Soil and Geographic Distance as Determinants of Floristic Composition in the Azuero Peninsula (Panama)

Cristina Garibaldi[1], Beatriz Nieto-Ariza[2,5], Manuel J. Macía[3], and Luis Cayuela[4]

[1] Departamento de Botánica, Universidad de Panamá, Av. Simón Bolívar, Manuel Espinoza Batista y José de Fábrega, Panama City, Republic of Panama

[2] Universidad Internacional Menéndez Pelayo, c/Isaac Peral 23, Madrid, 28040, Spain

[3] Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid, c/Darwin 2, Madrid, ES-28049, Spain

[4] Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, c/Tulipán s/n, Móstoles, Madrid, E-28933, Spain

ABSTRACT

Many studies analyzing the relative contribution of soil properties versus distance-related processes on plant species composition have focused on lowland tropical forests. Very few have investigated two forest types simultaneously, to contrast ecological processes that assemble the communities. This study analyses—at the landscape scale—the relative contribution of soil and distance on lowland and submontane tropical forests, which co-occur in two reserves of the Azuero peninsula (Panama). Floristic inventories and soil sampling were conducted in 81 0.1-ha plots clustered in 27 sites, and data were analyzed using Mantel tests, variance partitioning and non-metric multidimensional scaling. The largest differences in floristic composition occurred between reserves in both forest types. Soil variation and geographic distance were important determinants of floristic composition, but their effects were highly correlated; together they explained 7–25 percent and 46–50 percent of the variation in lowland and submontane forests, respectively. Soil variables that had the best correlations with floristic composition were iron, zinc, and silt content in lowland, and calcium, copper, iron, potassium, magnesium, phosphorus, zinc, and sand content in submontane forests. The studied forests showed a high beta diversity that seems to be related primarily with soils and, secondarily, with dispersal limitation and stochastic events. The results reveal a response of tree assemblages to environmental gradients, which are particularly conspicuous in Panama. The effects of limited dispersal seem to be more important in submontane than in lowland forests, probably as a result of higher isolation.

Abstract in Spanish is available in the online version of this article.

Key words: beta diversity; dispersal limitation; edaphic properties; species dissimilarity; tropical lowland forests; tropical submontane forests.

ONE OF THE MOST COMPELLING RESEARCH QUESTIONS IN ECOLOGY is to elucidate the factors that explain the high biodiversity of tropical forests. Many authors have emphasized the contribution of soil variation in determining floristic composition and species richness (Phillips *et al.* 2003, Tuomisto *et al.* 2003a, Poulsen *et al.* 2006, Leigh *et al.* 2014). Distance-related processes such as dispersal limitation, local extinction and other stochastic events—which are most simply represented by geographic distance (Terborgh & Andresen 1998)—can also play an important role in determining species composition in tropical forests (Chust *et al.* 2006, Bohlman *et al.* 2008, Guèze *et al.* 2013, López-Martínez *et al.* 2013).

For a better understanding of processes underlying floristic patterns in tropical forests it is necessary to test if species composition is more related to local factors, such as edaphic variables, or to distance-related processes (Pyke *et al.* 2001, Vormisto *et al.* 2004, Leigh *et al.* 2014). The hypothesis that floristic patterns exhibit strong spatial correlation emphasizes the neutral model:

species are ecologically equivalent and their assemblages result from random but spatially limited dispersal (Hubbell 2001, Condit *et al.* 2002). The hypothesis of environmental determinism, on the other hand, suggests that species assemblages respond to environmental gradients (Svenning *et al.* 2004). In tropical forests, such variability is represented mostly by soil gradients at the mesoscale (Tuomisto *et al.* 1995, Ruokolainen *et al.* 1997). To date, results from studies aiming to elucidate the relative contribution of soil properties versus geographic distances are inconsistent: the importance of distance and soils varies among regions and at different scales in response to evolutionary, climatic, geological, and ecological historical explanations (Bohlman *et al.* 2008, Chase & Myers 2011).

This study aimed to shed light on this issue by investigating floristic patterns in two forest types, namely tropical semi-deciduous lowland forests and tropical ombrophilous submontane forests, that co-occur within the same region. The study was conducted in two reserves of the Azuero peninsula (Republic of Panama), a highly diverse yet fairly unexplored region. Most of the currently available studies in the Neotropics have been conducted in lowland forests (*e.g.*, Valencia *et al.* 2004, Jones *et al.*

2006, Ruokolainen *et al.* 2007, Guèze *et al.* 2013). To our knowledge, only a few studies have compared the effects of soil characteristics and geographic distance on the floristic composition of different forest types (Baldeck *et al.* 2013, see John *et al.* 2007, for a general study in tropical forests). If the determinants of floristic composition and beta diversity are not the same, this might reflect differences in the ecological processes that assemble the biotic communities. This could have important consequences for forest management and conservation, for instance in the delimitation of priority conservation areas (Rodrigues *et al.* 2004).

We address the following three questions: (1) is the floristic composition similar within the same type of forest even between distant geographic locations? (2) To what extent can floristic patterns of the two types of forest be explained by geographic distance versus patterns in soil characteristics? (3) Which soil characteristics are the most important in determining floristic composition?

METHODS

Study area and aampling method.—Fieldwork was conducted in two forest reserves of the Azuero peninsula, Republic of Panama: El Montuoso (12,421 ha; 400–1000 m asl; Herrera Province) and La Tronosa (21,221 ha; 300–1000 m asl, Los Santos Province) (IGNTG 1988, ANAM 2010). The reserves are *ca* 40 km aside from each other (Fig. S1). Mean annual rainfall was 2031 mm in El Montuoso and 1603 mm in La Tronosa; and mean annual temperature was 25°C in El Montuoso and 28°C in La Tronosa (Garibaldi *et al.* 2005, 2009). The soils are clayey to loamy at both reserves. Silicic volcanic rocks are well developed in this region and porphyry copper mineralization is abundant (Kesler 1978). Each reserve contained two major forest types: tropical semi-deciduous lowland forest and tropical ombrophilous submontane forest (ANAM 2000). The former are dominated by drought-deciduous and often bottle-shaped upper canopy trees, with many evergreen and some sclerophyllous understory trees and shrubs (UNESCO 1973), and have been historically subjected to logging and cattle pressure. The latter consist mainly of evergreen trees neither cold nor drought resistant, with emergent trees largely absent and an even canopy layer (UNESCO 1973). Ombrophilous submontane forests are located on the top of the hills and maintain some of the last intact remnants of forest in the area due to their inaccessibility.

Woody plant communities and soil composition were recorded in 27 sites: 21 200 m × 5 m (0.1-ha) plots were sampled in El Montuoso (11 in submontane forests and 10 in lowland forests) and six 100 m × 100 m (1-ha) plots were sampled in La Tronosa (three at each forest type). The latter were further subdivided in ten 0.1-ha subplots. Fieldwork in El Montuoso was conducted from 2002 to 2004 and in La Tronosa from 2006 to 2008, in both cases mostly during the rainy season. The geographic coordinates of each plot were obtained with a hand-held Garmin GPS. Maximum distance among plots was 9.9 km in El Montuoso and 21.1 km in La Tronosa.

Data from El Montuoso and La Tronosa were collected in the context of different research projects, which explains differences in the sampling protocols, however sampling and identification of species was standardized and performed by the same research group (C. Garibaldi, pers. comm.). To keep plot size constant for statistical analyses, only one of the ten 20 m × 50 m (0.1-ha) smaller plots from La Tronosa was used at a time (see Data Analyses). In addition, it must be acknowledged that differences in plot shape (Fig. S1) might affect estimates of community composition. However, previous studies have demonstrated that long belts, rectangular, and square plots all provide similar estimates of tree species diversity and composition in tropical (Condit *et al.* 1996, Laurance *et al.* 1998) as well as in Mediterranean forests (Keeley & Fotheringham 2005).

Floristic inventories.—In each plot, we recorded all woody plants at least 10 cm in diameter at breast height (dbh). Mean number of stems per 0.1-ha plot was 59, with 90 percent confidence intervals between 13 and 127. Voucher specimens of all individuals that could not be identified to species level in the field were collected and deposited in the University of Panama Herbarium (PMA). We identified the vouchers to species using taxonomic keys (D'arcy 1987) or if in doubt assigned them to morphospecies. We accessed biological data freely available through the BIOTREE-NET database (http://portal.biotreenet.com/, Cayuela *et al.* 2012).

Soil sampling.—In each 0.1-ha plot in El Montuoso and La Tronosa, we took five soil subsamples from the topmost mineral soil layer, at a depth of *ca* 20 cm. We stored all five pooled subsamples in plastic airtight bags for transportation to the soil laboratory of the Faculty of Agriculture of the University of Panama. We air-dried them after 2–3 days at 25°C. We analyzed 15 variables from the soil samples: percentages of clay, sand and silt (as indicators of particle size), pH (using a potentiometer), percentage of organic matter (Walkley–Black method), and extractable Al, Cu, Ca, Fe, K, Mg, Mn, Na, P, and Zn with an atomic absorption spectrophotometer.

Data analyses.—To remove spatial autocorrelation derived from the use of clustered plots, we designed a novel procedure to randomly extract one 0.1-ha plot from each of the larger 1-ha plots in La Tronosa. This resulted in one of many possible subsets of 0.1-ha plots: all 21 0.1-ha plots in El Montuoso and six randomly selected 0.1-ha plots in La Tronosa. We iterated the randomization 1000 times to account for variability in floristic composition emerging from the random selection of 0.1-ha plots in La Tronosa, and the resulting datasets were used to perform all the analyses described below. We summarized the results of each analysis mostly in the form of means and standard deviations of the estimated parameters.

Distance matrices were computed independently for each forest type. We used the Steinhaus and Sørensen indices to calculate distance measures of floristic dissimilarity. These indices are mainly useful for ecological community data. They are

mathematically identical, but the Sørensen index uses only presence-absence information while the Steinhaus index also includes abundance information (Legendre & Legendre 2012). We used both indices to examine whether abundance data give different results than presence-absence data, and found that both indices gave relatively similar results in most analyses. This finding is in agreement with those reported in previous studies (e.g., Tuomisto et al. 2003b). Therefore, we only reported the results for the Steinhaus index, which uses all of the information in the floristic dataset.

Soil differences between plots were expressed in Euclidean distances computed separately for each soil variable. Before calculating the Euclidean distances, we transformed the concentrations of elements (Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, and Zn) to their natural logarithms, because a unit difference in element concentration has more weight ecologically when it is low than when it is high (Tuomisto et al. 2003b). We computed geographic distances from geographic coordinates (using the R function 'coord2dist'; package 'prabclus') and also transformed them to their natural logarithms, because dispersal limitation is expected to provide a linear similarity decay with logarithmic distance (Condit et al. 2002).

We used Mantel tests of matrix correspondence to determine whether similarities in floristic composition were correlated with similarities in soil variables and geographic distance. We used the standardized form of the Mantel test, which computes the Pearson's correlation coefficient. The statistical significance of each correlation was determined by a Monte Carlo test with 999 permutations. We ran partial Mantel tests to verify whether edaphic distance matrices remained correlated after the effect of geographic distance was taken into account (Legendre & Legendre 2012). Mean values and standard deviations for the Pearson's correlations were reported for the 1000 iterations using the procedure described above.

We also ran Mantel tests and partial Mantel tests for best possible subsets of soil variables (Clarke & Ainsworth 1993) on distance matrices to select the combination of explanatory variables that most contributed to explaining the variability in the floristic matrix of each forest type. As this procedure was repeated 1000 times to incorporate random selection of spatially autocorrelated plots in La Tronosa (see above), the results reported the relative contribution of each variable in the 1000 best subsets (i.e., frequency of appearance in the best subsets).

Next, we partitioned the amount of variation in species composition that could be explained exclusively or in combination by soil properties and geographic distance using redundancy analysis (RDA; Borcard et al. 1992). In RDA, Chi-square transformed data matrix is subjected to ordinary, unweighted linear regression and unweighted singular value decomposition (SVD) (Legendre & Legendre 2012). We reported mean and standard deviations for explained variances for the 1000 iterations.

Finally, we used non-metric multidimensional scaling (NMDS) to explore the overall pattern of dispersion in species composition; the resulting diagram shows the results from the 1000 iterations and their mean values in the ordination axes. We fit the soil variables that most contributed to explaining differences in floristic composition according to the partial Mantel tests for best subsets onto the NMDS diagram to help explain the results of the former analyses. We also explored non-linear relationships explored by fitting thin plate splines using general additive models and interpolating the fitted values on the unconstrained ordination diagram (Oksanen et al. 2012).

We performed all the analyses with the R software, including its packages 'vegan' (Oksanen et al. 2012), 'prabclus' (Henning & Hausdorf 2010), and 'rgdal' (Keitt et al. 2012).

RESULTS

Floristic inventories.—Overall, the 81 0.1-ha plots contained 4746 individuals from 309 species; 1807 individuals were found in El Montuoso and 2939 in La Tronosa. Lowland and submontane forests in El Montuoso contained 111 and 85 species, respectively; whereas in La Tronosa there were 138 and 81 species, respectively. Table 1 display the ten most frequent species found in each type of forest, where only 16 species (Table S1), 29 genera and 19 families were shared by both reserves for lowland forests. Garcinia madruno was the only species that was present in more than 30 percent of the plots in each reserve. In the case of submontane forests, 14 species (Table S2), 21 genera and 19 families were shared by both reserves, with two species (Dendropanax arboreus and Garcinia madruno) present in more than 30 percent of the plots in each reserve.

Soils.—Overall, the two reserves were edaphically distinct from each other, with a greater edaphic heterogeneity within La Tronosa than within El Montuoso (Table 2). On average, soils were more acidic in El Montuoso than in La Tronosa, and the concentration of all exchangeable bases (Ca, K, Mg, Na) was markedly increased in La Tronosa and, within reserves, was much higher in submontane forests. P, Mn, Zn, and organic matter were also higher in La Tronosa and in submontane forests within each reserve. The micronutrients (Cu, Fe) and Al reached a higher concentration in El Montuoso than in La Tronosa. In general, pH was positively related to the content of exchangeable bases (Ca, Mg, Na) and other micronutrients (Mn, Zn), and negatively related to Al and Fe content (Table S3).

The sand fraction dominated the soil texture, particularly in submontane forests. The clay fraction was higher in El Montuoso lowland forests, and the silt fraction was the least prominent in all forest types across reserves.

Assessing the relationship between floristic, edaphic and geographic patterns.—Mantel tests showed that there was a strong correlation between floristic and edaphic distances for most of the soil variables in each forest type (Table 3).

The soil properties that yielded the highest Mantel correlations ($r > 0.70$, $P < 0.05$ in at least 90% of iterations) in tropical lowland forests were Al, Ca, Fe, Mg, Mn, Na, P, pH, and Zn. In tropical submontane forests the highest correlations were attained

TABLE 1. *Most frequently occurring species in tropical lowland (A) and submontane forests (B) within El Montuoso and La Tronosa Forest Reserves in the Azuero Peninsula (Panama). S = percentage of occupancy in plots (in brackets, number of 0.1-ha plots).*

El Montuoso				La Tronosa			
Species	Family	S (%)	Total individuals	Species	Family	S (%)	Total individuals
(A) Tropical lowland forests							
Clethra lanata	Cletraceae	100 (10)	118	Cryosophila warscewiczii	Arecaceae	83.3 (25)	365
Pera arborea	Peraceae	90 (9)	70	Manilkara zapota	Sapotaceae	73.3 (22)	140
Cassipourea elliptica	Rhizophoraceae	90 (9)	46	Hura crepitans	Euphorbiaceae	53.3 (16)	79
Virola sebifera	Myristicaceae	70 (7)	46	Brosimum alicastrum	Moraceae	50 (15)	60
Byrsonima crassifolia	Malpighiaceae	70 (7)	40	Swartzia simplex	Leguminosae	50 (15)	31
Oenocarpus mapora	Arecaceae	70 (7)	30	Anacardium excelsum	Anacardiaceae	50 (15)	30
Roupala montana	Proteaceae	70 (7)	28	Pittoniotis trichantha	Rubiaceae	50 (15)	30
Licania hypoleuca	Chrysobalanaceae	70 (7)	25	Calycophyllum candidissimum	Rubiaceae	46.7 (14)	110
Simarouba amara	Simaroubaceae	70 (7)	23	Pouteria campechiana	Sapotaceae	46.7 (14)	30
Myrcia gatunensis	Myrtaceae	70 (7)	20	Garcinia madruno	Clusiaceae	43.3 (13)	25
(B) Tropical submontane forests							
Eugenia sp.	Myrtaceae	100 (11)	125	Dendropanax arboreus	Araliaceae	50 (15)	54
Calophyllum brasiliense	Clusiaceae	100 (11)	101	Protium sp. 1	Burseraceae	43.3 (13)	53
Quetzalia occidentalis	Celastraceae	100 (11)	60	Protium tenuifolium	Burseraceae	36.7 (11)	117
Cassipourea elliptica	Rhizophoraceae	100 (11)	52	Garcinia madruno	Clusiaceae	33.3 (10)	23
Podocarpus guatemalensis	Podocarpaceae	90.9 (10)	24	Alfaroa costaricensis	Juglandaceae	26.7 (8)	195
Ardisia sp. 1	Primulaceae	81.8 (9)	78	Protium panamense	Burseraceae	23.3 (7)	81
Dendropanax arboreus	Araliaceae	81.8 (9)	68	Ocotea sp. 1	Lauraceae	23.3 (7)	28
Garcinia madruno	Clusiaceae	81.8 (9)	54	Quercus lancifolia	Fagaceae	23.3 (7)	26
Lacistema aggregatum	Lacistemataceae	81.8 (9)	43	Cassipourea elliptica	Rhizophoraceae	23.3 (7)	14
Myrciaria floribunda	Myrtaceae	81.8 (9)	25	Cecropia insignis	Urticaceae	20 (6)	32

for Ca, Fe, K, Mg, Mn, Na, P, sum of exchangeable bases (Ca, K, Na, Mg), sand, pH, organic matter and Zn (Table 3).

Overall, the highest correlations between floristic distances and explanatory variables were achieved for geographic distances (Table 3). When accounting for the effect of geographic distance (*i.e.*, partial Mantel test), the correlation between floristic composition and most of the soil properties markedly decreased; pH in lowland forests and Ca, K, and Mg in submontane forests remained significant after removing the effect of geographic distance ($P < 0.05$ in at least 90% of iterations).

Three variables in lowland (Fe, Zn, and percentage of silt) and eight in submontane forests (Ca, Cu, Fe, K, Mg, P, Zn, and percentage of sand) maximized the correlation with floristic dissimilarities, according to partial Mantel tests for best possible subsets of soil variables (Table 4).

According to the variance partitioning results, the amount of variability in floristic composition that could be explained by geographic distance and soil was higher in submontane (44–46%) than in lowland forests (32–40%). Distance and soil together explained between 46 and 50 and 7–25 percent of the variation in submontane and lowland forests, respectively. In both forest types, distance alone and soil variables alone explained minor portions of the variation, and soil variables were more important

than distance. In submontane forests, the amount of variance explained by distance alone yielded a negative value, which can occur because fractions are calculated by subtracting different models, and these subtraction results can be negative when there are complicated or non-linear dependencies between fractions (Legendre & Legendre 2012).

The ordination diagram represented simultaneously the results of the NMDS with 1000 random subsets of six 0.1-ha plots from La Tronosa and the 21 0.1-ha plots from El Montuoso (Fig. 1). Two main groups were identified representing the two reserves. The clustering of plots was higher for El Montuoso than for La Tronosa, both between and within forest types. Lowland and submontane forests in El Montuoso were associated with larger concentrations of Fe and Cu than forests in La Tronosa. Within El Montuoso, lowland forests held the largest concentrations of Fe and submontane forests registered the highest concentration of Cu. High Mg, Zn and Ca concentrations characterized La Tronosa forests, with submontane forests showing the largest values as compared to lowland forests. Submontane forests likewise held the highest value for sand. Lowland forest of La Tronosa, on the other hand, contained the largest fractions of silt. Non-linear relationships better explained the effect of P and K concentration on floristic composition (results not shown),

TABLE 2. *Soil characteristics and elevation differences between lowland and submontane forests within each Forest Reserve: El Montuoso and La Tronosa (Panama). Cation concentrations are given in ppm (except for Ca, Mg, Al, which are given in meq/100 g), organic matter and texture components (clay, sand, silt) in percentages; elevation in m asl.*

| | Tropical lowland forests | | | | Tropical submontane forests | | | |
| | Montuoso | | Tronosa | | Montuoso | | Tronosa | |
Variables	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Elevation	–	582–753	–	326–605	–	687–912	–	485–936
pH	4.86 ± 0.14	4.71–5.10	6.34 ± 0.40	5.58–6.92	5.05 ± 0.21	4.67–5.20	5.60 ± 0.43	4.51–6.13
Ca	1.10 ± 0.81	0.20–2.41	18.34 ± 11.59	2.55–46.22	3.01 ± 1.55	1.27–4.36	29.83 ± 7.81	5.56–46.73
K	42.70 ± 33.01	5–73	49.23 ± 29.14	22–147	71.09 ± 10.64	52–79	156.10 ± 102.764	18–256
Mg	0.79 ± 0.35	0.54–1.29	4.99 ± 2.93	0.56–11.13	0.83 ± 0.27	0.37–1.14	12.30 ± 3.34	2.09–19.33
Na	24.20 ± 5.14	20–33	63.62 ± 38.42	3–150	37.09 ± 10.45	18–48	129.13 ± 100.24	14–272
Al	3.47 ± 1.85	0–5	0.00 ± 0.018	0–0	0.50 ± 0.60	0–1	0.24 ± 0.86	0–5
Organic matter	3.55 ± 0.82	2.86–4.72	5.83 ± 2.13	2–10.08	6.41 ± 1.76	4.17–7.91	9.41 ± 3.28	3.41–20.42
P	2.70 ± 0.95	0–3	2.70 ± 13.53	0–74	4.09 ± 1.05	3–5	9.07 ± 19.17	0–81
Cu	5.10 ± 1.45	4–7	4.07 ± 3.49	1–12	6.55 ± 4.80	3–14	4.07 ± 2.55	0–11
Fe	141.10 ± 54.20	69–216	39.07 ± 22.86	7–89	96.64 ± 19.13	67–109	63.23 ± 26.70	23–117
Mn	18.20 ± 6.49	6–22	85.07 ± 32.10	44–170	46.27 ± 10.99	28–55	120.03 ± 35.49	64–230
Zn	1.00 ± 0.00	1–1	4.43 ± 3.06	2–14	1.55 ± 0.93	1–3	5.77 ± 1.89	2–11
Clay	41.40 ± 2.55	37–44	34.67 ± 10.31	18–52	31.82 ± 6.72	22–40	25.00 ± 9.17	6–42
Sand	34.80 ± 6.60	28–46	35.00 ± 10.98	17–55	38.09 ± 4.30	35–46	47.73 ± 10.71	24–74
Silt	23.80 ± 4.05	17–28	30.30 ± 4.21	21–40	30.09 ± 8.72	14–39	27.27 ± 3.63	20–34

TABLE 3. *Mantel correlations (r mean values and standard deviation) between dissimilarity matrices based on floristic, soil and geographic distance (the two reserves were ca 40 km aside from each other) in lowland and submontane forests of Azuero Peninsula (Panama). The floristic distance matrices were calculated using Steinhaus index (abundance data); all distance matrices for explanatory variables were based on Euclidean distances. An analysis of 1000 random iterations was made and statistical significance level of each iteration was assessed with a Monte Carlo permutation test using 999 permutations.*

| | Lowland forests | | Submontane forests | |
Soil variables	Mantel	Partial mantel	Mantel	Partial mantel
pH	**0.83 ± 0.03**[**]	**0.50 ± 0.13**[*]	**0.67 ± 0.08**[*]	0.21 ± 0.08
Ca	**0.73 ± 0.07**[**]	**0.40 ± 0.16**[†]	**0.83 ± 0.02**[**]	**0.37 ± 0.05**[**]
K	−0.06 ± 0.04	−0.02 ± 0.03	**0.83 ± 0.03**[**]	**0.57 ± 0.06**[*]
Mg	**0.67 ± 0.09**[**]	0.35 ± 0.16	**0.89 ± 0.01**[**]	**0.64 ± 0.03**[**]
Na	**0.69 ± 0.08**[**]	0.26 ± 0.19	**0.62 ± 0.08**[*]	0.31 ± 0.06
Sum Ca + K + Mg + Na	0.11 ± 0.09	0.04 ± 0.05	**0.64 ± 0.04**[*]	0.37 ± 0.05
Al	**0.58 ± 0.02**[**]	**0.29 ± 0.15**[†]	−0.00 ± 0.03	−0.45 ± 0.02
Organic matter	**0.45 ± 0.14**[†]	0.20 ± 0.17	**0.42 ± 0.11**[*]	−0.15 ± 0.14
P	**0.67 ± 0.03**[**]	**0.36 ± 0.14**[†]	**0.75 ± 0.08**[**]	**0.42 ± 0.08**[†]
Cu	**0.50 ± 0.17**[†]	−0.02 ± 0.27	0.21 ± 0.12	−0.3848 ± 0.09
Fe	**0.62 ± 0.08**[**]	0.31 ± 0.10	**0.60 ± 0.11**[*]	0.13 ± 0.12
Mn	**0.63 ± 0.05**[**]	−0.01 ± 0.29	**0.71 ± 0.04**[**]	0.21 ± 0.07
Zn	**0.80 ± 0.06**[**]	**0.48 ± 0.15**[†]	**0.71 ± 0.07**[**]	**0.48 ± 0.15**[†]
Clay	**0.52 ± 0.12**[†]	0.20 ± 0.12	**0.37 ± 0.13**[†]	−0.16 ± 0.10
Sand	0.24 ± 0.15	0.04 ± 0.11	**0.54 ± 0.14**[*]	0.12 ± 0.12
Silt	**0.31 ± 0.15**[†]	0.06 ± 0.11	0.02 ± 0.06	−0.31 ± 0.02
Geographic distances	**0.76 ± 0.18**[*]	–	**0.85 ± 0.00**[**]	–

$P < 0.05$ in **100 percent, *90 percent, and †50 percent of iterations, Significant iterations in at least 50 percent appear in bold.

TABLE 4. *Mantel tests (r mean values and standard deviation) for best possible subsets of soil variables that maximize correlations with floristic dissimilarities in tropical lowland and submontane forests in the Azuero Peninsula (Panama). Occurrence frequency of each variable in best subsets is given; np indicates mean number of parameters selected in the best subsets.*

Soil variables	Lowland forests		Submontane forests	
	Mantel best subsets	Partial mantel best subsets	Mantel best subsets	Partial mantel best subsets
	Frequency		Frequency	
pH	**0.25**	0.25	0.41	0.27
Ca	0.16	0.13	0.48	**0.28**
K	0.01	0.08	0.21	**0.24**
Mg	**0.27**	0.19	**0.62**	**0.39**
Na	**0.27**	0.14	0.30	0.21
Al	0.15	0.14	0.08	0.03
Organic matter	0.08	0.14	0.16	0.07
P	**0.36**	0.26	**0.68**	**0.60**
Cu	0.25	0.25	0.46	**0.40**
Fe	0.25	**0.28**	0.54	**0.43**
Mn	0.11	0.26	**0.49**	0.27
Zn	**0.79**	**0.59**	0.39	**0.34**
Clay	0.10	0.12	0.32	0.23
Sand	0.06	0.07	0.35	**0.31**
Silt	**0.44**	**0.28**	0.02	0
$r \pm SD$	0.83 ± 0.02	0.62 ± 0.10	0.90 ± 0.01	0.56 ± 0.08
np	6	3	4	8

Variables with the highest ocurrence frequency in best subsets appear in bold.

with less clear patterns than those observed for other edaphic variables.

DISCUSSION

BETA DIVERSITY AND SPECIES COMPOSITION.—Tropical lowland and submontane forests in the Azuero peninsula showed high beta diversity, measured as turnover in species composition with distance (Duivenvoorden *et al.* 2002), as indicated by the distinctive species found between reserves and forest types. These results are consistent with those of Condit *et al.* (2002) for lowland rain forests in central Panama, where plots 50 km aside from each other typically shared between only 1 and 15 percent of their species. In this study, distance between the two reserves was approximately 40 km, and only between 6.9 and 9.2 percent of species were shared by both reserves. In contrast, Western Amazonian plots separated by 100 km shared from 30 to 40 percent of their species, and when this distance increased up to 1400 km, plots still shared, on average, 20 percent of their species (Condit *et al.* 2002). The higher beta diversity in Panama as compared to Western and Central Amazonia (Bohlman *et al.* 2008) might be related to larger variation in geology and climate at short distances (Condit *et al.* 2002, Duivenvoorden *et al.* 2002), which
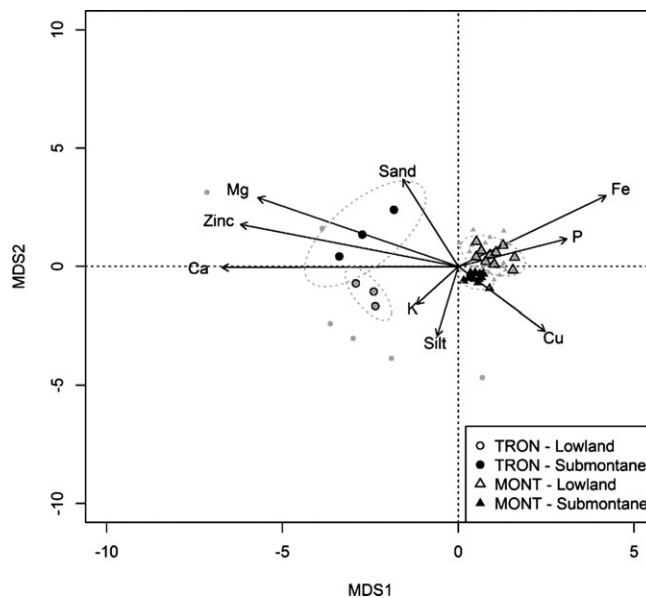

FIGURE 1. Non-metric multidimensional scaling (NMDS) ordination of tropical lowland and submontane forests of the Azuero Peninsula (Panama) with selected soil variables through best subset analyses fitted onto the ordination diagram. Gray points and triangles represent the ordination values for the 1000 iterations in La Tronosa and El Montuoso, respectively; and full-colored points and triangles show the centroids (*i.e.*, mean value of the 1000 iterations) for each set of 0.1-ha plots in La Tronosa and for each plot in the case of El Montuoso in lowland (white) and submontane (black) forests.

indicate that soil and precipitation gradients are strong in Panama (Pyke *et al.* 2001).

SOIL AND FLORISTIC HETEROGENEITY.—NMDS ordination identified a clear pattern of floristic composition: four rather distinct groups, each of which corresponds to sites with relatively similar soils and geographic proximity. Soil and floristic heterogeneity within La Tronosa was greater than within El Montuoso. On average, soils in El Montuoso were less nutrient-rich, more acidic and contained a higher concentration of Al than in La Tronosa, where the concentration of exchangeable bases (Ca, K, Na, Mg) and organic matter was higher. The floristic differences among plots that belong to the same type of forest were related to Fe, Zn and percentage of silt in lowland forests, and Ca, Cu, Fe, K, Mg, P, Zn and percentage of sand in the case of submontane forests.

Within reserves, submontane forest soils were more nutrient-rich than those in lowland forests, which is similar to results observed in comparisons of lowlands and submontane forests in Amazonia (Macía *et al.* 2007). Lowland and submontane forests are characterized by an elevational gradient that produces rapid shifts in soils and microenvironmental variables influencing floristic composition, as reported in both Amazonian (Macía *et al.* 2007) and montane forests (Gerold 2008, Vitousek 2008). Despite this, a surprising result emerged when lowland and sub-

montane forests were compared: the floristic composition of low-land forests tended to resemble more closely that of submontane forests within the same geographic region than the composition of lowland forests of adjacent regions. This result supported those of Terborgh and Andresen (1998), who concluded the same for inundated and *terra firme* forest in the Amazonian region. But whereas that study was carried out at a biographic scale, with thousands of kilometers between forests in some cases, this study was conducted at a much smaller scale. This implies that the same forest type, even at relatively short distances, can exhibit a variable degree of floristic differentiation (Emilio *et al.* 2010). In addition, these results might also indicate an imprecise or ambiguous definition of the major vegetation types within the reserves. Indeed, there is overlap in the elevational range between the two forest types at each of the reserves (Table 2), and some of the formerly classified lowland forests plots might turn out to be in transitional areas toward submontane forest (C. Garibaldi, pers. comm.).

In sum, lowland and submontane forests are heterogeneous forests. This heterogeneity is linked with variation in soils, which is ultimately determined by geological history and climate (Tuomisto *et al.* 1995, Andersen *et al.* 2010).

DETERMINANTS OF LOWLAND AND SUBMONTANE FOREST COMPOSITION.—Our results indicate that both soil properties and geographic distance control floristic patterns in lowland and submontane tropical forests in the Azuero peninsula. The inability to separate geographic distance and soil effects in the variance partition analysis suggests that both factors are contributing simultaneously to floristic composition, and that they are probably highly correlated across the landscape (Duivenvoorden *et al.* 2002). This is especially true in submontane forests, where the fraction explained by their joint effects was very high. Observed geographic limitation in this forest type could be the result of its occurrence on the tops of hills, which will ultimately lead to isolation of forest remnants.

In both cases, however, soil alone was a more important determining factor in the floristic patterns than geographic distance, as indicated by our Mantel tests. This suggests that dispersal limitation and random processes are overlain on a landscape primarily determined by environmental heterogeneity and are consistent with previous Amazonian and Central America studies (Pyke *et al.* 2001, Ruokolainen *et al.* 2007, Andersen *et al.* 2010, López-Martínez *et al.* 2013). In addition, when greater environmental heterogeneity is considered, local factors (*e.g.*, soil properties) usually have more explanatory power than spatial separation of sites (*e.g.,* Chust *et al.* 2006, Jones *et al.* 2006).

Other factors not considered in this study, such as the differences in the history of forest use by local populations and the resulting deforestation and habitat fragmentation, may be responsible for the large unexplained variance observed in the partitioning diagrams (Leigh *et al.* 2014). For example, the unexplained variance in submontane forests in our study region, which maintain some of the last intact remnants of forest in the area due to their inaccessibility, was much lower than that in lowland forests

that have been historically subjected to logging and cattle pressure. Similarly, habitat fragmentation has been shown to influence beta diversity in tropical dry forests of Mexico (López-Martínez *et al.* 2013), but this remains to be investigated in the forests of the Azuero peninsula.

Our results help disentangle the various processes responsible for spatial community structure (Dray *et al.* 2012). Yet there are some issues we did not consider that might influence our results. First, the amount of variance simultaneously explained by the environment and space (*i.e.*, the spatially structured environmental component), which is often quite large, can also carry the legacy of dispersal processes if dispersal spatially coincides environmental variables such as topography (Smith & Lundholm 2010). Secondly, some soil properties known to influence species composition were not measured in our study (*e.g.*, drainage, water-holding capacity topographic position [Sollins 1998, Valencia *et al.* 2004). These could also influence the results of variance partitioning because the spatial fraction is attributed to the effects of dispersal limitation and species responses to unmeasured environmental variables (Andersen *et al.* 2010, Baldeck *et al.* 2013). Third, chemical-extraction assays may not give an optimal measure of nutrient availability to plants and other soil properties at the root surface (Sollins 1998, Ruokolainen *et al.* 2007). Fourth, it is important to acknowledge that there might be scale-dependence in the degree to which environmentally based-deterministic patterns are differentially observed relative to dispersal-based patterns as the scale of observation increases (Garzon-Lopez *et al.* 2014). If so, then our results might be applicable only at the particular scale at which this study was conducted. Finally, the relative contribution of deterministic versus dispersal-based processes could be also influenced by patterns of tree co-occurrence in neighborhoods of different shapes. For example, conspecific clumping owing to dispersal limitation could be more readily detected in square plots than rectangular ones. This would result in a greater relative proportion of variance explained by geographic distance than environmental variables in square than rectangular plots. Mapping individual trees in plots, though time-consuming, might help solve this problem.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of the study area.

TABLE S1. *Shared species among tropical lowland forests of El Montuoso and La Tronosa Forest Reserves in the Azuero Peninsula.*

TABLE S2. *Shared species among tropical submontane forests of El Montuoso and La Tronosa Forest Reserves in the Azuero Peninsula.*

TABLE S3. *Pearson's correlation coefficients among soil properties measured in lowland and submontane forests of the Azuero Peninsula.*

LITERATURE CITED

ANAM (Autoridad Nacional del Ambiente). 2000. Mapa de vegetación de Panamá. ANAM, Panama.

ANAM. 2010. Cuarto informe nacional de Panamá ante el convenio sobre la diversidad biológica. ANAM, Panama.

ANDERSEN, K. M., B. L. TURNER, AND J. W. DALLING. 2010. Soil-based habitat partitioning in understorey palms in lower montane tropical forests. J. Biogeogr. 37: 278–292.

BALDECK, C. A., K. E. HARMS, J. B. YAVITT, R. JOHN, B. L. TURNER, R. VALENCIA, H. NAVARRETE, S. J. DAVIES, G. B. CHUYONG, D. KENFACK, D. W. THOMAS, S. MADAWALA, N. GUNATILLEKE, S. GUNATILLEKE, S. BUNYAVEJCHEWIN, S. KIRATIPRAYOON, A. YAACOB, M. N. NUR SUPARDI, AND J. W. DALLING. 2013. Soil resources and topography shape local tree community structure in tropical forests. Proc. R. Soc. B. 280: 20122532.

BOHLMAN, S. A., W. F. LAURANCE, S. G. LAURANCE, H. E. M. NASCIMENTO, P. M. FEARNSIDE, AND A. ANDRADE. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. J. Veg. Sci. 19: 863–874.

BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

CAYUELA, L., L. GÁLVEZ-BRAVO, R. PÉREZ PÉREZ, F. S. ALBUQUERQUE, D. J. GOLICHER, R. A. ZAHAWI, N. RAMÍREZ-MARCIAL, C. GARIBALDI, R. FIELD, J. M. REY BENAYAS, M. GONZÁLEZ-ESPINOSA, P. BALVANERA, M. A. CASTILLO, B. L. FIGUEROA-RANGEL, D. M. GRIFFITH, G. A. ISLEBE, D. L. KELLY, M. OLVERA-VARGAS, S. A. SCHNITZER, E. VELÁZQUEZ, G. WILLIAMS-LINERA, S. W. BREWER, A. CAMACHO-CRUZ, I. CORONADO, B. DE JONG, R. DEL CASTILLO, I. GRANZOW-DE LA CERDA, J. FERNÁNDEZ, W. FONSECA, L. GALINDO-JAIMES, T. W. GILLESPIE, B. GONZÁLES-RIVAS, J. E. GORDON, J. HURTADO, J. LINARES, S. G. LETCHER, S. A. MANGAN, J. A. MEAVE, V. E. MÉNDEZ, V. MEZA, S. OCHOA-GAONA, C. J. PETERSON, V. RUIZ-GUTIERREZ, K. A. SNARR, F. TUN DZUL, M. VALDEZ-HERNÁNDEZ, K. M. VIERGEVER, D. A. WHITE, J. N. WILLIAMS, F. J. BONET, AND R. ZAMORA. 2012. The Tree Biodiversity Network (BIOTREE-NET): Prospects for biodiversity research and conservation in the Neotropics. Biodivers. Ecol. 4: 211–224.

CHASE, J. M., AND J. A. MYERS. 2011. Disentangling the importance of ecological niches from stochastics processes across scales. Phil. Trans. R. Soc. B. 366: 2352–2363.

CHUST, G., J. CHAVE, R. CONDIT, S. AGUILAR, S. LAO, AND R. PÉREZ. 2006. Floristic composition across a climatic gradient in a neotropical lowland forest. J. Veg. Sci. 17: 83–92.

CLARKE, K. R., AND M. AINSWORTH. 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92: 205–219.

CONDIT, R., S. P. HUBBELL, J. V. LAFRANKIE, R. SUKUMAR, N. MAROKANAN, R. B. ROSTER, AND P. S. ASHTON. 1996. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. J. Ecol. 84: 549–562.

CONDIT, R., N. PITMAN, J. R. E. H. LEIGH, 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.

D'ARCY, W. G. 1987. Flora of Panama. Part I: The introduction and checklist, Monographs in systematic botany. Missouri Botanical garden, St. Louis, 325 pp.

DRAY, S., R. PÉLISSIER, P. COUTERON, M.-J. FORTIN, P. LEGENDRE, P. R. PERES-NETO, E. BELLIER, R. BIVAND, F. G. BLANCHET, M. DE CÁCERES, A.-B. DUFOUR, E. HEEGAARD, T. JOMBART, F. MUNOZ, J. OKSANEN, J. THIOULOUSE, AND H. H. WAGNER. 2012. Community ecology in the age of multivariate spatial analysis. Ecol. Monogr. 82: 257–275.

DUIVENVOORDEN, J. F., J.-C. SVENNING, AND S. J. WRIGHT. 2002. Beta diversity in tropical forests. Science 295: 636–637.

EMILIO, T., B. W. NELSON, J. SCHIETTI, S. J. M. DESMOULIERE, H. M. V. ESPÍRITO SANTO, AND F. R. C. COSTA. 2010. Assessing the relationship between forest types and canopy tree beta diversity in Amazonia. Ecography 33: 738–747.

GARIBALDI, C., S. AGUILAR, D. ARCIA, AND N. TORRES. 2005. La vegetación arbórea en los bosques fragmentados de la Reserva Forestal El Montuoso. In C. Garibaldi (Ed.). Diversidad biológica y servicios ambientales de los fragmentos de bosque en la Reserva Forestal El Montuoso, Panamá, pp. 39–70. Universal Books, Panama.

GARIBALDI, C., S. AGUILAR, A. ZAPATA, H. PÉREZ, F. FARNUM, O. CASTILLO, AND L. CARRASQUILLA. 2009. Riqueza, diversidad y dinámica de los bosques perturbados en la Reserva Forestal La Tronosa, península de Azuero. In C. Garibaldi (Ed.). Evaluación de la biodiversidad en la Reserva Forestal La Tronosa, provincia de Los Santos, Panamá, pp. 59–70. Novo Art, Panama.

GARZON-LOPEZ, C. X., P. A. JANSEN, S. A. BOHLMAN, A. ORDONEZ, AND H. OLFF. 2014. Effects of sampling scale on patterns of habitat association in tropical trees. J. Veg. Sci. 25: 349–362.

GEROLD, G.. 2008. Soil, climate, and vegetation of tropical montane forests –a case study from the Yungas, Bolivia. Biodiv. Ecol Ser. 2: 137–162.

GUÈZE, M., J. PANEQUE-GÁLVEZ, A. C. LUZ, J. PINO, M. ORTA-MARTÍNEZ, V. REYES-GARCÍA, AND M. J. MACÍA. 2013. Determinants of tree species turnover in a southern Amazonian rain forest. J. Veg. Sci. 24: 284–295.

HENNING, C., AND B. HAUSDORF. 2010. PRABCLUS, functions for clustering of presence-absence, abundance and multilocus genetic data. R package version 2.2-2. http://CRAN.Rproject.org/package=prabclus.

HUBBELL, S. P. 2001. The Unified Neutral Theory of biodiversity and biogeography. Princeton University Press, Princeton, 448 pp.

IGNTG (Instituto Geográfico Nacional Tommy Guardia). 1988. Atlas Nacional de la República de Panamá, 3rd edn. IGNTG, Panama.

JOHN, R., J. M. DALLING, K. E. HARMS, J. B. YAVITT, R. F. STALLARD, M. MIRABELLO, S. P. HUBBELL, R. VALENCIA, H. NAVARRETE, M. VALLEJO, AND R. FOSTER. 2007. Soil nutrients influence spatial distributions of tropical tree species. PNAS 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 rainforest ferns. J. Ecol. 94: 181–195.

KEELEY, J. E., AND C. J. FOTHERINGHAM. 2005. Plot shape effects on plant species diversity measurements. J. Veg. Sci. 16: 249–256.

KEITT, T. H., R. BIVAND, E. PEBESMA, AND B. ROWLINGSON. 2012. RGDAL, bindings for the geospatial data abstraction library. R package version 0.7-18. http://CRAN.Rproject.org/package=rgdal.

KESLER, S. E. 1978. Metallogenesis of the Caribbean region. J. Geol. Soc. 135: 429–441.

LAURANCE, W. F., L. V. FERREIRA, J. M. RANKIN-DE MERONA, AND R. W. HUTCHINGS. 1998. Influence of plot shape on estimates of tree diversity and community composition in Central Amazonia. Biotropica 30: 662–665.

LEGENDRE, P., AND L. LEGENDRE. 2012. Numerical ecology. 3rd edn. Elsevier Science BV, Amsterdam, 969 pp.

Leigh, E. G., A. O'Dea, and G. J. Vermeij. 2014. Historical biogeography of the Isthmus of Panama. Biol. Rev. 89: 148–172.

López-Martínez, J. O., J. L. Hernandez-Stefanoni, J. M. Dupuy, and J. A. Meave. 2013. Partitioning the variation of woody plant beta-diversity in a landscape of secondary tropical dry forests across spatial scales. J. Veg. Sci. 24: 33–45.

Macía, M. J., K. Ruokolainen, H. Tuomisto, J. Quisbert, and V. Cala. 2007. Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. Ecography 30: 561–577.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2012. VEGAN, community ecology package. R package version 2.0-3. http://CRAN.R-project.org/package=vegan.

Phillips, O. L., P. Núñez Vargas, A. L. Monteagudo, A. Peña Cruz, M.-E. Chuspe Zans, W. Galiano Sánchez, M. Yli-Halla, and M. S. Rose. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. J. Ecol. 91: 757–775.

Poulsen, A. D., H. Tuomisto, 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.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. Da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428: 640–643.

Ruokolainen, K., A. Linna, and H. Tuomisto. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographic patterns in Amazonian rain forests. J. Trop. Ecol. 13: 243–256.

Ruokolainen, K., H. Tuomisto, M. J. Macía, M. A. Higgins, and M. Yli-Halla. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae?. J. Trop. Ecol. 23: 13–25.

Smith, T. W., and J. T. Lundholm. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33: 648–655.

Sollins, P.. 1998. Factors influencing species composition in tropical lowland rain forests: does soil matter? Ecology 79: 23–30.

Svenning, J.-C., D. A. Kinner, R. F. Stallard, B. M. J. Engelbretch, and S. J. Wright. 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85: 2526–2538.

Terborgh, J., and E. Andresen. 1998. The composition of Amazonian forests: patterns at local and regional scales. J. Trop. Ecol. 14: 645–664.

Tuomisto, H., A. D. Poulsen, K. Ruokolainen, R. C. Moran, C. Quintana, J. Celi, and G. Cañas. 2003b. Linking floristic patterns with soil heterogeneity and satellite imagery in ecuadorian amazonia. Ecol. Appl. 13: 352–371.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodríguez. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003a. Dispersal, environment, and floristic variation of western Amazonian forests. Science 299: 241–244.

UNESCO (United Nations Educational, Scientific and Cultural Organization). 1973. International classification and mapping of vegetation. UNESCO, Paris, 102 pp.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J.-C. Svenning, C. Hernández, K. Romoleroux, E. Losos, E. Magard, and H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. J. Ecol. 92: 214–229.

Vitousek, P. P. M.. 2008. The structure and functioning of montane tropical forests: control by climate, soils, and disturbance. Ecology 79: 1–2.

Vormisto, J., J.-C. Svenning, P. Hall, and H. Balslev. 2004. Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. J. Ecol. 92: 577–578.