

ECOLOGICAL DETERMINISM IN PLANT COMMUNITY STRUCTURE ACROSS A TROPICAL FOREST LANDSCAPE

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Abstract. The ecological mechanisms hypothesized to structure species-rich communities range from strict local determinism to neutral ecological drift. We assessed the degree of ecological determinism in tropical plant community structure by analyses of published demographic data; a broad range of spatial, historical, and environmental variables; and the distributions of 33 herbaceous species (plot size = 0.02 ha) and 61 woody species (plot size = 0.09 ha) among 350 plots in a 16-km² forest landscape (Barro Colorado Island, Panamá). We found a strong degree of cross-landscape dominance by a subset of species whose identities were predictable from sapling survivorship rates under shade. Using canonical ordination we found that spatial and environmental–historical factors were of comparable importance for controlling within-landscape variability in species composition. Past land use had a strong impact on species composition despite ceasing 100–200 years ago. Furthermore, edaphic–hydrological factors, treefall gaps, and an edge effect all had unique impacts on species composition. Hence, ecological determinism was evident in terms of both cross-landscape dominance and within-landscape variability in species composition. However, at the latter scale, the large portion of the explained variance in species composition among plots uniquely attributed to spatial location pointed to an equally important role for neutral processes.

Key words: Barro Colorado Island; dispersal limitation; mesoscale plant distributions; niche differences; oligarchy hypothesis; partial RDA; plant community assembly; redundancy analysis; shade tolerance; spatial autocorrelation; tropical forest; variance decomposition.

INTRODUCTION

The forces that structure tropical rain-forest plant communities and other species-rich biotic communities are controversial. One tradition considers local community structure to be the deterministic result of interspecific interactions and differences in niche requirements among species (reviewed in Tilman 1997, Wright 1999, 2002, and Hubbell 2001). A more recent contrasting view considers local communities to be controlled by dispersal-dependent sampling of the regional species pool (Cornell and Lawton 1992, Hubbell 2001). In the extreme, this view posits that local communities are governed by ecological drift mediated by propagule limitation and demographic stochasticity (Hubbell et al. 1999, Bell 2001, Hubbell 2001). Evidence supporting the importance of drift include recent findings of (1) strong seed limitation (Hubbell et al. 1999, Dalling et al. 2002, Muller-Landau et al. 2002), and (2) nonenvironmental spatial dependency in species distributions (e.g., Svenning 1999, 2001a, Tuomisto et al. 2003b), which is predicted by neutral dis-

persal limitation (Bell 2001, Hubbell 2001, Condit et al. 2002). However, there is also much evidence in favor of ecological determinism, notably findings of (1) density dependence (Harms et al. 2000, Wright 2002), (2) environmentally dependent distributions and performance (e.g., Clark et al. 1999, Svenning 1999, 2001a, b, Webb and Peart 2000, Davies 2001, Harms et al. 2001, Potts et al. 2002, Wright 2002, Phillips et al. 2003, Tuomisto et al. 2003a, b), (3) a trade-off between growth rates at high resources and survival rates at low resources (Kitajima 1994, Wright et al. 2003), and (4) patterns of species dominance that cannot be accommodated by neutral models (Hubbell 2001, Pitman et al. 2001, Condit et al. 2002; also cf. Duivenvoorden et al. 2002).

Here, we contribute to this debate by investigating the landscape-scale patterns of plant species dominance and distribution within a 16-km² tropical forest. With regard to dominance, we investigate the hypothesis that tropical tree communities are dominated by an oligarchy of common species at all spatial scales (Pitman et al. 2001) and assess the degree to which species abundances are predictable from their shade tolerance, a key trait for determining dominance in extratropical forests (Kobe 1996, Pacala et al. 1996, Koike 2001). If drift predominates in tropical plant communities, cross-landscape abundance should not be predictable from species traits. Concerning distribution, we assess the

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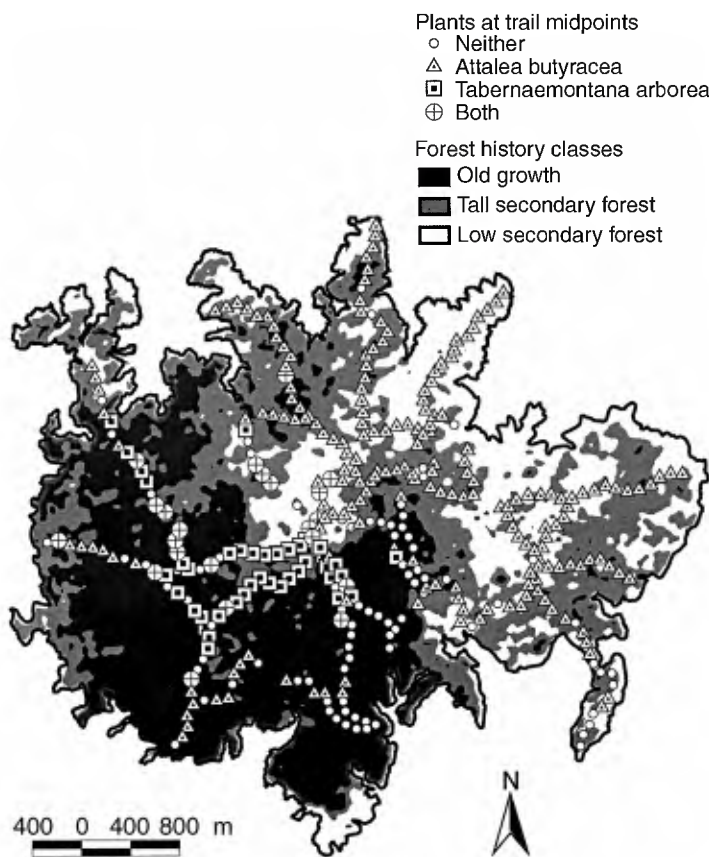


FIG. 1. The distribution across the 350 plots (0.09 ha each) of two woody species, *Attalea butyracea* and *Tabernaemontana arborea*, which according to Croat (1978) prefer young and old forest, respectively. Also shown is the distribution of the site history classes (see *Methods*), Barro Colorado Island, Panamá.

degree to which species distributions are controlled by environmental, historical, and spatial factors. Notably, we assess the relative importance of space vs. site history and local environment as determinants of within-landscape variability in species composition. If community structure is predominantly controlled by drift, then space should play a large role in determining species composition relative to history and environment (e.g., Tuomisto et al. 2003b). The few previous landscape-scale studies which have quantified the relative importance of space and environment–history as determinants of species distributions in tropical forests have generally found the latter to predominate (Dalle et al. 2002, Duque et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a; but cf. Potts et al. 2002). We investigate the determinants of species distributions using canonical ordinations and evaluate the relative importance of species and environment in determining plant distributions by employing Borcard et al. (1992)'s variance decomposition method. Our data sets include distributional data for 94 plant species, a broad range of explanatory variables, and published demographic data.

METHODS

The study site was Barro Colorado Island (BCI; 9°9' N, 79°51' W), a 16-km² former hilltop in the artificial

Gatun Lake in the Republic of Panamá (Croat 1978, Leigh et al. 1996, Leigh 1999) (Fig. 1). The vegetation is tropical semideciduous forest and the climate is seasonally dry. Mean annual precipitation is ~2600 mm, and elevation ranges between 27–160 m above sea level. The environment is a coarse-grained mosaic of old-growth and secondary forest (Fig. 1), soil types, lithologic units, and topographic structures (Leigh et al. 1996, Leigh 1999). About half the forest is old-growth, at least parts of which have not been under agriculture within the last 2000 years or more (Leigh 1999). Most of the secondary forest probably dates from the 1800s (Kenoyer 1929, Foster and Brokaw 1996).

The distribution of 33 species of herbs and 61 species of woody plants were inventoried along the complete 41-km trail system during July–August 2000 for herbs and December 2000–July 2001 for woody plants. We chose species that were easy to recognize and/or fairly common. The 94 species and their voucher numbers in the BCI Herbarium (Barro Colorado Island, Republic of Panamá) are listed in Appendix A. Our species selection seemed representative of at least the more common woody species in the BCI 50-ha plot (Appendix B). The trail-based sampling introduced only weak bias in the representation of the BCI environment (Appendix B). The trail system is divided into ~100-m segments by marker poles, and we scored presence–ab-



PLATE. 1. Low secondary forest with abundant *Cryosophila warscewiczii* (Arecaceae), J. D. Hood trail, Barro Colorado Island, Panamá. Photo credit: J.-C. Svenning.

sence of herbs (with adult-style leaf shape) and density of woody species (individuals ≥ 1.5 m tall, measured from the ground to the most distal point of the crown) along each of these segments. Herbs were scored within 1.0 m of each side of the trail and woody plants within 5.0 m to each side of the trail midline. Only segments with actual lengths of 85–115 m (99.1 ± 5.68 m; mean ± 1 SD) according to our GIS were used in the analyses ($n = 350$), excluding shorter or longer segments (Fig. 1). As the trails are ~ 1 m wide, the herb and woody plant plots were ~ 0.02 and ~ 0.09 ha, respectively. Plot size had no effect on species composition for herbs and at most a very weak effect for woody plants (Appendix B).

Twenty-one explanatory variables were determined for each plot, either from an Arc-Info geographic information system (GIS) for BCI, developed by R. Stallard and D. Kinner, or by new trail-wide surveys. The topographic base map for the GIS was digitized from 1:25 000 scale, 7.5 min quadrangle maps. Additional elevation data were collected through field surveys. A digital elevation model (DEM) was created from these data using the ANUDEM algorithm of Hutchinson (1989). The DEM was originally gridded with 25-m²

cells, but it was subsampled at 1-m² increments for calculation of the GIS variables. We note that subsampling does not improve the original resolution. Most explanatory variables were derived using the DEM and additional input maps (with 1-m² grid size). We extracted specific values for each GIS variable for each trail segment, calculating all areal variables for the area located within 5 m (perpendicular distance) from the trail midline. The GIS variables were:

1) Plot location (the geographical coordinates of the plot center) was used to compute nine spatial variables, namely, those of a cubic trend surface polynomial (the centered geographical coordinates $[X, Y]$ as well as X^2 , Y^2 , XY , X^3 , Y^3 , X^2Y , and XY^2), which is appropriate for capturing broad-scale spatial trends (Legendre and Legendre 1998).

2) Site history was derived from a dry-season 1927 aerial photograph of the island, rectified to the island DEM. The degree of canopy cover in a region of the island was quantified as a color index from the photograph: clear areas and deciduous tree canopies were lighter than areas with extensive leafed canopy (R. F. Stallard and D. A. Kinner, *personal observation*). The rectified photograph was converted into a grayscale

grid where each pixel received a value between 0 (black and forested) and 255 (white and cleared). The color values were put into three classes: (1) 0–95, (2) 95–160 and (3) 160–255, and pixel-scale anomalies were manually removed. Visual comparison with other BCI forest maps (Enders 1935, Foster and Brokaw 1996) indicated that these categories roughly correspond to the forest disturbance categories usually distinguished on BCI: old-growth, tall secondary, and low secondary forest (Fig. 1, Plate 1). The secondary forest probably dates back to 1800–1900, perhaps mostly ~1880 (Kenoyer 1929, Foster and Brokaw 1996). In the analyses, history was represented by two variables describing the percentage cover of site history type 1 (old growth forest, OG-for) and type 3 (low secondary forest, LS-for) per trail segment.

3) Distance to shore (mean distance [m] between the GIS cells of a trail segment and the lake edge). This variable represents an edge effect and was \log_e transformed, since edge effects decline rapidly and nonlinearly with distance from the edge in tropical forest fragments (Laurance et al. 1998).

4) Mean slope (maximum rate of change in elevation [$^\circ$] between a 1-m² cell and its eight neighbors; the variable used was the mean over all 1-m² cells in a given trail segment).

5) Hydrologic index ($\log_e[A/\tan \beta]$) represents topographic runoff potential of a stratified soil (Beven and Kirkby 1979, Wolock 1993). The first term in the index, A , is the hydrologic contributing area per grid-cell length. $\tan \beta$ represents the unitless topographic slope. Conceptually, an area with a high contributing area is likely to receive a lot of upslope water. If this location also has a low slope and, thus, a high value of $\log_e(A/\tan \beta)$, it likely drains slowly and will remain wetter during the dry season. Hydrologic field studies from BCI support this reasoning (Daws et al. 2002). The topographic-index algorithm of Wolock (1993) was used for computation of $\log_e(A/\tan \beta)$, the final variable being the trail segment mean for its 1-m² cells.

6) Lithology was based on Woodring (1958) and Johnsson and Stallard (1989) and digitized to represent the four island lithologies: basalt/andesite flows (type 1), Bohio Formation conglomerate (type 2), Caimito Volcanic Formation (type 3), and Caimito Marine Formation (type 4). In the analyses, it was represented by three variables describing the percentage cover of type 1 (BasaltFl), type 3 (CaimitoV), and type 4 (CaimitoM) per trail segment.

7) Soil type was derived from the lithology map and the DEM to estimate local soil types (Leigh 1999), based on relationships between soil type, slope, landscape curvature, and lithology established from soil surface samples from 39 sites around the island (R. Stallard and D. Kinner, *unpublished data*). The samples were analyzed for silica and aluminum. The $\text{Si}/(\text{Si} + \text{Al})$ ratios were used to establish whether the soils were rich in montmorillonite ($\text{Si}/[\text{Si} + \text{Al}] > 0.6$; soil type

1) or kaolinite ($\text{Si}/[\text{Si} + \text{Al}] < 0.6$; soil type 2). Montmorillonitic soils have higher cation exchange capacity than kaolinitic soils (Leigh 1999), which also makes them more likely to retain water in clay interstices and reduces drainage through clay swelling. The variable used was the trail segment mean for its 1-m² cells, each assigned 1 or 2 according to soil type.

Three environmental variables were determined independent of GIS:

1) Stream presence/absence was determined by streams crossing the trail and estimated to flow throughout the wet season (July–August 2000).

2) Gaps in the canopy were measured with the following ordinal index: 0, no large overhead or lateral gaps; 1, either exposed to very large lateral gap or 1–4 m of the trail exposed to the sky directly overhead as part of a major gap; or 2, ≥ 5 m of the trail exposed to the sky directly overhead and opening part of major gap (July–August 2000). A major gap was defined as an opening as large as the crown of one or more large canopy trees.

3) Soil moisture was determined by collecting samples of the upper 10 cm of the soil using standard soil corers during the late dry season (28 March–3 April 2001). No rain occurred just before or during the sampling period. A total of 1545 samples were collected across the whole trail system, 1 m off the trailside and at 25 m intervals within each trail segment. Gravimetric soil moisture was then determined for all of the samples using procedures similar to those outlined in Dietrich et al. (1996). Mean soil moisture by dry mass per segment was used in the analyses.

Hence, nine spatial variables, two historical, and 10 environmental variables were used in the analyses.

Analyses of dominance

We studied dominance by (1) looking at the interrelationship of landscape-scale plot frequency (number of plots in which a species is present) and density for the woody species (cf. Pitman et al. 2001), and (2) testing whether dominance is predictable from shade tolerance (e.g., Koike 2001), as represented by sapling survival rate (recalculated as a mortality rate by subtracting the percentage from 100) in shaded sites characterized by tall canopies in the BCI 50-ha plot (data taken from Welden et al. 1991).

Analyses of species distributions

We studied species distributions across the 350 plots using multivariate analyses. Three floristic data sets were used, herb species (presence–absence), woody species (presence–absence), and woody species (density). Detrended correspondence analysis (DCA) was used to estimate the amount of species turnover along the floristic gradients (i.e., gradient lengths) in the three species data sets (untransformed). DCA is well suited to estimate gradient lengths since its axes are scaled in units of the mean standard deviation (SD) of species

turnover (Legendre and Legendre 1998). A complete turnover in species composition occurs in ~ 4 SD units, while a half change occurs in $\sim 1\text{--}1.4$ SD units (Legendre and Legendre 1998). We used linear redundancy analysis (RDA) to investigate the degree of environmental, historical, and spatial control of within-landscape variability in species composition. RDA can be viewed as the canonical extension of principal component analysis (PCA), with the ordination vectors being constrained by multiple regression to be linear combinations of the original explanatory variables (Legendre and Legendre 1998). The species distribution data were Hellinger distance-transformed before use in RDA (Legendre and Gallagher 2001). This transformation allows species distribution data to be analyzed by Euclidean-based ordination methods like RDA, which thereby offer an often preferable alternative to chi-square based ordination methods such as canonical correspondence analysis (CCA, Legendre and Gallagher 2001). Notably, the Hellinger distance does not give rare species differential weighting, in contrast to the chi-square distance, and RDA does not give sites with many individuals higher weighting, in contrast to CCA (Legendre and Gallagher 2001). Since canonical ordination using RDA on Hellinger distance-transformed species data is a new method (but see Dalle et al. 2002), we repeated the analysis using the full set of explanatory variables as well as the variance partitioning using CCA as well as RDA on the untransformed species data. Unless specified otherwise the canonical ordination results reported are from RDA using the Hellinger distance-transformation. Significance of the canonical models, both in terms of the first canonical axis and all canonical axes, was tested using 999 permutations.

Following Borcard et al. (1992) we used canonical ordination to partition the variation in species composition into independent variance components (also cf. Økland and Eilertsen 1994, Økland 1999), however, we expanded the method to three classes of variables (environmental, historical, and spatial) rather than two. Hence, the total explained variance (R_t , the variance explained using the full set of 21 explanatory variables) was divided into seven nonoverlapping fractions, namely the pure environmental (R_{pe}), pure historical (R_{ph}), pure spatial (R_{ps}), mixed environmental–historical (R_{e+h}), mixed environmental–spatial (R_{e+s}), mixed historical–spatial (R_{h+s}), and mixed environmental–historical–spatial (R_{e+h+s}) fractions. The four mixed fractions (R_{e+h} , R_{e+s} , R_{h+s} , R_{e+h+s}) refer to variance exclusively shared by the component variable classes. The seven fractions were computed using RDAs and partial RDAs with the appropriate combinations of variable classes as explanatory variables and/or covariables (cf. Borcard et al. 1992). For example, R_{ph} was computed from a partial RDA with the historical variables as explanatory variables and the environmental and spatial variables as covariables, while R_{h+s} was computed

as $R_t - R_e - R_{ps} - R_{ph}$, where R_e is the variance explained by all the environmental variables combined. We investigated the importance of each explanatory variable using RDAs and partial RDAs with each variable as the only explanatory variable. Furthermore, we used the automatic forward selection procedure in CANOCO (ter Braak and Smilauer 2002) to provide an estimate of the best set of nonredundant variables for predicting species composition and to provide a ranking of the relative importance of the individual explanatory variables (ter Braak and Smilauer 2002). Variables were selected sequentially by the residual variance explained, judging the significance of the explanatory effect of the candidate variable by a permutation test (using 999 permutations) before its addition. When encountering the first variable included at $P \geq 0.05$, we terminated the variable selection to the exclusion of this variable.

The validity of the conclusions reached from the canonical analyses depends on the extent to which the explanatory variables represent the major factors controlling floristic composition. We investigated this issue in two ways. First, we compared the floristic gradients found by indirect gradient analysis (here, PCA on the Hellinger distance-transformed species data) to those found by RDA. This comparison allows us to determine whether our set of explanatory variables allowed the RDAs to capture the major floristic gradients identified by the PCA. The second method used to evaluate whether our explanatory variables captured the major factors controlling floristic composition involved an examination of residual floristic variation from a partial PCA, which used all 21 explanatory variables as covariables. This analysis will help determine if there are residual gradients in species composition caused by unmeasured or incompletely represented explanatory factors (cf. Clark et al. 1999).

RDA and PCA were computed after centering, but not standardizing the species data table. Thus, the RDA and PCA were computed on the covariance cross-products matrix (McCune and Grace 2002). CCA and DCA were computed without downweighting of rare species. The DCA was computed using detrending by segments. Trend surface variables were computed using SpaceMaker (Borcard and Legendre 2002). RDA, CCA, and DCA were computed using CANOCO 4.5 (ter Braak and Smilauer 2002). All other analyses were done in JMP 4.0.4 (SAS Institute 2001).

RESULTS

Dominance

A total of 56 350 stems of the 61 woody species were found in the 350 plots. The woody and herbaceous plants had totals summed over all species of 7592 and 2435 presences, respectively. There was a strong positive log–log correlation between the frequency of woody species in the 350 plots and their mean and

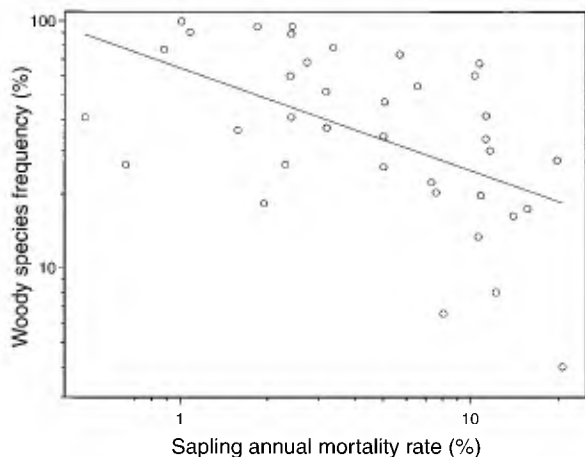


FIG. 2. Landscape-scale frequency of woody species (percentage of plots where present) across the 350 0.09-ha plots decreases with sapling annual mortality (annualized percentage, 1982–1985) in high-canopy sites (from Welden et al. 1991): linear regression, both variables \log_{10} -transformed, $r^2 = 0.28$, $P = 0.0007$, $n = 37$ woody species.

maximum density per plot (mean density over all plots, $r = 0.94$, $P < 0.0001$; mean density in occupied plots, $r = 0.65$, $P < 0.0001$; maximum density, $r = 0.74$, $P < 0.0001$; $n = 61$). Nearly one third of the variation in frequency was explained by differences in sapling mortality rates beneath a tall canopy (Fig. 2). Log-log linear regressions of density on sapling mortality rate under high canopy produced even stronger negative relationships: $r^2 = 0.36$, $P < 0.0001$ (for mean density over all plots), $r^2 = 0.34$, $P = 0.0002$ (for mean density in occupied plots), and $r^2 = 0.36$, $P < 0.0001$ (for maximum density in any plot).

Distributions

The vegetation on BCI exhibits only short compositional gradients (in species turnover SD units) as estimated using DCA: herbs (axis 1, 2.75; axis 2, 2.72;

axis 3, 2.78; axis 4, 2.36), woody plants (presence-absence; axis 1, 1.70; axis 2, 1.65; axis 3, 1.80; axis 4, 1.54), and woody plants (density; axis 1, 2.71; axis 2, 2.45; axis 3, 1.78; axis 4, 1.58).

About 22–24% of the variation in distributions of presences and absences of both herbs and woody plants was explained by environmental, historical, and spatial variables using RDA on the Hellinger distance-transformed species data (Table 1). The total explained floristic variation (TVE) rose to 38% of the variation in the distribution of stem densities of woody species (Table 1). The RDA on the untransformed species data gave nearly identical results, while CCA consistently resulted in moderately smaller TVE (Appendix D). The first four environmental–historical–spatial gradients accounted for 69–80% of TVE (Table 1). For woody plants, the first RDA axis separated species considered typical (Croat 1978, Foster and Brokaw 1996) of young (e.g., *Astrocaryum standleyanum*, *Attalea butyracea*, *Cryosophila warscewiczii*, and *Gustavia superba*; see Plate 1) and old forest (e.g., *Beilschmiedia pendula*, *Calophyllum longifolium*, *Poulsenia armata*, *Prioria copaifera*, *Quararibea asterolepis*, *Socratea exorrhiza*, *Tabernaemontana arborea*, and *Tetragastris panamensis*) for both presence-absence and density data (Appendix C). For herbs, the second RDA axis separated species considered typical (Croat 1978, Foster and Brokaw 1996) of young forest and disturbed habitats (e.g., *Oplismenus hirtellus*, *Xanthosoma helleborifolium*, and *Xiphidium caeruleum*) and old forest (e.g., *Asplenium delitescens* and *Pharus parvifolius*, Appendix C).

Spatial and environmental–historical factors exhibited correlations of similar magnitude on the first four RDA axes for all three floristic data sets (Fig. 3). Considering only the environmental–historical factors, for the woody plants, the first axis could be interpreted as a historical gradient, the fourth (presence-absence) or second (density) as an edge gradient, and the remaining axes as edaphic–hydrologic gradients (Fig. 3). For

TABLE 1. Linear redundancy analysis (RDA) of the environmental–historical–spatial control of plant species distributions (Hellinger distance-transformed), Barro Colorado Island, Panamá.

Species group	Data†	P ‡	Sum of all canonical eigenvalues§	Cumulative percentage of canonical variance accounted for by axes 1–4			
				I	II	III	IV
Herbs	P–A	0.001	0.236	30.8	54.0	64.3	72.1
Woody	P–A	0.001	0.223	31.5	50.6	60.6	68.9
Woody	Density	0.001	0.377	33.4	57.3	71.5	79.8

Notes: The full set of 10 environmental, two historical, and nine spatial explanatory variables was used.

† P–A, presence–absence data.

‡ Based on 999 permutations: tests of significance of the first canonical axis vs. all canonical axes gave identical results.

§ The sum of all canonical eigenvalues equals the proportion of the total variance explained, because CANOCO always sets the total variance at 1 in PCA/RDA (ter Braak and Smilauer 2002).

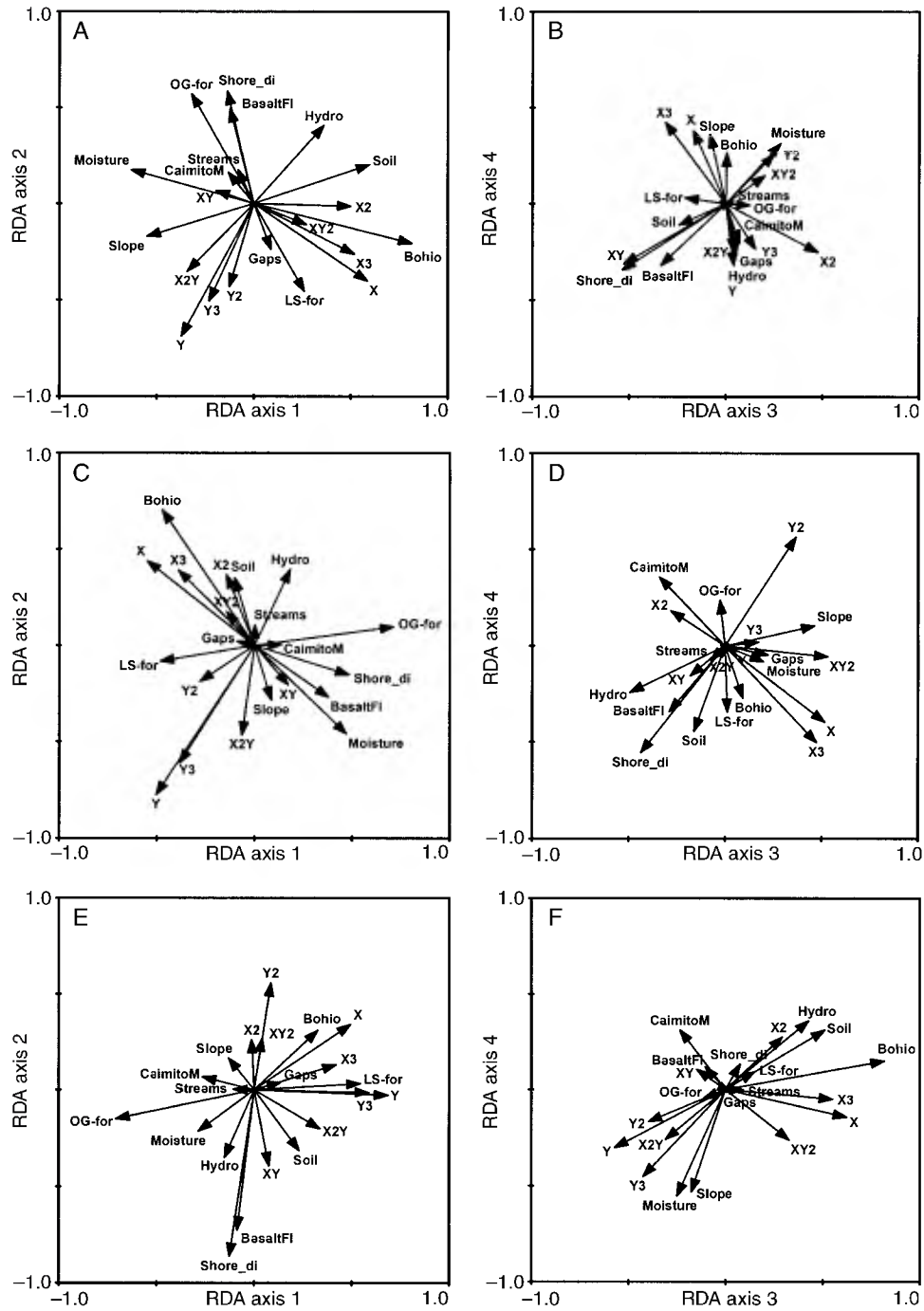


FIG. 3. Redundancy analysis scores (biplot arrows) for the 21 explanatory variables on the first four ordination axes (in species scaling) for (A, B) herbs, (C, D) presence-absence of woody plants, and (E, F) density of woody plants. Panels A, C, and E present axes 1 and 2; panels B, D, and F present axes 3 and 4. All RDAs were calculated using Hellinger distance-transformed species data; numerical results are in Table 1. Key to abbreviations: Hydro, hydrologic index; moisture, soil moisture; Soil, mean soil type; Shore_di, distance to shore; BasaltFl, lithology type 1; CaimitoV, lithology type 3; CaimitoM, lithology type 4; OG-for, old-growth forest (site history type 1); LS-for, low secondary forest (site history type 3).

TABLE 2. Variance decomposition by linear redundancy analysis (RDA) of species distribution data (Hellinger distance-transformed) into its purely environmental (R_{pe}), purely historical (R_{ph}), purely spatial (R_{ps}), and various mixed components for plants from Barro Colorado Island, Panamá.

Variance components fractions	Herbs (presence-absence)		Woody plants (presence-absence)		Woody plants (density)	
	TV (%)	TVE (%)	TV (%)	TVE (%)	TV (%)	TVE (%)
R_{pe}	6.5	27.5	5.1	22.9	6.8	18.0
R_{ph}	0.8	3.4	0.7	3.1	0.8	2.1
R_{ps}	6.5	27.5	7.3	32.7	12.4	32.9
R_{e+h}	0.4	1.7	0.5	2.2	1.0	2.7
R_{e+s}	7.3	30.9	5.6	25.1	11.1	29.4
R_{h+s}	1.1	4.7	2.4	10.8	4.2	11.1
R_{e+h+s}	1.0	4.2	0.7	3.1	1.4	3.7
Residuals	76.4		77.7		62.3	

Note: TV, total variance; TVE, total variance explained.

herbs, the first and fourth RDA axes seemed largely to represent edaphic-hydrologic gradients, the second axis a historical-edge gradient, and the third an edge gradient (Fig. 3).

For all three floristic data sets, the three greatest variance components were the mixed spatial-environmental (R_{e+s}), the pure spatial (R_{ps}), and the pure environmental component (R_{pe}). For herbs, pure spatial and pure environmental effects accounted for equal proportions of TVE, while the purely spatial effect was clearly the greater for the woody plants, in particular for the density data (Table 2). While small, the pure historical effect (R_{ph} ; Table 2) was always significant at $P = 0.001-0.003$ (partial RDA) for the three data sets (as were R_{pe} and R_{ps}). The CCA and RDA on the untransformed species data produced qualitatively similar variance components, although the CCA for herbs allocated a greater fraction of TVE to R_{pe} (37% instead of 28%; Appendix D).

With automatic forward selection, the first five variables selected (in order selected) were CaimitoV (lithology type 3), Y , shore distance, soil moisture, and X^2 for herbs; Y , CaimitoV, shore distance, X , and soil moisture for woody plants (presence-absence data); and Y , distance to shore, CaimitoV, X , and soil moisture for woody plants (density data). The following variables were excluded by the forward selection procedure: streams, soil type, low secondary forest (site history type 3), X , X^3 , Y^2 , X^2Y , and XY^2 for herbs; basalt flows (lithology type 1), hydrological index, and XY for woody plants (presence-absence data); and gaps, soil type, and streams for woody plants (density data). We note that for herbs many of the excluded variables did enter at $P < 0.05$, but only after the procedure encountered the first variable entered at $P \geq 0.05$. Partial RDA showed that lithology and soil moisture had the highest unique contributions to the explained floristic variation among the explanatory factors, while soil type and streams never had significant unique contributions (Table 3). Lithology probably captured most variation in species composition associated with soils.

To determine whether the explanatory variables captured the main floristic gradients, we compared sample scores from the RDAs using the full set of explanatory variables to sample scores from the PCAs (both RDAs and PCAs were in sample scaling on the Hellinger distance-transformed species matrices). In all but one case, the PCA axes had the highest correlation with the RDA axes of the same number. RDA and PCA sample scores were moderately to highly correlated, notably for axis 1 and 2: herbs (axis 1, $r = 0.957$; axis 2, $r = -0.942$; axis 3, $r = 0.404$; axis 4, $r = 0.253$), woody plants (presence-absence data; axis 1, $r = 0.993$; axis 2, $r = 0.975$; axis 3, $r = -0.514$; axis 4, $r = 0.756$), and woody plants (density data; axis 1, $r = -0.928$; axis 2, $r = -0.900$; axis 3, $r = 0.761$; axis 4, $r = -0.569$; $P < 0.0001$ and $n = 350$ in all cases). The one exception for which PCA and RDA axes of different number had the highest correlation was for the density of woody plants for which PCA axis 4 was slightly better correlated with RDA axis 3 ($r = -0.636$) than RDA axis 4. Hence, the set of explanatory variables used was sufficient to capture the main floristic gradients on BCI.

Using partial PCA to investigate patterns in the residual variation suggested a relatively weak tendency for geographically close plots to have similar species composition (see plots of sample scores in Appendix E). Plots of species scores suggested no simple ecological explanations for the residual gradients for the herbs (Appendix E). However, the first partial PCA axis for woody plants (presence-absence data; Appendix E) showed some tendency for separating species considered typical of young and old forest (cf. Croat 1978; Foster and Brokaw 1996). The first partial PCA axis for woody plants (density data) mainly represented a contrast of *Oenocarpus mapora* vs. *Faramaea occidentalis* and *Hybanthus prunifolius* (Appendix E).

DISCUSSION

Oligarchic dominance

Pitman et al. (2001) found a positive correlation between the mean density of individuals and the fre-

quency of plots occupied for trees in two Amazonian forest landscapes (both Spearman correlations were 0.53, $P < 0.0001$). We find similar, but stronger, correlations between interplot frequency and mean density across all plots, mean density in occupied plots, as well as maximum density in any plot for 61 woody species on BCI. Both frequency and mean density across all plots depend on the number of empty plots. However, the relationships between mean density in occupied plots or maximum density in any plot and frequency are not similarly mathematically constrained, and their positive relationship must reflect real processes. These could be neutral and/or deterministic (cf. Gaston and Blackburn 2000, Bell 2001).

Previously, there has been little success finding plant trait correlates of landscape-scale abundance in tropical forests (Pitman et al. 2001). Here, we found that sapling mortality rate in the shade explains about a third of the variation in landscape-scale frequency and density, hence showing that there is a strong deterministic component to these landscape-scale aspects of plant community structure on BCI (as found for the BCI 50 ha plot; Duivenvoorden et al. 2002). High sapling mortality can result from a response to light conditions per se (Wright et al. 2003), or reflect low survivorship irrespective of canopy conditions. In any case, species with higher sapling survivorship under shade are more likely to be widespread in the landscape as well as locally abundant. In this respect, the BCI forest apparently is similar to extratropical forests (Kobe 1996, Pacala et al. 1996; also cf. Koike 2001).

Our findings agree with the hypothesis of Pitman et al. (2001) that Amazonian tree communities are dominated by an oligarchy of common species at all spatial scales. Pitman et al. (2001) suggested that areas dominated by predictable oligarchies may be small where environmental heterogeneity is high. Hence, the particularly strong frequency–density relationship found here may reflect a low level of habitat heterogeneity on BCI. Notably, DCA gradient lengths are short: 2–3 SD for both herbs and woody plants on BCI. The main floristic gradients on BCI are moderate in strength and do not involve complete turnover in species composition (cf. Legendre and Legendre 1998). Since our species selection was biased towards the more common species, it is possible that we would have found higher beta diversity if we had studied the full BCI flora (cf. Pitman et al. 2001, Phillips et al. 2003). However, in a study of all trees ≥ 10 cm dbh, Duivenvoorden (1995) likewise documented low beta diversity in well-drained uplands in a western Amazonian landscape.

Spatial and environmental–historical determinants of species composition

Several landscape-scale studies of species distributions in tropical forests have found that environmental–historical factors predominate over space as determinants of species composition (Dalle et al. 2002, Duque

et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a; also cf. Svenning 1999). Other landscape-scale studies have come to the opposite conclusion (Svenning 2001a, Condit et al. 2002) or suggested that the balance might depend on soil fertility (Potts et al. 2002). Our results regarding species composition of woody plants on BCI, notably for the density data, assigned more of the total variance explained (TVE) to pure spatial variation (R_{ps}) than to all sources of historical and environmental variation combined (i.e., R_{ph} , R_{pe} , and R_{e+h} combined; Table 2). However, the pure spatial and combined pure environmental–historical TVE fractions were of similar magnitude for woody plants, and for herbs, R_{ph} , R_{pe} , and R_{e+h} were assigned a greater fraction of the TVE than R_{ps} (Table 2). In terms of overall TVE, species composition was much more predictable when densities rather than presence–absence data were considered (Table 1). Interestingly, the increase in predictability mainly resulted from an increase in R_{ps} and R_{e+s} (Table 2). Hence, there must be broad-scale variation in species abundances independent of environmental gradients and site history on BCI. These patterns are congruent with the view that local ecological determinism and dispersal-limited ecological drift are both important controls of species distributions in tropical forest at the landscape scale (cf. Potts et al. 2002, Tuomisto et al. 2003b). While we believe the spatial structure (at least R_{ps} , see Table 2) is likely to reflect dispersal limitation, an alternative explanation would be that we missed one or more important spatially autocorrelated abiotic or biotic variables. In favor of the dispersal interpretation is a seed trap study from the BCI 50-ha plot, which indicates extensive seed limitation for nearly all species (Hubbell et al. 1999, Wright 2002). Furthermore, in a landscape-scale study of temperate forest herb distributions strong nonenvironmental clumping was associated with poor propagule dispersal ability (Svenning and Skov 2002).

The major canonical axes of floristic variation from the RDA correlated with site history, edaphic–hydrologic conditions, and distance to shore in all three data sets (Fig. 3). While similar landscape-scale relationships have been reported from other tropical forests (e.g., Clark et al. 1995, 1999, Guariguata et al. 1997, Svenning 1998, Webb and Peart 2000, Potts et al. 2002), no previous analyses at this scale have considered edaphic and nonedaphic factors and spatial dependency simultaneously (except the study by Dalle et al. [2002] on 23 useful plant species in an indigenous territory, Panamá). The fact that both spatial, historical, and environmental variables correlated with the major canonical axes for all three floristic data sets (Fig. 5) clearly points to importance of simultaneous consideration of these factors (as do the large mixed variance fractions, notably R_{e+s}).

The major floristic gradient for woody plants and the second most important floristic gradient for herbs was the historical gradient contrasting old-growth and low

TABLE 3. Partial linear redundancy analysis (RDA) testing the unique contribution of each environmental factor to the environmental–historical–spatial control of plant species distributions (Hellinger distance-transformed). Barro Colorado Island, Panamá.

Factor	Unique contribution to total canonical variance					
	Herbs (presence–absence)		Woody plants (presence–absence)		Woody plants (density)	
	TVE (%)†	P ‡	TVE (%)	P	TVE (%)	P
Shore distance§	1.7	0.008	1.8	0.010	1.1	0.001
Gaps	3.0	0.001	1.8	0.003	0.8	0.081
Slope	2.1	0.003	1.3	0.078	0.8	0.017
Hydrologic index	2.1	0.004	0.9	0.519	1.3	0.001
Streams	1.3	0.072	1.3	0.078	0.8	0.070
Soil moisture	5.9	0.001	4.9	0.001	3.4	0.001
Lithology	5.5	0.001	6.3	0.001	5.3	0.001
Soil type	0.8	0.782	0.9	0.383	0.5	0.325

Notes: A partial RDA is calculated for each environmental factor using all other environmental, historical, and spatial factors as covariables.

† TVE, total variance explained.

‡ Based on 999 permutations.

§ Log_e-transformed.

|| Lithology includes the three variables BasaltFI, CaimitoV, and CaimitoM.

secondary forest. This interpretation was evident not only from the RDA scores for the explanatory variables (Fig. 3), but also from the species scores (Appendix C). The importance of site history for floristic composition on BCI agrees with the observations of Croat (1978) and Foster and Brokaw (1996). Past human disturbance has also been reported to influence plant distributions in other tropical forests (Clark et al. 1995, Guariguata et al. 1997, Svenning 1998, Thompson et al. 2002). However, hitherto evidence for the legacy of past land use has mostly been limited to more recent human activity. The human activities that created secondary forest on BCI largely ceased as early as 100–200 years ago (Kenoyer 1929, Foster and Brokaw 1996). The importance of site history as indicated by the RDA axes would seem to contrast with small TVE fractions assigned to R_{PH} and the mixed fractions involving history. Part of the explanation probably is that site history is represented by fewer variables ($n = 2$) in the analyses than environment ($n = 10$) or space ($n = 9$).

Apart from site history, the RDA and partial RDA results also showed that edaphic–hydrologic factors, distance to shore, and, to a smaller extent, gaps all had unique effects on species composition on BCI (Table 3). Among these soil moisture, lithology, and distance to shore were most important (Fig. 3, Table 3; also cf. forward selection results). In particular, the importance of edaphic–hydrological variation in controlling floristic composition in tropical forest landscapes is becoming well established (e.g., Clark et al. 1995, 1999, Duivenvoorden 1995, Svenning 1999, Webb and Peart 2000, Harms et al. 2001, Duque et al. 2002, Potts et al. 2002, Thompson et al. 2002, Phillips et al. 2003, Tuomisto et al. 2003a).

Substantial amounts of floristic variation could not be attributed uniquely to environment, history, or space. Thus, R_{e+s} included 25–31% of TVE, while the other mixed fractions together included 11–17% of TVE. The main reason for the large mixed variance fractions is the coarse-grained nature of the environmental and historical variation across BCI. Old-growth and secondary forest (Fig. 1), soil type (Leigh 1999), lithology (Leigh et al. 1996), topography (Leigh et al. 1996), and distance to shore (as a simple consequence of geographical constraints) all exhibit large-scale patchiness on BCI. Consequently, when attempting to sample the landscape at random, as we did, it is unavoidable that there will be considerable intercorrelation within the set of environmental and historical variables and in particular between these and the spatial variables. We included distance to shore among the environmental variables despite its spatial definition since its purpose was to represent edge effects (Laurance et al. 1998). If distance to shore was excluded from the analyses, R_{e+s} remained high (22–29% of TVE). Large mixed spatial–environmental TVE fractions are common in large-scale studies of plant distributions or diversity (e.g., Heikkinen and Birks 1996, Lobo et al. 2001, Duivenvoorden et al. 2002, Tuomisto et al. 2003b; but cf. Dalle et al. 2002). If the objective is to study distributional determinants along predefined gradients rather than across the landscape as a whole, the problem of joint variation among the explanatory variables can be minimized through the sampling design (e.g., Phillips et al. 2003).

It is likely that the large amount of unexplained floristic variance (62–78%; Table 1) in large part reflects lack of fit to the model implicit in the ordination method (Økland 1999). Other potential sources include (cf.

Borcard and Legendre 1994) demographic stochasticity (cf. Hubbell 2001), missing small-scale or nonspatial explanatory factors, incomplete representation of the measured explanatory factors, and trivial sampling noise (cf. Clark et al. 1999). The partial PCA sample plots indeed suggested the occurrence of modest small-scale spatial dependency in species composition (Appendix E). Furthermore, for woody plants (presence–absence) the first partial PCA axis (Appendix E) tended to separate species considered typical of young and old forest (cf. Croat 1978, Foster and Brokaw 1996), suggesting that there is small-scale variation in past land use on BCI left unaccounted for by the site history variables. For woody plants (density), the first partial PCA axis (Appendix E) contrasted the midstory palm *Oenocarpus mapora* with the treelet *Faramea occidentalis* and the shrub *Hybanthus prunifolius* (all abundant on BCI). An explanation for this pattern can possibly be found in Foster and Brokaw (1996:75), who noted that abundant *Oenocarpus mapora* is (1) typical of former massive blowdowns and (2) inhibits undergrowth to some degree. While a complete coverage of all factors driving species composition has not been achieved, the close agreement between the RDA and PCA results shows that the set of explanatory variables used was sufficient to capture the main floristic gradients on BCI. A low percentage variance explained is frequent in landscape-scale studies of spatial variation in floristic structure in tropical forests (Duivenvoorden 1995, Clark et al. 1999, Svenning 1999) and other vegetation types (e.g., Borcard et al. 1992, Heikkinen and Birks 1996, Svenning and Skov 2002; also cf. Økland 1999).

Conclusion

Our main findings were (1) a strong degree of oligarchic dominance, with landscape-scale abundance being moderately predictable from sapling survivorship rates under shade for woody plants, (2) that space and environmental–historical factors were of comparable importance for controlling herb species composition while space was of somewhat greater importance for woody plants, (3) that past human land use on BCI still had a strong impact on species composition despite having ceased 100–200 years ago, and (4) that with regard to environmental control, edaphic–hydrological factors, gaps, and an edge effect all had unique impacts on within-landscape variability in species composition on BCI. We believe the above results provide support for a joint role of ecological determinism and ecological drift in controlling plant community structure in tropical forest landscapes. Furthermore, it seems that ecological determinism may be particularly strong when considering aspects of average landscape-scale community structure (such landscape-scale frequency and abundance), while ecological drift may play a greater role for structuring species distributions within landscapes.

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APPENDIX A

A total species list, including family, growth form, and voucher number is available in ESA's Electronic Data Archive: *Ecological Archives* E085-073-A1.

APPENDIX B

Evaluations of the potential methodological problems in relation to the species selection, the spatial sampling, and the variable plot sizes are available in ESA's Electronic Data Archive: *Ecological Archives* E085-073-A2.

APPENDIX C

Biplots of species and samples based on RDAs involving the full set of 21 explanatory variables are available in ESA's Electronic Data Archive: *Ecological Archives* E085-073-A3.

APPENDIX D

Variance decomposition by two alternative procedures, RDA and CCA, of the untransformed species data is available in ESA's Electronic Data Archive: *Ecological Archives* E085-073-A4.

APPENDIX E

The results of partial principal components analysis (PCA) of the Hellinger distance-transformed species data using the complete set of environmental, historical, and spatial variables as covariables are available in ESA's Electronic Data Archive: *Ecological Archives* E085-073-A5.