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The relative roles of environment, history and local dispersal in controlling the distributions of common tree and shrub species in a tropical forest landscape, Panama

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Abstract: We used regression models and information-theoretic model selection to assess the relative importance of environment, local dispersal and historical contingency as controls of the distributions of 26 common plant species in tropical forest on Barro Colorado Island (BCI), Panama. We censused eighty-eight 0.09-ha plots scattered across the landscape. Environmental control, local dispersal and historical contingency were represented by environmental variables (soil moisture, slope, soil type, distance to shore, old-forest presence), a spatial autoregressive parameter (ρ), and four spatial trend variables, respectively. We built regression models, representing all combinations of the three hypotheses, for each species. The probability that the best model included the environmental variables, spatial trend variables and ρ averaged 33%, 64% and 50% across the study species, respectively. The environmental variables, spatial trend variables, ρ, and a simple intercept model received the strongest support for 4, 15, 5 and 2 species, respectively. Comparing the model results to information on species traits showed that species with strong spatial trends produced few and heavy diaspores, while species with strong soil moisture relationships were particularly drought-sensitive. In conclusion, history and local dispersal appeared to be the dominant controls of the distributions of common plant species on BCI.

Key Words: Barro Colorado Island, dispersal limitation, drought tolerance, environmental control, soil

INTRODUCTION

Understanding the controls of species distributions is a central issue in ecology and conservation. In tropical plant ecology, the relative importance of the potential determinants of species distributions has been hotly debated for several decades (Ashton 1964, Hubbell 1979, 2001; Poore 1968, Tuomisto & Ruokolainen 1993). The debate has been inconclusive because several possible determinants have received strong, but variable support. Many studies have shown that local- and landscape-scale plant distributions depend on the local environment in tropical forests, notably on edaphic factors and topography (Ashton 1964, Clark *et al.* 1999, Harms *et al.* 2001, Phillips *et al.* 2003, Potts *et al.* 2002, Svenning 1999, Svenning *et al.* 2004, Tuomisto *et al.* 2003a, Webb & Peart 2000).

There are, however, two important alternatives to environmental control of plant distributions in tropical forests. (1) Localized dispersal has long been recognized as a likely cause of patchiness in the distributions of many species in tropical forests (Ashton 1969, Poore 1968) and has received much attention recently due to its central role in neutral community theory (Bell 2001, Hubbell 2001). Evidence from spatial analyses, seed trap studies, and seed addition experiments indicate that distributions

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are often strongly limited by localized dispersal (Condit *et al.* 2000, 2002; Dalling *et al.* 2002, Harms *et al.* 2000, Hubbell *et al.* 1999, Makana & Thomas 2004, Svenning & Wright 2005, Uriarte *et al.* 2005). (2) Historical contingency has received relatively little attention in tropical vegetation ecology (but see Thompson *et al.* 2002, White & Hood 2004) despite the widespread evidence that many tropical forests are undergoing successional processes after past anthropogenic disturbances (Clark *et al.* 1995, Foster & Brokaw 1996, Svenning 2001, Svenning *et al.* 2004) or are experiencing broad-scale plant migrations (Beard 1946, Charles-Dominique *et al.* 2003). The limited focus on history is particularly striking given the evidence for pervasive climate changes and prehistoric human disturbance of tropical forests during preceding millennia and their strong vegetation impacts (Behling 2003, Burbridge *et al.* 2004, Bush *et al.* 2000, Colinvaux *et al.* 1988, Heckenberger *et al.* 2003, Ledru *et al.* 1998, Mayle *et al.* 2004, Willis *et al.* 2004).

In the present paper we use spatial regression modelling to represent the three competing hypotheses (environmental control, localized dispersal and broad-scale historical contingency) for the distribution of common plant species in a tropical forest landscape and an information-theoretic approach to assess the relative support for each model (Burnham & Anderson 2002, Johnson & Omland 2004). Given that empirical evidence already exists that local environment, history and dispersal all exert some control on plant distributions in tropical forests, simple null hypothesis testing of the individual mechanisms is not likely to yield much further progress. Instead the focus should shift to estimating their relative importance. The information-theoretic approach is specifically designed to assess the relative levels of support for a set of competing hypotheses and to allow inferences to be drawn from the whole set of competing models (Burnham & Anderson 2002, Johnson & Omland 2004). Contrary to traditional null hypothesis testing, model selection is based on the simultaneous confrontation of several competing hypotheses with data. The three primary advantages of the information-theoretic approach are that one is not restricted to evaluating a single model against an arbitrary probability threshold, relative support for competing hypotheses can be quantified, and model averaging can be used to make robust parameter estimates and predictions when several models have similar support (Johnson & Omland 2004). We used the information-theoretic approach not only to evaluate the relative support for the three hypotheses studied, but also to assess whether the parameter estimates for species-environment relationships and local spatial autocorrelation were related to species traits that potentially influence distribution and abundance.

METHODS

Study site

The BCI study site (9°09′N, 79°51′W) is a 16-km^2 former hilltop (27–160 m asl) in the artificial Gatun Lake, Republic of Panama. The climate is seasonally dry and annual precipitation averages *c.* 2600 mm. The vegetation consists of old-growth and 100–200-y-old secondary tropical semi-deciduous forest, which cover roughly the south-western and north-eastern halves of BCI, respectively (Foster & Brokaw 1996). A palaeobotanical study conducted in the old-growth found no evidence for agriculture at any time, continuous presence of many forest plant genera, and evidence for brief low intensity human occupations 500 and 1500 y BP, possibly on a seasonal basis (Piperno 1990). The secondary forest is mainly the result of clearing in the 1800s during the French attempt to construct a canal. Detailed descriptions of BCI can be found in Croat (1978), Leigh (1999) and Leigh *et al.* (1996).

Species and environmental data

The 26 study species (Table 1), all trees and shrubs, were chosen because they were included in at least one of two previous studies on BCI (Engelbrecht & Kursar 2003, Svenning *et al.* 2004) and were present in $\geq 50\%$ of the 88 study plots (see below). By focusing on common species, we minimized problems caused by zero-inflated data. Plant distributions were inventoried along the 41-km trail system during 2000–2002 (see Svenning *et al.* 2004 for further details). The trail system is divided into segments by marker poles, and 350 of these segments (plots) are approximately 100 m long (mean ± SD = 99 ± 6 m; Svenning *et al.* 2004). To ensure adequate sampling of the edaphic gradients on BCI, all 350 plots were classified as having values above or below the median soil type, soil moisture, and slope (see below), and 11 plots were selected at random from each of the eight possible combinations of 'above' or 'below' values, i.e. n = 88. Individuals ≥ 1.5 m tall (measured from the ground to the top of the crown) of the study species were counted for each plot within 5.0 m to each side of the trail midline. Since the trails were ≈ 1 m wide, effective plot size was ≈ 0.09 ha.

A previous study using constrained ordinations found that the environmental factors most strongly related to quantitative woody plant species composition gradients on BCI were soil moisture, topographic slope inclination, type of bedrock or soil, distance to lake shore, and presence of old-growth forest (Svenning *et al.* 2004). As soil type has more direct relevance to plants than bedrock, we included the first at the expense of the latter.

Hence, the set of environmental variables included were: (1) Moisture; mean gravimetric soil moisture determined for samples of the upper 10 cm of the soil, collected at 25-m intervals using 12–25-mm-diameter soil corers during the late dry season 28 March to 4 April 2001. (2) Slope; the plot average maximum rate of change in elevation between a 1-m^2 cell and its eight neighbours calculated using a Geographic Information System (GIS) topographic map developed for BCI by R. F. Stallard and D. A. Kinner. (3) Soil type; soil mineralogical composition on BCI is largely controlled by lithology and slope, with abundant kaolinite on gently sloping areas underlain by igneous rocks, while montmorillonite predominates on steep slopes and sedimentary rocks (Johnsson & Stallard 1989). Accordingly, a soil map was derived from maps of lithology and slope (map by D. A. Kinner, p. 73 in Leigh 1999). The soil type of each plot was scored as montmorillonite (scored as 0, 41 plots) or kaolinite (scored as 1, 47 plots) according to the most frequent soil type among the 1-m^2 GIS cells in each plot. However, for the edaphic classification of the 350 plots (above) the average soil type per plot was computed instead. Kaolinite has lower cation exchange capacity (CEC), particle surface area, and water retention than montmorillonite (Birkeland 1999). (4) Shore distance; the mean distance (m) between the 1-m^2 GIS cells of a plot and the lake edge, $\log_e$-transformed to represent non-linear edge effects. (5) Old-forest; absence (0; 43 plots) or presence (1; 45 plots) of old-growth forest, based on a 1927 aerial photograph of BCI. Svenning *et al.* (2004) provide further description of the environmental variables.

Model building

We used ordinary least-squares regression (OLS) and conditional autoregressive (CAR) models to relate species abundance to sets of explanatory variables and parameters representing the three hypotheses (Lichstein *et al.* 2002). Species abundance was square-root-transformed to reduce skewness. The transformed abundances had |skewness| <1, except for *Attalea butyracea* (skewness = 1.75), *Gustavia superba* (1.27) and *Picramnia latifolia* (1.14).

The environmental control hypothesis was represented by the five environmental variables, all known to affect plant species distributions on BCI (Croat 1978, Harms *et al.* 2001, Knight 1975, Svenning *et al.* 2004). The three continuous variables were standardized and had |skewness| <1. Quadratic terms were not considered, as only 2–3 species had significant (at $P < 0.05$) correlations with the squares of moisture and slope with $|r|$ always <0.30. While the young forest on BCI is a product of past anthropogenic disturbance, we chose to include the old-forest variable in the environmental variable set. Old-growth and secondary forest differ structurally on BCI (Croat 1978, Foster & Brokaw 1996) and, elsewhere, in light regime (Nicotra *et al.* 1999). Succession in plant communities may be constrained by either dispersal or environmental conditions (Pacala & Rees 1998). By placing the old-forest variable in the environmental variable set, we emphasized the latter mechanism. It is nevertheless clear that the old-forest variable also has an historical component (Svenning *et al.* 2004) and might also reflect dispersal (Capers *et al.* 2005).

On BCI broad-scale historically contingent patterns are likely to have arisen through the impact of past anthropogenic disturbance and subsequent dispersal- and time-limited successional processes as well as through broad-scale natural migrations (Foster & Brokaw 1996, Piperno 1990). In the present paper species abundance differences caused by persistent environmental changes due to past disturbance were considered to be consistent with the environmental control hypothesis (as discussed above), while patterns were only considered as historically contingent when they reflect past conditions or time-accumulative processes. Broad-scale historical processes are expected to leave their mark as spatial trends in species distributions. Hence, the historical contingency hypothesis was represented by four trend-surface variables, namely the centred planar coordinates (X, Y; in 100-m units) as well as X^2 and Y^2. XY and higher order terms were not included due to the limited sample size and because of their generally lower importance in a previous study (Svenning *et al.* 2004).

Localized dispersal is expected to create positive spatial autocorrelation in species occurrences particularly at small scales (Bleher *et al.* 2002, Chave *et al.* 2002, Condit *et al.* 2002). Here, the local dispersal limitation hypothesis was represented by inclusion of an autoregressive spatial parameter using conditional autoregressive modelling (CAR; Cressie 1993, Lichstein *et al.* 2002). The CAR model is specified as $\mathbf{Y} = \mathbf{X}\beta + \rho\mathbf{C}(\mathbf{Y} - \mathbf{X}\beta) + \varepsilon$, where $\mathbf{Y}$ is a vector of observations of the response variable, $\mathbf{X}$ is the matrix of explanatory variables, β is vector of regression coefficients, ρ is the spatial autoregressive coefficient, $\mathbf{C}$ is a symmetric neighbourhood matrix with elements (w_{ij}) representing the degree of connection between locations i and j, and ε is a vector of random errors. Hence, the model is similar to the OLS regression model, except that the response variable is also modelled as dependent on the residuals at neighbouring locations. We did not define an arbitrary distance d_{ij} at which $w_{ij} = 0$, but used the distance weighting $w_{ij} = 1/{d_{ij}}^2$ to emphasize near neighbours. Using $w_{ij} = 1/{d_{ij}}^k$, $k = 1$–4 caused only negligible differences in model fit.

Given that the three hypotheses are mutually compatible we built a series of regression models for each species, representing all possible combinations of the three sets of variables/parameters, i.e. OLS models with just an intercept (M_0; to represent the situation where all three hypotheses are unimportant), the five environmental variables (M_E), the four trend-surface variables (M_T), or both environmental and trend-surface variables (M_{E+T}), and CAR models with just an intercept (M_ρ), the five environmental variables ($M_{\rho+E}$), the four trend-surface variables ($M_{\rho+T}$), or both environmental and trend-surface variables ($M_{\rho+E+T}$).

Among the explanatory variables the largest pairwise correlations were between shore distance and Y^2 ($r = 0.659$) and shore distance and soil type ($r = 0.529$). Tolerance values ranged from 0.495–0.792, except that shore distance and Y^2 had tolerance of 0.250 and 0.382, respectively. As all tolerances were well above 0.1, multicollinearity should not be a problem (Quinn & Keough 2002).

OLS regressions were performed using JMP 5.0 (SAS Institute, Cary, NC, USA), while CAR models were computed in S-PLUS 6.2 (Insightful Corporation, Seattle, Washington, USA) using the S+ SpatialStats module (Kaluzny *et al.* 1998).

Model selection and multi-model inference

The information-theoretic approach described by Burnham & Anderson (2002) was used to assess the relative degree of support for the three hypotheses and to provide robust parameter estimates based on the full suite of models (see also Johnsson & Omland 2004). For each species, the relative support for each of the eight models was assessed using Akaike's Information Criterion ($AIC = -2\ln(L) + 2K$), which estimates the Kullback–Leibler information lost by approximating full reality with a given model and simultaneously accounts for model fit (L, model loglikelihood) and complexity (K, number of model parameters, including the intercept) (Burnham & Anderson 2002, Johnson & Omland 2004). Given that K exceeded $n/40 = 2.2$ in most models, we used the small-sample bias-corrected version of AIC, $AIC_c = AIC + 2K(K + 1)/(n - K - 1)$. Different mathematical routines scale likelihoods differently, so to obtain comparable likelihood estimates for the OLS and CAR models we computed the OLS likelihood estimates from CAR models with $\rho = 0$ (Bahn 2005) using the method described in Lichstein *et al.* (2002). To assess the relative support for each model, we computed AIC differences, $\Delta AIC_c(i) = AIC_c(i) - AIC_c(min)$, where $AIC_c(i)$ is the observed value of AIC_c for model i and $AIC_c(min)$ is the minimum AIC_c value in the set of models for a species. Thus, $\Delta AIC_c = 0$ for the best model. Models with $\Delta AIC_c \leq 2$, $4-7$, and >10 have substantial, considerably less, and essentially no support, respectively (Burnham & Anderson 2002).

To provide a more synthetic assessment of the relative support for the three hypotheses for each species, we first computed the Akaike weight of model i as

$$W(i) = \exp(-1/2\Delta AIC_c(i))/\Sigma \exp(-1/2\Delta AIC_c(i)),$$

where the denominator is summed across all eight models for a given species (Burnham & Anderson 2002). This value can be interpreted as the probability that model i is the best model in the set for the observed data (Burnham & Anderson 2002). Following Burnham & Anderson (2002), we then computed the probability that the best model for a given species includes the environmental variables as

$$W(E) = W(M_E) + W(M_{E+T}) + W(M_{\rho+E}) + W(M_{\rho+E+T}),$$

the trend-surface variables as

$$W(T) = W(M_T) + W(M_{E+T}) + W(M_{\rho+T}) + W(M_{\rho+E+T}),$$

the spatial parameter as

$$W(\rho) = W(M_\rho) + W(M_{\rho+T}) + W(M_{\rho+T}) + W(M_{\rho+E+T}),$$

or just the intercept as

$$W(0) = W(M_0).$$

The choice of a best model becomes problematic when there is substantial support for several models (Burnham & Anderson 2002). Hence, we used model averaging to provide robust parameter estimation, and computed the parameter estimate for a given variable as the weighted average of its standardized regression coefficient, $\beta_{MA} = \Sigma W(i)\beta_i$, in the eight models for a given species, with $\beta_i = 0$ for models without the variable (Burnham & Anderson 2002). A model-averaged estimate of the spatial autoregressive coefficient was computed in a similar way, standardizing ρ analogously to the regression coefficients following Bahn (2005).

Spatial variograms

We computed classical variograms to assess spatial dependency in the original abundance variables (square-root-transformed) as well as in the residuals of the regression model with strongest support for each species (Legendre & Legendre 1998). To allow comparison of the variograms they were standardized by dividing the semi-variance value (γ) by the overall sample variance (s^2) of the variable in question (Rossi *et al.* 1992).

Relationships between model parameter and species traits

We tested for functional relationships between species traits and distribution patterns, the latter represented by the model-averaged parameter estimates, comparing (1) edaphic parameter estimates with experimentally determined seedling drought sensitivity; (2) ρ estimates as well as W(ρ) and W(T) with minimum adult size, diaspore fresh weight and fecundity; and (3) old-forest parameter estimates to gap growth and recruitment rates for saplings and minimum adult size, diaspore fresh weight and fecundity.

We expect drought-sensitive species to be associated with moist plots, steep slopes (Becker *et al.* 1988, Daws *et al.* 2002), and montmorillonite (Birkeland 1999). Thus, drought-sensitive species are expected to have large positive parameter estimates for soil moisture and slope and large negative parameter estimates for soil type. Furthermore, we expect drought-tolerant species to be relatively indifferent to hydrologic conditions. Hence, we tested whether species with parameter estimates for soil moisture and slope greater than 0.10 or soil type −0.10 or less are more drought-sensitive than other species using one-tailed t-tests. Seedling drought sensitivity was experimentally determined as $100 \times (1 - S_D/S_W)$, where S_D and S_W are survival over 22 wk in dry and irrigated treatments, respectively (Engelbrecht & Kursar 2003 and unpubl. data). We used values for *Virola nobilis* to represent *V. sebifera*, as these species exhibit similar abundance-environment relationships on BCI (Svenning *et al.* 2004).

Localized dispersal is expected to produce strong local spatial autocorrelation (Bleher *et al.* 2002, Chave *et al.* 2002, Condit *et al.* 2002) and may also be involved in creating broad-scale trends. Hence, ρ estimates as well as W(ρ) and W(T) were tested for positive correlations with diaspore weight and negative correlations with adult size and fecundity using one-tailed tests. Lighter, more numerous diaspores produced on larger plants are expected to disperse further causing smaller ρ, W(ρ) and W(T). We did not expect relationships between dispersal and particular trend-surface variables, but only between dispersal and the combined importance of the trend-surface variables (represented by W(T)), and consequently did not test for correlations involving the trend-surface parameter estimates. Minimum adult size (typical stem diameter at 1.30 m above ground (dbh) at which individuals become reproductive) was estimated for all study species by Robin Foster. This estimate of adult size proved to be remarkably accurate in a quantitative assessment of reproductive size thresholds for 16 tree species (Wright *et al.* 2005). Diaspore fresh weight (g) was determined for mature diaspores for 21 study species (Wright *et al.* 2003). Fecundity (seeds y^{-1} m^{-2} basal area) was determined for 25 study species as the area-standardized number of seeds divided by the summed basal area of trees larger than the species-specific minimum adult size for a 50-ha plot where all trees larger than 1 cm dbh were identified and measured and seeds and fruit were collected weekly for 13 y from 200 0.5-m^2 traps (Wright *et al.* 2003).

As already discussed, associations with young or old forest might reflect modern environment and/or past disturbance and subsequent dispersal processes. Old-forest association is expected to be negatively related to growth and recruitment rates in gaps in either case. Old-forest association is also expected to be negatively related to fecundity and adult size and positively related to diaspore weight if past disturbance and subsequent dispersal are important. Gap growth and recruitment rates of saplings were available in Welden *et al.* (1991) for 21 and 22 study species, respectively.

RESULTS

Inventory data

The 88 plots contained 17 925 individuals belonging to the 26 study species (Table 1). The most abundant species were the treelet *Faramea occidentalis*, the shrub *Hybanthus prunifolius*, the treelet *Swartzia simplex*, the midstorey palm *Oenocarpus mapora* and the shrub *Psychotria horizontalis* (Table 1).

Average support for the competing models

The summed Akaike weights for the environmental variables (W(E)), the trend-surface variables (W(T)) and the spatial parameter (W(ρ)) were 33.3%, 63.9% and 50.0% on average across species, respectively, while the average Akaike weight for the model with just an intercept (W(0)) was 9.9% (Table 1). Hence, broad-scale trend and local spatial autocorrelation were both fairly strongly supported as ‘controls’ of tree species distributions on BCI, while local environmental control also received some, albeit substantially less, support. Among the eight different models on average the $M_{\rho+T}$ and M_T were most strongly supported, the $M_{\rho+E+T}$ and M_{E+T} also had some support, while the remaining models were essentially unsupported (Table 2). Hence, the general pattern was that broad-scale trends appeared to characterize the distributions of most species, with local spatial autocorrelation and, less importantly, environmental control as additional constraints in some cases. The best regression models (Table 1) generally accounted for most of the spatial autocorrelation in the species abundances (Figure 1). If only the species where the best model was a CAR model were considered then the variogram for the residuals was essentially flat, with the mean semivariance at the larger distance classes not being significantly different from that of the first distance class (results not shown).

Table 1. Model selection results for 26 common tree and shrub species on BCI, Panama. The number of plot presences (n_p; total number of plots = 88) and individuals (n_i) are given. The most strongly supported regression model M_i (M_{best}: just i is given), its Akaike weight (W_{best}; in %), the summed Akaike weights for the intercept-only model (W(0)), the models with environmental variables (W(E)), trend-surface variables (W(T)), or the autoregressive spatial parameter (W(ρ)) are listed. Bold face indicates the set of variables with the highest Akaike weight.

Species	n_p	n_i	M_{best}	W_{best}	W(0)	W(E)	W(T)	W(ρ)
Alseis blackiana Hemsl.	85	768	$\rho+T$	41	0	56	80	**97**
Astrocaryum standleyanum Bailey	60	164	E+T	34	0	44	**100**	34
Attalea butyracea (Mutis ex L. f.) Wess. Boer	55	431	T	75	0	0	**100**	25
Brosimum alicastrum Sw.	51	107	$\rho+T$	50	0	30	**70**	67
Cupania sylvatica Seem.	77	671	E+T	25	2	61	**67**	32
Faramea occidentalis Standl.	87	3963	0	27	27	19	37	**46**
Garcinia intermedia (Pittier) Hammel	81	970	$\rho+T$	72	0	1	**100**	72
Gustavia superba (H.B.K.) Berg	59	472	$\rho+T$	65	0	1	**100**	66
Hybanthus prunifolius (Schult.) Schulze	77	1293	E	65	0	**100**	15	23
Lacistema aggregatum (Berg) Rusby	69	290	E+T	50	0	63	**100**	29
Miconia argentea (Sw.) DC.	53	129	0	66	**66**	1	2	31
Mouriri myrtilloides (Sw.) Poir.	82	920	$\rho+E$	91	0	**100**	9	100
Oenocarpus mapora H. Karst.	84	1087	T	67	0	1	**100**	32
Ouratea lucens (H.B.K.) Engler	65	253	ρ	31	31	9	30	**42**
Picramnia latifolia Tul.	53	173	T	41	20	17	**58**	26
Pouteria unilocularis (Donn. Sm.) Baehni	47	104	$\rho+T$	45	3	6	**90**	52
Psychotria horizontalis Sw.	73	1051	0	50	**50**	5	22	29
Psychotria marginata Sw.	56	299	T	70	0	1	**100**	29
Pterocarpus rohrii Vahl	53	194	E	32	9	**45**	43	26
Quassia amara L.	64	331	$\rho+T$	97	0	3	**100**	100
Sorocea affinis Hemsl.	80	658	0	41	41	8	15	**44**
Swartzia simplex (Sw.) Spreng.	82	1227	T	35	4	6	**64**	59
Tachigali versicolor Standl. & L. O. Wms.	55	235	E	47	3	**79**	9	46
Tetragastris panamensis (Engler) O. Kuntze	77	887	E+T	36	0	56	**100**	56
Trichilia tuberculata C. DC.	84	934	$\rho+E$	42	0	55	51	**84**
Virola sebifera Aubl.	66	314	$\rho+E+T$	50	0	97	**99**	52

Table 2. The eight regression models (M_i, just i is given), their total number of estimated parameters (K) including the intercept and the variance estimate, their mean (±SD) ΔAIC_c across the 26 study species, and the number of times a model was selected as the best (n_{best}), i.e. $\Delta AIC_c = 0$, or not the best, but with substantial support ($n_{subst.}$), i.e. $0 < \Delta AIC_c \leq 2$, or with less, albeit still some support (n_{some}), i.e. $2 < \Delta AIC_c \leq 10$. Sum = $n_{best} + n_{subst.} + n_{some}$.

Model	K	ΔAIC_c	n_{best}	$n_{subst.}$	n_{some}	Sum
0	2	16.5 ± 15.2	4	2	5	11
E	7	11.2 ± 10.3	3	1	11	15
T	6	3.7 ± 5.1	5	10	8	23
E+T	11	7.6 ± 4.9	4	1	12	17
ρ	3	13.5 ± 12.6	1	5	6	12
$\rho+E$	8	10.3 ± 9.9	2	4	10	16
$\rho+T$	7	3.0 ± 4.1	6	8	10	24
$\rho+E+T$	12	7.6 ± 4.5	1	2	15	18

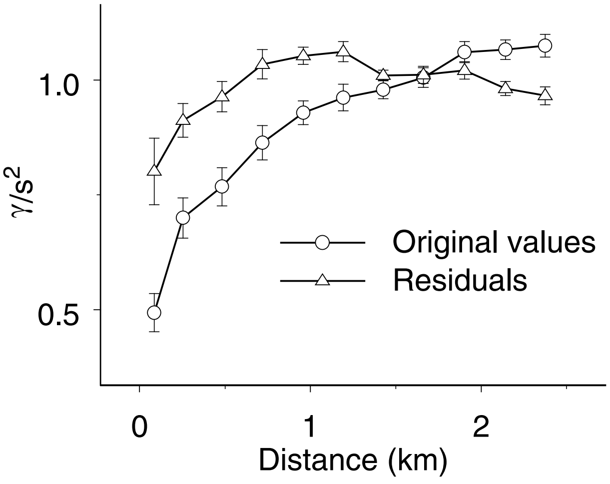

Figure 1. Empirical variograms of square-root-transformed abundance per plot and its residuals from the best regression model (Table 1) for each of the 26 tree and shrub species studied. The cross-species mean (±SE) standardized semi-variance (γ/s^2) is shown as a function of the average distance between all pairs of points in a given distance class.

Species-specific support for the competing models

These average figures hide the highly variable results for the individual species (Tables 1 and 2). Notably, all eight models were selected as the best model for at least one species and had substantial support for at least three species (Table 2). The environmental variables, trend-surface variables, ρ, and the simple intercept model had the strongest support for 4, 15, 5 and 2 species, respectively (Table 1). Furthermore, the probability that the best model for a given species included the

Table 3. The model-averaged standardized regression parameter estimates for the species abundance-environment relationships and the autoregressive spatial parameter ρ. For soil type, a positive parameter indicates an association with kaolinite. Bold face indicates parameter estimates of at least 0.100 in absolute value. † indicates ρ estimates larger than any of the environmental parameter estimates (absolute values).

Species	Moisture	Slope	Soil type	Shore distance	Old-forest	ρ
Alseis blackiana	**0.100**	**−0.114**	0.094	0.060	**0.107**	**0.370**†
Astrocaryum standleyanum	−0.028	0.053	−0.023	**−0.158**	0.018	0.038
Attalea butyracea	0.000	0.000	−0.001	0.000	0.000	0.009†
Brosimum alicastrum	0.035	−0.024	−0.009	0.091	0.060	**0.135**†
Cupania sylvatica	−0.088	−0.022	**0.102**	**0.130**	−0.089	0.025
Faramea occidentalis	−0.024	−0.031	−0.012	0.050	−0.021	0.062†
Garcinia intermedia	0.000	−0.001	0.001	−0.001	−0.001	**0.172**†
Gustavia superba	0.000	0.000	0.000	0.001	−0.001	0.083†
Hybanthus prunifolius	**0.142**	−0.024	**0.217**	**0.508**	0.033	0.003
Lacistema aggregatum	**0.153**	0.028	**0.221**	−0.009	0.010	0.025
Miconia argentea	0.001	−0.001	0.000	−0.001	0.001	0.038†
Mouriri myrtilloides	0.069	**−0.107**	**0.214**	**0.471**	**0.172**	**0.410**
Oenocarpus mapora	0.000	0.000	0.000	0.001	0.000	0.030†
Ouratea lucens	−0.016	−0.009	0.006	−0.004	−0.006	0.066†
Picramnia latifolia	0.032	−0.008	0.000	0.045	−0.012	0.016
Pouteria unilocularis	0.000	−0.008	−0.015	0.016	0.003	0.086†
Psychotria horizontalis	0.004	−0.004	−0.007	0.012	−0.011	0.029†
Psychotria marginata	0.001	−0.001	0.001	0.001	0.000	0.045†
Pterocarpus rohrii	0.060	−0.046	−0.008	**0.162**	−0.072	0.016
Quassia amara	−0.004	−0.001	−0.003	0.001	−0.004	**0.395**†
Sorocea affinis	−0.003	0.006	0.004	0.019	−0.011	0.069†
Swartzia simplex	0.008	−0.002	0.014	−0.002	−0.010	**0.104**†
Tachigali versicolor	**0.124**	0.071	**0.137**	0.085	**0.214**	0.067
Tetragastris panamensis	−0.037	0.027	−0.050	**−0.249**	0.025	0.076
Trichilia tuberculata	**0.109**	−0.073	0.015	**0.214**	−0.048	**0.179**
Virola sebifera	**0.375**	−0.047	**0.303**	−0.079	−0.048	0.072

environmental variables, the trend-surface variables, ρ, or just the intercept was 90% or more for 3 species (*Hybanthus prunifolius*, *Mouriri myrtilloides*, and *Virola sebifera*), 11 species, 3 species (*Alseis blackiana*, *Mouriri myrtilloides* and *Quassia amara*) and 0 species (Table 1).

Species–environment relationships and local spatial dependence

Given that the best model only had W > 0.90 for two species (Table 1), it was clearly appropriate to use model averaging to provide robust parameter estimation. It was noteworthy that the standardized estimate for ρ exceeded all five standardized environmental parameter estimates in absolute size for 58% of the species (Table 3). Considering the five environmental factors, all had parameter estimates of considerable size for some species (Table 3). Notably, six species had non-negligible positive relationships to soil moisture, and six species were associated with kaolinitic soils, while none was associated with dry or montmorillonitic soils. In contrast, five species clearly increased and two clearly decreased (*Astrocaryum standleyanum* and *Tetragastris panamensis*) in abundance away from the lake shore. Only two and three species had non-negligible relationships to slope (both negative) and old-forest (all positive), respectively. Nevertheless, even the strongest abundance-environment relationships were only of moderate strength (Figure 2).

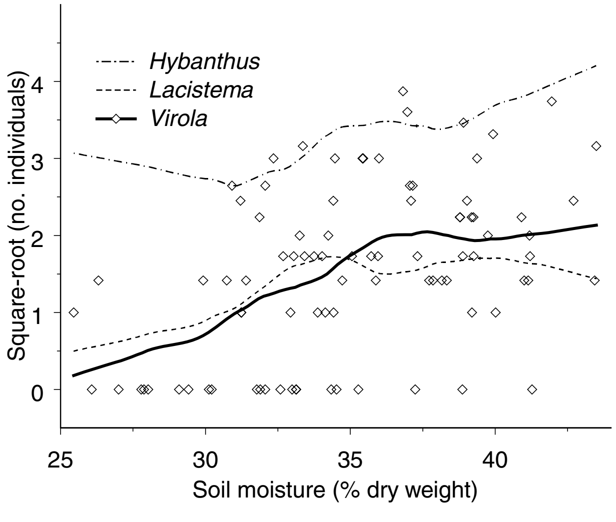

Figure 2. Abundance as a function of soil moisture for the three species with the strongest abundance-soil moisture relationships (Table 3): *Virola sebifera*, *Lacistema aggregatum* and *Hybanthus prunifolius* versus soil moisture. The fits are locally weighted linear Gaussian regression fits implemented using cross-validated automatic span selection in S-PLUS. The data points are only shown for *Virola sebifera* (diamonds).

The average absolute sizes of the model-averaged parameter estimates for soil moisture, slope, soil type, shore distance and old-forest were 42%, 34%, 49%, 47% and just 21% of the corresponding parameter values for the M_E models, respectively (results not shown). Furthermore, while old-forest had the second largest average absolute M_E parameter estimate among the five environmental variables, it had the smallest average absolute model-averaged parameter estimates. As the average absolute $M_{\rho+E}$, M_{E+T} and $M_{\rho+E+T}$ old-forest parameter estimates were 95%, 51% and 52% of the M_E value (results not shown), the reduction in the importance of the old-forest variable was mainly caused by the trend-surface variables and not by the modelling of local spatial autocorrelation using ρ.

Model parameter–species trait relationships

Species with parameter estimates for soil moisture of 0.10 or more (n = 4) were more drought-sensitive (mean ± SD = 30% ± 14%) than other species (18% ± 14%, n = 13) using a one-tailed t-test (square-root-transformed drought sensitivity, $t = -2.42$, $P = 0.014$) (Figure 3). As no species had slope parameter estimates exceeding 0.10 or soil type parameter estimates less than −0.10, t-tests of drought sensitivity were not carried out for these variables. Spearman correlations of ρ and $W(\rho)$ with minimum adult size, diaspore weight and fecundity were all non-significant (one-tailed tests). While W(T) was also unrelated to minimum adult size, it decreased with fecundity (Spearman $r = -0.434$, one-tailed $P = 0.015$ and increased with diaspore weight (Spearman $r = 0.472$, one-tailed $P = 0.015$). Spearman correlations of old-forest parameter estimates with gap growth and recruitment rates and minimum adult size, diaspore weight and fecundity were all insignificant (one-tailed tests). The correlations remained insignificant if the M_E old-forest parameter estimates were used instead of the model-averaged estimates (one-tailed tests).

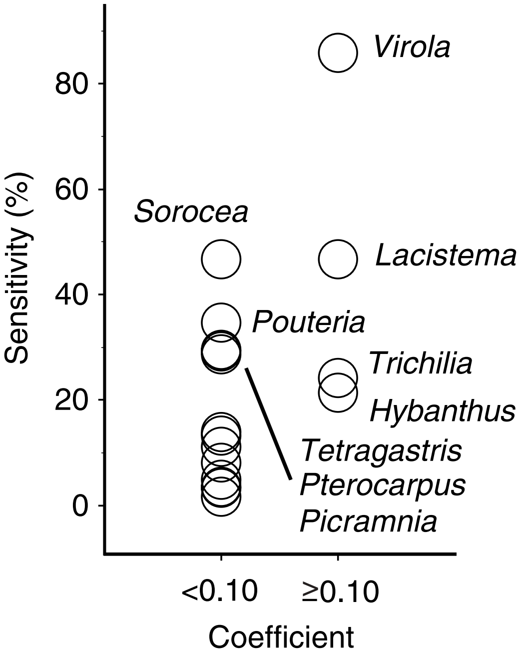

Figure 3. Seedling drought sensitivity of species with model-averaged standardized regression coefficients for soil moisture <0.10 (n = 13) or ≥0.10 (n = 4). Note that drought sensitivity estimates were only available for the subset of species studied by Engelbrecht & Kursar (2003).

DISCUSSION

To the extent that broad-scale trends and local spatial autocorrelation represent historical contingencies and localized dispersal, respectively, these hypothesized controls of species distributions were clearly of stronger general importance than environmental control for 26 common tree and shrub species in the tropical forest landscape on Barro Colorado Island, Panama. However, as expected, given the empirical evidence for all three competing hypotheses from both BCI and other tropical forests, historical contingency, local dispersal and environmental control all received some support. While our results thus provide further support for the combined importance of these potential controls of plant species distributions in tropical forest landscapes, they also support the view that history and dispersal are of greater importance at least at the landscape scale (Condit *et al.* 2002, Hubbell 2001, Hubbell *et al.* 1999, Svenning 2001, Thompson *et al.* 2002, Tuomisto *et al.* 2003b) and perhaps particularly so for common species (Poore 1968). However, the results were highly variable among the species, with all eight models being selected as the best model for at least one species (Tables 1 and 2). Hence, the way environmental control, broad-scale historical contingencies, and local dispersal limitation act to control landscape-scale species distributions of tropical forest plant species appear to vary idiosyncratically among species. This idiosyncrasy becomes even more apparent when the highly variable species–environment relationships are considered (Table 3).

Is it reasonable to interpret the broad-scale trends and local spatial autocorrelation (the ρ estimate) to represent patterns caused by historical contingencies and localized dispersal, respectively? Given that environmental heterogeneity has some spatial structure this will contribute to the spatial trend and ρ estimates. Furthermore, it is impossible to rule out the possibility that other spatially structured processes that were unaccounted for by our set of environmental variables also contribute to these patterns. While the set of environmental variables represents the main environmental factors proposed to have important effects on plant species distributions on BCI (Croat 1978, Harms *et al.* 2001, Knight 1975, Svenning *et al.* 2004) and in other tropical forests (Clark *et al.* 1999, Svenning 1999, Thompson *et al.* 2002, Valencia *et al.* 2004), undescribed heterogeneity in these or other environmental factors could contribute to the spatial trend or ρ estimates. Localized historical events such as landslides and large blowdowns are known to have occurred on BCI and to have had strong impacts on the local vegetation (Foster & Brokaw 1996) and might contribute to the ρ estimates. Nevertheless, these environmental and historical effects can hardly account for the much stronger support for broad-scale trend and local spatial autocorrelation relative to the environmental variables.

Alternatively, undescribed population dynamic processes might contribute to broad-scale trends and local spatial autocorrelation. Negative conspecific density dependence is known to affect the performance of many plant species on BCI (Condit *et al.* 1992, Harms *et al.* 2000, Uriarte *et al.* 2004) and in other tropical forests (Blundell & Peart 2004, Silman *et al.* 2002, Uriarte *et al.* 2005). However, the impact of negative density dependence acts principally at scales of 10 m or less (Condit *et al.* 1992), and it decreases conspecific spatial aggregation (Chave *et al.* 2002) and hence is not a likely cause of the broad-scale trends or the positive local spatial autocorrelation. Nevertheless, there is some evidence that seed predator satiation may induce positive density-dependence at the 1-ha scale (Schupp 1992), which would contribute to the observed spatial dependence.

While it is clear that the spatial trend and ρ estimates may have been enhanced by environmental effects, positive density-dependence and (only ρ) localized historical events, broad-scale historical events or processes and localized dispersal still seem likely to be their main driving agents, respectively. Several studies have documented that the main floristic gradient on BCI is related to the age of the forest (Knight 1975, Svenning *et al.* 2004). The variable old-forest presence/absence was included with the environmental variables in the present analysis because the old-growth and secondary forest are expected to differ environmentally, e.g. in the understorey light environment (Nicotra *et al.* 1999), susceptibility to storm damage (Thompson *et al.* 2002), and soil conditions (White & Hood 2004). Furthermore, succession is likely to be at least partly driven by environmental changes (Pacala & Rees 1998). Nevertheless, most of the old-forest effect was captured by the trend-surface variables, as was evident from the strong reduction in the importance of the old-forest regression coefficient in the model-averaged results relative to the M_E results. This is to be expected if the species associations with old or young forest were largely historical rather than environmental, as recolonization out from the old forest and associated successional processes would tend to erase any local-scale relationships that are not maintained by environmental differences. Other broad-scale trends in the distributions of certain plant species on BCI have been explained as related to immigration from neighbouring areas (Foster & Brokaw 1996). The finding that species that produce few and heavy diaspores exhibited the strongest spatial trends (as measured by W(T)) support the interpretation that the spatial trends reflect historically contingent distribution restrictions. Notably, heavy-seeded tree species have been found to exhibit particularly limited recolonization of secondary tropical forests elsewhere (Chazdon 2003). With respect to localized dispersal, a number of recent studies have concluded that the distribution and abundance of many plant species on BCI are strongly constrained by limited dispersal (Condit *et al.* 2000, Dalling *et al.* 2002, Muller-Landau *et al.* 2002) or limited seed availability more generally (Hubbell *et al.* 1999, Svenning & Wright 2005). Furthermore, theoretically localized dispersal is expected to cause clumped distribution patterns (Bleher *et al.* 2002, Chave *et al.* 2002). The absence of significant correlations of ρ or W(ρ) with minimum adult size, diaspore weight, and fecundity in the present study may reflect that the degree of local clumping is controlled not only by dispersal ability, but also by other factors, notably density dependence, adult density and breeding system (Bleher *et al.* 2002, Chave *et al.* 2002).

The finding that a considerable minority (42%) of the common plant species studied had non-negligible environmental relationships (see Table 3) agrees with previous findings from BCI (Croat 1978, Foster & Brokaw 1996, Harms *et al.* 2001, Svenning *et al.* 2004) and other tropical forests (Ashton 1964, Clark *et al.* 1999, Phillips *et al.* 2003, Potts *et al.* 2002, Svenning 1999, Svenning *et al.* 2004, Tuomisto *et al.* 2003a, Webb & Peart 2000). Given BCI's seasonally dry climate it is not surprising to find that a number of species are associated with sites that stay relatively moist during the dry season. The result that these species are particularly drought-sensitive as seedlings (Engelbrecht & Kursar 2003) provides compelling evidence that the species abundance–soil moisture relationships really are caused by species-specific responses to soil water availability. Similar relationships between drought sensitivity and plant species distributions also exist at local scales on BCI and at regional scales across the Isthmus of Panama (Engelbrecht *et al.* 2005).

The exact mechanisms behind the other environmental relationships were more elusive. Given that common species may be expected to be generalists (Pitman *et al.* 2001, Poore 1968), it is noteworthy that the probability that the best model for a given species included the environmental variables was ≥50% for 9 out of 26 species. Furthermore, the second-most abundant species *Hybanthus prunifolius* was one of the three species with the strongest environmental relationships, both in terms of W(E) and the size of the environmental parameter estimates (Tables 1 and 3). Nevertheless, only a few species–environment relationships could be characterized as strong (Figure 2, Table 3).

Our study provides evidence that broad-scale historical contingencies and localized dispersal were the dominant controls of the distributions of common species on BCI. This supports non-equilibrium views of tropical plant distributions (Beard 1946, Charles-Dominique *et al.* 2003, Hubbell 2001, Poore 1968) and exemplifies the strong impact of past human disturbance in many tropical forests (Chazdon 2003, Clark *et al.* 1995, Svenning 2001, Svenning *et al.* 2004, Thompson *et al.* 2002, White & Hood 2004). Nevertheless, environmental heterogeneity also had a non-negligible effect on some species distributions and the differential species–environment relationships could to some extent be linked to species' autecology. However, the way environmental control, broad-scale historical contingencies and local dispersal limitation acted to control landscape-scale species distributions varied substantially among species, and an important avenue for future research will be to provide a better understanding of the mechanisms behind this variability.

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LITERATURE CITED

ASHTON, P. S. 1964. Ecological studies in the mixed dipterocarp forest of Brunei State. *Oxford Forestry Memoirs* 25:1–75.

ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* 1:155–196.

BAHN, V. 2005. *Implications of spatial autocorrelation and dispersal for the modeling of species distributions*. Ph.D. thesis. University of Maine, Orono, Maine. 118 pp.

BEARD, J. S. 1946. The *Mora* forests of Trinidad, British West Indies. *Journal of Ecology* 33:173–192.

BECKER, P., RABENOLD, P. E., IDOL, J. R. & SMITH, A. P. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* 4:173–184.

BEHLING, H. 2003. Late glacial and Holocene vegetation, climate and fire history inferred from Lagoa Nova in the southeastern Brazilian lowland. *Vegetation History and Archaeobotany* 12:263–270.

BELL, G. 2001. Neutral macroecology. *Science* 293:2413–2418.

BIRKELAND, P. W. 1999. *Soils and geomorphology*. Oxford University Press, New York. 430 pp.

BLEHER, B., OBERRATH, R. & BÖHNING-GAESE, K. 2002. Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach. *Basic and Applied Ecology* 3:115–123.

BLUNDELL, A. G. & PEART, D. R. 2004. Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology* 85:704–715.

BURBRIDGE, R. E., MAYLE, F. E. & KILLEEN, T. J. 2004. Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* 61:215–230.

BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer-Verlag, New York. 514 pp.

BUSH, M. B., MILLER, M. C., DE OLIVEIRA, P. E. & COLINVAUX, P. A. 2000. Two histories of environmental change and human disturbance in eastern lowland Amazonia. *Holocene* 10:543–553.

CAPERS, R. S., CHAZDON, R. L., BRENES, A. R. & ALVARADO, B. V. 2005. Successional dynamics of woody seedling communities in wet tropical secondary forests. *Journal of Ecology* 93:1071–1084.

CHARLES-DOMINIQUE, P., CHAVE, J., DUBOIS, M.-A., DE GRANVILLE, J.-J. & VEZZOLI, C. 2003. Colonization front of the understory palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography* 12:237–248.

CHAVE, J., MULLER-LANDAU, H. C. & LEVIN, S. A. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* 159:1–23.

CHAZDON, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbance. *Perspectives in Plant Ecology, Evolution, and Systematics* 6:51–71.

CLARK, D. A., CLARK, D. B., SANDOVAL, M. R. & CASTRO, C. M. V. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* 76:2581–2594.

CLARK, D. B., PALMER, M. W. & CLARK, D. A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80:2662–2675.

COLINVAUX, P. A., FROST, M., FROST, I., LIU, K. & STEINITZ-KANNAN, M. 1988. Three pollen diagrams of forest disturbance in the western Amazon basin. *Review of Palaeobotany and Palynology* 55:73–81.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist* 140:261–286.

CONDIT, R., ASHTON, P. S., BAKER, P., BUNYAVEJCHEWIN, S., GUNATILLEKE, S., GUNATILLEKE, N., HUBBELL, S. P., FOSTER, R. B., ITOH, A., LAFRANKIE, J. V., LEE, H. S., LOSOS, E., MANOKARAN, N., SUKUMAR, R. & YAMAKURA, T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288:1414–1418.

CONDIT, R., PITMAN, N., LEIGH, E. G., CHAVE, J., TERBORGH, J., FOSTER, R. B., NÚÑEZ, V. P., AGUILAR, S., VALENCIA, R., VILLA, G., MULLER-LANDAU, H., LOSOS, E. & HUBBELL, S. P. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.

CRESSIE, N. A. C. 1993. *Statistics for spatial data*. (Revised edition). John Wiley & Sons, Inc., New York. 922 pp.

CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford. 954 pp.

DALLING, J. W., MULLER-LANDAU, H. C., WRIGHT, S. J. & HUBBELL, S. P. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology* 90:714–727.

DAWS, M. I., MULLINS, C. E., BURSLEM, D. F. R. P., PATON, S. R. & DALLING, J. W. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panamá. *Plant and Soil* 238:79–90.

ENGELBRECHT, B. M. J. & KURSAR, T. A. 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136:383–393.

ENGELBRECHT, B. M. J., KURSAR, T. A. & TYREE, M. T. 2005. Drought effects on seedling survival in a tropical moist forest. *Trees* 19:312–321.

FOSTER, R. B. & BROKAW, N. V. L. 1996. Structure and history of the vegetation of Barro Colorado Island. Pp. 67–82 in Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC.

HARMS, K. E., WRIGHT, S. J., CALDERÓN, O., HERNÁNDEZ, A. & HERRE, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.

HARMS, K. E., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89:947–959.

HECKENBERGER, M. J., KUIKURO, A., KUIKURO, U. T., RUSSELL, J. C., SCHMIDT, M., FAUSTO, C. & FRANCHETTO, B. 2003. Amazonia 1492: pristine forest or cultural parkland? *Science* 301:1710–1714.

HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–1309.

HUBBELL, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton. 390 pp.

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

JOHNSON, J. B. & OMLAND, K. S. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.

JOHNSSON, M. J. & STALLARD, R. F. 1989. Physiographic controls on the composition of sediments derived from volcanic and sedimentary terrains on Barro Colorado Island, Panama. *Journal of Sedimentary Petrology* 59:768–781.

KALUZNY, S. P., VEGA, S. C., CARDOSO, T. P. & SHELLY, A. A. 1998. *S + SpatialStats: user's manual for Windows and UNIX*. Insightful Corporation, Seattle. 344 pp.

KNIGHT, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecological Monographs* 45:259–284.

LEDRU, M.-P., SALGADO-LABOURIAU, M. L. & LORSCHEITTER, M. L. 1998. Vegetation dynamics in southern and central Brazil during the last 10,000 yr B.P. *Review of Palaeobotany and Palynology* 99:131–142.

LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. (Second edition). Elsevier, Amsterdam. 870 pp.

LEIGH, E. G. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, New York. 262 pp.

LEIGH, E. G., RAND, A. S. & WINDSOR D. M. (eds) 1996. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC. 503 pp.

LICHSTEIN, J. W., SIMONS, T. R., SHRINER, S. A. & FRANZREB, K. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72:445–463.

MAKANA, J. R. & THOMAS, C. 2004. Dispersal limits natural recruitment of African mahoganies. *Oikos* 106:67–72.

MAYLE, F. E., BEERLING, D. J., GOSLING, W. D. & BUSH, M. B. 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society of London, Series B* 359:499–514.

MULLER-LANDAU, H. C., WRIGHT, S. J., CALDERÓN, O., HUBBELL, S. P. & FOSTER, R. B. 2002. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. Pp. 35–53 in Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution, and conservation*. CABI Publishing, Wallingford.

NICOTRA, A. B., CHAZDON, R. L. & IRIARTE, S. V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.

PACALA, S. W. & REES, M. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist* 152:729–737.

PHILLIPS, O. L., VARGAS, P. N., MONTEAGUDO, A. L., CRUZ, A. P., ZANS, M. E. C., SANCHEZ, W. G., YLI-HALLA, M. & ROSE, S. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91:757–775.

PIPERNO, D. 1990. Fitolitos, arquelogia y cambios prehistoricos de la vegetacion en un lote de cincuenta hectáreas de la isla de Barro Colorado. Pp. 153–156 in Rand, A. S., Windsor, D. M. & Leigh, E. G. (eds.) *Ecologia de un Bosque Tropical*, Smithsonian Institution Press, Washington, DC.

PITMAN, N. C. A., TERBORGH, J. W., SILMAN, M. R., NÚNEZ, V. P., NEILL, D. A., CERÓN, C. E., PALACIOS, W. A. & AULESTIA, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82:2101–2117.

POORE, M. E. D. 1968. Studies in Malaysian rain forest: I. The forest on Triassic sediments in Jengka Forest Reserve. *Journal of Ecology* 56:143–196.

POTTS, M. D., ASHTON, P. S., KAUFMAN, L. S. & PLOTKIN, J. B. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83:2782–2797.

QUINN, G. P. & KEOUGH, M. J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge. 555 pp.

ROSSI, R. E., MULLA, D. J., JOURNEL, A. G. & FRANZ, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* 62:277–314.

SCHUPP, E. W. 1992. The Janzen–Connell model for tropical tree diversity: population implications and the importance of spatial scale. *American Naturalist* 140:526–530.

SILMAN, M. R., TERBORGH, J. W. & KILTIE, R. A. 2002. Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* 84:431–438.

SVENNING, J.-C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* 87:55–65.

SVENNING, J.-C. 2001. Environmental heterogeneity, recruitment limitation, and the mesoscale distribution of palms in a tropical montane rain forest (Maquipucuna, Ecuador). *Journal of Tropical Ecology* 17:97–113.

SVENNING, J.-C. & WRIGHT, S. J. 2005. Seed limitation in a Panamanian forest. *Journal of Ecology* 93:853–862.

SVENNING, J.-C., KINNER, D. A., STALLARD, R. F., ENGELBRECHT, B. M. J. & WRIGHT, S. J. 2004. Ecological determinism in plant community structure across a tropical forest landscape. *Ecology* 85:2526–2538.

THOMPSON, J., BROKAW, N., ZIMMERMAN, J. K., WAIDE, R. B., EVERHAM, E. M., LODGE, D. J., TAYLOR, C. M., GARCÍA-MONTIEL, D. & FLUET, M. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.

TUOMISTO, H. & RUOKOLAINEN, K. 1993. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science* 4:25–34.

TUOMISTO, H., RUOKOLAINEN, K., AGUILAR, M. & SARMIENTO, A.. 2003a. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology* 91:743–756.

TUOMISTO, H., RUOKOLAINEN, K. & YLI-HALLA, M. 2003b. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241–244.

URIARTE, M., CONDIT, R., CANHAM, C. D. & HUBBELL, S. P. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92:348–360.

URIARTE, M., CANHAM, C. D., THOMPSON, J., ZIMMERMAN, Z. K. & BROKAW, N. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *Journal of Ecology* 93:291–304.

VALENCIA, R., CONDIT, R., ROMOLEROUX, K., FOSTER, R. B., MUÑOS, G. V., LOSOS, E. C., BALSLEV, H., SVENNING, J.-C. & MAGÅRD, E. 2004. Tree-species diversity and distribution in a forest plot at Yasuní National Park, Amazonian Ecuador. Pp. 107–118 in Losos, E. C. & Leigh, E. G. (eds.). *Tropical forest diversity and dynamism. Findings from a large-scale plot network*. The University of Chicago Press, Chicago.

WEBB, C. O. & PEART, D. R. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.

WELDEN, C. W., HEWETT, S. W., HUBBELL, S. P. & FOSTER, R. B. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* 72:35–50.

WHITE, D. A. & HOOD, C. S. 2004. Vegetation patterns and environmental gradients in tropical dry forests of the northern Yucatan Peninsula. *Journal of Vegetation Science* 15:151–160.

WILLIS, K. J., GILLSON, L. & BRNCIC, T. M. 2004. How 'virgin' is virgin rainforest? *Science* 304:402–403.

WRIGHT, S. J., MULLER-LANDAU, H. C., CONDIT, R. & HUBBELL, S. P. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185.

WRIGHT, S. J., JARAMILLO, M. A., PAVON, J., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21:307–315.