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Neighbourhood structure and light availability influence the variations in plant design of shrubs in two cloud forests of different successional status

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● **Background and Aims** Plant design refers to the construction of the plant body or its constituent parts in terms of form and function. Although neighbourhood structure is recognized as a factor that limits plant survival and species coexistence, its relative importance in plant design is not well understood. We conducted field research to analyse how the surrounding environment of neighbourhood structure and related effects on light availability are associated with changes in plant design in two understorey plants (*Palicourea padifolia* and *Psychotria elata*) within two successional stages of a cloud forest in Costa Rica.
● **Methods** Features of plant neighbourhood physical structure and light availability, estimated using hemispherical photographs, were used as variables that reflect the surrounding environment. Measures of plant biomechanics, allometry, branching and plant slenderness were used as functional plant attributes that reflect plant design. We propose a framework using a partial least squares path model and used it to test this association.
● **Key Results** The multidimensional response of plant design of these species suggests that decreases in the height-based factor of safety and increases in mechanical load and developmental stability are influenced by increases in maximum height of neighbours and a distance-dependence interference index more than neighbourhood plant density or neighbour aggregation. Changes in plant branching and slenderness are associated positively with light availability and negatively with canopy cover.
● **Conclusions** Although it has been proposed that plant design varies according to plant density and light availability, we found that neighbour size and distance-dependence interference are associated with changes in biomechanics, allometry and branching, and they must be considered as key factors that contribute to the adaptation and coexistence of these plants in this highly diverse forest community.

Key words: Economic plant design, *Palicourea padifolia*, plant allometry, plant biomechanics, *Psychotria elata*, plant competition.

INTRODUCTION

'Economic plant design' refers to the construction of the plant body or its constituent parts in terms of form and function so as to minimize the allocation of energy and/or biomass of different genotypes (Givnish, 1987; Niklas, 1993*a*) and phenotypes. Any design is determined by the anatomical, developmental and mechanical properties of the tissues (Rowe and Speck, 2005), attributes that are important for plant growth, reproductive performance and fitness in different environments (Tremmel and Bazzaz, 1995; Henry and Aarssen, 1999; Weiner, 2004). In nature there is no optimal design (Niklas, 1986), because any form and function of the plant body depend directly on the cost–benefit of the investments, which may provide an advantage to survival and coexistence in different environments (McNickle and Dybzinski, 2013). In many cases, design responses are influenced by ontogenetic effects (Barthélémy and Caraglio, 2007) or environmental interactions in terms of abiotic stresses, like physical laws (Niklas and Hammond, 2013), light availability (Henry and Aarssen, 1999) and soil properties (Fitter and Stickland, 1991), and biotic stresses (Read and

Stokes, 2006), like plant density (Mäkelä and Vanninen, 1998) and herbivory (Hambäck and Beckerman, 2003).

In the tropical understorey, where species experience great light heterogeneity (Chazdon and Fetcher 1984), plant design plays an important role in survival and energy capture (Valladares *et al.*, 2002; Cooley *et al.*, 2004). Many hypotheses have been proposed to explain how the designs of understorey species, especially shade-tolerant plants, survive and coexist in different environments (Valladares and Niinemets, 2008). For example, it is proposed that plants within shaded sites present greater leaf area, petiole length and bifurcation ratio, which maximizes light interception (Horn, 1971; Delagrange *et al.*, 2004; Weijschedé *et al.*, 2006), as well as lower plasticity, related to greater capacity to conserve resources (Valladares *et al.*, 2000). The literature shows few examples of how understorey plant designs (e.g. allometry, biomechanics, branching) could be affected by neighbourhood structure and how these designs could allow coexistence in communities. It can be expected that plant design features that are under strong competition for light express the same patterns as those found in experiments with deep shade treatments. But what is the relative

importance of neighbourhood structure in plant design? And what are the properties of neighbourhoods that most influence plant design patterns?

Because the interpretation of the effects of competition on plants is related to the way in which the competition is measured or defined (Freckleton and Watkinson, 1999; Weigelt and Jolliffe, 2003), in this study we use the practical definition of competition by Grime (1979) and Trinder *et al.* (2012) – 'the capture of essential resources from a common, finite pool by neighbours' – considering here light availability as a common limiting resource in the tropical understorey (Chazdon and Fetcher, 1984). Perspectives of how plant design changes as a function of neighbourhood structure or competition could be used to answer questions related to trait-based tests of survival and coexistence (e.g. Adler *et al.*, 2013; Lasky and Uriarte, 2014; Kraft *et al.*, 2015). We consider that changes in plant design associated with variations in neighbourhoods and light availability could be used as key factors that contribute to community structure in highly diverse tropical ecosystems.

The aim of this paper is to analyse the importance of neighbourhood structure and light availability on the plant designs of two understorey species (*Palicourea padifolia* and *Psychotria elata*) as traits that may explain the coexistence of these two species within two cloud forests with communities of different successional status in Costa Rica. We propose a new framework in which the ecological variables (neighbourhood structure and light availability) affect different sectors of plant design, specifically, allometry, biomechanics and plant attributes like bifurcation and slenderness (Fig. 1). We address the general hypothesis that adjustments in plant design are associated with variations in the neighbourhood structure and light availability of the surrounding environment. From this we show which ecological variable has the greatest contribution in the variation of plant design and in which direction. The conclusions obtained here allow an understanding of how changes in the 'optimal plant design' with respect to neighbourhood structure and light availability could provide an adaptive advantage in spatially heterogeneous environments and promote their coexistence in regenerating tropical cloud forest communities.

MATERIALS AND METHODS

Study site and plant species

We conducted this study at two sites in Río Macho, Cartago, Costa Rica. The first site is a secondary old forest (SOF) of 21·26 ha near Estación de Biología Tropical y Acuicultura (EBTARM) ($9°45'52·64''$ N, $83°51'44·13''$ W, 1700 masl). Annual rainfall is 2416 mm and the monthly mean temperature is 15·8 °C (Pérez-Molina and Cordero, 2012). The most abundant tree species are *Viburnum costaricanum*, *Lozania mutisiana*, *Symphonia globulifera*, *Ilex lamprophylla* and *Dendropanax arboreus*. The second site is a secondary young forest (SYF) of 11·62 ha to the west of EBTARM ($9°45'24·42''$ N, $83°50'59·16''$ W, 1700 masl). The average rainfall is similar to that of the SOF, but monthly mean temperature is 16·5 °C (Pérez-Molina and Cordero, 2012). Some of the most common plant species in this site are *Syzygium jambos*, *Vismia baccifera*, *Miconia dodecandra*, *Myrsine coriacea* and *V. costaricanum*. According to aerial photographs and interviews, the SOF and
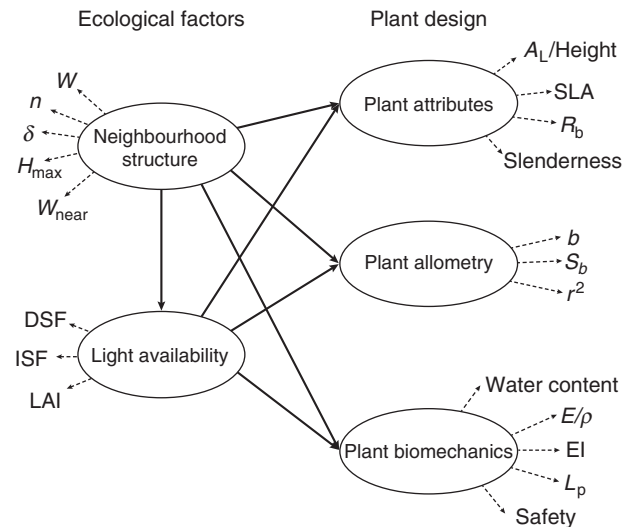

Fig. 1. Partial least squares path model to test the effect of ecological factors on plant design. Solid and dashed lines represent the inner and outer model, respectively.

SYF had undergone natural regeneration for 53 and 20 years at the time of sampling, respectively, both from abandoned pastures and soils derived from Ultisol. Both sites are classified within the rainy tropical lower montane life zone (ITCR, 2008).

Two Rubiaceae plants were used in this study: *Palicourea padifolia* and *Psychotria elata*. *P. padifolia* is a common shrub (2–7 m in height) found in cloud forests from southern Mexico to Panama (Taylor, 1989). It can be recognized by its reddish-purple pyramidal, terminal inflorescences with yellow, 1-d flowers organized in cymose clusters (Taylor, 1989). *Psychotria elata* is an understorey shrub (5–8 m in height) of premontane and wet forests from southern Mexico to Ecuador, easy to recognize by its inflorescences surrounded by two ovate red involucral bracts.

Field design

At each study site we choose 27 plants of *P. padifolia* and 22 of *P. elata* as target plants to measure the physical structure and light availability of the neighbourhood and different plant design traits described below. We chose plants with no apparent mechanical damage, low herbivory, growing in sites with little slope, far from trails, and considering plant heights between 1 and 1 m. Each target plant was separated from other target plants by >5 m but including different areas along each site. For each target plant, we measured in the field the individual stem height (m) and basal diameter 5 cm above ground (D_b, cm) and made schematic representations of the entire plant bifurcations. Later, plants were collected, cut at ground level, put into large bags and taken to the station. Thereafter, we extracted a segment of three mature and fully expanded leaves from the top crown to measure lamina thickness (mm) with a digital micrometer (293-349, Mitutoyo, Miyazaki, Japan). Likewise, total fresh leaf area (cm^2) was measured with a leaf area meter (Li-3100, LI-COR, Lincoln, NE, USA). Then, the leaf segment was extracted and total leaf biomass was determined by drying at 58 °C for >72 h to calculate specific leaf area (SLA, $cm^2\ g^{-1}$)

and total dry leaf weight (g). We used the remaining plant material to estimate several allometric and biomechanical features, described later.

Neighbourhood structure

All neighbouring woody plants (excluding woody climbers and palms) within a 5-m radius that exceeded the horizontal height of the target plant were measured. For each neighbour plant, height (h, m), circumference at breast height (c, m), horizontal orientation with respect to magnetic north (α) and distance to the target plant (d, m) were measured. The value of c was measured with a tape (± 0.05 cm), α with a digital compass (BG, Bushnell, Overland Park, KS, USA) and d using a laser range-finder (Disto D2, Leica Geosystems, Heerbrugg, Switzerland). Tree height was determined in two ways according to the visibility of the tree top crown: direct measurements of the tallest leaf by laser distance measurement and trigonometric height estimations with a digital clinometer (Forestry Pro, Shinagawa-ku, Tokyo, Japan) and a laser range-finder (Disto D2, Leica Geosystems AG, Heerbrugg, Switzerland).

We extracted five characteristics of the neighbourhood structure that influence plant features: (1) the number of neighbours (n) or the number of plants falling within the 5-m radius as a density-dependent factor; (2) maximum neighbour height (H_{max}, m), which relates to neighbourhood size; (3) the tree aggregation index (δ), which is related to the neighbours' dispersion; (4) near-tree interference (W_{near}, $m^3\ m^{-1}$), which is related to the nearest interaction factor; and (5) distance-dependent plant interference (W, $m^3\ m^{-1}$), which is related to neighbourhood size distance pressure. W was calculated according to the Weiner model (1984), which defines W as:

$$W = \sum_{i=1}^{n} h_i c_i^2 d_i^{-1}, \tag{1}$$

where i is each neighbour plant, n is the total number of neighbours, and h, c and d are the height, circumference at breast height and distance described above. W varies between 0 and ∞, where higher values correspond to higher interference and competition. W_{near} was calculated in the same way, except that we used the value of the nearest neighbour. We calculated δ according to Zar (2010) considering the horizontal orientation of the neighbours as follows:

$$\delta = 1 - \sqrt{\left(\frac{\sum_{i=1}^{n} sin_{\alpha i}}{n}\right)^2 + \left(\frac{\sum_{i=1}^{n} cos_{\alpha i}}{n}\right)^2} \tag{2}$$

where i and n are as described above, and α is the horizontal angle of orientation of each neighbour plant. The value of δ varies between 0 and 1, where 0 describes completely aggregated neighbourhoods and 1 completely dispersed neighbourhoods.

Understorey light environment measurement

We measured the neighbourhood light characteristics of each target plant using hemispherical photographs (Rich, 1989) after the harvest. Photographs were taken with a digital camera (EX SD14, Sigma, Setagaya-ku, Japan) equipped with a fisheye lens of 35 mm focal length. The camera was levelled at 1.50 m by a tripod and the photograph was taken oriented to the magnetic north. Five pictures with different shutter speeds were taken; however, for analysis we selected only the picture with the best contrast. Resulting images were analysed with HemiView 2·1 software (Delta-T Instruments, Cambridge, UK). Image processing was performed by creating 160 sky sectors (eight azimuth classes and 20 elevation angle classes) and, for a specific harvest day, the time series (1-min intervals) of openness along the solar track. From these analyses, the direct site factor (DSF, %), indirect site factor (ISF, %) and global site factor (GSF, %) were estimated. DSF and ISF estimate the fraction of direct and diffuse radiations, respectively, expected to reach the spot where the photograph was taken. GSF is the mean of DSF and ISF. Likewise, the leaf area index (LAI, amount of leaf surface area per unit ground area) was estimated as an indicator of forest cover above each plant.

Diameter–height allometry

For each species and site, the relationships between plant height and D_b and between plant height and total leaf area were used to show the effect of the type of forest on the allometric scaling of the plants. Interspecific differences in slope and intercept reflect the trade-off between height growth and leaf area extension for understorey species across growth forms (King, 1990; Kohyama and Hotta, 1990).

Plant bifurcation

We studied the plant branching patterns according to the branch order method of Strahler (1957) and Shukla and Ramakrishnan (1986). This method assumes that the forking order of each branch is independent of age. For this, the last branch was designated as the first order; where two first-order branches came together the resulting proximal segment was assigned the second order and so forth. However, if two or more branches of unequal order were joined, the resulting branch maintained the higher order (for a schematic description see Supplementary Data Fig. S1). We calculated the natural antilogarithm of the slope of the linear regression between the natural base logarithm of the number of branches per order and the branch order per plant, as an indicator of the scale pattern of plant bifurcation (bifurcation ratio, R_B). Even though there is great variability in branching ratios by species, growth form and light environment, a general expected trend for understorey shrubs is reducing bifurcation with increasing light (Valladares et al., 2012).

Plant allometry

We studied the relationships of segment length (L, cm) and diameter (D, cm) with segment order (N) as entities of pattern scale and stability of development on each plant. For this purpose, a plant segment was considered as the section between consecutive intersections of branches, stems or both. The same

logic of branch ordering as that utilized for plant bifurcation was used to study segment order. From this, linear regression models between L and N and between D and N were inspected to calculate the scaling exponent (b) and interception (a) per target plant. Also, the accuracy of the regression was evaluated using the coefficient of determination (r^2), as well as the standard error of the intersection (S_a) and slope (S_b). These parameters are good estimators of homeostasis disruption and the developmental stability of the plant (Alados *et al.*, 1999), which help to describe the patterns of homogeneity of growth in plants in different ecosystems.

Biomechanical properties

Young's modulus of elasticity (E, MNm^{-2}), flexural stiffness (EI, Nm^2), tissue density (ρ, g cm^{-3}) and the percentage of stem water content were measured in a segment of the main stem at the top of the crown of each harvested individual. E was calculated for each segment by bending experiments considering the segment of a cantilevered beam fixed at one end and measuring the deflections from the initial horizontal after putting a concentrated load at the free end. Ten discrete loads were used as bending forces (F) through the bending tests while increasing one by one and measuring the maximum deflection (X_{max}) after 60 s (Speck 1994*a, b*). To remain in the linear part of the force–deflection curve, total deflection was <20 % of the segment length. To reduce shearing effects present during bending of anisotropic materials like stems, the ratio of stem length to stem radius was well above 24, which is the minimum recommended value (Cannell and Morgan, 1987; Niklas, 1992). We fitted a regression model using the linear part of the force–deflection curve (Hookean range), using the slope b to extract EI (Niklas, 1992) and E (Speck, 1994*a*):

$$X_{max} = bF, \tag{3}$$

$$EI = \frac{l_s^3}{3b}, \tag{4}$$

$$E = \frac{EI}{I_m}, \tag{5}$$

where l_s is stem length between the holder and its free end and I_m is the mean second moment of area of the segment under test. I_m was calculated from the mean diameter of the segment at three points as:

$$I_m = \frac{\pi r^4}{4}, \tag{6}$$

where r is the stem-over-bark radius. All segment tests in which the correlation coefficients of the force–deflection data were <0·95 were eliminated from the analyses. Calculations of E reported in this study are assumed to represent the biomechanical properties of the entire stem, which consists of several tissues. Thus, E is termed the apparent modulus E_{app} (as in Gartner, 1991). The value of ρ was calculated as the ratio of stem segment dry weight and fresh volume displaced in a test tube filled with water, and percentage water content as the ratio of the difference of fresh weight less dry weight between the fresh

weight multiplied by a hundred. In both cases, ρ and water content were estimated from wood pieces with bark of 3.43 ±1.56 cm^3 sectioned from the segment in which we performed the bending experiments. Density-specific stiffness (E/ρ, MNm kg^{-1}) was calculated as the ratio of E_{app} and ρ, following Niklas (1993*b*).

From the above measurements, we determined the mechanical load parameter (L_p, dimensionless) and the factor of safety (S, dimensionless) by the critical height (h_{cr}, m). L_p is the ratio of the dimensions of the static load at the end of the stem segment and its bending stiffness (Niklas 1990*a*). This was calculated as:

$$L_p = \frac{W_t l_s^2}{EI_m}, \tag{7}$$

where W_t is the total fresh weight supported at the end of the stem segment, and l_s, E and I_m are as described above. Likewise, S was calculated as the ratio between the maximum height (critical height, h_{cr}) that the main stem could sustain and actual plant height (h). When $S = 1$ the plant has a height that it can maintain without breaking, when $S = 2$ the plant has half of the h_{cr}, which means that the plant is 2-fold safer biomechanically. We calculated h_{cr} in two different ways, according to Holbrook and Putz (1989) (eqn 8), where the tree is described as a uniform column, and according to Niklas (1992) (eqn 9), where the tree stem tapers uniformly.

$$h_{cr} = 1.26 \left(\frac{E}{w}\right)^{\frac{1}{3}} (D_b)^{\frac{2}{3}}, \tag{8}$$

$$h_{cr} = 1.97 \left(\frac{E}{w}\right)^{\frac{1}{3}} (D_b)^{\frac{2}{3}}, \tag{9}$$

where E is the modulus of elasticity previously estimated for each individual stem, w is the ratio of fresh weight to volume (Nm^{-3}) and D_b is basal diameter. Two factors of safety according to Holbrook and Putz (1989) ($S_{H\&P}$) and Niklas (1992) (S_N) were calculated.

Statistical analyses

We compared the light environment and neighbourhood characteristics for each species across sites using multivariate analysis of variance (MANOVA). Then we used univariate analysis of variance (ANOVA) to interpret the overall multivariate effects on each variable. For each species we compared plant attributes (allometric and biomechanical) across sites using MANOVA and extracted the univariate ANOVA in each comparison. We also applied one-way analysis of covariance (ANCOVA) to measure the effect of D_b on plant height, plant height on leaf area, I_m on E_{app}, and I_m on EI, using the site as predictor variables. We conducted the previous analysis using R software version 3.1.1 (R Development Core Team, 2014). We applied partial least squares (PLS) path modelling for each plant species to measure how ecological factors can affect plant design as a method for maximizing the amount of variance to predict variable relationships, rather than the statistical accuracy of the estimates. The latent variables consisted of

TABLE 1. *Neighbourhood and light characteristics of all the studied plants as estimated by interference measures and hemispherical canopy photography in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF). Values are mean and standard deviation. Significant differences between sites are represented by the univariate ANOVA extracted from MANOVA*

Characteristic	Species					
	Palicourea padifolia			*Psychotria elata*		
	SYF	SOF	F	SYF	SOF	F
Neighbourhood characteristics						
n	36.04 ± 14.31	28.54 ± 10.09	4.57[*]	43.05 ± 9.32	32.05 ± 9.71	14.85[***]
H_{max}	14.69 ± 3.37	22.86 ± 7.01	26.8[***]	13.76 ± 2.67	19.40 ± 5.36	23.92[***]
W_{near}	1.67 ± 1.87	2.01 ± 4.38	0.60	4.66 ± 8.03	2.17 ± 2.93	1.04
W	25.05 ± 10.39	32.88 ± 16.31	3.28	29.27 ± 13.00	30.81 ± 14.96	0.10
δ	0.84 ± 0.08	0.80 ± 0.11	1.96	0.86 ± 0.07	0.85 ± 0.08	0.45
Light characteristics						
LAI	2.32 ± 0.46	3.26 ± 0.64	48.99[***]	2.98 ± 0.43	2.98 ± 0.62	22.31[***]
DSF	0.20 ± 0.06	0.14 ± 0.04	18.26[***]	0.20 ± 0.07	0.15 ± 0.04	10.61[**]
ISF	0.18 ± 0.04	0.11 ± 0.04	34.11[***]	0.17 ± 0.04	0.12 ± 0.03	26.19[***]
GSF	0.20 ± 0.06	0.13 ± 0.04	19.77[***]	0.19 ± 0.06	0.14 ± 0.04	11.66[**]

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

neighbourhood characteristics and the light environment as ecological factors, and plant attributes, allometry and biomechanics as indicators of plant design (Fig. 1). From this, the variables for ecological factors were n, H_{max}, δ, W_{near} and W for neighbourhood characteristics and DSF, ISF and LAI for the light environment, while plant designs were A_L/height, SLA, R_B, and plant slenderness for plant attributes, b, S_b and r^2 from the segment D–N regression for plant allometry and water content, and E/ρ, EI, L_p and $S_{H\&P}$ for plant biomechanics. We used SmartPLS 3.1 software (Ringle *et al*., 2014) to conduct this analysis, in which we implemented a path weighting scheme to estimate the inner values of the standardized latent variable and a bootstrapping of 5000 iterations based on the individual changes to extract the variation of the inner and outer variables and their significance according to two-tailed *t*-tests.

RESULTS

Neighbourhood and light features

The ecological factors of neighbourhood and light environment differed between the SOF and SYF for each species (*P. padifolia*: Hotelling–Lawley$_{(9,44)}$ = 2·45, $P > 0.001$; *P. elata*: Hotelling–Lawley$_{(9,34)}$ = 3·37, $P > 0.001$) (Table 1). In general, neighbourhood parameters like n and H_{max} were different between sites in both species, plants in the SOF showing higher values of H_{max} and fewer neighbours than plants in the SYF. Neighbourhood characteristics like δ, W and W_{near} did not differ between sites in either of the two species. All light parameters extracted were different in both species, the plants in the SYF having lower values of LAI and higher values of DSF, ISF and GSF than those in the SOF.

Plant attributes

The multivariate response of the plant attributes within each species showed that plant attributes differed between sites

(*P. padifolia*: Hotelling–Lawley$_{(8,45)}$ = 1·39, $P < 0.001$; *P. elata*: Hotelling–Lawley$_{(8,35)}$ = 2·88, $P < 0.001$). These analyses suggest that the differences included leaf thickness, slenderness, SLA and R_B in *P. elata*, but only SLA and R_B in *P. padifolia*. In both species the values of SLA and plant slenderness were higher and leaf thickness was lower in the SOF than in the SYF, respectively. Surprisingly, plants of *P. elata* showed higher values of R_B in the SYF than in the SOF, while in plants of *P. padifolia* the higher values of R_B were found in the SOF. ANCOVA results showed that D_b had a strong relationship with plant height in both species (Fig. 2, Supplementary Data Table S1), but this relationship did not differ between sites, or their site-D_b interaction. Likewise, the relationship of plant height with total leaf area showed the same pattern in both species (Fig. 2), plant height having a strong effect on total leaf area, although variation between sites (except *P. padifolia*) and their site-plant height interaction were not significant (Table S1).

Plant allometry

The multivariate comparisons of the allometric patterns across sites within each species showed that allometric plant design did not differ between sites (*P. padifolia*: Hotelling–Lawley$_{(11,45)}$ = 0·48, $P = 0.08$; *P. elata*: Hotelling–Lawley$_{(8,35)}$ = 0·63, $P = 0.09$). Despite this, the univariate responses extracted from these comparisons in *P. padifolia* showed that the parameters a, b and r^2 from the L-N relationship were different between sites. None of the extracted variables from the D-N relationship in either species differed between sites.

Plant biomechanics

The multivariate response of the biomechanics across sites within each species showed that the biomechanical plant designs differed between sites in *P. padifolia* (Hotelling–Lawley$_{(9,45)}$ = 0·55, $P = 0.02$), but not in *P. elata*

TABLE 2. *Leaf and plant attributes of* Palicourea padifolia *and* Psychotria elata *in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF). Values are mean and standard deviation. Significant differences between sites across species are represented by the univariate ANOVA extracted from MANOVA*

Attribute	Species					
	Palicourea padifolia			*Psychotria elata*		
	SYF	SOF	F	SYF	SOF	F
Plant height	2.55 ± 0.78	2.26 ± 0.62	1.71	1.90 ± 0.54	1.52 ± 0.80	1.79
Plant diameter	2.03 ± 0.75	1.73 ± 0.70	2.52	1.58 ± 0.37	1.32 ± 0.53	1.93
Total leaf area	5316.37 ± 5111.07	6173.81 ± 4906.46	0.78	4051.31 ± 2591.61	4176.60 ± 2997.81	0.29
Total leaf biomass	44.88 ± 19.39	29.81 ± 52.11	0.22	26.69 ± 55.50	35.07 ± 20.92	0.04
SLA	160.13 ± 32.18	237.72 ± 56.43	38.65[***]	197.34 ± 42.01	243.42 ± 22.18	30.40[***]
Leaf thickness	0.22 ± 0.08	0.20 ± 0.04	0.01	0.27 ± 0.11	0.18 ± 0.05	41.64[***]
Slenderness	130.15 ± 20.15	138.52 ± 28.92	1.16	120.36 ± 22.44	154.94 ± 27.80	23.19[***]
R_B	6.84 ± 3.38	4.56 ± 1.87	9.83[**]	3.33 ± 0.66	3.48 ± 1.81	5.41[*]

[*]$P < 0.05$; [**]$P < 0.01$; [***]$P < 0.001$.

TABLE 3. *Plant-scale properties of* Palicourea padifolia *and* Psychotria elata *in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF).Values are mean and standard deviation. Significant differences between sites across species are represented by the univariate ANOVA extracted from MANOVA*

Property	Species					
	P. padifolia			*P. elata*		
	SYF	SOF	F	SYF	SOF	F
Segments	44.93 ± 42.52	36.50 ± 23.11	0.11	31.23 ± 25.73	37.05 ± 34.91	0.02
Length–order relation						
a	19.74 ± 13.94	8.99 ± 11.94	9.15[**]	12.96 ± 15.96	22.98 ± 23.48	2.74
b	4.20 ± 10.33	11.91 ± 12.18	7.29[**]	7.44 ± 9.50	3.47 ± 13.90	1.55
S_a	10.84 ± 6.74	11.16 ± 7.91	0.30	10.98 ± 6.75	16.33 ± 15.07	0.89
S_b	6.88 ± 4.43	7.18 ± 5.91	0.18	6.43 ± 4.50	10.07 ± 10.44	0.63
r^2	0.06 ± 0.15	0.12 ± 0.13	11.16[**]	0.13 ± 0.13	0.08 ± 0.11	2.48
Diameter–order relation						
a	-1.44 ± 1.33	-1.07 ± 0.88	1.43	-0.20 ± 0.74	0.19 ± 1.00	2.16
b	4.45 ± 1.08	3.98 ± 0.96	2.59	3.69 ± 0.72	3.30 ± 0.80	3.36
S_a	1.15 ± 0.56	0.94 ± 0.62	0.81	0.88 ± 0.42	0.92 ± 0.53	1.21
S_b	0.74 ± 0.42	0.60 ± 0.45	2.29	0.51 ± 0.28	0.55 ± 0.37	0.01
r^2	0.62 ± 0.14	0.68 ± 0.12	3.08	0.74 ± 0.10	0.71 ± 0.08	1.71

[**]$P < 0.01$.

(Hotelling–Lawley$_{(8,35)} = 0.48$, $P = 0.13$). Within *P. padifolia*, differences between sites were represented by changes in stem water content and I_m, plants in the SOF presenting higher values of water content and lower values of I_m than plants in the SYF. Differences across sites in *P. elata* were shown only in $S_{H\&P}$ and S_N, plants in the SYF presenting higher values than plants in the SOF. ANCOVA results showed in both species that I_m, the site and their interaction did not have an effect on E_{app} (Fig. 3A, B, Supplementary Data Table S2). However, there was a strong relationship between I_m and EI in both species (Fig. 3C, D), but the EI pattern was not effected by site or the I_m–site interaction.

Structural equation model

The PLS path analysis showed that not all ecological factors affected plant design in both species (Fig. 4). The analysis suggested two ways in which plant designs of these species are affected by ecological factors: (1) the neighbourhood structure influences the allometric and biomechanical patterns; and (2) the changes in light availability associated with the neighbourhood structure influence the plant attributes. According to the outer loadings in both species (Table 5), H_{max} and W were the variables that had a significant effect on the neighbourhood structure. The neighbourhood structure explained 29 and 10 % of light availability variance in *P. padifolia* and *P. elata* environment, respectively (Supplementary Data Table S3), increases in the neighbour's structure leading to decreases in light availability. In this latter latent group in both species, all variables (ISF, DSF, LAI) had strong effect. In relation to plant design, neighbourhood and light characteristics together explained 30 and 52 % of the variance of plant attributes in *P. padifolia* and *P. elata*, respectively. In both species R_B and SLA had an effect on plant attributes, but only in *P. elata* did plant slenderness also influence their design. Likewise,

TABLE 4. *Biomechanical and tissue properties of stem sections of* Palicourea padifolia *and* Psychotria elata *in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF). Values are mean and standard deviation. Significant differences between sites across species are represented by the univariate ANOVA extracted from MANOVA*

| Property	Species					
	P. padifolia			*P. elata*		
	SYF	SOF	F	SYF	SOF	F
I_{m} (10^{-9})	1.58 ± 0.10	1.34 ± 0.08	7.63**	2.37 ± 0.17	1.61 ± 0.15	0.01
E_{app} (10^{+9})	2.57 ± 0.97	2.70 ± 1.37	1.45	2.37 ± 1.52	2.84 ± 1.30	1.39
EI	0.38 ± 0.28	0.38 ± 0.29	0.77	0.48 ± 0.43	0.41 ± 0.40	0.27
ρ	302.40 ± 61.84	302.78 ± 91.99	2.86	335.12 ± 75.02	302.70 ± 73.68	0.08
Water content	65.72 ± 6.80	70.39 ± 4.96	10.61**	72.14 ± 3.34	71.38 ± 6.04	0.49
E_{app}/ρ (10^{+6})	9.00 ± 3.79	8.95 ± 4.51	3.01	7.60 ± 5.04	10.22 ± 5.80	0.45
L_{p} (10^{-5})	28.59 ± 38.56	24.48 ± 32.34	0.01	16.63 ± 19.21	28.65 ± 45.36	0.01
$S_{H\&P}$	2.21 ± 0.71	2.39 ± 0.62	1.25	2.68 ± 0.51	2.25 ± 0.50	6.70*
S_{N}	3.46 ± 1.12	3.74 ± 0.97	1.65	4.19 ± 0.80	3.52 ± 0.78	6.23*

*$P < 0.05$; **$P < 0.01$.
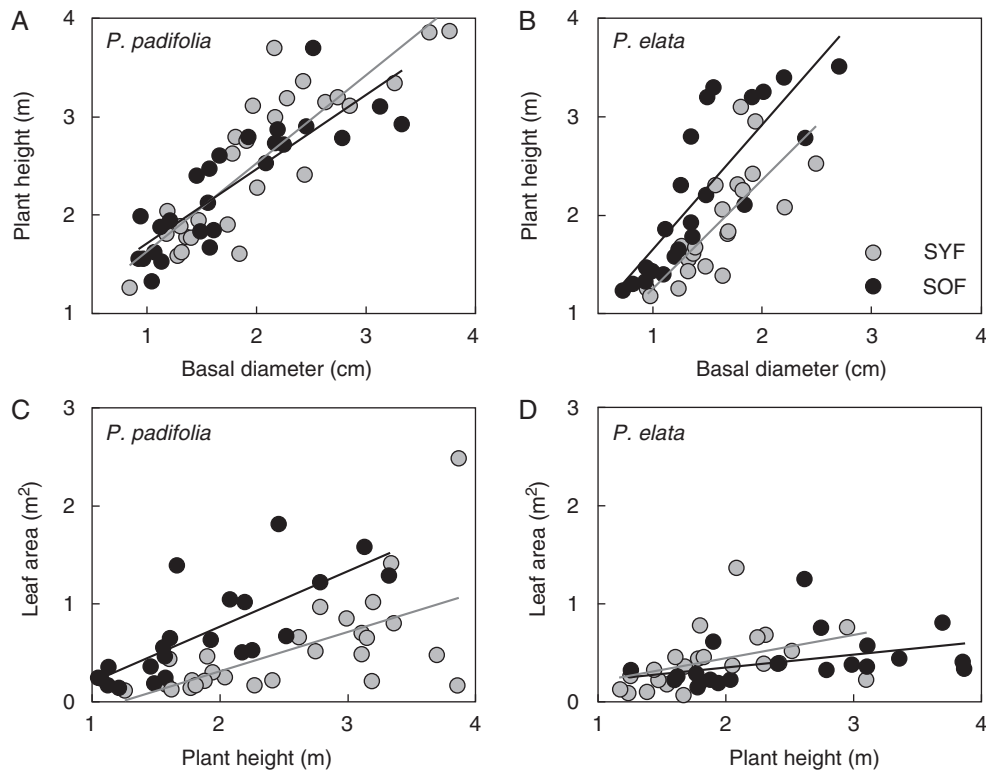
FIG. 2. Relationship of basal stem diameter with plant height (A, B) and of plant height with total leaf area (C, D) in *Palicourea padifolia* (A, C) and *Psychotria elata* (B, D) in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF). The two-way ANCOVA results are shown in Table S1.

neighbourhood and light features explained 9 and 6 % of the variance of plant allometry in *P. padifolia* and *P. elata*, respectively; however only the neighbourhood structure significantly affected this latent group. In both species increases in the structure of the neighbours (H_{max} and W mainly) led to increases in S_{b} and decreases in r^2 of the plant allometric design, the latter

being the only parameters that had a significant effect on the allometry latent group. The biomechanical plant design suggests that the neighbourhood structure influenced their properties; however, only in *P. padifolia* were these properties affected jointly with light availability. Together, neighbourhood and light availability explained 23 and 24 % of the variance in
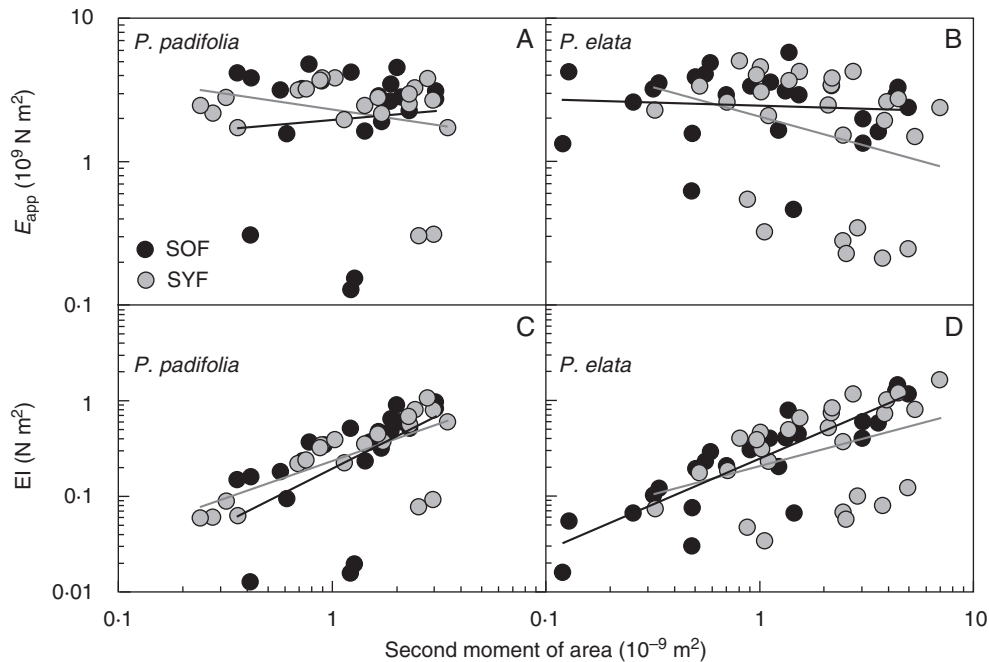
FIG. 3. Relationship of apparent Young's modulus of elasticity (E_{app}) (A, B) and flexural stiffness (EI) (C, D) with second moment of area of *Palicourea padifolia* (A, C) and *Psychotria elata* (B, D) stem in two cloud forests of different successional status in Río Macho, Costa Rica: secondary young forest (SYF) and secondary old forest (SOF). The two-way ANCOVA results are shown in Table S2.

biomechanical design in *P. padifolia* and *P. elata*, respectively. In this last latent variable, the outer loadings showed that E/ρ was related to the changes in plant biomechanics in both species. In *P. elata* this change was also related to tissue water content and L_p, while in *P. padifolia* it was also related to $S_{H\&P}$.

DISCUSSION

Ecological factors

This study shows strong effects of neighbourhood structure on understorey plant design in highly diverse and heterogeneous ecosystems such as these tropical cloud forests. We show that these sites with different successional status have contrasting physical structure and light availability around these two understorey shrubs. Differences between sites in terms of neighbourhood structure were explained mainly by n and H_{max}. In general, the highest value of n in the SYF corresponds to higher plant density, which is typical of early successional stages (Finegan, 1996; Guariguata *et al.*, 1997), while the highest H_{max} values in the SOF are indicative of forests during later successional states (Huston and Smith, 1987). The understorey light environments in the SYF had higher light availability than understories in the SOF, probably due to its forest structure, with small neighbours and low leaf cover. According to the PLS path model, increases in the parameters of neighbourhood structure (lower values of n) are associated with decreases in light availability, which suggests the capture of light by neighbouring plants, and perhaps plant competition. This analysis suggests also that W and H_{max} were the neighbourhood characteristics that have the greater effects on the increases in LAI

and decreases in ISF and DSF. In this sense, the tested model showed that neighbourhood features affected the light environment and plant design more by effects of distance and size-dependence than by nearness interference or density-dependent effects. Some studies have shown that distance-dependence indices like W could be used to determine the canopy light index (Grote *et al.*, 2013); therefore, it would be expected that, in terms of size (H_{max}) and distance (W), neighbour trees determine the light patterns of the surrounding plant environment.

Even though W did not show differences between sites, its calculation can compensate itself as a consequence of the number and size of neighbours within each site. In this sense, the light availability resulting from light interception by a distance-dependent neighbourhood structure could affect target plants through these variables. In addition, this problem may be a result of greater variation in W between sites than within sites. This suggests that observed variations in plant design of these species in relation to the light environment may depend not only on the differences in light availability between sites, but also on the properties of light generated by the heterogeneity of the neighbourhood structure between and within sites. The above statement may have strong implications for the quality of light that these and other species may experience in the understorey, which could determine the niche partitioning of the populations within this community. For example, studies in tropical forests suggest that the percentage of light transmitted below the adult crowns of late successional trees is much lower than the percentage of light transmitted through the tree crowns of early successional forest (Kabakoff and Chazdon, 1996; Kitajima *et al.*, 2005). This would mean that the performance of these species within these kinds of forest depends not only
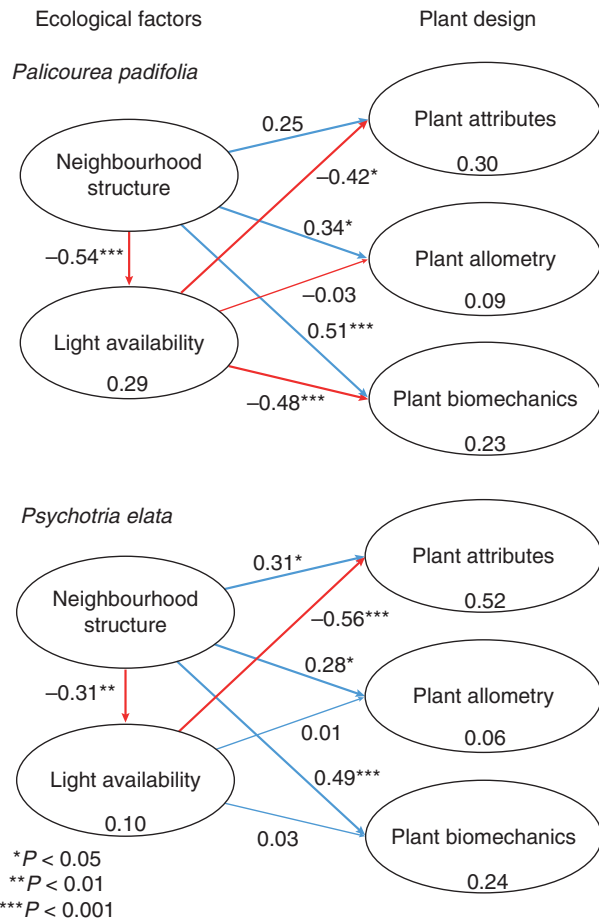
FIG. 4. Partial least squares path model results showing the effect of ecological factors on plant design. Path coefficients and their significances extracted by bootstrapping are shown near the arrows; values within ellipses represent the proportion of variance explained by the model. Outer loadings are presented in Table 5.

on the ability to adapt their traits depending on the amount of light available in a distance-dependent environment, but also on their capacity to adapt their traits to the light quality generated by this same environment, although this latter aspect was not addressed in this study.

Plant attributes

In both species we found important changes in some attributes associated with forest structure. Changes in SLA, leaf thickness and plant slenderness between sites in both species strongly respond to the previously described ecological factors, as found elsewhere (Ackerly *et al*., 2002; Valladares *et al*., 2012). Plants within sites with higher environmental exposure (e.g. high solar radiation and low forest cover) had lower values of SLA and slenderness and higher values of leaf thickness. Changes in SLA and leaf thickness between sites could be associated with the energetic costs of leaf maintenance in understorey light intensities (Lusk and Warton, 2007). Likewise, the observed increase in plant slenderness in the SOF could be associated with increased

long-term survival in the understorey for this strategy to be adaptive (Valladares *et al*., 2012). Although the species showed differences in R_B across sites, the direction of change between species differed by site, indicating an adjustment in plant design according to forest succession. Some studies suggest that plant branching is an indicator of adaptation of design to different environments (Whitney, 1976); therefore, bifurcation traits respond to the needs of resource exploration by changing reiteration design and branch mortality. Within each species, plant height, diameter, total leaf area and total leaf biomass were not different between sites, although the allometric relationship showed a species–site interaction and an effect of plant size (diameter or height) on plant design. As previously found, these plants change their resource allocation to achieve an 'optimal plant design' as a product of dynamic interaction with the surrounding environment (King, 1990; Weiner and Thomas, 1992; Farnsworth and Niklas, 1995; Alados *et al*., 1999; Henry and Aarssen, 1999). According to the PLS path model by species, plant attributes may be more affected by light availability than by neighbourhood structure. This may be due to the great plastic phenotypic capacity of these understorey shade-tolerant species to change their branch bifurcation and SLA under different light regimens (Valladares and Niinemets, 2008).

Plant allometry

The plant-scale properties showed that the order–diameter relationship can represent the pattern of development of the plant better than the order–length relationship, due to the higher coefficient of determination and the lower standard error of the slope and intercept. Although increases in stem diameter have been associated with optimal plant design in a higher density-dependent structure (Weiner and Thomas, 1992; Escós *et al*., 1997), here we did not find evidence of the effects of neighbourhood structure on increases in stem diameter. According to the PLS path model, increases in neighbourhood structure (W and H_{max}) have a direct effect on the allometric design in both species, specifically on the developmental stability described by S_b and r^2 of the order–diameter relation. These results suggest that a surrounding environment with higher capture of the light resource produces plants with lower development stability.

Plant biomechanics

Even though some mechanical features (E_{app}, EI and L_p) of stem segments in both species were not affected by the type of forest, some studies claim that changes in stem size (I_m) are more than enough to achieve higher biomechanical stability than changes in tissue mechanical properties *per se* (Holbrook and Putz, 1989; Niklas, 1990*a*, *b*; Gartner, 1991). In ecological terms, biomechanical stability is a concept that describes the likelihood of damage and constrains the extension rate of plants by requiring an increment in diameter per unit of biomass or load (King, 1990). In this sense, changes in flexural stiffness dominated by stem size and decreases in plant slenderness in the SYF in both species are a viable strategy to achieve higher biomechanical stability in plant design. In many cases, studies have recognized that increases in mechanical load are associated with the loss of stability of the design (Niklas, 1990*a*),

TABLE 5. *Loadings of the outer model and bootstrapping results (mean ± standard error) and* t-*test of the partial least square path model for the effects of ecological factors on plant design. The inner variables are presented in bold*

Outer model	Species					
	P. padifolia			*P. elata*		
	Loadings	Mean ± s.e.	*t*-test	Loadings	Mean ± s.e.	*t*-test
Neighbourhood structure						
W	0.81	0.89 ± 0.06	13.94[***]	0.86	0.69 ± 0.22	3.94[***]
n	−0.03	−0.25 ± 0.17	0.18	−0.51	−0.41 ± 0.23	2.17[*]
δ	0.02	0.21 ± 0.18	0.12	0.03	0.25 ± 0.18	0.99
H_{max}	0.77	0.72 ± 0.16	4.83[***]	0.60	0.55 ± 0.20	2.97[**]
W_{near}	0.01	0.23 ± 0.16	0.01	0.25	0.43 ± 0.23	1.06
Light availability						
DSF	0.91	0.90 ± 0.06	17.38[***]	0.88	0.85 ± 0.10	9.33[***]
ISF	0.96	0.95 ± 0.03	28.01[***]	0.96	0.94 ± 0.08	13.20[***]
LAI	−0.84	−0.83 ± 0.06	13.65[***]	−0.70	−0.71 ± 0.12	5.56[***]
Plant attributes						
A_L/height	0.26	0.47 ± 0.26	0.98	−0.10	−0.23 ± 0.17	0.58
R_B	−0.60	−0.51 ± 0.18	3.38[**]	0.42	0.46 ± 0.18	2.35[*]
Plant slenderness	0.10	0.41 ± 0.24	0.44	0.75	0.69 ± 0.16	4.76[***]
SLA	0.87	0.73 ± 0.18	4.60[***]	0.86	0.84 ± 0.10	8.30[***]
Plant allometry						
b	0.02	0.35 ± 0.23	0.10	0.45	0.59 ± 0.30	1.50
S_b	0.90	0.81 ± 0.17	5.14[***]	0.96	0.67 ± 0.26	3.33[***]
r^2	−0.89	−0.81 ± 0.17	5.27[***]	−0.56	−0.60 ± 0.28	2.01[*]
Plant biomechanics						
Water content	0.20	0.36 ± 0.23	0.86	0.79	0.56 ± 0.25	3.13[**]
E/ρ	0.50	0.49 ± 0.22	2.29[*]	0.36	0.44 ± 0.21	2.33[*]
EI	0.11	0.28 ± 0.20	0.53	0.27	0.51 ± 0.25	1.08
L_p	−0.03	−0.37 ± 0.23	0.14	−0.63	−0.48 ± 0.26	2.40[*]
Safety factor	−0.94	−0.76 ± 0.18	5.21[***]	−0.28	−0.38 ± 0.23	1.18

*P < 0.05; **P < 0.01; ***P < 0.001.

which may impact the production of different structures, such as branches, flowers and fruits (Gartner, 1991). Likewise, some studies have recognized that strategies to optimize biomechanical fitness, such as increases in stem and branch diameters, have been developed to avoid the effects of environmental stress like sites with low coverage or high wind exposure (Cordero, 1999; Henry and Thomas, 2002; Cooley *et al.*, 2004). Although changes in the factor of safety suggest that height growth of *P. elata* in the SOF could affect its height stability, these effects only represent a 16 % reduction in plant safety and plants remain 2- to 3-fold safer in both environments. From a whole-plant perspective, plant slenderness and developmental and biomechanical stability in both species suggest that changes in diameter and their homeostasis between forests with different succession could be an adaptation to optimize biomechanical fitness in relation to neighbourhood structure. Moreover, studies suggest that increases in stem water content can increase E_{app} (Cannell and Morgan, 1987), but we did not find any evidence of this effect between sites in both species.

Implication of the neighbourhood structure for plant design

Here the approach of defining whole-plant design responses by variations in neighbourhood structure could be related to the struggle of the species to find the 'optimal plant design' in different environments that could provide an adaptive advantage in spatial heterogeneous systems. We consider that changes in design in neighbourhoods in which there is high or low competitiveness may be related to an economic advantage in exploiting and using efficiently the light resource according to its availability. In this sense, it is likely that the observed variations in plant design are related to the resource-conservative and resource-acquisitive strategies (Adler *et al.*, 2013), as proposed for different functional traits as ways that drive the coexistence in the plant communities. For example, in this study increases in plant slenderness in the SOF could be associated with a resource-conservative design for the exploration of resources in a low-light environment or a highly competitive neighbourhood. This last idea has been indirectly tested by King (1990, 1994), who described saplings that adapted their plant allometry as a strategy to make efficient use of biomass for height growth in the forest understorey. Likewise, increases in SLA in the SYF could be associated with a resource-acquisitive leaf economics strategy in high-light-gap environments or neighbourhoods with low competitiveness (Adler *et al.*, 2013). If plant design responds to conservative-acquisitive strategies, it could prevent the environmental filtering of the species and promote coexistence in spatially heterogeneous environments. If the above is true, species coexistence based on adaptive plant design could predict the composition of communities in well-studied systems.

In summary, this study demonstrates that plant design, in terms of the allometric and biomechanical traits of two understorey species, varies concomitantly with the degree of neighbourhood structure in terms of size and distance, while plant

bifurcation and SLA design respond more to light availability than to neighbourhood structure. Our results strongly suggest that changes in plant design by ecological factors may have important consequences for the coexistence of the understorey species in face to neighbourhood structure. Future works should demonstrate how plant design is associated with stabilizing processes (Chesson, 2000), and fitness equality (Hubbell, 2001) in the coexistence among communities and how this association allow the survivals and assembly of the species with different designs.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Figure S1: schematic description of the method of measuring plant bifurcation proposed by Strahler (1957) and Shukla and Ramakrishnan (1986). Table S1: one-way ANCOVA results of the effect of basal plant diameter on plant height and plant height on total leaf area in *Palicourea padifolia* and *Psychotria elata* in two cloud forests of different successional status in Río Macho, Costa Rica. Table S2: one-way ANCOVA results on the effect of the second moment of area (I_m) to the apparent Young's modulus of elasticity (E_{app}) and flexural stiffness (EI) of *Palicourea padifolia* and *Psychotria elata* plants in two cloud forests of different successional status in Río Macho, Costa Rica. Table S3: path coefficients of the inner model and bootstrapping results (mean $\pm$ standard error and *t*-test) of the partial least squares path model of the effect of ecological factors on plant design.

ACKNOWLEDGEMENTS

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