



Canopy height variation and environmental heterogeneity in the tropical dry forests of coastal Oaxaca, Mexico

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ABSTRACT

Despite its importance for carbon storage and other ecosystem functions, the variation in vegetation canopy height is not yet well understood. We examined the relationship between this community attribute and environmental heterogeneity in a tropical dry forest of southern Mexico. We sampled vegetation in 15 sites along a 100-km coastal stretch of Oaxaca State, and measured the heights of all woody plants (excluding lianas). The majority of the ca. 4000 individuals recorded concentrated in the 4–8 m height range. We defined three plant sets to describe overall community canopy height at each site: a set including all plants, a set made up by the tallest plants representing 10 percent of all individuals, and a set comprising the 10 tallest plants. For each site we computed maximum height and the mean and median heights of the three sets. Significant collinearity was observed between the seven resulting height variables, but null distributions constructed through bootstrap revealed their different behaviors as functions of species richness and density of individuals. Through linear modeling and a model selection procedure, we identified 21 models that best described the variation in canopy height variables. These models pointed out to soil (measured as PC1 of a principal component analysis performed on 10 soil variables), water stress, and elevation as the main drivers of canopy height variation in the region. In the event of increasing water stress resulting from global climate change, the studied tropical dry forests could become shorter and thus decrease their carbon storage potential.

Abstract in Spanish is available with online material.

Key words: elevation; environmental drivers; latitudinal gradient; potential evaporation; soil properties; tree height measurement; vegetation structure; water stress.

UNDERSTANDING THE INTRICATE RELATIONSHIP BETWEEN VEGETATION AND ENVIRONMENT REMAINS A MAJOR CHALLENGE FOR PLANT ECOLOGISTS (Austin 2005, van der Maarel 2005). This is particularly true for tropical regions (Walter 1973, Richards 1996), where a complex mosaic of plant communities exists, ranging from those typical of very humid regions to those subjected to a marked seasonal drought (e.g., Sagar & Singh 2005, González-Rivas *et al.* 2006, Lott & Atkinson 2006, Velázquez & Gómez-Sal 2008, Madeira *et al.* 2009).

The physical structure of the plant community is affected by local factors such as abiotic conditions and interspecific interactions, and by regional and long-term climatic and historical-biogeographical processes (Ricklefs 1987, Menge & Olson 1990, Aiba & Kitayama 1999, Lortie *et al.* 2004). Canopy height represents an integrated expression of overall vegetation development (Bongers 2001, Westoby *et al.* 2002). Plant height is involved in the ability to fix carbon, and potentially affects seed production, breeding age, longevity, and distance of seed dispersal (Moles & Leishman 2008, Thomson *et al.* 2011, Pérez-Harguindeguy *et al.* 2013). All these traits can be scaled from the individual to the community level, with important consequences on functional

properties such as the magnitude of carbon stocks (Poorter *et al.* 2016). Despite its importance, relatively little is known about canopy height variation in different forests (King *et al.* 2006, Moles *et al.* 2009).

Tree height varies considerably across regions and continents (Feldpausch *et al.* 2011, Banin *et al.* 2012). The heights of individual trees in a forest, and therefore the maximum community canopy height, depend primarily on climate. For example, Larjavaara (2014) found a global correlation between temperature and the spatial distribution of the tallest trees, and Tao *et al.* (2016) described a hump-shaped global pattern of canopy height along a water availability gradient. In tropical regions, trees reach their largest sizes under conditions of high humidity and protection from strong, desiccating winds (Crawley 1986, Fajardo *et al.* 2005).

From an ecological viewpoint, canopy height is relevant because a higher canopy is associated with a more heterogeneous microenvironment in the understory, depending upon the amount of foliage, and the number and positions of branches and stems that filter light and affect other physical factors along the vertical dimension (Welden *et al.* 1991, Bongers 2001). Such vertical differentiation provides multiple opportunities for species adapted to different conditions, so that a more complex vertical structure is usually related to a higher diversity (Crawley 1986, Montgomery & Chazdon 2001).

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In this paper, we address the following questions: How much does canopy height of a tropical dry forest vary at the regional scale? What are the main environmental drivers of this variability? How is canopy height related to community diversity? Our main objective was to examine potential relationships between forest height variability and environmental factors in a tropical dry forest region of southern Mexico. To this end, we first attempted to define the dataset for tropical dry forest height that best represents overall community canopy height.

METHODS

STUDY AREA.—The studied forests are located in the coastal region of eastern Oaxaca State, southern Mexico (15°42′–16°12′ N; 91°15′–96°18′ W; 0 to ca. 500 m asl; Fig. 1, upper panel). Despite its moderate extent (150,000 ha), the region comprises considerable environmental heterogeneity (Fig. 1A–F). Following García's (2004) modification of Köppen's climate classification system, two climates characterize the region; an Aw_0 climate (i.e., the driest of the sub-humid tropical climate) is present in the lowest portions, whereas at elevations >500 m climate is also warm sub-humid, but less dry (Aw_1). Precipitation concentrates in the summer months across the entire region (June–October; Salas-Morales *et al.* 2015); total annual precipitation is highly variable (Fig. 1A), whereas both mean annual temperature and potential evaporation clearly decrease from east to west (Fig. 1B,C). Bedrock comprises a variety of substrates with different ages and origins, among which the most common are metasedimentary rocks and a metamorphic complex, whereas prevailing soil types are Haplic Pheozems and Chromic Cambisols. Observations made during a long-term floristic survey focused on primary forest revealed a substantial variation in canopy height (Salas-Morales *et al.* 2003).

SITE SELECTION AND ENVIRONMENTAL DESCRIPTION.—On the basis of thematic cartography (scale 1:250,000), we selected 15 sites for vegetation and soil sampling. The main criterion was a good conservation status of the plant community, but access and distance between sites (always >3 km to minimize spatial autocorrelation) were also considered. At each site, elevation, slope, and aspect were recorded (Table S1).

A soil profile was described at each site in a soil trench. Due to soil shallowness, samples were taken from two horizons only. Soil analyses were conducted in the Edaphology Laboratory, Facultad de Ciencias, Universidad Nacional Autónoma de México, for pH (distilled water), texture (Bouyoucos flotation method), bulk density (weight/volume ratio), cationic exchange capacity (CEC; EDTA versenate method), organic matter content and carbon (Walkley-Black method), phosphorous (Bray I method), and total nitrogen (Kjeldahl method) (Page *et al.* 1982, Klute 1986).

Only Sites 5 and 12 are located very close to a weather station. However, within and around the region there are six weather stations with sufficiently long climate records to confidently infer mean climatic conditions for the remaining 13

localities through interpolation. Estimated climate variables were the weighted means of the values from neighboring weather stations (weights were inversely related to the distances from these stations). Climate variables obtained for these stations were total annual precipitation, potential evaporation (as measured in evaporation pans), and mean annual temperature (Fig. 1A–C).

VEGETATION SAMPLING.—We used Gentry's (1982) method for vegetation sampling (10 rectangular plots totaling 0.1 ha). Within the plots we measured all woody plants (trees, shrubs, and columnar cacti) ≥ 2.5 cm in diameter at breast height (1.3 m; dbh). Shrubs were defined as plants extensively branched at their base. As tree height measurement may be associated with large errors (Pérez-Harguindeguy *et al.* 2013), we were particularly meticulous in assessing this variable. In measuring the height of a tree, two or three observers standing in different points around the tree guided the person using a 9.5 m telescopic measuring rod; they had a better judgment when standing at a position higher than the tree base, and having the tree top almost at eye level. For the few trees higher than the measuring rod, we estimated a multiplication factor for the rod height to attain total tree height. Vouchers were prepared for all species when first encountered, and deposited at SERO and MEXU.

DATA ANALYSES.—The definition of forest canopy, particularly regarding its boundaries, is controversial (Bongers 2001), and consequently a single, straightforward way of measuring canopy height is still lacking (Parker & Brown 2000, Kohyama *et al.* 2003, King *et al.* 2006). For this reason, here we defined three plant sets for describing community canopy height: (i) all individuals sampled at each site (hereafter referred to as the TOT set); (ii) trees accounting for the tallest 10 percent of all trees at each site (hereafter, the TOP10% set); and (iii) the ten tallest trees at each site (hereafter, the TOP10 set). For each site we extracted the maximum height (i.e., the tallest plant), and calculated the mean and median heights for the three sets. We assessed collinearity between these height variables, as well as their associations with community structure and diversity variables, through Pearson product-moment correlations (Zar 1999).

A principal component analysis (PCA) was used to reduce the large number of soil variables to fewer, synthetic ones. First, we discarded some variables with high collinearity between the two horizons; thus the PCA was based only on 10 soil variables (N, C, pH, bulk density, P, and CEC for horizon 1; N, C, and CEC for horizon 2; and total soil depth). The first three PCA axes accounted together for 99.2 percent of total variation (PC1 = 78.8%, PC2 = 14.8%, and PC3 = 5.6%). P concentration in horizon 1 had the largest loading on PC1 (Fig. 1F).

The analysis of potential environmental variables driving canopy height variation was done through a linear modeling approach. For each response (height) variable, we constructed all possible models including none, one, two or three predictive (environmental) variables. Despite degrees of freedom limitations, we decided to include a maximum of three factors in the models because this opened the possibility to include one factor from

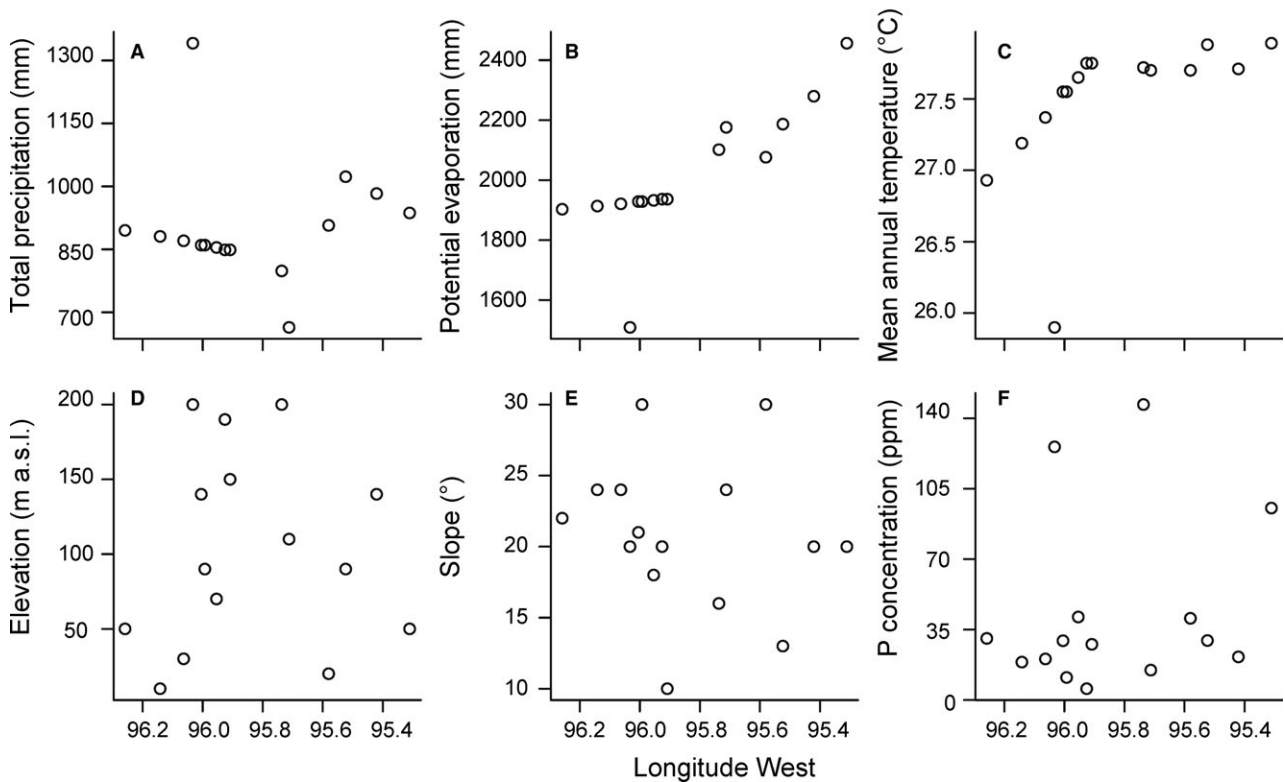
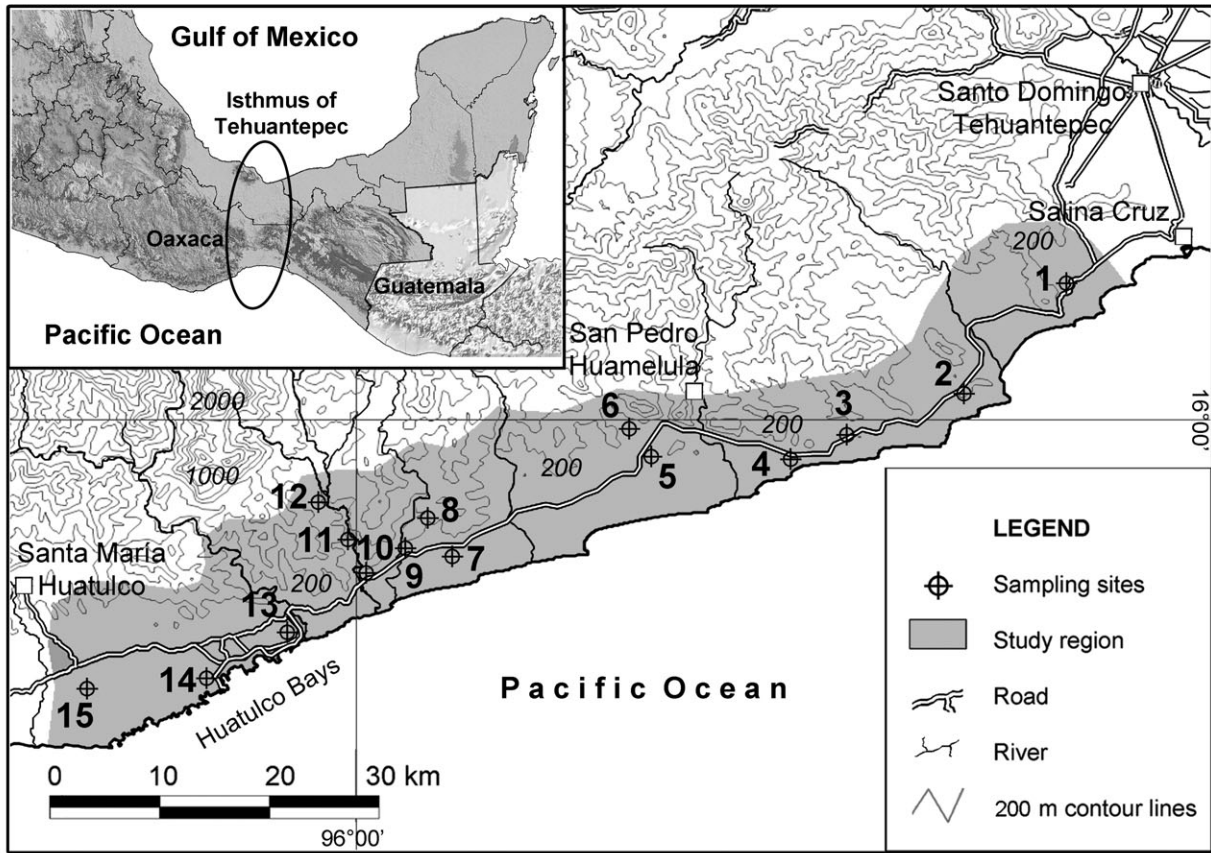


FIGURE 1. Location of the 15 tropical dry forest study sites in coastal Oaxaca, Mexico (upper panel), and geographical distribution of the most important environmental variables according to the linear regression models (lower panels). See Table S1 for locality names.

each of three groups of potential drivers of height variability, namely climate, soil, and topography. The models also included quadratic terms to allow for non-monotonic trends (Tao *et al.* 2016). We constructed a total of 220 models for each response variable, i.e., a total of 1,540 models, as follows:

$$Y = \beta_0 + \varepsilon, \quad (1)$$

$$Y = \beta_0 + \beta_1 X_i + \varepsilon, \quad (2)$$

$$Y = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \varepsilon, \quad (3)$$

$$Y = \beta_0 + \beta_1 X_i + \beta_2 X_j + \varepsilon, \quad (4)$$

$$Y = \beta_0 + \beta_1 X_i + \beta_2 X_j + \beta_3 X_j^2 + \varepsilon, \quad (5)$$

$$Y = \beta_0 + \beta_1 X_i + \beta_2 X_j + \beta_3 X_k + \varepsilon, \quad (6)$$

where Y is any of the seven canopy height variables (in logarithmic scale), X is any of the nine environmental variables ($i \neq j \neq k$), and ε is a normally distributed error term. By considering all possible combinations of variables we developed 7, 63, 63, 252, 567, and 588 different models corresponding to equations (1–6), respectively. The seven models associated with equation (1) represent null models, as they do not include any environmental factor as explanatory variable. We then applied a model selection procedure for each response variable separately based on the corrected Akaike's Information Criterion (AICc; Burnham & Anderson 2002). For each model we calculated ΔAICc by comparison with the model having the smallest AICc; models with $\Delta\text{AICc} < 2$ were considered to have similar support. Response variables were log-transformed to achieve normality; thus, R_{adj}^2 values were also calculated to compare model performance between height variables while accounting for different number of parameters between models. Spatial autocorrelation between model residuals was assessed through Moran's I test (Gittleman & Kot 1990).

To assess whether variation in species richness or sample size across sites affected the probability of having large height values by chance, we produced null distributions through bootstrap for each height variable. First, we defined a total pool by combining all plants from all sites and the species they represented. For each richness value < 100 species, we randomly chose

this number of species from the total pool and computed the height variables for the individuals associated to those species. We repeated this procedure 100 times to obtain the null distribution associated to each richness value, along with a 95% C.I. The same procedure was performed for all sample sizes < 500 individuals.

To examine the relationship between canopy height and community diversity, we calculated true diversity indices (species richness and effective number of species; 0D and 1D ; Jost 2006) per site, and computed correlations between these two sets of variables. Then, to examine the relationship between canopy height and the heights of individual species, mean heights by site of the most frequent species (i.e., those occurring in 10 sites or more with at least three individuals per site) were correlated with TOT and TOP10% mean heights.

All analyses were performed in R (R Core Team 2017), with the AICcmodavg (Mazerolle 2016), ape (Paradis *et al.* 2004), and vegan libraries (Oksanen *et al.* 2016).

RESULTS

COMMUNITY STRUCTURE AND DIVERSITY.—In the entire area (1.5 ha) sampled across the 15 localities we recorded 3,998 individuals, with a mean (± 1 SD) density by site of 266.5 ± 84.8 individuals (range: 158–425 individuals; Table 1). Most individual plants (3,105, 77.7%) were trees, whereas shrubs (552, 13.8%) and cacti (342, 8.5%) were scarcer. Maximum and mean diameters ranged between 31.0 and 54.6 cm, and between 5.74 and 9.87 cm, respectively. Total richness was 199 woody species. Species richness by site ranged from 36 to 79 species, whereas the range for the effective numbers of species was 14.95–44.21 (Table S1). This implies an almost 3-fold difference between the true diversity of the least diverse site (Site 9), located centrally in the study area, and the most diverse one (Site 15), located on its western end.

CANOPY HEIGHT VARIATION.—Mean height (± 1 SD) for the TOT set ($N = 3,998$) was 5.53 ± 1.04 m (Table 1). The frequency distributions of individual tree heights for all sites (Fig. 2) show that most values concentrated in the 4–8 m range, with very few values in the tallest plant classes. Interestingly, the large frequency of individuals in this height range was independent of the maximum heights recorded at each site. Expectedly, frequency distributions for trees of the TOP10% sets shifted toward the right, with modes between 10 and 14 m (Fig. 2). Mean values conceal the large variability observed at the study sites, which spread over one order of magnitude (1.3–25 m) for all heights measured. Likewise, maximum height was very heterogeneous, ranging from 8.3 m at Site 1 to the largest recorded value of 25 m at Site 8. The mean (± 1 SD) maximum height for all sites ($N = 15$) was 16.5 ± 4.69 m. At Sites 1 and 6 no single tree measured > 10 m, whereas at Sites 8, 11, and 12, trees surpassing this value accounted for 18.8, 9.2, and 12.7 percent of the total, respectively. Only 55 individuals (1.2%) had heights > 15 m, most of them occurring at Sites 8, 9, and 11.

TABLE 1. Structural variables assessed in 15 tropical dry forest sites in coastal Oaxaca (Mexico).

Site	Plant density (ind. 0.1/ha)				Max. height (m)	Mean height (m)			Median height (m)		
	Trees	Shrubs	Cacti	Total		TOT	TOP10%	TOP10	TOT	TOP10%	TOP10
1	159	27	3	189	8.3	3.79	6.5	6.9	3.5	6.3	6.8
2	115	32	11	158	15.5	5.80	10.8	12.5	5.5	10.2	11.0
3	208	54	18	280	13.5	5.80	9.9	11.0	5.3	9.5	10.6
4	165	16	80	261	12.0	3.66	7.6	8.9	3.4	7.4	8.7
5	132	90	1	223	16.0	5.27	10.0	11.4	4.8	9.4	10.5
6	241	94	7	342	10.0	4.89	8.3	9.3	4.6	8.1	9.3
7	313	10	102	425	18.0	5.17	10.0	13.7	4.9	9.2	13.0
8	194	26	4	224	25.0	7.63	18.1	21.7	6.4	16.5	22.5
9	335	20	10	365	22.0	6.05	11.5	18.8	5.4	11.0	18.5
10	127	21	13	161	16.0	6.10	11.5	12.5	5.4	11.0	11.5
11	293	19	2	314	24.0	6.55	14.2	18.0	5.8	14.0	17.0
12	114	44	0	158	15.5	6.62	13.0	13.8	6.1	13.3	13.5
13	241	23	65	329	17.5	5.20	11.7	14.4	4.3	11.0	14.3
14	294	33	24	351	18.5	4.90	10.8	14.5	4.4	10.0	13.0
15	174	42	2	218	16.0	5.57	11.5	13.1	4.8	11.5	12.8
Mean	207	36.73	22.8	266.53	16.52	5.53	11.0	13.37	4.96	10.56	12.87
SD	75.29	25.23	32.29	84.8	4.69	1.04	2.78	3.90	0.87	2.61	4.03

SD, standard deviation; Max., Maximum. The largest and the smallest values of each column are highlighted in bold typeface. TOT, the entire set of plants recorded at each site; TOP10%, the set comprising the tallest plants representing 10% of the total number at each site; TOP10, the set comprising the tallest 10 plants at each site.

For the TOP10% set (364 individuals), canopy height ranged from 8.8 to 25 m. TOP10% mean height was >15 m at one site only, whereas only at four sites it was <10 m. Similarly, for the TOP10 set, mean height was >15 m in three sites, and also in three sites was this variable <10 m. Median values for all datasets were also quite variable (Table 1).

ENVIRONMENTAL FACTORS AFFECTING CANOPY HEIGHT VARIATION.—The model selection procedure allowed us to identify 21 models that best described canopy height variation (Table 2). Maximum height, a variable that is the same for the TOT, TOP10%, and TOP10 sets, was best described by two models only: one with three terms and another with two. Regardless of plant set, the number of models describing the variation in mean canopy height was always smaller than that of models describing the variation in median canopy height (3 vs. 5 for TOT, 1 vs. 2 for TOP10%, and 3 vs. 5 for TOP10; Table 2). No single univariate model had better support than the best multivariate model for each height variable (Table S2).

Almost all three-term models included one variable from each group of environmental variables; the only exception was one model for the median height of the TOT set, which included elevation both as a linear and a quadratic term. Overall, the selected models coincided in pointing a prime role for soil properties in canopy height variation, as PC1 was the most frequently included environmental variable (it appeared in 19 models, and it was part of all but one two-term models). Incidentally, topsoil P concentration was the edaphic variable with the largest (positive)

loading on PC1. Notably, no selected model included any of the other two axes of the PCA considered in the modeling procedure (PC2 and PC3). PC1 was followed closely by potential evaporation and elevation, with each of them being included in 15 models, indicating also their important role in determining canopy height variation. In addition, three more environmental variables were included in the models, but with very low frequencies (mean annual temperature, 5 models; slope, 2 models; and precipitation, 1 model).

Generally, PC1 was negatively related to canopy height, and so was potential evaporation; in contrast, elevation was always positively related to all canopy height variables, except when included as a quadratic term. Mean annual temperature showed an inconsistent pattern, because although it tended to be negatively related to canopy height, it showed a positive relationship with TOT median height. TOP10% mean height was the only response variable for which a single linear model was selected.

Overall, the R_{adj}^2 values of the selected models showed their good performance, as they always accounted for >50% of total variation in the canopy height variables (Table 2). Moreover, four models had R_{adj}^2 values >0.7 (maximum height, $R_{adj}^2 = 0.767$; TOP10% mean height, $R_{adj}^2 = 0.739$; TOP10% median height, $R_{adj}^2 = 0.710$; and TOT median height, $R_{adj}^2 = 0.701$).

Moran's I was not significant for almost all selected linear models but one. Model residuals showed significant spatial autocorrelation for a two-term model selected for TOT mean height ($P = 0.004$).

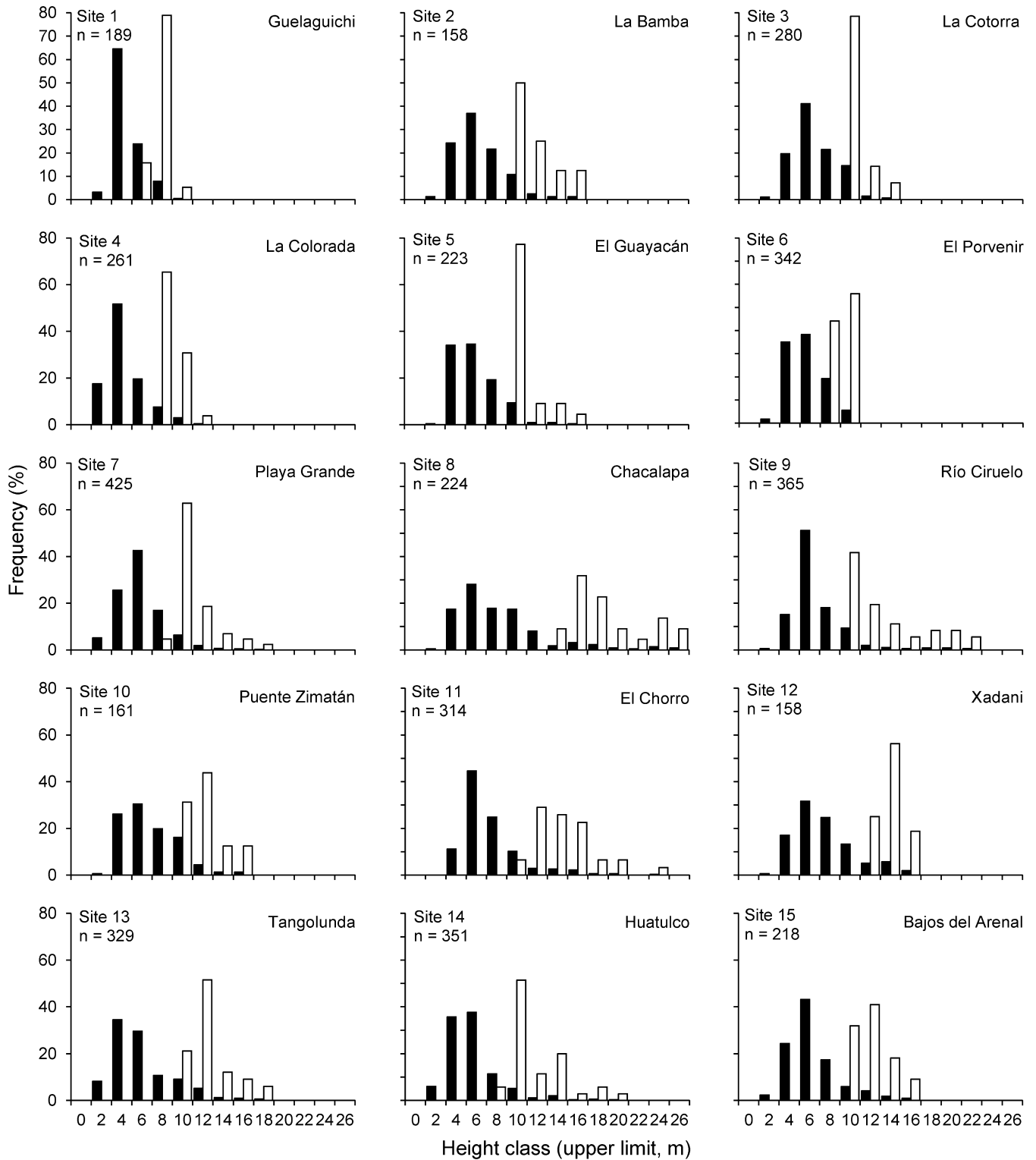


FIGURE 2. Frequency distributions of heights of all trees (TOT set; black bars) and of the trees representing the tallest 10 percent of all trees (TOP10% set; white bars) occurring in 15 tropical dry forest sites in coastal Oaxaca, Mexico. Sites are arranged geographically, from the easternmost one (site 1, upper left corner) to the westernmost one (site 15, lower right corner); n , number of woody plants (trees, shrubs, and cacti) recorded at each site.

TABLE 2. Linear regression models describing the variation in height variables. Only competing models with $\Delta AICc < 2$ are shown. The terms included in the models (X_1 , X_2 , and X_3) are presented along with the signs of their coefficients. The significance of Moran's I (I P-value) to test for spatial autocorrelation is given in the last column.

Height variable (m)	X_1	X_2	X_3	$\Delta AICc$	R_{adj}^2	I P-value
Maximum	PE (–)	PCA1 (–)	Elev. (+)	0.000	0.767	0.480
	PE (–)	PCA1 (–)		0.874	0.692	0.724
Mean, TOT	Elev. (+)	PCA1 (–)	MAT (–)	0.000	0.664	0.726
	Elev. (+)	PCA1 (–)	PE (–)	0.096	0.662	0.468
Median, TOT	Elev. (+)	PCA1 (–)		1.910	0.523	0.004
	Elev. (+)	PCA1 (–)	MAT (–)	0.000	0.701	0.426
	Elev. (+)	PCA1 (–)	PE (–)	0.922	0.682	0.414
	Elev. (+)	PCA1 (–)		1.081	0.598	0.074
	Elev. (+)	PCA1 (–)	Prec. (+)	1.399	0.672	0.107
Mean, TOP10%	Elev. (+)	(Elev.) ² (–)	PE (–)	1.977	0.659	0.433
	Elev. (+)	PE (–)	PCA1 (–)	0.000	0.739	0.694
Median, TOP10%	Elev. (+)	PCA1 (–)	PE (–)	0.000	0.710	0.669
	Elev. (+)	PCA1 (–)	MAT (–)	1.362	0.682	0.720
Mean, TOP10	PE (–)	PCA1 (–)	Elev. (+)	0.000	0.666	0.520
	PE (–)	PCA1 (–)		0.434	0.570	0.630
Median, TOP10	PE (–)	PCA1 (–)	Slope (–)	1.718	0.626	0.560
	PE (–)	MAT (+)		0.000	0.524	0.522
	PE (–)	PCA1 (–)		0.185	0.518	0.658
	PE (–)	PCA1 (–)	Elev. (+)	0.508	0.607	0.492
	PE (–)	PCA1 (–)	Slope (–)	1.546	0.578	0.578
	PE (–)	PCA1 (–)	MAT (+)	1.917	0.568	0.427

TOT: the set of all trees at the study sites; TOP10%, the set comprising the tallest trees representing 10% of all trees at the site; TOP10, the set comprising the ten tallest trees at the site; PE, potential evaporation (mm/yr); Elev., elevation (m asl); Prec., total annual precipitation (mm/yr); MAT, mean annual temperature (°C); PC1, site scores on axis 1 of PCA performed on soil variables; P, phosphorus concentration (ppm); Slope, slope inclination (°); R_{adj}^2 , adjusted coefficient of determination of the model.

DEPENDENCY OF CANOPY HEIGHT VARIABLES ON SPECIES RICHNESS AND DENSITY.—The 14 null distributions constructed to examine the dependency of canopy height variables upon increasing species richness (S) and density of individuals (N) showed strikingly different behaviors for the different variables (Fig. 3). The largest difference was observed between height variables for the TOT set (including maximum height, which is the same for the other sets), and those for the TOP10% and TOP10 sets; this difference consisted in the lack of asymptotic trends of canopy height variables both with increasing S and N for the TOT set, whereas estimated height variables became constant starting at low S and N values for TOP10% and TOP10.

For the height variables corresponding to the TOP10% and TOP10 sets, constant values emerged with as few as five species for the former and two or three species for the latter. Likewise,

very few individuals suffice to reach constant values of height variables for these two sets. In addition, the confidence intervals tended to decrease with increasing species richness and density of individuals, a trend that was not observed for height variables modeled for the TOT set. The graphs depicting the models for canopy height variables as a function of species richness (Fig. 3, left panels) or of density of individuals (Fig. 3, right panels) also include the positions of the 15 study sites. Although many sites were included in the 95% confidence intervals, some were not, indicating that not all of the observed variation can be explained by chance.

RELATIONS BETWEEN HEIGHT VARIABLES AND OTHER STRUCTURAL VARIABLES.—Overall, height variables were strongly correlated among themselves (Table 3). TOP10% mean height was the most redundant because it had the strongest correlations with the other height variables.

Correlations between height variables and dbh means by plant set were significant for the TOT set only ($r = 0.60$, $P = 0.017$). No significant correlation was found between height variables and density. Correlations between species richness (0D) and mean height were not significant for the TOT ($r = 0.310$, $P = 0.259$) and TOP10% ($r = 0.459$, $P = 0.085$) sets. Conversely, significant positive correlations were found between the effective number of species (1D) and mean heights of the TOT ($r = 0.517$, $P = 0.048$) and TOP10% ($r = 0.523$, $P = 0.045$) sets.

INDIVIDUAL SPECIES ANALYSES.—Twenty five species belonging to 11 families (mostly Leguminosae), had individuals reaching heights >15 m. The largest heights (ca. 25 m) were recorded for the legumes *Pterocarpus robrii* Vahl and *Lonchocarpus emarginatus* Pittier. Only six species occurred in 10 sites or more with at least three individuals per site; four of them were typically upper canopy trees (*Lonchocarpus constrictus* Pittier, *Lysiloma microphyllum* Benth., *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, and *Apoplanesia paniculata* C.Presl), whereas the remaining two, *Randia nelsonii* Greenm. and *Cnidocolus tubulosus* (Müll. Arg.) I.M. Johnst., were sub-canopy shrubs, attaining maximum heights of 6 and 16 m, respectively. Except for the correlations of mean heights by site of *H. impetiginosus* with mean heights of the TOT and TOP10% sets, and of the mean height by site of *L. microphyllum* with mean height of TOP10%, all remaining correlations were significant, often highly so, and the positive r coefficients imply that these associations are strong, particularly for *L. constrictus* and *A. paniculata* (Table 4).

DISCUSSION

ENVIRONMENTAL EFFECTS ON CANOPY HEIGHT VARIATION.—The tropical dry forests that still cover large areas of Oaxaca's coastal region are highly heterogeneous. Canopy height is a major component of such heterogeneity, with short communities where the tallest trees barely measure 8 m contrasting with much taller communities where the biggest trees are three times as tall. At first glance, such variation seemed to be organized along an east

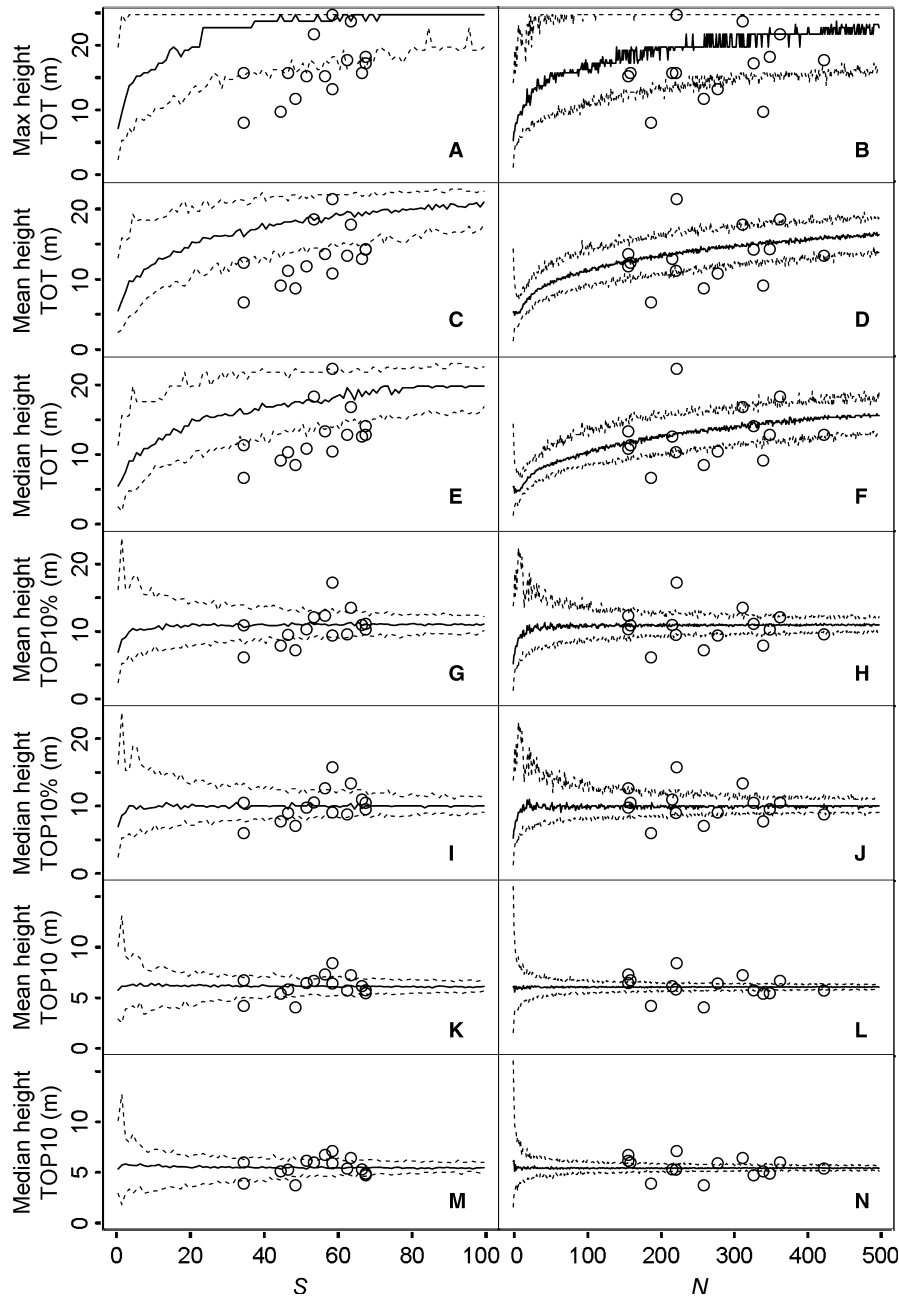


FIGURE 3. Null distributions of the seven canopy height variables defined in the study, constructed through bootstrap, to assess the potential influence of species richness or sample size variation across sites on height variables. Pools for species and individuals were obtained by grouping all woody plants (trees and shrubs) from all sites and the species they belong to. Continuous lines represent mean values for each canopy height variable after 100 iterations; broken lines represent 95% confidence intervals. Left panels (A, C, E, G, I, K, M), null distributions for species richness (S); right panels (B, D, F, H, J, L, N), null distributions for number of individuals (N). Open circles are observed height variables at the 15 vegetation sampling sites.

to west gradient, but the precise sources of this structural heterogeneity were unclear. We hypothesized that climate, edaphic factors, and topography could be the main drivers of the structural heterogeneity in these forests. Generally, the analyses conducted for the three datasets defined here to describe canopy height confirmed the existence of such geographical gradient and allowed us to gain new insight on the causes of canopy height variability.

As in many tropical regions around the world, climatic records for coastal Oaxaca are scattered and discontinuous. Fortunately, we were able to gather sufficient climatic information to characterize our sites through linear interpolation. These data revealed substantial variation in the prevailing climatic conditions, with the least water-stressed portions located at the western end, and the driest ones concentrating toward the eastern part of the

TABLE 3. Pearson product-moment correlations between height variables for 15 sites in the tropical dry forest of coastal Oaxaca, Mexico.

Height variables	1	2	3	4	5	6	7
1	—	0.75	0.66	0.86	0.83	0.97	0.94
2	0.0013	—	0.97	0.92	0.93	0.81	0.80
3	0.007	0.000000	—	0.83	0.84	0.72	0.70
4	0.000037	0.000001	0.00015	—	0.99	0.90	0.91
5	0.00013	0.000001	0.00008	0.000000	—	0.88	0.88
6	0.000000	0.00026	0.0023	0.000004	0.000018	—	0.98
7	0.000000	0.00033	0.0035	0.000003	0.000017	0.000000	—

1: Maximum height among all individuals; 2: TOT mean height; 3: TOT median height; 4: TOP10% mean height; 5: TOP10% median height; 6: TOP10 mean height; 7: TOP10 median height. Upper triangle, correlation coefficients; lower triangle, significance (P exact values).

TABLE 4. Results of the correlation analyses for the six most frequent species in 15 tropical dry forest sites in coastal Oaxaca, Mexico, between their mean heights and TOT mean height by site and TOP10% mean height by site.

Species	N	Fr	Height range (m)	Mean height		Mean height	
				r	P	TOT	TOP10%
<i>Cnidocolus tubulosus</i>	215	11	1.5–16.0	0.77	0.006	0.63	0.035
<i>Randia nelsonii</i>	135	11	1.9–6.1	0.70	0.016	0.66	0.027
<i>Lonchocarpus constrictus</i>	131	11	2.1–16.0	0.89	0.0002	0.83	0.001
<i>Lysiloma microphyllum</i>	128	13	2.3–24.0	0.68	0.01	0.48	0.095
<i>Handroanthus impetiginosus</i>	116	10	2.7–19.5	0.20	0.57	0.17	0.64
<i>Apoplanesia paniculata</i>	73	10	3.7–16.5	0.83	0.003	0.85	0.002

N, total number of individuals for each species across all sites; Fr, number of sites where the species was present.

study area. Yet, it also became evident that climate was not the only source of environmental heterogeneity, as soil properties and topography also varied considerably across the region.

Our modeling approach recognized the potential influence of these three sets of environmental factors (climate, soil, and topography), so models were constructed to allow the possibility to include one factor from each group, at least potentially. Interestingly, among the numerous potential models describing canopy height variation, more than half of the selected ones (15 of 21), included one term from each group of environmental variables. Besides, most two-term models also included predictive variables belonging to different groups. This result is highly relevant, as the criterion used in selecting the best-supported models (AICc) penalizes models with many terms. In other words, the likelihood component of AICc in models with only one term never compensated the penalization due to having two or three terms. The ecological implication of this finding is that canopy height heterogeneity cannot be explained by a single factor; rather, it responds in a complex fashion to several factors affecting it simultaneously. In particular, and based on the frequency of inclusion of terms in the models, these results point out to soil (measured through

PC1 of a PCA that included 10 soil variables), water stress (measured as potential evaporation) and topography (measured as elevation), as the main drivers of canopy height heterogeneity in the region.

Water is the factor most strongly limiting tropical dry forest structure and functioning (Murphy & Lugo 1986, Holbrook *et al.* 1995, Maass & Burgos 2011). Therefore, the prevalent role of soil among the best models describing canopy height variation came as a surprise. Actually, many studies in tropical regions have acknowledged the role of soil properties as drivers of plant community attributes. For example, soil texture explained abundance and distribution patterns of some species in Kenya (Patten & Ellis 1995), and tree density in South Africa (Witkowski & O'Connor 1996). Also, soil nitrogen deficiency was identified as a main driver of vegetation structure and physiognomy in Amazonian caatingas, in Bolivia soil was more important in determining structure and diversity in dry than in moist forests (Peña-Claros *et al.* 2012), and plant diversity of an Indian tropical dry forest showed a significant positive relationship with soil moisture content, clay, and total N (Chaturvedi & Raghubanshi 2014). Although there is less evidence regarding the role of edaphic properties on canopy height variation, Coomes and Grubb (1996) showed that the depth of aerated soil affects this variable. Unfortunately, due to sample size (and thus degrees of freedom) limitations for the analysis, we faced the need to create soil synthetic variables, given the impossibility to include in the analysis the original 21 soil variables. Hence, it is difficult to precisely identify those soil factors most strongly responsible for canopy height variation. There are some clues suggesting that fertility is involved in this relationship, as P concentration had the largest loading on PC1. However, this result is puzzling, as P was positively related to PC1 scores and PC1 always had negative coefficients in the models, leading to the conclusion that soil fertility is negatively related with canopy height in our study region. This possibility is consistent with the well-established negative P availability-rainfall relationship, as a result of enhanced leaching in areas of greater rainfall (Austin & Vitousek 1998). Nonetheless, that PC1 is not a direct representation of P availability, but a mathematical function integrating many soil properties with potentially complex synergisms between them, must not be overlooked.

The other two environmental variables with high frequencies in the best-supported models explaining canopy height variation were potential evaporation and elevation. Unlike the results related to soil properties, this finding is consistent with the basic tenets of tropical dry forest ecology, as these two environmental factors are related to water availability. Previous studies have recognized this factor as a major driver of vegetation height (Moles *et al.* 2009, Givnish *et al.* 2014, Tao *et al.* 2016). Notably, however, the effect of water was not best described through precipitation, i.e., water input into the region, as precipitation was included in one model only (TOT median height). Rather, it is water stress, better reflected in potential evaporation, the climatic factor emerging as a main driver of canopy height; this agrees with Givnish *et al.* (2014), who concluded that evaporation is the main driver of maximum height attained by *Eucalyptus* species in Victoria, Australia. Generally, potential evaporation depends mainly upon air temperature, and in turn this latter variable decreases significantly with increasing elevation (Holdridge 1996, Salas-Morales *et al.* 2015), but local factors may distort this relationship, as discussed below. Therefore, the interpretation of the effects of elevation and mean annual temperature should be similar, as all these factors help sizing the magnitude of water stress. Unlike PC1 for soil properties, these three variables had consistent behaviors regarding canopy height: our study communities are shorter with increasing evaporation and temperature, but they are taller at higher elevations. In addition, changes in canopy height tend to be linearly related to these environmental factors, as only one model included elevation as a quadratic term.

In coastal Oaxaca potential evaporation decreases from east to west, although the change is less marked west of the 95.8th meridian (see Fig. 1). Being located on the Pacific watershed of tropical southern North America, the cause of this strong gradient was not evident at first sight. In fact, this appears to be a good example of local conditions overriding regional climatic effects (Fridley 2009, Suggitt *et al.* 2011, Ashcroft & Gollan 2012). Our study region lies very close to the Isthmus of Tehuantepec, a narrow section of the continent separating the Atlantic and Pacific oceans. Climatic conditions in the Isthmus of Tehuantepec are strongly influenced by the Trade Winds, which gain speed while crossing the continent over this low-elevation narrow pass. This meteorological singularity creates a strong asymmetry in precipitation between the northern and southern sides of the Isthmus, as the humidity is released gradually from north to south. Consequently, when the winds reach the Pacific side of the Isthmus they are very dry and highly desiccating (Trasviña *et al.* 1995, Romero-Centeno *et al.* 2003). This phenomenon may explain the attributes of the vegetation located at the eastern end of our study region: shorter canopies may result from higher water stress, but also perhaps because of a strong wind shear on treecrowns (Jones 1983, King 1990). The western portion of coastal Oaxaca, farther away from the Isthmus of Tehuantepec, is not influenced by this climatic effect. On the contrary, the prevailing winds in that area approach it from the sea and therefore they carry larger humidity loads. This situation may be related to the close location of the Southern Sierra Madre, whose highest

peaks (up to 3,750 m asl) are located nearby. The combined influence of marine winds and this sharp elevational gradient may determine the existence of better conditions for vegetation development (Salas-Morales *et al.* 2015), ultimately allowing for bigger trees and a higher canopy in the area.

CAVEATS ABOUT MEASURING CANOPY HEIGHT.—This investigation required a definition as to what the best way is to measure vegetation height (a community-level attribute) from height data of individual trees (an individual-level attribute). In fact, most vegetation descriptions that include canopy height data are very imprecise regarding how this variable was measured. Calculating mean height values using all data for the sampled community resulted in a large bias toward the most frequent heights, which in our forests ranged between 4 and 8 m. In fact, Parker and Brown (2000) warned against the use of mean height values, as they tend to hide ‘ecologically interesting diversity’. To overcome this problem, we defined various height variables for different plant sets. All these variables showed high collinearity between them, so it is difficult to make suggestions as to which one is better to use based on these correlation values. Only TOP10% mean and median heights seemed to outdo the other height variables because they have the strongest correlations with all of them (mean $r = 0.901$ and 0.891 , respectively). The null distributions for these canopy height variables as functions of species richness or density of individuals were more informative, because they revealed different properties of these variables. In particular, the null distributions showed very stable behaviors of the estimated variable for the TOP10% and the TOP10 sets, even at low richness or density values, which are potential outcomes of having small sample sizes. On the basis of these results and because the TOP10% set always involves more plants than the TOP10 set (except in very small vegetation samples), we recommend using the TOP10% set as a standard for the assessment of canopy height derived from individual plant measurements.

Taking height measurements only of the TOP10% set in the field would result in considerable cutbacks in sampling time. However, in practice this procedure may face complications, because defining the group that accounts for 10 percent of the tallest plants cannot be done without first measuring all plants in the plot. Yet, in communities where a visual overview of the canopy is feasible, one could count the number of individuals in the study plot, then measure the height of the tallest tree first, and proceed downwards measuring the height of shorter individuals until the heights of the tallest 10 percent of all individuals are measured. Although this would be an imperfect process because one cannot guarantee that the measured trees correspond exactly to the tallest 10 percent of the trees in the community, the estimated canopy height variable would probably be accurate enough.

RELATIONSHIPS BETWEEN CANOPY HEIGHT AND OTHER COMMUNITY AND POPULATION ATTRIBUTES.—The examination of the relationship between canopy height and other community attributes was only done for mean canopy values for the TOT and TOP10%

sets. Overall, canopy height was not correlated with community structure, except for the significant correlation between TOT mean height and mean dbh. The lack of significance for those correlations involving plant density is intriguing, as we expected that communities with taller, and therefore bigger trees, would contain fewer stems. In fact, correlations between mean dbh and density were significant and negative, in agreement with this idea (results not shown). A different situation was observed for those correlations involving diversity attributes: the significant correlations between the two canopy height variables and the effective number of species, although not very strong, suggest that sites with taller canopies tend to be more diverse, in agreement with generalizations made by Gentry (1982, 1988) and Clinebell *et al.* (1995). In fact, canopy height is often correlated with the diversity of other biological groups, both of plants (lianas; Putz 1984, epiphytes, Benzing 1983), and animals (Gillespie & Walter 2001, Seavy & Alexander 2011, Powell & Steidl 2015).

A particularly interesting result of this study was the significant relationships observed between the mean height of the most frequent species and mean canopy height by site, confirming that broadly distributed species across the study area had taller individuals in forests with taller canopies. This result implies that the structural variability in these forests seems to match population level responses for some species. However, there were two important exceptions to this pattern, namely *Lysiloma microphyllum* and *Handroanthus impetiginosus*. The relative independence of the heights of these two upper canopy species from the overall community height hints to the existence of strong physiological or mechanical limitations imposing fixed limits to the heights attained by some species (Friend 1993, Niklas 2007, Givnish *et al.* 2014). Although this result could also be due to small sample sizes, this seems unlikely as this analysis was performed for abundant species only.

CONCLUSIONS

The examination of canopy height variability in the tropical dry forest of coastal Oaxaca shed new light on the potential drivers of this variation. Perhaps the most far-reaching finding is that canopy height is not only an elusive attribute regarding its measurement, but also a complex community attribute driven by multiple environmental factors. Admittedly, the effects of the environmental variables analyzed by us may be mediated by other factors ignored in our study, such as human influence, as past uses of these forests may have left undetectable structural legacies. Of particular importance may be firewood extraction, a highly selective activity toward some species (Sassen *et al.* 2015). Future studies should address this issue.

Despite the wide recognition of environmental humidity as a good predictor of forest height globally (Moles *et al.* 2009, Tao *et al.* 2016), it is clear that regionally soil properties may also play an important role in determining canopy height variation. However, which soil factors are more important, and through what mechanisms they operate, remains obscure. These findings bear important implications in the light of different global change

future scenarios (IPCC 2014). Although soil properties are less likely to be severely altered, important changes in the temperature and precipitation regimes of the region may take place. Therefore, in the event of increasing water stress resulting from climate change, a likely outcome could be a significant reduction in the stature in the studied tropical dry forests. Ultimately, this could cause an important decline in their potential to store carbon, as this process has been shown to be closely related to water availability and forest structure in the tropics (Poorter *et al.* 2016).

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DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.8n4f6> (Salas-Morales *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Environment, structure, and diversity of 15 tropical dry forest sampling sites in the Coastal Region of Oaxaca (Mexico).*

TABLE S2. *Univariate linear regression models describing the variation in height variables.*

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