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Can terrestrial laser scanners (TLSs) and hemispherical photographs predict tropical dry forest succession with liana abundance?

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Abstract. Tropical dry forests (TDFs) are ecosystems with long drought periods, a mean temperature of 25 °C, a mean annual precipitation that ranges from 900 to 2000 mm, and that possess a high abundance of deciduous species (trees and lianas). What remains of the original extent of TDFs in the Americas remains highly fragmented and at different levels of ecological succession. It is estimated that one of the main fingerprints left by global environmental and climate change in tropical environments is an increase in liana coverage. Lianas are non-structural elements of the forest canopy that eventually kill their host trees. In this paper we evaluate the use of a terrestrial laser scanner (TLS) in combination with hemispherical photographs (HPs) to characterize changes in forest structure as a function of ecological succession and liana abundance. We deployed a TLS and HP system in 28 plots throughout secondary forests of different ages and with different levels of liana abundance. Using a canonical correlation analysis (CCA), we addressed how the VEGNET, a terrestrial laser scanner, and HPs could predict TDF structure. Likewise, using univariate analyses of correlations, we show how the liana abundance could affect the prediction of the forest structure. Our results suggest that TLSs and HPs can predict the differences in the forest structure at different successional stages but that these differences disappear as liana abundance increases. Therefore, in well known ecosystems such as the tropical dry forest of Costa Rica, these biases of prediction could be considered as structural effects of liana presence. This research contributes to the understanding of the potential effects of lianas in secondary dry forests and highlights the role of TLSs combined with HPs in monitoring structural changes in secondary TDFs.

1 Introduction

Lianas (woody vines) are a key structural component of tropical forests; they account for 25–40 % of the woody stems and more than 25 % of the woody species (Schnitzer and Bongers, 2011). Lianas are structural parasites that use trees to ascend to the forest canopies and move from tree to tree. Lianas have been defined as hyper-dynamic elements of the canopy structure (Phillips et al., 2005; Sánchez-Azofeifa and Castro, 2006). Lianas can be detrimental to host trees by competing with them for above- and belowground resources (Chen et al., 2008), reducing tree growth rates and increasing tree mortality (Schnitzer and Carson, 2010; van der Heijden et al., 2013).

In the last two decades lianas have increased in density and biomass in old-growth forests (Phillips et al., 2002; Schnitzer and Bongers, 2011). This increment is considered to be one of the major structural changes in tropical forests (Phillips and Lewis, 2014). These structural changes may have potentially negative effects on carbon stocks since they tend to reduce carbon storage and uptake in old-growth tropical forests (Durán and Gianoli, 2013; van der Heijden et al., 2015). Liana dynamics in secondary forests and their impact on forest structure, however, are not yet understood despite the fact that secondary forests are becoming increasingly dominant in tropical regions and currently occupy more area than old-growth forests (Durán and Sánchez-Azofeifa, 2015; Wright, 2005).

Lianas are considered light-loving plants, because they tend to respond positively to disturbance and show high density in areas of secondary forest succession (Paul and Yavitt, 2011). Furthermore, secondary forests may promote liana abundance because they provide both high light availability and an abundance of trellises (Schnitzer and Bongers, 2002). As tree turnover increases gaps due to mortality, lianas can take advantage of this process and form dense tangles which in turn reduce the amount of light reaching the forest understory (Paul and Yavitt, 2011; Schnitzer et al., 2000). These liana tangles can persist for long periods (up to 13 years) and alter the successional pathway stalled by liana abundance by inhibiting the regeneration, growth, and density of late successional species (Schnitzer et al., 2000).

As of today, it is still unknown whether lianas can alter successional trajectories in secondary forests resulting from anthropogenic disturbance (Durán and Sánchez-Azofeifa, 2015). Two studies in secondary wet forests have found an increment in liana density in the first 20 years of regeneration (age since land abandonment), with a subsequent decline (DeWalt et al., 2000; Letcher and Chazdon, 2009). This decline of lianas in wet forests appears to be related to reductions in light availability due to greater tree and shrub biomass at later stages of succession (Letcher and Chazdon, 2009). Nonetheless, it remains unclear whether this pattern holds true with more open forest types and whether other factors such as structure, canopy openness, plant density, and the volume of forest stands can also influence the successional trajectories of lianas (Durán and Sánchez-Azofeifa, 2015; Sánchez et al., 2009).

Despite the important effect of lianas on the biomass distribution within tropical forests (Schnitzer and Bongers, 2011; Ledo et al., 2016) and their potential role as fingerprints of climate change (Phillips et al., 2005), remote sensing tools aimed at measuring their presence or absence and their distribution within tropical forests are limited (Foster et al., 2008; Kalacksa et al., 2007a, b; Zhang et al., 2006). Current knowledge based on leaf spectroscopy approaches provides two key messages regarding liana extent mapping: first, that lianas in tropical rainforests tend to confuse the spectral reflectance of their host trees making it, in many cases, impossible to use remote sensing to create species maps (Castro-Esau et al., 2004); and second, that there is a higher degree of probability of success for efforts aiming to map liana coverage in tropical dry forests (TDFs) than in rain forests environments (Sánchez-Azofeifa et al., 2009; Kalacska et al., 2007b). Moreover, studying the impact of lianas on tropical dry forest structure, Sánchez-Azofeifa et al. (2009) used hemispherical photography (HP) over a succession of tropical dry forests in Mexico, Costa Rica, and Brazil, finding that liana-infested sites were significantly different in both canopy openness and woody area index (WAI).

Initial attempts aimed to start untangling the effects that lianas have on remote sensing observations may require data fusion techniques in which hyperspectral remote sensing approaches (leaf spectroscopy findings) are merged with ground-based forest structure information derived from terrestrial laser scanners (TLSs) and hemispherical photography (e.g. LAI, leaf area index; WAI, woody area index; and PAI, plant area index). Terrestrial laser scanners have demonstrated their capability to measure canopy properties such as height, cover (Ramírez et al., 2013), and tree architecture (Lefsky et al., 2008; Dassot et al., 2011; Richardson et al., 2014). In the last decade, there has been rapid development in portable TLSs (Dassot et al., 2011; Richardson et al., 2014). When laser pulses emitted in the visible or near-infrared come into contact with an object, part of that energy is reflected back toward the instrument which triggers the recording of its distance and intensity (Beland et al., 2014). TLS systems typically employ vertical and horizontal scanning around a fixed point of observation, providing a hemispherical representation of biomass distribution in the forest-leaves, branches, and trunks – which allows for the exploration of foliage angle distributions and clumping (Clawges et al., 2007; Jupp et al., 2009; Strahler et al., 2008).

Until now, there has been no concrete evidence about how liana abundance can affect the prediction of the forest structure using TLSs or HPs, which in turn can drive the development of better remote sensing techniques for mapping their extent. Because of this, the objective of this study was to evaluate the feasibility of using a TLS named VEGNET in combination with HPs to assess changes in forest structure in secondary TDFs with different levels of liana abundance. The VEGNET is a TLS that automatically scans a forest plot and produces a vertical foliage density profile. Given its automated mode of operation and semipermanent installation, the VEGNET instrument is described as an in situ monitoring lidar (IML) (Culvernor et al., 2014; Portillo-Quintero et al., 2014).

In this paper we first assess the changes of tropical dry forest structure due to liana presence and forest succession. Then we analyze the potential of VEGNET and HPs to detect the vertical structure of forest stands at different successional stages. Finally, we examine how liana abundance could affect the bias of prediction of VEGNET and HPs in detecting the level of succession of a given forest stand. Therefore, in well known ecosystems such as the tropical dry forest of Costa Rica, this bias of prediction could be considered as the effect of liana presence on forest structure.

2 Methods

2.1 Study Area

The study area is located in the Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS), which is a part of the Guanacaste Conservation Area in Costa Rica (10°48″ N, 85°36″ W) (Fig. 1). This site covers an area of 50 000 ha, receives 1720 mm of annual rainfall, and has a mean annual temperature of 25 °C and a 6 month dry season (December–May) (Kalácska et al., 2004). The SRNP-EMSS site has suffered intense deforestation in the past 200 years due to the expansion of pasturelands (Calvo-Alvarado et al., 2009). Original land management practices in the park included pasture rotation between different large corrals surrounded by fences that can still be identified today. More recently (early 1970's) with the creation of the Santa Rosa National Park, a process of secondary regeneration has become the dominant land-cover change force in the region. Today and after the creation of the SRNP, the uplands of the park are a mosaic of secondary forests in various stages of regeneration and with different land-use histories related to anthropogenic fires, intense deforestation, and clearing lands for pasture (Kalácska et al., 2004; Arroyo-Mora et al., 2005a; Cao et al., 2015).

2.2 Definition of forest cover and plot age.

A map of forest cover and forest cover ages was generated using aerial photographs collected by the US Army in 1956 (Scale 1 : 24 000); a Landsat Multispectral Scanner image from 1979 (80 m spatial resolution); four Landsat Thematic Mapper images from 1986, 1997, 2000, and 2005 (28.5 m spatial resolution); one SPOT multispectral image from 2010 (20 m spatial resolution); and a Landsat 8 image from 2015. All images had less than 10 % cloud cover.

The 1986 image was georeferenced to 1 : 50 000 topographic maps from the Costa Rica National Geographic Institute with a Root Mean Square Error (RMSE) of 0.5 pixels or 14.25 m. We defined this as our master image in order to georeference all of the other images. All other images were then georeferenced to the 1986 image seeking a RMSE close to 0.5 pixels between the master and the target image. The pixels of the georeferenced images were then classified as either forest or non-forest using a supervised classification to create forest cover maps. Image accuracy was determined for the 1997, 2000, 2005, and 2010 satellite images as part of independent validation efforts conducted by Costa Rica's National Forest Financing Fund (FONAFIFO). Overall accuracy for the forest and non-forest images was 90 %. Further information on image processing can be found in Sánchez-Azofeifa et al. (2001).

Final quality-controlled forest cover maps (forest non-forest) for 1956, 1979, 1986, 1997, 2000, 2005, 2010, and 2015 were cross referenced to produce a tropical dry forest age map. Specifically, forests that were 60 years old correspond to woodlands which were being observed in images since 1956; forests that were 40 years old were not detected in 1956 but have been recognized as forests since 1979; on the other hand, woodlands that were referred to as being 10 years old have a minimum of 10 years of distinguishable forest coverage. Based on Arroyo-Mora et al. (2005b) and Kalascka et. al's (2005a) studies, the following successional classification was developed: ages 10 to 40 years (early) and ages 40 to 60 (intermediate). Figure 1 presents the final land cover and forest age map for our study area.

2.3 Plots selection and description

Based on Fig. 1, 28 randomly stratified 0.1 ha plots were selected. The number of plots chosen for each forest successional stage was based upon each stage's total forest cover area. Plot sizes of 0.1 ha follow conventions used in tropical forest studies at this site (Kalascka et al., 2005a). Fieldwork was conducted in July 2016 in order to characterize the diameter at breast height (DBH), tree height, total biomass, VEGNET observations (canopy vertical profiles), and hemispherical photographs (canopy openness and leaf area index).

The characterization of successional stages was performed following previous approaches for the seasonally dry forests of Costa Rica (Arroyo-Mora et al., 2005b; Kalácska et al., 2005b) and adjusted according to the estimated forest ages (Fig. 1). These approaches categorized the secondary regeneration in different successional stages such as early and intermediate successional stages (E and I, respectively) (Arroyo-Mora et al., 2005a). The E stage is a forest area with patches of sparse woody vegetation composed of shrubs, small trees, and saplings, with a thick herbaceous understory and a single stratum of tree crowns with a maximum height of less than 10 m (Castillo et al., 2012). Some of the common species that are characteristic of this early stage of succession include *Genipa americana*, *Cochlospermum vitifolium*, *Gliricidia sepium*, and *Randia monantha* (Hilje et al., 2015; Kalácska et al., 2004). In contrast, the I stage has two vegetation strata composed of deciduous species of woody plants. The first stratum is comprised of fast-growing deciduous tree species that reach a maximum height of 10–15 m (e.g., *Cydista aequinoctialis*). The second stratum is represented by lianas and vines, adults of shade-tolerant and slow-growing evergreen species, and the juveniles of many species such as *Annona reticulata*, *Ocotea veraguensis*, and *Hirtella racemosa* (Arroyo-Mora et al., 2005a; Kalácska et al., 2004). No lianas were present in the early successional stage plots. Liana abundance tends to increase in early forests during their transition to intermediate stages. We did not select "late forests" at our study site since they tend to reflect structural characteristics (DBH, three height and species composition) associated with tropical moist forests (J. T. Tosi, personal communication, 2000).

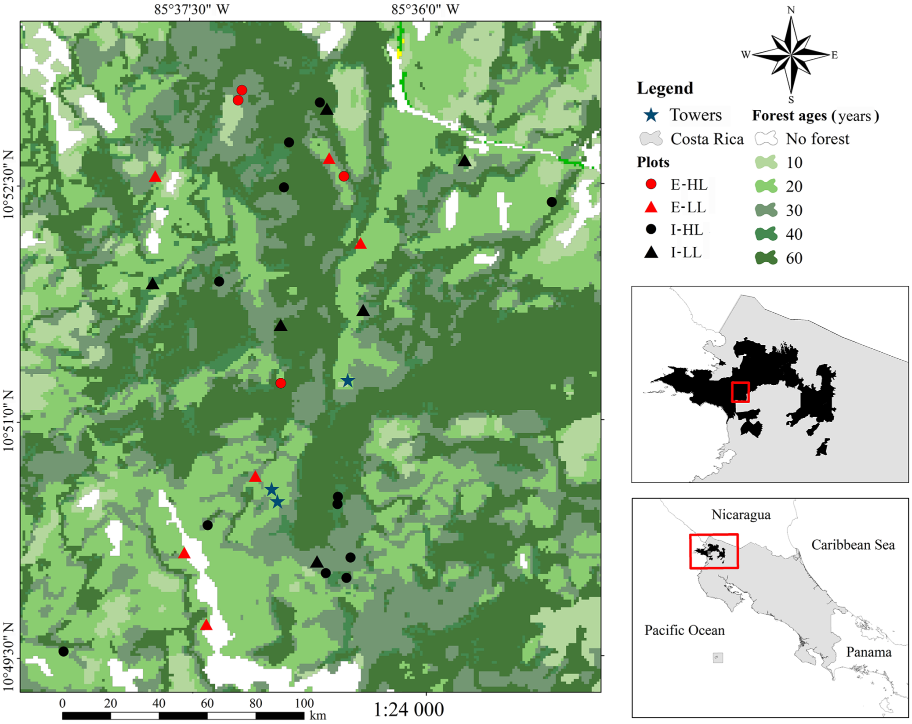

Figure 1. Location of the sampled forest plots at the Santa Rosa National Park Environmental Monitoring Super Site in Guanacaste, Costa Rica. E-HL indicates early successional stage with a high relative abundance of lianas; E-LL indicates early successional stage with a low relative abundance of lianas; I-HL indicates intermediate successional stage with a high relative abundance of lianas; I-LL indicates intermediate successional stage with a low relative abundance of lianas. Forest ages refer to 60 forests detected since 1956; 40 forests detected since 1979; 30 forests detected since 1986; 20 forests detected since 1997; 10 forests detected since 2005; and no forest, corresponding to non-related to woodlands.

The characterization of the plots according to the liana abundance was based on the structure of plants that compose the tropical dry forest of SRNP-EMSS. In this way, we classified the 28 plots according to the relative abundance of stems of lianas over the total number of stems. Plots with a relative abundance greater than 0.1 were categorized as having high liana abundance (HL); plots with a relative abundance lower than 0.1 were categorized as having a low liana abundance (LL). Although this classification seems to be indeterministic, this kind of classification represents an important ecological component which is very difficult to study as a continuum due to its spatial and temporal variation. This characterization can help to improve the understanding of ecological processes like many other ecological categories.

At the end of this characterization, ours plots for the study consisted of 5 E-LL (early successional stage with a low relative abundance of lianas) plots, 6 E-HL (early successional stage with a high relative abundance of lianas) plots, 7 I-LL (intermediate successional stage with a low relative abundance of lianas) plots, and 10 I-HL (intermediate successional stage with a high relative abundance of lianas) plots. In each of these plots we extracted all the information available to describe the dry forest according to its structure. At the same time, we deployed the ground lidar and hemispherical photograph measurements to predict and describe the structure. Information about the parameters used and estimated according to the forest structure, ground lidar, and hemispherical photographs is described in the following sections.

2.4 Forest structure

Four parameters that characterize the forest structure were used in this study. These parameters were selected because they are easily obtained in any forest inventory, which could help in the applicability of this study in other regions. Specifically, we selected the stem density (stems/ha) as a parameter to describe the number of individuals per plot, the mean diameter at breast height (1.3 m) ($\mathrm{DBH}_{\mathrm{mean}}$, cm) as a parameter that can describe the mean size of the individuals, the total basal area (TBA, m^2) as a parameter that can describe the biomass of each plot, and the ratio of liana basal area to TBA (L/TBA) as a parameter that can describe the contribution of liana biomass to the total biomass of each plot. Each of these parameters was extracted from DBH measurements for lianas (> 2.5 cm) and trees (> 5 cm).

2.5 Ground lidar measurements

The VEGNET ground lidar system was deployed in the middle of each of the selected plots, in which a single successful scan was performed between 12 and 27 June 2016. The VEGNET IML instrument uses a phase-based laser rangefinder with a wavelength of 635 nm in which a laser beam is directed at a rotating prism that reflects the laser at a fixed angle of 57.5° zenith or the "hinge angle" (Jupp et al., 2009). The prism is designed to perform full 360° azimuth rotations at this fixed zenith angle (no vertical scanning motion) and has the capability to be programmed to obtain up to 7360 range measurements for a full azimuth scan (an average of 20.6 measurements per azimuth degree) (Culvenor et al., 2014). Because sunlight irradiance may cause interference with the VEGNET laser at the same wavelength (Culvenor et al., 2014; Portilllo-Quintero et al., 2014), measurements for VEGNET were conducted at night. Some tests of the measurement process by VEGNET at nighttime indicated that at distances greater than 60 m or in areas larger than 3600 m^2 (0.36 ha) the laser beam does not provide reliable measurements (Culvenor et al., 2014). In a tropical forest setting, data analysis and interpretation may be restrained to the footprint, which is dependent on forest height at each site. Based on the forest heights of our study sites, the effective footprint of lidar measurements was within 0.1 ha of our original sampling area.

From these measurements at night, six parameters were estimated: the maximum tree height ($H_{\max}$), the plant area index (PAI), the plant area volume density (PAVD), the centroid of x (C_x) and y (C_y), and the radius of gyration (RG). To estimate these parameters, the height (h) was initially calculated as the cosine of the laser zenith angle (57.5°) multiplied by the laser distance measurement (d) assuming that the terrain is flat as describes by Culvenor et al. (2014).

Canopy "hits" and "gaps" were recorded to enable the calculation of angular gap fraction or gap probability (P_{gap}) at each h where a leaf, trunk, or branch was hit by the laser (Lovell et al., 2003). P_{gap} at a given h is the ratio of the number of valid returns below z ($\#z_i < h$) to the total number of laser shots (N) (Culvenor et al., 2014):

$$P_{\text{gap}(z)} = [\#z_i < h]/N. \tag{1}$$

Consequently, the estimation of the cumulative plant area index by the conversion of $P_{\text{gap}(z)}$ was performed using the following the equation (Culvenor et al., 2014):

$$\text{PAI}_{(z)} = -1.1 \times \ln(P_{\text{gap}(z)}). \tag{2}$$

From this calculation, the density of vegetation components at any level of z was computed as the derivative of PAI with respect to h. This calculation is commonly referred to as the plant area volume density (Culvenor et al., 2014) described by

$$\text{PAVD}_{(z)} = \delta \text{PAI}_{(z)}/\delta_z. \tag{3}$$

It is important to note that these calculations represent tridimensional variations (x, y, z) of the forest structure (Culvenor et al., 2014). Because of this, we used the maximum h estimated by the lidar per plot ($H_{\max}$), the cumulative PAI as a function of the canopy height, and the mean PAVD at different heights ($\text{PAVD}_{\text{mean}}$) in our statistical analysis. These calculations were extracted using the "VEGNET Data Display and Export Version 2.5" software developed by Environmental Sensing Systems Inc (Melbourne, Australia).

Likewise, from the lidar measurements we also used shape metrics such as the centroid (C) and radius of gyration to understand how the vertical profile of the forest could change according to successional stages and liana abundance. The RG and the C are metrics that are mainly used in lidar waveforms to describe the motion of objects and the manner in which material is distributed around an axis (Muss et al., 2013). We used a similar approach by calculating the C and RG for the PAVD vertical profile of each plot. Specifically, C represents the geometric center of a two-dimensional (x and y) region (e.g., the arithmetic mean position) of all the points (n) in the shape of the PAVD profile. It could be interpreted as the variability of PAI with height and it will change as a function of understory changes along the path of succession (grasses to shrubs to short trees). Moreover, RG is the root mean square of the sum of the distances for all points on the PAVD vertical profile, which is described as

$$\text{RG} = \sqrt{\frac{\sum (x_i - C_x)^2 + \sum \left(y_i - C_y\right)^2}{n}}. \tag{4}$$

This parameter can be visualized as the relationship between the total length of the PAVD vertical profile and its shape and position, which are determined using the sum of x or y coordinates divided by the total length of the profile (Muss et al., 2013). In general, the RG captures the manner in which the PAVD profile is distributed around the centroid, making it a better descriptor of the vertical profile shape than just the centroid itself and thus more suitable for relating VEGNET measurements to forest structure (Muss et al., 2013; Culvenor et al., 2014). Therefore, we used the RG to relate the shape of the PAVD profile to forest biomass at the footprint level. For a more detailed explanation on the functioning of the VEGNET in the field please refer to Portillo-Quintero et al. (2014) as well as Culvenor et al. (2014). A single successful scan was performed during the wet season using the VEGNET instrument at each site on clear nights.

2.6 Hemispherical photographs

Hemispherical photographs were taken during the early morning in the middle of each plot using a digital camera (E4500, Nikon, Tokyo, Japan) equipped with a fisheye lens of 35 mm focal length. The camera was leveled at 1.50 m by a tripod and orientated towards the magnetic north in order to ensure photographic standardization. The resulting pictures were analyzed using the Gap Light Analyzer version 2.0.4 software (Frazer et al., 1999). This analysis was performed by creating 340 sky sectors (36 azimuth classes and 9 elevation angle classes) with a time series of 2 min along the solar track. The leaf area index and the canopy openness were subsequently extracted by this analysis; however, the LAI was extracted using the "four rings" routine (with a zenith angle between 0 to 60°) which is a more accurate depiction of the site than using the "five rings" routine because the latter takes into account trees that are not immediately surrounding the site and which are found outside of the plot footprint.

2.7 Statistical analysis

This study compared the effect of the successional stages, the abundance of lianas, their interaction on the parameters of forest structure, and VEGNET–HPs parameters using a multivariate analysis of variance (MANOVA) in order to demonstrate that this study had been conducted in contrasting environments. For each MANOVA, we extracted the univariate analysis of variance (ANOVA) to describe the multivariate effects of each parameter. To show the potential of the VEGNET and HPs to predict variations in the structure of the dry forest, we applied a canonical correlation analysis (CCA) using the VEGNET–HPs parameters as independent variables and the features of the forest stand as dependent variables. Due to the CCA's sensitivity to the collinearity among variables (Quinn and Keought, 2002), we only used RG, PAI, $\text{PAVD}_{\text{mean}}$, $H_{\max}$, LAI, and canopy openness as independent parameters. Specifically, the CCA was used to extract the canonical correlation between VEGNET–HPs and forest structure (eigenvalues), the correlation between the canonical variates and each matrix (eigenvectors), and the scores that describe the multidimensional variation of each plot according to its correlation. To extract the statistical significance of the canonical correlation coefficients, we computed an asymptotic test on the first canonical dimensions to extract the F-approximations of Wilks' lambda along with its significance. This statistical significance was subsequently validated by 10 000 iterations of a permutation test on each dimension.

After describing the potential of the VEGNET–HPs parameters to predict variations in the structure of the dry forest, we were interested in demonstrating how the relative abundance of lianas could affect the bias of prediction extracted from these sensors. In ecological terms, it is a perceived expectation that during successional transitions increases in basal area, height, and vertical strata of the vegetation should be observed; consequently, these transitions could be translated into increases in VEGNET–HPs parameters (except canopy openness which is inverse). However, from hypothesis derived from previous studies, it is possible that the abundance of lianas may actually arrest the forest succession and reduce the biomass accumulation of woody vegetation (Paul and Yavitt, 2011; Schnitzer et al., 2000). If the above is true, correlations between descriptors of forest structure and parameters extracted from VEGNET and HPs could be diffuse or stochastic in the dry forest, and their application under the presence of lianas could prove ineffective. Under this reasoning, we compare the parametric correlations of four parameters according to the successional stages and the liana abundance separately. The four parameters selected were those with the two highest correlation values for the VEGNET–HPs matrix and the two parameters with the highest correlation values for forest structure, determined by the first two canonical dimensions described by the CCA. This comparison was conducted using an ordinary resampling method to replicate the correlation 5000 times, in which the resampled values were used to build density plots to describe the bias of prediction according to its overlap.

The previous analyses were conducted in R software version 3.3.1 (R Development Core Team, 2016) using the "CCA" package (González and Déjean, 2015) to extract the canonical correlations, the "CCP" package (Menzel, 2012) to extract the significance of the CCA and its permutation, and the "boot" package (Canty and Ripley, 2016) to extract the resampled values. When the normality of the data was not reached, each parameter was previously transformed using the Box-Cox transformation for the analysis.

3 Results

3.1 Changes on forest structure along the path of succession and liana abundance

According to the MANOVA, the forest structure of our plots differed between successional stages (Wilks' $\text{Lambda}_{(4,21)} = 0.51$; $p<0.01$) and liana abundance (Wilks' $\text{Lambda}_{(4,21)} = 0.58$; $p<0.05$) but without interaction between these categories (Wilks' $\text{Lambda}_{(4,21)} = 0.76$; $p = 0.20$). This analysis suggests that the DBH_{mean} and TBA were the only parameters affected by the interaction between successional stages and liana abundance, where E successional plots with LL and I plots with HL showed lower values of DBH_{mean} and TBA than E and I plots with HL and LL, respectively (Table 1). In terms of the effect of the liana abundance, the univariate analysis suggests that plots with LL showed lower values of L/TBA in comparison with HL plots.

3.2 VEGNET–HPs, forest succession, and liana abundance

The multivariate comparisons of the VEGNET–HPs parameters showed that the sensor estimations did not differ between successional stages (Wilks' $\text{Lambda}_{(8,17)} = 0.58$; $p = 0.21$) and liana abundance (Wilks' $\text{Lambda}_{(8,17)} = 0.62$; $p = 0.29$); these categories did not show an interaction (Wilks' $\text{Lambda}_{(8,17)} = 0.53$; $p = 0.14$). Despite the absence of a multivariate effect of the liana abundance, the univariate responses extracted from this comparison suggest that the LAI

Table 1. Mean (±SD) of parameters of forest structure extracted from plots with different successional stages and different relative abundance of lianas in the dry forest at the Santa Rosa National Park in Costa Rica. Significant differences (F values and their p values) according to the successional stages, relative abundance of lianas, and their interaction are represented by a posteriori ANOVA text extracted from a MANOVA. Stem density (stems/ha); $\mathrm{DBH}_{\mathrm{mean}}$, mean stem diameter at breast height (cm); TBA, total basal area (m^2); L/TBA, ratio of liana basal area to TBA.

Parameters	Early		Intermediate		ANOVA		
	LL	HL	LL	HL	Stage	Condition	Interaction
Stem density	1054 ± 370.72	1218.33 ± 603.24	1027.14 ± 379.02	1021 ± 331.54	0.55	0.15	0.27
$\mathrm{DBH}_{\mathrm{mean}}$	10.91 ± 2.36	11.83 ± 1.57	14.17 ± 1.85	11.56 ± 1.89	2.72	2.73	5.65*
TBA	1.44 ± 0.90	2.08 ± 1.01	2.61 ± 0.80	1.84 ± 0.61	1.39	0.48	5.15*
L/TBA (10^{-2})	0.38 ± 0.35	1.48 ± 0.84	0.35 ± 0.32	2.93 ± 2.14	2.76	14.11***	1.86

* $p<0.05$; *** $p<0.01$

Table 2. Mean (±SD) of parameters calculated by the VEGNET system and HPs in plots with different successional stages and different relative abundance of lianas in the dry forest at the Santa Rosa National Park in Costa Rica. Significant differences (F values and their p values) according to the successional stages, relative abundance of lianas, and their interaction are represented by a posteriori ANOVA text extracted from the MANOVA. RG, radius of gyration; PAI, plant area index; $\mathrm{PAVD}_{\mathrm{mean}}$, plant area volume density; H_{max}, maximum tree height (m); LAI, leaf area index.

Parameters	Early		Intermediate		ANOVA		
	LL	HL	LL	HL	Stage	Condition	Interaction
RG	4.21 ± 1.42	4.85 ± 0.92	4.69 ± 1.11	4.34 ± 0.91	0.03	0.01	1.41
C_x	0.19 ± 0.06	0.13 ± 0.04	0.14 ± 0.03	0.16 ± 0.04	0.12	0.14	5.95*
C_y	7.56 ± 2.96	8.43 ± 1.63	8.22 ± 2.07	7.56 ± 1.59	0.07	0.01	0.96
PAI	2.45 ± 0.28	2.10 ± 0.28	2.13 ± 0.34	2.31 ± 0.33	0.06	0.05	4.75*
$\mathrm{PAVD}_{\mathrm{mean}}$	0.19 ± 0.05	0.13 ± 0.04	0.14 ± 0.03	0.16 ± 0.04	0.14	0.22	7.26*
H_{max}	17.42 ± 5.51	18.17 ± 3.90	23.26 ± 7.73	18.01 ± 6.00	0.99	1.53	1.61
LAI	2.30 ± 0.32	2.46 ± 0.64	2.34 ± 0.46	2.92 ± 0.39	2.97	6.91*	1.32
Canopy openness	13.90 ± 3.94	12.59 ± 5.89	12.74 ± 5.27	8.67 ± 1.47	5.77*	6.78*	0.79

* $p<0.05$

and canopy openness differed between plots with HL and LL, where LL plots showed lower values of LAI and higher values of canopy openness in comparison with HL plots (Table 2). Moreover, the univariate responses showed that the canopy openness was affected by the successional stages, where E successional plots showed higher values of canopy openness than I plots. Likewise, the univariate comparisons suggest that C_x, PAI, and $\mathrm{PAVD}_{\mathrm{mean}}$ were affected by the interaction of the successional stages and liana abundance, where E successional plots with LL and I plots with HL showed higher values of C_x, PAI, and $\mathrm{PAVD}_{\mathrm{mean}}$ in comparison with E and I successional plots with HL and LL, respectively.

3.3 Canonical correlation analysis and trends of forest structure

The CCA showed that sensor parameters are strongly associated with the trends in forest structure (Fig. 2). In general, the first and second canonical dimension showed correlations of 0.81 (Wilks' $\mathrm{Lambda}_{(24,64.01)} = 0.13$; $p<0.01$) and 0.72 (Wilks' $\mathrm{Lambda}_{(15,52.85)} = 1.46$; $p = 0.16$) between our sensors and forest structure. Specifically, the correlation between the canonical variates in the first canonical dimension suggested that canopy openness and the LAI had a great weight in the sensor matrix, while L/TBA and stem density had an important effect on the forest structure (Fig. 2a). Likewise, the correlation between the canonical variates in the second canonical dimension showed that H_{max} and $\mathrm{PAVD}_{\mathrm{mean}}$ had a strong correlation with the sensor parameters while TBA and steam density had a strong correlation on the forest structure. The scores that described the multidimensional variation of each plot did not reflect a visual aggregation according to the successional stages and liana abundance (Fig. 2b). In terms of the validation of the significance of the canonical correlation coefficients, the permutations test showed that there was an important increase in the significance of the first two canonical dimensions (Figs. 2c, 1d), where the first dimension presented an increase of 0.21 points for the Wilks' statistic while the sec-

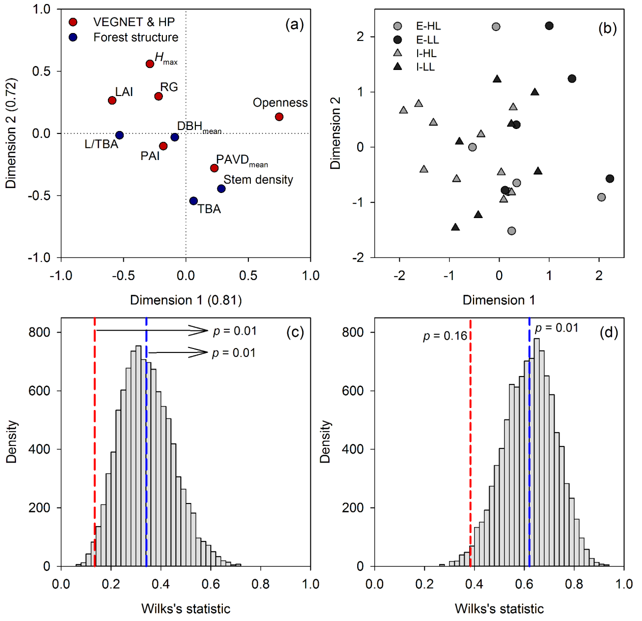

Figure 2. Canonical correlation analysis to describe the association between the parameters estimated by the VEGNET system–hemispherical photographs (HPs) and the forest structure. **(a)** VEGNET–HP coefficients are represented by red points, while forest structure coefficients are represented by blue points. **(b)** Individual scores for each plot of the canonical variates are represented according to successional stages (E, early; I, intermediate) and relative liana abundance (LL, low liana abundance; HL, high liana abundance). Panels **(c)** and **(d)** represent the permutation distribution of the Wilks' Lambda test to assign the statistical significance of canonical correlation coefficients considering four and three canonical correlations; the red line represent the original value of Wilks' Lambda, while the blue line represent the mean value permutated. The *p* values next to each line represent the significance of the Wilks' Lambda test.

ond dimension showed an increase of 0.25 points, which results in a significant effect.

3.4 Comparison of correlations between successional stages and liana abundance

The different trends of correlation showed that the successional stages and mainly the liana abundance had an important effect in the prediction of the forest structure using VEGNET-HPs parameters (Fig. 3) but, at the same time, these trends showed that some of these parameters have the potential to predict the implications of the liana abundance on the forest structure. Specifically, variation in the correlations of canopy openness on L/TBA (Fig. 3a, b, c) and H_{max} on TBA (Fig. 3g, h, i) showed that the correlation trends between successional stages overlapped while the correlations trends between liana abundance separated. Therefore, low values of canopy openness and H_{max} were associated with high values of L/TBA and TBA and, consequently, with the discrimination of HL plots. Likewise, variation in the correlation between LAI and L/TBA showed that the trends might not be used to separate successional stages or liana abundance (Fig. 3d, e, f). However, the correlation between H_{max} and TBA suggests that H_{max} can not discriminate between different successional stages but can discriminate between different liana abundances since lower values of correlation are associated with HL plots (Fig. 3j, k, l).

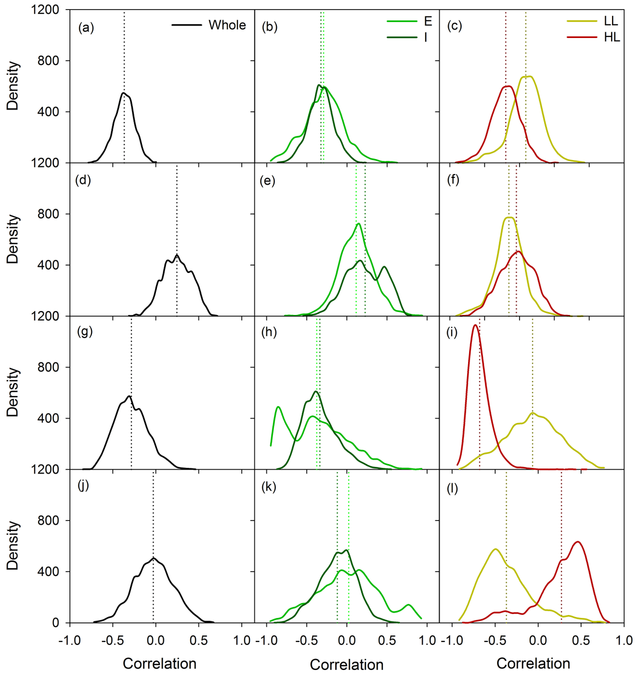

Figure 3. Density distribution of the bootstrapped correlation coefficients with and without distinction between successional stages (E, early; I, intermediate) and relative liana abundance (LL, low liana abundance; HL, high liana abundance). Panels **(a)**, **(b)**, and **(c)** correspond to the correlation of canopy openness and the ratio of liana basal area to total basal area (L/TBA); **(d)**, **(e)**, **(f)** correspond to leaf area index-L/TBA correlation; **(g)**, **(h)**, and **(i)** correspond to the maximum tree height to TBA correlation; **(j)**, **(k)**, and **(l)** correspond to plant area volume density to TBA correlation. Each dotted line represents the mean value of the bootstrapped correlation.

4 Discussion

4.1 Potential of VEGNET and HPs to detect the vertical structure of forest stands at different successional stages

Woody vines (lianas) tend to proliferate in disturbed forest stands such as regenerating forests (Paul and Yavitt, 2011). Much research on liana ecology, however, has focused on old-growth forests despite the fact that secondary forests currently cover a larger area than old-growth forests and may become the dominant ecosystem in tropical regions (Wright, 2005). Due to shorter stature and a higher variability of light in secondary forests, lianas may be particularly abundant in these ecosystems, but little is understood about the role of lianas in forest succession (Letcher and Chazdon, 2009). In this study, we used VEGNET, a terrestrial lidar system combined with HPs, to assess the impact of liana abundance on forest succession. Our overall analysis indicated that VEGNET parameters, in combination with HP-derived information, were able to characterize changes in forest structure at different successional stages with and without lianas. Changes observed using HPs, along the successional gradient, were similar to those observed in other tropical dry forest environments where parameters such as biomass, LAI, canopy openness, and H_{max} changed as trees grew (Sánchez-Azofeifa et al., 2009). Our work using the TLS suggested that this technology could also used to detect differences along the forest succession trajectory when lianas were integrated into the analysis. In terms of the comparison of VEGNET parameters between our categories, the effects of the interaction of the successional stages and liana abundance on C_x, PAI, and $\mathrm{PAVD_{mean}}$ are probably some of the most reveling. As lianas emerge along the path of succession, they create a more heterogeneous space which is captured by the variability in C_x. C_x is affected by PAI and $\mathrm{PAVD_{mean}}$ as function of understory components (shrubs, grasses, and also liana tangles). A higher value of C_x may be interpreted on an E-LL as a high dominance of shrubs, tall grasses, and short trees. A high value of C_x on aa E-HL may, however, mean a high density at low height of tangles combined with shrubs which makes accessibility to some sites impossible due to a high density of understory liana tangles.

4.2 How can liana abundance affect the predictions of VEGNET and HPs in detecting the level of succession of a given forest stand?

When we consider the bias of correlations between the forest structure and the parameters extracted from our two sensors at different successional stages and liana abundance, our results suggest that this latter variable has an important effect on the bias of prediction for a given forest structure. The main reason is probably a result of lianas introducing random tangles into the 3-D space that is occupied by all forest biomass at a given plot. In other words, lianas tend to randomize or reduce the degree of organization of the natural space which is typically utilized by trees. This randomization of the 3-D space occupied by trees and lianas is an element that has not been considered as of today, since most studies do not consider the space occupied by lianas because of a lack of TLS information.

This change in the deterministic patterns of the forest structure is probably due to competition between lianas and trees in forest stands within a random 3-D space. In disturbed sites such as secondary forests, lianas deploy leaves in the canopy and create large amounts of tangles in both the ground and mid canopy. This high density of tangles contributes to a reduction on the amount of transmitted incoming solar radiation available for photosynthesis at the understory (Sánchez-Azofeifa et al., 2009; Graham et al., 2003). Moreover, in regenerating stands within forests (e.g., treefall gaps), high densities of lianas can inhibit the regeneration of tree species and reduce the abundance of shade-tolerant trees (Schnitzer et al., 2000) which in turn can affect the 3-D arrangement of species within a given area. These ecological processes may cause a shift in forest structure, which is detected as a shift in the vertical structure signature by TLSs or even HPs in sites with high liana abundance. These differences in structures have been confirmed in a recent study which found that a liana-infested forest had a more irregular canopy with canopy heights between 10 and 20 m, while the surrounding forests had a significantly taller canopy between 25 and 35 m along with a denser canopy (Tymen et al., 2016). Our results together with the Tymen et al. (2016) observations could highlight the potential of entropy analysis of the forests to detect the presence and the effect of lianas on the forest structure and the pathways of succession.

4.3 A cautionary tale associated to emergent TLS and HPs monitoring technologies applied to liana-infested sites

Our observations from changes on $\mathrm{DBH_{mean}}$, TBA, PAI, $\mathrm{PAVD_{mean}}$, LAI, and canopy openness as function of liana abundance provide evidence that these variables can be used to estimate the impact of lianas on forest structure along the path of succession, although not all parameters, such as stem density and L/TBA, were significant. In other words, there is a strong need to carefully select which parameters should be considered if we want to estimate changes in the forest structure as function of liana abundance. One key example is the use of PAI ($\mathrm{PAI} = \mathrm{LAI} + \mathrm{WAI}$) as a tool to evaluate the impact of liana abundance on forest succession. PAI as a single measurement could theoretically provide insights into the impact of liana abundance on successional stages; as such we could expect that PAI would increase as leaf and wood biomass increased during succession (Quesada et al., 2009). Furthermore, the PAI could be better understood if specific measurements of TLS could be done during the dry season to quantify the real value of WAI to PAI. Tropical dry forests in contrast to tropical rainforests could provide a significant advantage in better understanding the PAI (Kalascka et al., 2005b). It is surprising that we did not find differences in the PAI values between stands that did and did not have lianas. It is possible that the PAI is not the best parameter to differentiate between plots with and without liana presence. Instead, variables more related with leaf components, such as LAI and WAI, may be more suitable for finding the differences in liana signature across sites, especially when the contribution of lianas to the WAI to overall plot PAI is relatively small in comparison to the allocation of the WAI from trees (Kalascka et al., 2005b; Sánchez-Azofeifa et al., 2009).

A recent study assessing the role of lianas on forest dynamics in the Amazon indicated that a liana-infested forest appeared to be in an arrested stage of ecological succession due to the evidence provided by lidar surveys from 2007 to 2012 which showed that the overall extent of forest area had remained stable, with no notable net gain or loss over the surrounding forest (Tymen et al., 2016). It is possible that studying forest dynamics in forest stands across successional stages, with different levels of liana abundance integrated into the TLS and HP parameters, may allow us in the future to provide stronger evidence as to whether lianas can arrest succession in dry forests as it appears to occur in humid forests (Schnitzer et al., 2000; Tymen et al., 2016).

Moreover, our work seeks to strength the argument for the inclusion of lianas in global terrestrial vegetation models (Verbeek and Kearsley, 2016). We argue here that the first step in the development of such models is to have a clear understanding of how lianas affect ecosystem structure and composition, which in turn will affect tree mortality, recruitment, and carbon storage above ground and below ground (Poulsen et al., 2016; Schnitzer et al., 2014). Furthermore, lianas, because of their impact on the 3-D structure of a given forest space, may have the ability to change faunal diversity (e.g. birds), an impact that has not been fully documented as of today. As such, our study also supports the arguments by Schnitzer et al. (2016) that call for the need to develope a network of observational and experimental sites that can provide insights into the impact of lianas at different ecological levels.

We extend the previous argument to remote sensing studies as well. Since lianas represent a significant ecological component of tropical ecosystems (with a stronger presence in intermediate stages than in early or late successional stages), we also argue that the development of more robust global vegetation models must start with understanding the liana impact of forest structure which in turn will drive the other components of those models.

5 Conclusions

This study evaluated the potential for TLSs and hemispherical photographs to observe the differences between the successional stages of a tropical dry forest chronosequence and liana abundance. Our work provided five main conclusions: (1) that TLS data combined with hemispherical photography data can help predict the forest structure of the tropical dry forest as demonstrated before; (2) that these predictions get blurry when liana abundance is considered; (3) that variations in TLS and HP parameters can be used to predict the effect of liana abundance on the successional path; (4) that not all the parameters could address the effect of the presence or impact of lianas along a successional gradient; and (5) we suggest that the impact of lianas on successional stages changes the deterministic nature of forest structure by randomizing the 3-D space where they grow at a given plot – the higher the abundance of lianas, the higher the randomization.

Our study provides important insights into the contributions of lianas to the successional process, and highlights the potential that TLSs and HPs have in monitoring liana presence in tropical dry forests environments. Lianas are increasing in density and biomass in tropical forests, but it is unknown whether this pattern is also found in secondary forests, which are suitable for liana proliferation. TLS systems and, to a lesser extent, HPs are capable of providing unbiased estimations for the vertical structure of a given site and thus constitute powerful tools in monitoring the increases in liana density and biomass. Although our study is limited to one single site in Costa Rica, this is a first step in the development of more comprehensive approaches which take advantage of advanced technology to understand the effects of liana abundance on tropical dry forest structure. The approach presented in this paper presents important contributions to efforts directed at estimating the potential effects of lianas on forest carbon in secondary forests (Durán and Sánchez-Azofeifa, 2015) elements that seem to not be fully considered yet in the tropical literature.

6 Data availability

The data used in this article are available at doi:10.5061/dryad.69kq2 (Sánchez-Azofeifa et al., 2017).

Competing interests. The authors declare that they have no conflict of interest.

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