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Structural effects of liana presence in secondary tropical dry forests using ground LiDAR

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Abstract

Lianas, woody vines, are a key component of tropical forest because they may reduce carbon storage potential. Lianas are increasing in density and biomass in tropical forests, but it is unknown what the potential consequences of these increases are for forest dynamics. Lianas may proliferate in disturbed areas, such as regenerating forests, but little is known about the role of lianas in secondary succession. In this study, we evaluated the potential of the ground LiDAR to detect differences in the vertical structure of stands of different ages with and without lianas in tropical dry forests. Specifically, we used a terrestrial laser scanner called VEGNET to assess whether liana presence influences the vertical signature of stands of different ages, and whether successional trajectories as detected by the VEGNET could be altered by liana presence. We deployed the VEGNET ground LiDAR system in 15 secondary forests of different ages early (21 years old since land abandonment), intermediate (32–35 years old) and late stages (> 80 years old) with and without lianas. We compared laser-derived vegetation components such as Plant Area Index (PAI), plant area volume density (PAVD), and the radius of gyration (RG) across forest stands between liana and no-liana treatments. In general forest stands without lianas show a clearer distinction of vertical strata and the vertical height of accumulated PAVD. A significant increase of PAI was found from intermediate to late stages in stands without lianas, but in stands where lianas were present there was not a significant trend. This suggests that lianas may be influencing successional trajectories in secondary forests, and these effects can be captured by terrestrial laser scanners such as the VEGNET. This research contributes to estimate the potential effects of lianas in secondary dry forests and highlight the role of ground LiDAR to monitor structural changes in tropical forests due to liana presence.

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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 as such, 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 (van der Heijden et al., 2013). Thus, lianas are able to reduce carbon storage and uptake in old-growth forests (Durán and Gianoli, 2013; van der Heijden et al., 2013). In the context of remote sensing, lianas have been defined as hyperdynamic elements of the canopy structure (Sanchez-Azofeifa and Castro, 2006). In the last two decades lianas have increased in density and biomass in old-growth forests (Phillips et al., 2002; Schnitzer and Bongers, 2011), and this increment is considered one of the major structural changes in tropical forests (Phillips and Lewis, 2014), because it can have potential negative effects on carbon stocks. Liana dynamics in secondary forests, however, are not yet understood despite that secondary forests are becomingly increasingly dominant in tropical regions, and currently occupy more area than old-growth forests (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). Secondary forests may promote liana abundance because they provide both high light availability and abundant of trellises (Schnitzer and Bongers, 2002). In treefall gaps, lianas can form dense tangles and 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 to one stalled by liana abundance by inhibiting the regeneration, growth, and density of late successional species (Schnitzer et al., 2000).

As today, it is still unknown whether lianas can alter successional trajectories in secondary forests resulting from anthropogenic disturbance (Durán and Sánchez-Azofeifa,

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2015). Two studies in secondary wet forests have found an increment of 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 related with 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 can hold to more open forest types, and whether other factors such as structure, canopy openness, plant density and volume of forest stands can also influence successional trajectories of lianas (Durán and Sánchez-Azofeifa, 2015; Sánchez et al., 2009).

Assessments of forest structure in different stands are often constrained by accessibility, and cost of personnel and equipment. Remote sensing offers an efficient alternative to detect changes in vegetation and examine how lianas may change across stands with different structures. Nonetheless, few studies have assessed the potential of remote sensing (space-borne or airborne) to detect the presence of lianas in tropical forests with the objective of providing tools to map their extent from local to landscape level, and measure their ecological footprint (Foster et al., 2008). Sanchez-Azofeifa et al. (2009) used hemispherical photography over a succession of tropical dry forests and found that liana contributed substantially to forest-level Wood Area Index (WAI). Other studies found differences between the biochemical, structural and hyperspectral properties of lianas and trees in tropical dry forests (Castro-Esau et al., 2004; Sanchez-Azofeifa et al., 2009). These studies emphasized the potential of using remote sensing to map liana abundance at regional scales. However, given the important effect of lianas on the biomass distribution within tropical forests (Schnitzer and Bongers, 2011), remote sensing tools capable of measuring the vertical distribution of biomass within tropical forest are probably more adequate for detecting the presence and variation of liana density across forest stands.

Ground LiDAR has demonstrated the capability to measure canopy properties such as height and cover (Ramírez et al., 2013) and tree architecture (Lefsky et al., 2008), using terrestrial laser scanning systems (TLS) (Dassot et al., 2011; Richardson et al.,

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2014). In the last decade, there has been a rapid development in portable Terrestrial Laser 65 Scanners – TLS – (Dassot et al., 2011; Richardson et al., 2014). When laser pulses emitted in the visible or near-infrared comes into contact with an object, part of that energy is reflected back toward the instrument and 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 exploring foliage angle distributions and clumping (Clawges et al., 2007; Jupp et al., 2009; Strahler et al., 2008). As part of its program on vegetation monitoring, Australia’s Commonwealth Scientific and Industrial Research Organisation (CSIRO) has developed a new experimental TLS named VEGNET. The VEGNET instrument automatically scans the forest producing a vertical foliage density profile. Given its automated mode of operation and semi-permanent installation, the VEGNET instrument is described as an in situ Monitoring Lidar (IML) (Culvernor et al., 2014; Portillo-Quintero et al., 2014).

The objective of this study was to assess changes in forest stands in secondary dry forests with and without the presence of lianas. To this end, we used the VEGNET instrument to assess changes in the vertical vegetation profile across stands of different ages with the presence and absence of lianas. First, we assess the potential of the VEGNET to detect differences in the vertical structure of forest stands of different ages. Second, we examine whether the differences in vertical structure are influenced by liana presence. Third, we explore whether successional trajectories as captured by VEGNET could be altered by liana presence. Significant increases in vertical structure with stand age (e.g., as a result of increases in basal area, height and volume with stand age) would indicate that lianas are not influencing successional trajectories, while no significant increases or no change in vertical structure would suggest that lianas may be altering successional pathways.

2 Study area

The study area is located in the Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS), 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 and receives 1720 mm of annual rainfall, has a mean annual temperature of 25 °C and a 6 month dry season (December–May), with 40–60 % of deciduous species (Kalácska et al., 2004). The SRNP-EMSS site has suffered intense deforestation due to the expansion of pasture lands since the early 1700s. Today and after the creation of SRNP-EMSS, the uplands of the park are a mosaic of secondary forest in various stages of succession and with different land use histories related to anthropogenic fires (Kalácska et al., 2004). Forest inventories have been conducted in the study area since 2004 to evaluate the influence of previous land use on woody species structure and composition (Hilje et al., 2015; Kalácska et al., 2004).

Forest stands within the study area have been classified in different ages (e.g., age since land abandonment) using a combination of forest structure data (e.g., number of vertical strata), land use history, and remote sensing data (e.g., reflectance signatures of forest stands with known age) following previous approaches for seasonally dry forests (Arroyo-Mora et al., 2005; Kalácska et al., 2005). The early stage constitutes a very open and patchy canopy, with a thick herbaceous understory; the intermediate state is a forest with a range of canopy openness, and the late stage constitutes a canopy with two layers of vegetation: dominant canopy trees and shade tolerant species (Castillo et al., 2012). The forest ages in 2007 for these stages were 21 years old (early stage), 32–35 years old (intermediate stage) and more than 80 years old (late stage) according to Kalácska et al. (2004). Liana abundance in these forests is high and lianas are commonly found in the intermediate and late forest stands (Sanchez-Azofeifa et al., 2009).

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3 Methods

3.1 Ground LiDAR

The VEGNET IML instrument uses a phase-based laser rangefinder with a wavelength of 635 nm. The 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 VEGNET instrument provides indirect measurements of leaf area index (LAI) at a fixed angle based on optimized algorithms for LAI retrieval. The prism is designed to perform full rotations of 360° azimuth at this fixed zenith angle (no vertical scanning motion) and the VEGNET instrument can 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). A more detailed explanation of the functioning of the VEGNET instrument, as well as a photograph of the instrument deployment in the field, is provided by Portillo-Quintero et al. (2014) as well as on Culvenor et al. (2014).

Processing data from VEGNET requires first estimating the height h aboveground for all measured objects. Assuming flat terrain, height h is calculated as the cosine of the laser zenith angle (57.5°) and the laser distance measurement d (Culvenor et al., 2014):

$$h = \cos(57.5^\circ)d \quad (1)$$

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

$$P_{\text{gap}}(z) = [\#z_i < h]/N \quad (2)$$

The density of vegetation components at any level z is then computed as the derivative of LAI with respect to height, and it is referred to as the plant area volume density

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(PAVD):

$$\text{PAVD}(z) = \delta \text{LAI}(z) / \delta z \quad (3)$$

It is important to note that the method of LAI retrieval, just like all other indirect methods, does not estimate leaf area index, as the laser does not differentiate between forest structural elements. Therefore, the term Plant Area Index (PAI) is preferred if no correction to remove branches and stems is made. Plant Area Index was calculated following methods by Jupp et al. (2009) and Lovell et al. (2003) for PAI retrieval based on LiDAR data. The PAI estimates are typically presented in three forms: (i) a cumulative PAI as a function of canopy height, (ii) the cumulative PAI derivative, termed the Plant Area Volume Density (PAVD), which is the density of vegetation components at any height level, and (iii) the maximum cumulative PAI, which represents the top-of-canopy PAI, incorporating intercepted laser measurements through the full canopy depth. The process was automated using the “VEGNET Data Display and Export Version 2.5” software developed by Environmental Sensing Systems Inc. PAVD values obtained at each plot were compared against height in order to construct a graph showing the vertical distribution of plant area (Fig. 2). Tests of the measurement process by VEGNET at night time indicated that at distances greater than 60 m or areas larger than 3600 m² (0.36 ha) the laser beam does not provide reliable measurements (Culvenor et al., 2014). Thus, data analysis and interpretation may be restrained to a footprint of 3600 m².

We also used shape metrics such as the centroid and radius of gyration (RG) to understand how the vertical profile of vegetation changes across successional stages and with liana presence. The RG and the centroid 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 centroid and the RG for the PAVD vertical profile. The centroid then represents the geometric center of a two-dimensional region (e.g., the arithmetic mean position) of all the points in the shape of the PAVD profile. The RG is the root mean square of the

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sum of the distances that all points on the PAVD vertical profile are from its centroid:

$$RG \sqrt{\frac{\sum (x_i - C_x)^2 + \sum (y_i - C_y)^2}{n}} \quad (4)$$

The centroid (C_x , C_y) 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). 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 (3600 m² or 0.36 ha). We hypothesize that the RG will increase during succession in stands without lianas, while it will show no trend or a reduction in stands with liana presence. This hypothesis is derived from previous literature that indicate that lianas may arrest forest succession and reducing the biomass accumulation of woody vegetation in regenerating forest stands (Paul and Yavitt, 2011; Schnitzer et al., 2000).

3.2 Sampling design

The VEGNET ground LiDAR system was deployed in fifteen different tropical dry forest locations, which include 9 sites without lianas, and 6 sites with lianas. Sites with and without lianas were chosen based on previous inventories conducted in the study area (Hilje et al., 2015; Kalácska et al., 2004). The sites without lianas included forest stands in early, intermediate and late successional stages, while the sites with lianas were only in intermediate and late succession. A single successful scan was performed during the wet season using the VEGNET instrument at each site on clear nights between 29 March and 10 April 2014.

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3.3 Data analysis

To evaluate the potential of the VEGNET to detect differences in the vertical structure of forest stands in the presence of lianas, we built vegetation profiles of PAVD as a function of height for all the different successional stages. To examine the potential of VEGNET to detect differences across sites we conducted non-parametric Kruskal–Wallis tests to compare successional stages with and without lianas. To explore whether liana presence could alter successional trajectories, we correlate PAI as a function of RG to assess whether PAI will increase during succession (e.g., from early to late stage), and whether this increase could be affected by liana presence. A change or no significant increase in PAI as a function of RG during succession would suggest that lianas may be altering the successional trajectories of vertical structure in the forest stands.

4 Results

Plant Area Index (PAI) values ranged from 0.54–1.55 in early succession sites, 1.59–2.07 in intermediate succession sites and 1.65–2.32 in late succession sites. Similarly, the radius of gyration (RG) showed a significant increase along in succession in plots with no lianas (Table 1), a progression that is expected with increases in leaf and wood biomass in forest chronosequences. However, significant differences in PAI were only found between the early succession sites and intermediate/late sites, but no differences were found between no-liana and liana stands in PAI treatments within the intermediate and late succession sites (Table 2).

The vertical distribution of plant area differed between no-liana and liana treatments. Figure 2 shows the vertical PAVD profiles for the different five treatments: (a) early successional stage with no lianas, (b) intermediate successional stage with no lianas, (c) intermediate successional stage with lianas, (d) late successional stage with no lianas and (e) late successional stage with lianas. At the early site PAVD concentrates between 2–8 m from the ground, with the highest biomass between 2–4 m as measured

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by the VEGNET system (Fig. 2). At the intermediate site (no lianas) PAVD is lower in the first 2–5 m from the ground and reaches higher values between 6–12 m, which corresponds, as expected, to the vertical distribution of canopy and subcanopy leaves and branches (Fig. 2). On the other hand, at the intermediate site (with lianas) PAVD values in the lower forest strata are as high as the subcanopy and canopy layers (Fig. 2). At the late successional stages (no lianas) PAVD values show two distinctive peaks (canopy and understory, one occurring at the first 5 m from the ground and the other one between 8 and 14 m).

At the late successional sites (with lianas, Fig. 2), most PAVD is concentrated between 2–10 m with no clear distinction between forest strata.

Although PAI did not capture differences between liana and no-liana sites, the Radius of Gyration (RG) values calculated from the PAVD vertical profiles were significantly different between no liana and liana treatments in intermediate successional stages (Table 2, Fig. 1) and marginally significant for late successional stages ($H = 2.3$, $P = 0.12$, Table 2, Fig. 1). Moreover, when PAI and RG are plotted against each other (Fig. 3), a significant progressive increase of RG and PAI as a function of succession is evident when lianas are not present ($R^2 = 0.71$, Fig. 3). In contrast, accumulation of PAI as a function of RG in stands with lianas did not show a significant trend over time (e.g., from intermediate to late stages).

5 Discussion

Woody vines or lianas tend to proliferate in disturbed forest stands such as regenerating forests (Paul and Yavitt, 2010). Much research on liana ecology, however, has focused on old-growth forests despite 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 high amount 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

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this study, we evaluated the role of VEGNET, a ground LiDAR system to assess the differences in vertical structure of secondary forests with and without lianas. Overall, parameters from ground LiDAR were able to identify structural patterns of stands of different ages and in some cases with and without lianas.

5 The PAI as a single measurement per plot does not seem sensitive to changes in liana, neither to changes between intermediate and late successional stages, but values of PAI showed increases across all successional stages, which is expected from leaf and wood biomass increase in forest chronosequences (Quesada et al., 2009). The PAI was able to detect differences from early succession, but intermediate and
10 late stages were similar in PAI values. This coincides with comparisons within the study area between intermediate and late stages in structural parameters (e.g., tree density, basal area) using forests inventory data (Kalacska et al., 2004). It is surprising that we did not find differences in stands with and without lianas on the PAI values. It is possible that PAI is not the best parameter to differentiate plots with liana presence, and
15 instead variables more related with leaf components, such as leaf area index (LAI) may be more suitable for finding differences in liana signature across sites, especially when the contribution of lianas to the woody area index (WAI) to overall plot PAI is relatively small when compared with the allocation to WAI from trees (Sanchez-Azofeifa et al., 2009).

20 The PAVD and RG appears more sensitive to detect changes in forest structure, since it captures the vertical distribution of the vegetation (Muss et al., 2013), which in turn is a measurement of the spatial distribution of PAI along a vertical gradient in a plot. RG and PAVD indicated changes between stands of different ages, and with liana presence. In general, stands without lianas show different vertical strata, specifically in late succession, but in the presence of lianas, stratum recognition becomes
25 more difficult. This is may be due to the high contribution of lianas to forest structure, but also probably the result of competition between lianas and trees in forest stands. In disturbed sites, such as secondary forests, lianas deploy leaves on the canopy, reducing light availability and incoming solar radiation available for photosynthesis by other

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plant species (Graham et al., 2013). Moreover, in regenerating stands within forests (e.g., treefall gaps), high density of lianas can inhibit the regeneration of tree species and reduce the abundance of shade-tolerant trees (Schnitzer et al., 2000). These ecological processes may cause a shift in forest structure, which is detected as a shift in the vertical structure signature by the ground LiDAR in sites with and without lianas.

Assessing the relationship between PAI as a function of RG suggested changes in the successional trajectories in secondary dry forests under the liana presence. Stands without lianas showed a significant gradual increase in the RG. This is consistent with accumulation of basal area, vegetation material and biomass accumulation in secondary dry forests (Quesada et al., 2009). On stands with lianas, however, there was not a significant trend in the successional path across stand ages, which suggests that lianas may be modifying the successional path in these regenerating dry forests. In treefall gaps, lianas can interrupt the successional sequence and change the trajectory to a pathway dominated by lianas and stalled in a low canopy state for many years (Schnitzer et al., 2000). This interruption in the successional sequence is due to a variety of causes, including plant competition for light, reduction in recruitment and growth rates of trees due to liana infestation, and belowground competition (Schnitzer et al., 2000; Schnitzer and Carson, 2010). This could explain the differences in vertical signature in the accumulation of the PAVD between intermediate and late. Further research is necessary to determine whether the mechanisms explaining changes in the vertical profile of vegetation in secondary dry forests are similar to what it has been found in treefall gaps.

The stronger differences of stands with and without lianas in intermediate, rather than late stages may be related with reductions in liana density along succession. Liana density in humid forest appears to increase in the first 20 years of succession, following by a decline in older stands (DeWalt et al., 2000; Letcher and Chazdon, 2009). The intermediate stages in our study area are older than 32 years. It is possible that declines in liana density in dry forests occurs at an older stand age due to a shorter stature of the forests and higher light availability in dry forests compared to humid

forests. Future studies should compare liana patterns during succession using ground LiDAR in humid and dry forests to determine whether this unimodal pattern in liana density is common across sites, and to identify the stand age at which this reduction begins to occur.

6 Conclusions

This study evaluated the potential of ground LiDAR to detect differences in stands of different ages with and without liana presence in secondary tropical dry forests. We found that stands with lianas have different vertical structure signature than stands without lianas as detected by the ground LiDAR system. The radius of gyration (RG), estimated from the Plant Area Volume Density (PAVD) showed differences in the vertical signature of forest stands under liana presence, specifically in the number of vertical strata and the vertical height of PAVD. Liana presence also appears to influence the successional trajectories of vegetation accumulation over time. Our study provides important insights on the contributions of lianas to successional process, and highlights the potential of LiDAR systems to monitor liana presence in tropical forests. 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. LiDAR systems provide unbiased estimations of the vertical structure of PAI for a given site, thus constitute a powerful tool to monitor the increase of liana density and biomass. The approach presented in this paper, presents important contributions to efforts directed to estimate the potential effects of lianas on forest carbon in secondary forests (Durán and Sanchez-Azofeifa, 2015), elements that seems not fully considered yet in the tropical literature.

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Table 1. Structural characteristics of forests stands of different ages with and without lianas in secondary tropical dry forests.

Successional Stage	Liana presence	Symbol	C_x	C_y	RG	PAI	Max. height (m)
Early 1	No Lianas	E–NL	0.012	5.150	1.8	0.84	8.3
Early 2	No Lianas		0.006	5.950	2.3	0.54	9.9
Early 3	No Lianas		0.016	6.450	2.6	1.55	10.9
Intermediate 1	No Lianas	I–NL	0.010	7.800	3.9	1.66	15.5
Intermediate 2	No Lianas		0.013	7.400	3.1	1.69	12.8
Intermediate 3	No Lianas		0.012	8.150	3.6	1.59	14.3
Late 1	No Lianas	L–NL	0.011	10.600	4.9	2.08	19.2
Late 2	No Lianas		0.011	8.900	4.0	1.65	15.8
Late 3	No Lianas		0.010	9.800	4.5	1.65	17.6
Intermediate 1	Lianas	I–L	0.012	9.438	4.4	1.89	17.0
Intermediate 2	Lianas		0.005	9.602	4.2	1.24	19.3
Intermediate 3	Lianas		0.012	9.600	4.4	2.07	17.2
Late 1	Lianas	L–L	0.015	9.100	4.1	2.32	16.2
Late 2	Lianas		0.012	8.750	3.9	1.81	15.5
Late 3	Lianas		0.013	8.500	3.8	1.80	15.0

C_x , C_y , centroid coordinates in x and y axis, C_y , RG, radius of gyration, PAI, plant area index, Max.height, maximum height.

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Table 2. Results from the Kruskal Wallis test to compare Plant Area Index (PAI) and the Radius of Gyration (RG) across successional stages with (L) and without lianas (NL).

Variable		<i>H</i> (Kruskal–Wallis test)	<i>P</i> -value
PAI	E-NL vs. I-NL, L-NL	3.857	< 0.05
	I-NL vs. L-NL	0.04762	0.82
	I-NL vs. I-L	0.4286	0.51
	L-NL vs. L-L	1.19	0.26
RG	E-NL vs. I-NL, L-NL	7.2	< 0.05
	I-NL vs. L-NL	3.857	< 0.05
	I-NL vs. I-L	3.857	< 0.05
	L-NL vs. L-L	2.333	0.12

E, early succession; I, intermediate succession; L, late succession.

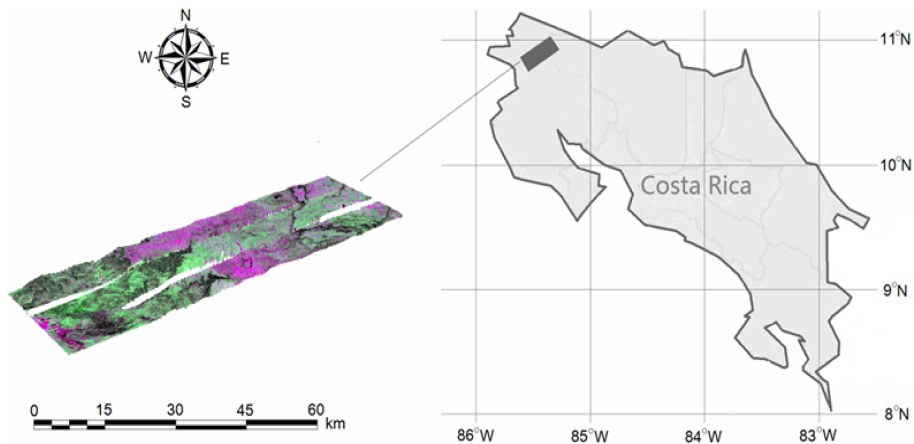


Figure 1. Localization of the sampled forests stands in Santa Rosa National Park (shaded area) in Costa Rica.

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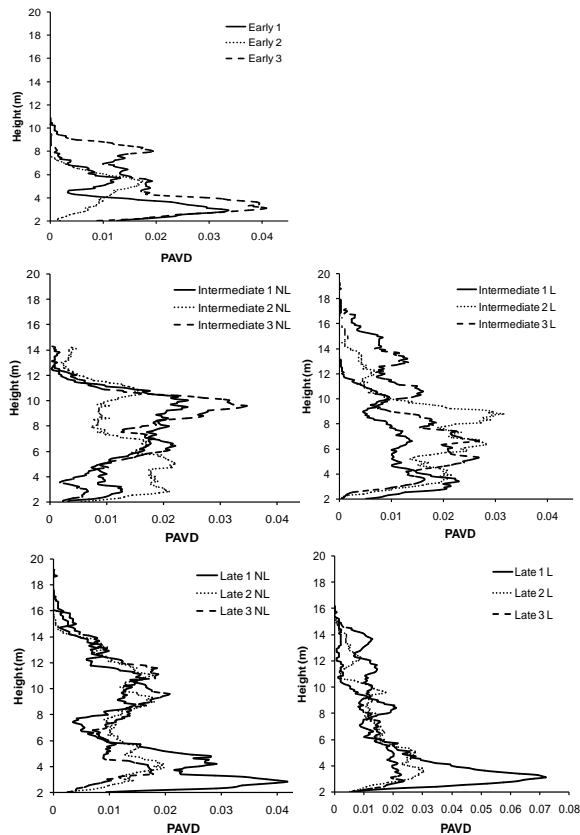


Figure 2. Time-series of Plant Area Volume Density (PAVD) values calculated by the VEGNET IML during 29 March and 10 April 2014. The height is plotted against volume density distribution in order to show the vertical distribution of biomass in the forest; values have been averaged by forest stand for visualization purposes. NL are stands without lianas, and L represent stands with liana presence.

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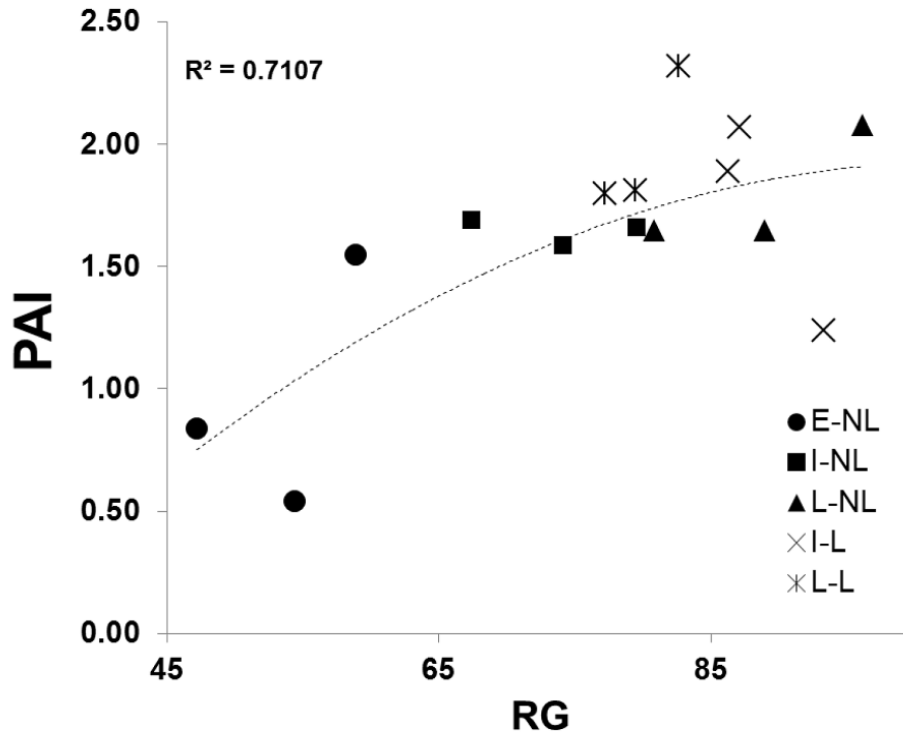


Figure 3. Relationship of plant area index (PAI) as a function of the radius of gyration (RG) for forest stands of different ages (I, intermediate; L, late) with (L) and without lianas (NL). Full symbols represent sites with no lianas (NL), and asterisks represent sites with lianas. The dashed line represents fitted regression lines for significant relationships between PAI and RG.

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