

November 1st, 2016

Editorial Board

Biogeosciences Editorial Office
European Geosciences Union
Munich, Germany

Dear editor,

First of all we want to thank you for the extra time provided to us in order to complete this paper, it has been a very intense few months with a large field campaign in order to satisfy the requests of the reviewers. We hope now that the manuscript is acceptable. As such, we resubmit for your consideration the manuscript entitled “Can Terrestrial Laser Scanner (TLS) and hemispherical photographs predict Tropical Dry Forest Succession with liana abundance?”, please notice the change of title as requested by reviewer No. 1. This article has significantly evolved from our first submission given the request for additional data and explanations from the reviewers. This request, led us to:

1. Increase our sampling scheme from 9 plots to 28 plots.
2. Conduct a full set of field measurements on all new plots, specifically DBH and hemispherical photographs (June 2016)
3. Conduct additional ground LiDAR measurements at all sites (June 2016).
4. We have conducted an analysis to map the extent of tropical dry forests at our study area since 1950, which is allowing us to approximately date our plots more accurately than before.

Furthermore, we have extended our analysis using univariate techniques; this novel field study addresses how the forest structure of the tropical dry forest is correlated with measures from ground LiDAR and hemispherical photography. Then, we show how the abundance of lianas affects the bias of correlation in regards to the ground LiDAR and the hemispherical photographs. Therefore, in well-known ecosystems such as the tropical dry forest of Costa Rica, these biases of prediction could be considered as artifacts from the structural effects of liana presence. In the next pages, we enclose an explanation of how we dealt with the reviewers' or editor's comments.

We want to also thank the reviewers for their positive comments. We hope that now the paper is satisfactory.

Sincerely,

Arturo Sánchez-Azofeifa,

Explanation of how we dealt with the reviewers' or editor's comments

REVIEWER #1

General

In their revised version the authors made some efforts to respond to the comments of both reviewers, which I appreciate. Additional information was provided on the methods and analysis. However, with this additional information included, it became even more clear to me that the analysis is too weak and the assumptions are too shaky to support the conclusions (see my major comments). I can therefore not recommend this manuscript for publication in Biogeosciences.

R: In order to satisfy the reviewer concerns we have spend a significant amount of time in both the laboratory and the field.

In my opinion the authors have to make a choice: or (1) they make an assessment of VEGNET to detect differences in tropical forest structure, (2) or they use VEGNET to study the impact of liana's on forest structure, or (3) they combine both. In their response letter the authors state that the actual purpose of the paper is to assess whether TLS (but you are actually testing VEGNET, which is due to the fixed zenith angle quite different from most other TLS approaches) can detect differences in aboveground structure across plots. This is actually option (1), but this is not what is presented in the paper.

R/. We agree with the reviewer comment. Our final goal is to combine both methods to describe the forest structure using VEGNET and then predict the effect of the presence of lianas. Currently, there is a substantial change in terms of how we present our results and our background. In this manuscript, we applied a canonical correspondent analysis to make an assessment about how VEGNET detects differences in tropical dry forest structure and then we applied individual correlations between VEGNET parameters and forest structure using categories of liana abundance to study the impact of lianas on forest structure.

For each option more data is needed:

(1) To assess the potential of VEGNET to study differences in the structure of tropical forests, you need another quantitative method to observe forest structure, to compare VEGNET to. Now the VEGNET is just applied on rather arbitrarily chosen plots, for which you assume they have a different structure, but no quantitative comparison is made with other data. You could compare the vegnet information with inventory data, hemispherical photo's, tree height measurements, other type of TLS... etc... some of this information is apparently available (page 8 line 168-176 in the manuscript) but not included in a quantitative analysis.

(2) To study the impact of lianas on forest structure you need more information on the plots. (and the plots probably need to be larger to do a decent study). You need background information on the plots to be sure that you are looking toat the effects of lianas and not to at the effects of other factors (species composition, soil, hydrology, topography, disturbance). Some of this info might be in the other studies whichere the authors refer to, but in that case that information should be integrated in this manuscript. Apparently the authors do have access to

some information on the number of lianas per hectare (see response to reviewer 2), this information should really be integrated in the paper. In addition you really need young plots with lianas to study the impact of lianas along a successional gradient.

(3) To study both in one paper, you need all the info of 1 and 2.

I hope the authors can use my comments to improve their work in the future, by adding new data and doing a different analysis.

R/. We agree, more data and samples were included. In this manuscript, we added tables that describe the forest structure and the VEGNET parameters according to successional stages and liana abundance. Likewise, we compared the effect of the successional stage and liana abundance on all of these parameters to show that this study was conducted in contrasting environments.

Major comments:

1. It became clear for me that the VEGNET approach is different from other TLS approaches in the sense that it scans at a fixed zenith angle. This really limits the info that you can extract from the scans compared to other TLS approaches that can produce full 3D point clouds. This needs to be mentioned in the discussion.

R/. We agree with the reviewer on the fixed zenith angle issue when compared with other more expensive instrument, but the VEGNET has the advantage over other 3D instruments that is more versatile and significantly cheaper than any other TLS in the market. Therefore, albeit of their limitations, the information provided is very unique, and we have mentioned this in the discussion. Sometimes more data, as those provided by 3D scanners, is fundamentally overkill for some applications as the one presented in this paper.

2. The authors added some information to show that the plots are randomly selected. However, I still doubt that the setup is sufficient to study the selected research questions. The plots are probably independent replicate (yes I meant replicates) samples of ‘the forest’, but are they replicate samples of the categories that you define? (in terms of succession and in terms of liana presence?). I doubt. In addition, the plots are very small in size. Only 0.1 ha, means that the plots are very prone to edge effects. You might have 0 rooting liana stems in such a small plots, but the crowns might be full of lianas due to lateral ingrowth.

R/. To address this comment we want to mention first that we increased our sample size from 9 plots to 28 plots in our study site. We partially disagree with the comment because this is making a classical perception of the pseudoreplication and independence of samples in study sites that need to be considered as unique in the world. This topic is widely and well discussed by Hurlbert (1984), when he started to explain that the replication of the number of experimental units (in our case the plots) in mensurative experiments needs to be randomly selected when very large-scale systems are studied (like our study) and when the study site is unique (there are no similar systems); Hurlbert (1984) concluded that the independence of these experimental units depends mainly on the number of samples, more than the remote chance (yes we meant chance) of proximity or aggregation. In addition, we consider that the distribution of forest patches, the ages of these patches, the remaining history in these patches (fires, management, distance to major highways), and the number of samples can produce independence in our plots and

treatments. The comment of the reviewer could be valid if the plots of each treatment are aggregated in a single patch of forest, but this is not our case as you can see in Figure 1.

Furthermore, our selection of plot size (0.1 ha) is typical of tropical environments, and this has been used constantly across the tropics (See Kalascka et al. 2005 as an example for dry forests).

3. An additional weak point is for me the fact that only 1 scan per plot is performed. In combination with the fact that VEGNET is scanning at 1 fixed azimuth angle, I suspect that the observed structure is really depending on the scanning location. Did you do any tests by scanning at different locations within the plot? Moreover, no information is given on the actual location of the scanning position within the plot.

R/. This is not a weak point, and we did not test different locations because this is not necessary. A scan of VEGNET can cover ~0.1 ha of forest, which means that we do not need to make multiple measurements. If we perform a measure in the edge of the plot we can extract information outside of the plot which could produce noise in our correlations. Likewise, we performed our measures in the middle of each plot, this information was included. In addition, conducting one single measurement using the VEGNET takes between 2-3 hours every night. The argument that the structure will depend on the scanning location is a logical one but the area measured by the instrument covers our plot completely, so we do not see a reason to conduct additional measurements.

4. The authors state that they want to test the impact of lianas on canopy structure, but due to the lack of information about the plots and the rather weak set-up, the resulting patterns seen in the VEGNET data might not be caused by lianas at all.

R/. As we explained above, information about the forest structure and abundance of lianas was included. Currently, using bias of correlation the resulting patterns can be attributed to liana abundance.

5. It is now more clear for me what the RG parameter actually means. The authors use this index to explore if successional trajectories could be altered by lianas, by assuming that if they don't see a change in vertical structural complexity, this would mean that lianas are altering the successional pathway. I really don't understand this assumption. Why would an altered succession be reflected in a none-change in vertical structure? In addition the authors assume that if they don't find an RG trend along the successional gradient for the plots with lianas, that this would indicate an arrested succession by lianas... But on the other hand the late successional plots are selected based on their structure. I really think this a weak setup. Also on page 13 (line 278) the authors write that "a change or no significant increase in PAI as a function of RG would suggest that lianas are altering the successional trajectory of vertical structure". This sentence is very confusing. "a change" is contradicting "no significant increase". I agree that VEGNET might be used to make observations of canopy structure of tropical forest, but even this probably needs to be tested. But to test if lianas are altering successional trajectories, you really need to present more information on the plots, come up with a setup that really allows you to study lianas of successional gradients, make scans in plots that are large enough, make multiple scans per plot, ...

R/. In this new submission, we correct the above framework. Currently, using a canonical correspondent analysis we are showing how the forest structure could be predicted by VEGNET measurements, but at the same time, using univariate analysis of correlations we show how the presence of lianas affects the bias of prediction. Therefore, variations in the parameters of correlations could be used to describe that the successional trajectories are altered by the liana abundance.

6. The answer of the authors to my comment 8, is not sufficient. The authors provide indeed some more information on the trends they found in fig 3. However this does not answer the key point of my comment: the fact that you find a significant positive relation for plots without lianas is mainly driven by the fact that you have observation in early successional plots. You don't have observations in early plots with lianas, leading to a non-significant trend for the plots with lianas. Try to fit a curve through the plots without lianas, but only considering the intermediate and late successional plots, the trend will probably be lost...

R/. We have removed this from the analysis but we need to make a clarification to the reviewer regarding the ecological succession of tropical dry forests and the presence of lianas. In general, lianas are never present in young early successional forest in the dry forest, in fact during our long term work in Mexico, Costa Rica and Brazil, we have never observed lianas in early successional stages (< ~20 years). They are present, and more dominant, in old early or intermediate stages (> ~30 years) with a reduction within late succession. So the fact that we did not use young early successional stages is (1) because they do not have lianas, (2) they are a combination of grasses, scrubs, and short trees. Thus, our original graph was correct, but given the new focus we have made the decision to drop it from the paper. In this new manuscript, we used the term early successional plots to make a reference to forest with less than 35 years of succession, while we used the term intermediate plots to make a reference of forest with more than 35 years of succession. The trend in fact exists, given the fact that no lianas are present in the young early forests.

Specific comments

1. Depending on which option the authors choose, the title of a future study should be adapted: if they chose option (1), the title should be adapted: e.g. 'the potential of VEGNET to observe canopy structure in tropical forests'.

R/. We agree with this comment because we are not looking the effect of liana abundance on the forest structure, we are looking how the prediction of forest structure by VEGNET-hemispherical photographs could be affected by the liana abundance, and therefore in well-known ecosystems, these biases of prediction could be considered the structural effects of liana presence. However, we have made the decision to use the suggested title.

2. Line 25: vegetation 'components', I guess you mean 'indices'?

R/. We agree, this was corrected.

3. Line 206: PAVD is estimated based on the derivative of LAI, but how is LAI estimated?

R/. We agree, this was corrected. PAVD is estimated based on PAI.

4. Line 245: ‘RG is a measured that has..’ something is wrong with this sentence.

R/. We agree, this was corrected.

5. Line 286: ‘liana treatments’ here and elsewhere this is confusing terminology, because a lot of readers will interpret it as if you experimentally added or removed lianas.

R/. We agree, this was corrected. In this version, we use the terminology of “liana abundance”.

6. Table 1: units of variables are missing: Cx, cy, RG, PAI

R/. We agree, but the Table 1 was replaced by a new Table 1.

7. Table 1: the plots are 20x50 m. I assume that the centroid coordinates Cx and Cy are in meters. Does this mean that the Cy coordinates which are close to 10 are located really at the edge of the plot? What about edge effects?

R/. We agree, but the Table 1 was replaced by a new Table 1.

8. Fig 3, y axis, units are missing. Are these boxplots based on only 3 observations per boxplot? Probably not the best way to represent the data.

R/. We agree, but the Table 1 was deleted.

REVIEWER #2

General comment

The author addresses the very interesting question of the effect of liana presence on secondary forest regeneration. The use of terrestrial LiDAR is interesting and has high potential in forest structure studies. However the study takes place in an area where forest inventory data are available according to them and they don’t use it. Moreover, the structure of the article needs to be improved. The study setup and the hypothesis still need to be explained more clearly. The result section is not structured enough and the discussion should be enriched by quantitative rather than qualitative comparisons. The article does currently not appear suitable for a publication in Biogeoscience and I suggest major revision.

Comments will re-address comment already made by previous referee but not well enough answered in my opinion. I grouped the major comments in 4 sections.

Major Comments

1. Site selection and succession stages: A better description of site selection is needed. What forest structure data are used in quantitative terms to distinguish different forest categories? What are their specific land use history? What remote sensing data (airplane photography, satellite optical measures) are used and at which resolution?

R: We have conducted a new land use history of the site, providing probably the first comprehensive study of forest succession for the Santa Rosa National Park. This study involved aerial photography (Scale 1:24,000) from the US Army produced in 1950 which was scanned and resampled to 80 m resolution. This provided us with the initial forest class to detect potential old growth at the park. Second we use 1979 MSS interpreted data (80 m resolution); 1986, 1997, 2000, 2005 TM data (28 m resampled to 80 m), 2010 SPOT (10 m resolution resampled to 80 m), and finally 2015 Landsat 8 data resampled as well to 80 m. For each one of these images a forest/non-forest map was produced using a supervised classification. In order to compare the different maps to the 1979 MSS data, which is a key image since the Park was created in 1971 the rest of the data was resampled to 80m resolution.. With the 1950, 1979, 1986, 1997, 2000, 2005, 2010, and 2015 data we were able to produce Figure 1 which presents information about forest age and allows us to better define the differences between early, intermediate and late forests found within the park.

Spectral reflectance may change with liana abundance (Castro-Esau, Sánchez-Azofeifa, and Caelli 2004; Kalácska et al. 2007; Asner and Martin 2012), as well as other parameters used to distinguish forest age (canopy height, stem diameter...). As pointed out by previous referees, this might reduce the strength of your conclusions. I think it has to be discussed.

R: Indeed this is a good point and an element that we are continuing to work on in our research group since it seems that the impact of lianas is totally ignored by researchers working on the remote sensing of tropical environments (Foster et al. 2008 is one of the few examples that bring the importance of lianas into the light of correct remote sensing processes). Having said that we have made the decision not to bring the concept of remote sensing identification of lianas from trees in the discussion of our paper since it is not part of our main goals. Our work on this paper is strictly on forest structure and succession and the impact of liana abundance; adding a new dimension associated to remote sensing will be out of context.

The best option would be to select forest site based on their age. Can you approximate the ages of forest stands selected? The first mention of the forest stand age is line 395. It would be good to have this information in the Table 1.

R: This is an excellent suggestion and we appreciate the reviewer to move us in that direction. Figure 1 now presents the requested information.

Are the plots the same as in (Kalácska et al. 2004)?

R:/ No they are not. We are using a different sampling scheme. Kalacska et al. (2004) plots (9 of them) are our long term monitoring plots in Santa Rosa and where not used in this paper.

The PAI values are very low compared to Kalácska et al.'s LAI estimate, especially for late succession. I think it should be discussed because it might explain the weakness of the result concerning PAI alteration by liana presence.

R/. We agree and in this new version of our manuscript, we included in Table 1 a quantitative description of forest structure using two categories: early and intermediate successional stages. In addition, we include a new Figure 2 that was created by integrating interpreted aerial photographs for the ages of forest patches in our study site which were estimated and included in this version using a Figure. These ages were used to describe the successional stages for our plots.

Unfortunately, in this new version, we cannot make a direct comparison with Kalacska's plots because we increased our number of samples. However, the method implemented by Kalacska et al. is different in comparison with our method. They used LAI-2000 Plant Canopy Analyzer and we used hemispherical photographs. The trend that you described could be an effect of the method implemented which has been documented previously by other researchers that suggest that hemispherical photographs tend to underestimate LAI when compared with other techniques.

2. Description of liana presence, explanation of its quantification.
How where selected stands with and without lianas?

R/. please refer to our new section 2 which provides detail information about our sample selection.

Citations made are not enough in my opinion, you should mention in the method what has been measured. Is it a number of lianas bigger than 5cm dbh? What about the basal area of lianas and the crown occupancy index (G. M. F. van der Heijden et al. 2010)? What is a stand with liana? I guess it means a liana presence above certain threshold (1 per stand?). liana presence measures of each stand could be added to the Table 1.

The significance of liana densities should also be discussed? They seem to be quite variable, is it relevant to consider in the same category a stand with more than 30 lianas (or whatever is the measure) and another one with 11 (or even less I suppose if you wrote the result in the form mean \pm standard error).

R/. We agree, a better explanation about the liana abundance was included in methods under the description of plots. We hope that our new section 2, which has been significantly expanded covers your concerns.

3. Relation between measures issued from terrestrial LiDAR point cloud and ecologically relevant features

Structural features issued from forest inventory data should be related more rigorously to terrestrial LiDAR measurement (RG and PAI). You mention line 243 "we used RG to relate the shape of the PAVD profile to forest biomass". I don't see any relation between RG and biomass in the article. I think it would be a great thing to do so, you should at least explain briefly Muss et al's results (2013). If RG is related to biomass, can you evaluate biomass from RG? Several articles hypothesize a reduction of biomass accumulation due to liana presence. Why not testing this hypothesis and showing the ability of terrestrial LiDAR in doing so? Tree >5cm are

measured since 2003 you should also find some trends tree growth which could differ according to liana presence or not. Finally quantifying biomass or basal area would allow a better interpretation of PAI increase. PAI in stands with a lot of liana is supposed to be mainly due to branches while contribution of trunks and Branches is expected to be higher in stands with no lianas.

The comparison of the relation $PAI=f(RG)$ between liana-infested and free of liana patches should be explained more clearly. Hypothesis about PAI evolution in forest stands with liana should also be explained more clearly.

The discussion on the different component of the PAI (wood vs leaves) is interesting and should be more precise. The use of biomass estimation in the different stand as well as carbon turnover would probably feed interestingly the discussion.

R/. We agree, but in this version, we change dramatically this perspective of association of VEGNET and biomass. Currently, our central focus is the relation of VEGNET – hemispherical photographs with forest structure, and the effect of the presence of liana abundance on this relationship. Notice that we use the term liana abundance which we think is a term that covers more our main goals.

4. Forest dynamic

Line 173 You mention the quantification of litterfall. There is no more mention of litterfall in the article! it would be interesting to use litterfall data and forest inventory data to have a proxy of carbon turnover/residence time (Chave et al. 2010). Carbon residence time is expected to be lower in liana presence (van der Heijden et al. 2013; Tymen et al. 2016). Moreover it may be interesting to discuss the relative contribution of leaves and woody parts to the PAI in the different forest stands.

R/. We agree; we correct that in this version. In this version, we do not include information about litterfall, and do not discuss the relative contribution of leaves and woody parts to the PAI in different forest stands as this could be very far from our goals; therefore this was not discussed.

Minor comments

Abstract

Line 15 the potential consequences of liana presence on forest dynamic is not completely unknown see at least Tymen et al. (2016).

R/. Fully agree and even more in tropical dry forests where studies on liana abundance and their impact on forests dynamics are close to none. In fact, it seems that our paper helps to confirm the same argument presented by Tymen at al. (2016) but for dry forests using a totally different methodological approach.

Introduction

Line 114 Why making the hypothesis that increase in structural complexity would indicate no effect of lianas ? A comparison between forest stands with and without liana should be enough to show a relation between liana and forest development.

R/. We thank the reviewer for his/her suggestion. This is not the goal of the paper as indicated by the following: “As such in this paper we first, we assess the potential of VEGNET and HPs to detect the vertical structure of forest stands at different successional stages. Second, we examine how liana abundance could affect the bias of prediction of VEGNET and HPs to detect 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.” We hope that the goals of the paper are better defined now.

Line 155-159 Forest structure description is not really clear for me.

R/. We agree, a better description of the measures of forest structure was included under the section of “Forest structure”.

Methods

Line 195 Is the ground really flat? If topography is known, it would be a good thing to add elevation lines to the Fig.1. A better option would be to compute the canopy height as a distance to a terrain model (i.e adding to the current calculation the point of measurement height from the ground situated vertically to the focal point).

R/. We have been tried to select all our plots on flat sites, but we fail to see how this can contribute to the outcome of our paper. Although, we appreciate very much the suggestion from the reviewer we have not implemented it.

Line 245-249 I don't really get this paragraph.

R/. We have significantly changed that section thus the paragraph is no longer present.

Results

Line 287: I wouldn't say five treatments since there is no experimental manipulation in your study.

R/. We agree, this was corrected.

Line 291 I disagree with the interpretation of high PAVD as a zone of high biomass. In old growth forest typically, most of the biomass is situated in tree trunk while PAVD is highly driven by leaf repartition and maximal PAVD will thus be at the crown level.

R/. We agree, but the results were rewritten.

Line 300 When you say PAVD was higher do you mean sum of the PAVD (which is PAI if I well understood)? This result should be shown in Table 1.

R/. We agree, but the results were rewritten.

Line 304-307 Reformulate sentence. What are PAI treatments? Consider moving this part at the beginning of the result section where PAI along forest succession is described. In my opinion, comparison of PAI values between liana and non liana stands should be clearly exposed at the beginning of the result section. It be interesting to discuss this point in comparison it to biomass accumulation (as well as carbon turnover) differences?

R/. We agree, but the results were rewritten.

Line 317 Liana density unit?

R/. We agree, but the results were rewritten.

Discussion

Line 359 Are you able to detect horizontal variations in canopy structure such as canopy height irregularity you mention. They could explain the blurry signal you get.

R/. No, with the VEGNET we cannot detect horizontal variations. We have been conducting work in the same plots with a different TLS (Leica C10) and we are observing those variations but mostly because of the nature of the 3D cloud obtained by the Leica C10.

Line 364 The increase of basal area, vegetation material and biomass accumulation could be shown and quantified thanks to forest inventory data.

R/. This is correct and it is observed on our new plots.

Line 378 You could also cite Foster, Townsend, and Zganjar (2008) and Tymen et al. (2016).

R:/ Thanks for the suggestions, we have include them in the references.

Line 386 A reference would be welcome

R/. We have added a new one.

Line 390 Putz (1984) can also be an interesting reference

R/. Indeed, very good point.

Line 390-392 You showed in the result that decrease in liana density was not significant. You should discuss this point. Pinard, Putz, and Licona (1999) could be interesting to read for the discussion.

R/. We agree but since our data and objectives (driven by Reviewer No. 1 comments) significantly changed, our new results no longer cover this section.

REFERENCES

Hurlbert, S. H. 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs. 54:187-211.

1 Can Terrestrial Laser Scanner (TLS) and hemispherical photographs predict Tropical
2 Dry Forest Succession with liana abundance?
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30 **Abstract**

31 Tropical Dry Forests (TDFs) are ecosystems with long drought periods, a mean temperature
32 of 25°C, a mean annual precipitation that ranges from 900 to 2000 mm, and that possess a
33 high abundance of deciduous species (trees and lianas). What remains of the original extent
34 of TDFs in the Americas remains highly fragmented and at different levels of ecological
35 succession. It is estimated that one of the main fingerprints left by global environmental and
36 climate change in tropical environments is an increase in liana coverage. Lianas are non-
37 structural elements of the forest canopy that eventually kill their host trees. In this paper we
38 evaluate the use of a Terrestrial Laser Scanner (TLS) in combination with hemispherical
39 photographs (HPs) to characterize changes in forest structure as a function of ecological
40 succession and liana abundance. We deployed a TLS and HP system in 28 plots throughout
41 secondary forests of different ages and with different levels of liana abundance. Using a
42 canonical correspondence analysis, we addressed how the VEGNET and HPs could predict
43 TDF structure. Likewise, using univariate analysis of correlations we show how the liana
44 abundance could affect the prediction of the forest structure. Our results suggest that TLS
45 and HPs can predict differences in the forest structure at different successional stages, but
46 that these differences disappear as liana abundance increases. Therefore, in well-known
47 ecosystems such as the tropical dry forest of Costa Rica, these biases of prediction could be
48 considered as structural effects of liana presence. This research contributes to the
49 understanding of the potential effects of lianas in secondary dry forests and highlights the
50 role of TLS combined with HPs to monitor structural changes in secondary TDFs.
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Deleted: 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 ground LiDAR to detect differences in the vertical structure of stands of different ages with and without lianas in a tropical dry forest. 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 canopy height. 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 from a structural point of view, 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 dry forests due to liana presence. - ... [4]

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94 | **1 Introduction**

95 | Lianas, woody vines, are a key structural component of tropical forests; they account
96 | for 25-40% of the woody stems and more than 25% of the woody species (*Schnitzer and*
97 | *Bongers, 2011*). Lianas are structural parasites that use trees to ascend to the forest canopies,
98 | and as such, can be detrimental to host trees by competing with them for above- and
99 | belowground resources (*Chen et al., 2008*), reducing tree growth rates, and increasing tree
100 | mortality (*van der Heijden et al., 2013*). Thus, lianas are able to reduce carbon storage and
101 | uptake in old-growth tropical forests (*Durán and Gianoli, 2013; van der Heijden et al.,*
102 | *2015*).

103 | Lianas have been defined as hyper-dynamic elements of the canopy structure
104 | (*Sanchez-Azofeifa and Castro, 2006*). In the last two decades lianas have increased in
105 | density and biomass in old-growth forests (*Phillips et al., 2002; Schnitzer and Bongers,*
106 | *2011*), and this increment is considered to be one of the major structural changes in tropical
107 | forests (*Phillips and Lewis, 2014*), because it can have potential negative effects on carbon
108 | stocks. Liana dynamics in secondary forests, however, are not yet understood despite the
109 | fact that secondary forests are becoming increasingly dominant in tropical regions, and
110 | currently occupy more area than old-growth forests (*Durán and Sánchez-Azofeifa, 2015;*
111 | *Wright, 2005*).

112 | Lianas are considered light-loving plants, because they tend to respond positively to
113 | disturbance and show high density in areas of secondary forest succession (*Paul and Yavitt,*
114 | *2011*). Secondary forests may promote liana abundance because they provide both high light
115 | availability and an abundance of trellises (*Schnitzer and Bongers, 2002*). In treefall gaps,
116 | lianas can form dense tangles and reduce the amount of light reaching the forest understory

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123 (Paul and Yavitt, 2011; Schnitzer et al., 2000). These liana tangles can persist for long
124 periods (up to 13 years) and alter the successional pathway to one(?) stalled by liana
125 abundance by inhibiting the regeneration, growth, and density of late successional species
126 (Schnitzer et al., 2000).

127 As of today, it is still unknown whether lianas can alter successional trajectories in
128 secondary forests resulting from anthropogenic disturbance (Durán and Sánchez-Azofeifa,
129 2015). Two studies in secondary wet forests have found an increment in liana density in the
130 first 20 years of regeneration (age since land abandonment), with a subsequent decline
131 (DeWalt et al., 2000; Letcher and Chazdon, 2009). This decline of lianas in wet forests
132 appears to be related with reductions in light availability due to greater tree and shrub
133 biomass at later stages of succession (Letcher and Chazdon, 2009). Nonetheless, it remains
134 unclear whether this pattern holds true with more open forest types, and whether other
135 factors such as structure, canopy openness, plant density and the volume of forest stands can
136 also influence successional trajectories of lianas (Durán and Sánchez-Azofeifa, 2015;
137 Sánchez et al., 2009).

138 Assessments of forest structure in different stands are often constrained by
139 accessibility, and the cost of personnel and equipment. Remote sensing offers an efficient
140 alternative to detect changes in vegetation and examine how lianas may change across stands
141 with different structures. Nonetheless, few studies have assessed the potential of remote
142 sensing (space-borne or airborne) to detect the presence of lianas in tropical forests with the
143 objective of providing tools to map their extent from local to landscape level, and measure
144 their ecological footprint (Foster et al., 2008). Sanchez-Azofeifa et al. (2009) used
145 hemispherical photography over a succession of tropical dry forests and found that lianas

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149 contributed substantially to forest-level Wood Area Index (WAI). Other studies found
150 differences between the biochemical, structural and hyperspectral properties of lianas and
151 trees in tropical dry forests (*Castro-Esau et al., 2004; Sanchez-Azofeifa et al., 2009*). These
152 studies emphasized the potential of using remote sensing to map liana abundance at regional
153 scales. However, given the important effect of lianas on the biomass distribution within
154 tropical forests (*Schnitzer and Bongers, 2011*), remote sensing tools capable of measuring
155 the vertical distribution of biomass within tropical forests are probably more adequate for
156 detecting the presence and variation of liana density across forest stands.

157 Terrestrial Laser Scanners (TLS) have demonstrated their capability to measure canopy
158 properties such as height and cover (*Ramirez et al., 2013*) and tree architecture (*Lefsky et al.,*
159 *2008*), (*Dassot et al., 2011; Richardson et al., 2014*). In the last decade, there has been a rapid
160 development in portable TLS (*Dassot et al., 2011; Richardson et al., 2014*). When laser
161 pulses emitted in the visible or near-infrared come into contact with an object, part of that
162 energy is reflected back toward the instrument which triggers the recording of its distance
163 and intensity (*Beland et al., 2014*). TLS systems typically employ vertical and horizontal
164 scanning around a fixed point of observation, providing a hemispherical representation of
165 biomass distribution in the forest -leaves, branches and trunks- which allows for the
166 exploration of foliage angle distributions and clumping (*Clawges et al., 2007; Jupp et al.,*
167 *2009; Strahler et al., 2008*).

168 Until today, there has been no concrete evidence about how liana abundance can
169 affect the prediction of the forest structure by TLS or HPs (HPs). Because of this, the
170 objective of this study was to evaluate the feasibility of a TLS named VEGNET in
171 combination with HPs to assess changes in forest structure in secondary TDFs with different

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187 | levels of lianas abundance. The VEGNET is a TLS that automatically scans a forest plot
188 | producing a vertical foliage density profile. Given its automated mode of operation and
189 | semi-permanent installation, the VEGNET instrument is described as an *in situ* Monitoring

190 | LiDAR (IML) (Culvernor et al., 2014; Portillo-Quintero et al., 2014).

191 | As such, in this paper we first assess the potential of VEGNET and HPs to detect the
192 | vertical structure of forest stands at different successional stages. Second, we examine how
193 | liana abundance could affect the bias of prediction of VEGNET and HPs to detect the level
194 | of succession of a given forest stand. Therefore, in well-known ecosystems such as the
195 | tropical dry forest of Costa Rica, this bias of prediction could be considered as the effect of
196 | liana presence on forest structure.

198 | **2. Methods**

199 | **2.1 Study Area**

200 | The study area is located in the Santa Rosa National Park Environmental Monitoring Super
201 | Site (SRNP-EMSS), which is a part of the Guanacaste Conservation Area in Costa Rica
202 | (10°48" N, 85°36" W) (Figure 1). This site covers an area of 50,000 ha, receives 1720 mm
203 | of annual rainfall, has a mean annual temperature of 25°C and a 6-month dry season
204 | (Dec–May)

205 | (Kalácska et al., 2004). The SRNP-EMSS site has suffered intense deforestation in the past
206 | 200 years due to the expansion of pasturelands (Calvo-Alvarado et al., 2009). Original land
207 | management practices in the park included pasture rotation between different large corrals
208 | surrounded by life fences that can still be identified today. More recently (early 1970's) with
209 | the creation of Santa Rosa National Park, a process of secondary regeneration has become

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239 | the dominant land cover change force in the region. Today and after the creation of SRNP,
240 | the uplands of the park are a mosaic of secondary forest in various stages of regeneration
241 | and with different land use histories related to anthropogenic fires, intense deforestation, and
242 | clearing for pasture lands (*Kalácska et al., 2004; Arroyo-Mora et al., 2005a, Sen et al.,*
243 | *2015*).

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245 | 2.2 Definition of forest cover and plot age.

246 | A map of forest cover and forest cover ages was generated using aerial photographs
247 | collected by the US Army in 1956 (Scale 1:24,000), a Multispectral Scanner (MSS) image
248 | from 1979 (80 m spatial resolution); 4 Landsat Thematic Mapper [TM] images from 1986,
249 | 1997, 2000 and 2005 (28.5 m spatial resolution); one Spot Multispectral image from 2010
250 | (20 m spatial resolution); and a Landsat 8 image from 2015. All images had less than 10%
251 | cloud cover.

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252 | The 1986 image was georeferenced to 1:50,000 topographic maps from the Costa Rica
253 | National Geographic Institute with a Root Mean Square Error (RSME) of 0.5 pixels or 14.25
254 | m. We defined this as our master image in order to georeference all of the other images, as
255 | such all other images were then geo-referenced to the 1986 image seeking a RMSE close to
256 | 0.5 pixels between the master and the target image. All images were then classified using a
257 | supervised classification. Image accuracy was conducted for the 1997, 2000, 2005 and 2010
258 | satellite images as part of independent validation efforts conducted by the Costa Rica's
259 | National Forest Financing Fund (FONAFIFO). Overall accuracy for the forest/non-forest
260 | images was 90%. Further information on image processing can be found in Sanchez-
261 | Azofeifa et al. (2001).

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284 Final quality controlled forest cover maps (forest non-forest) for 1956, 1979, 1986, 1997,
285 2000, 2005, 2010 and 2015 were cross referenced to produce a tropical dry forest age map.
286 Specifically, forest coverage with 60 years old correspond to woodlands which were being
287 observed in images since 1956; forests that were 40 years old were not detected in 1956 but
288 have been recognizing as forests since 1979; on the other hand, woodlands that were referred
289 to as being 10 years old have a minimum of 10 years as a discriminable forest coverage.
290 Based on Arroyo-Mora et al (2005) and Kalascka et. al's (2005) studies the following
291 successional classification was developed: Ages 10 to 40 years (Early), and ages 40 to 60
292 (Intermediate). Figure 1 presents the final land cover and forest age map for our study area.
293 Figure 1 presents the final land cover and forest age map for our study area.

2.3 Plots selection and description

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295
296 Based on Figure 1, twenty-eight randomly stratified 0.1ha plots were selected. The number
297 of plots chosen for each forest successional stage was based upon each stages total forest cover
298 area. Plot sizes of 0.1 ha follows convention used in tropical forest studies at this site (Kalascka
299 et al. 2005). Fieldwork conducted in July 2016 was conducted in order to characterize diameter
300 at breast height (DBH), tree height, total biomass, VEGNET observations (canopy vertical
301 profiles) and hemispherical photos (Canopy openness and Leaf Area Index).

302 The characterization of successional stages was performed following previous approaches
303 for seasonally dry forests of Costa Rica (Arroyo-Mora et al., 2005b; Kalácska et al., 2005) and
304 adjusted according to the estimated forest ages (Figure 1). These approaches categorized the
305 secondary regeneration in different successional stages such as early and intermediate
306 successional stages (E and I, respectively) (Arroyo-Mora et al., 2005a). The E stage is a

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314 forest area with patches of sparse woody vegetation composed of shrubs, small trees, and
 315 saplings, with a thick herbaceous understory, and with a single stratum of tree crowns with a
 316 maximum height of less than 10 m (Castillo *et al.*, 2012). Some of the common species that
 317 are characteristic of this early stage of succession includes *Genipa americana*,
 318 *Cochlospermum vitifolium*, *Gliricidia sepium*, *Randia monantha* (Hilje *et al.*, 2015;
 319 Kalácska *et al.*, 2004). In contrast, the I stage has two vegetation strata composed of
 320 deciduous species of woody plants. The first strata is comprised of fast-growing deciduous
 321 tree species that reach a maximum height of 10–15 m (e.g., *Cydista aequinoctialis*) and the
 322 second stratum is represented by lianas and vines, adults of shade-tolerant and slow-growing
 323 evergreen species as well as the juveniles of many species such as *Annona reticulata*,
 324 *Ocotea veraguensis*, and *Hirtella racemosa* (Arroyo-Mora *et al.*, 2005a; Kalácska *et al.*,
 325 2004). No lianas were present in the early successional stage plots. Lianas in early forests
 326 tend to be present more later in the succession, specifically in the transition from early to
 327 intermediate stages. We did not select “late forests” since they tend to reflect the
 328 characteristics of tropical moist forests with significant structural characteristics very
 329 different from true late tropical dry forests sites (Tosi, personal communication).
 330 On the other hand, the characterization of the plots according to the liana abundance was
 331 based on the structure of plants that compose the tropical dry forest of SRNP-EMSS. In this
 332 way, we classified the 28 plots according to the relative abundance of stems of lianas, where
 333 plots with a relative abundance greater than 0.1 were categorized as plots having high liana
 334 abundance (HL), while plots with a relative abundance lower than 0.1 were categorized as
 335 having a low liana abundance (LL). Although this classification seems to be in-
 336 deterministic, this kind of classification represents an important ecological component which

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Deleted: 2005; Kalácska *et al.*, 2004). The late successional stage is characterized by three layers of vegetation: the upper layer consists of trees 15–30 m height; the second layer is composed of juveniles of all ages and heights, and the understory species; the third layer is represented by a dense canopy composed by deciduous and evergreen species, with the latter ones accounting for 50–90 percent of the canopy composition (Arroyo-Mora *et al.*, 2005
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407 is very difficult to study as a continuum due to its spatial and temporal variation, and its
408 categorization can help to improve the understanding of ecological processes as many other
409 ecological categories.

410 At the end of this characterization, we used 11 *E* plots and 17 *I* plots, with 12 of those
411 plots being LL and the other 16 plots being HL. Altogether, ours plots for the study
412 consisted of 5 *E*-LL plots, 6 *E*-HL plots, 7 *I*-LL plots, and 10 *I*-HL plots. In each of these
413 plots we extracted the available information that described the complexity of the dry forest
414 according to its structure, but at the same time deployed the ground LiDAR and
415 hemispherical photograph measurements to predict and describe that complexity.
416 Information about the parameters used and estimated according to the forest structure,
417 ground LiDAR, and hemispherical photographs is described below.

418

419 **2.4 Forest structure**

420 Four parameters that characterize the forest structure were used in this study. These
421 parameters were selected because these are easily obtained in any forest inventory, which
422 could help in the applicability of this study in other regions. Specifically, we selected the
423 stem density (stems/ha) as a parameter to describe the number of individuals per plot, the
424 mean diameter at breast height (1.3 m) (DBH_{mean} , cm) as a parameter that can describe the
425 mean size of the individuals, the total basal area (TBA, m^2) as a parameter that can describe
426 the biomass of each plot, and the ratio of liana basal area to TBA (L/TBA) as a parameter
427 that can describe the contribution of lianas biomass to the total biomass of each plot. Each
428 of these parameters was extracted from DBH measurements for lianas (>2.5 cm) and trees
429 (>5 cm).

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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 June 12th to June 27th, 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; Portillo-Quintero et al., 2014), measurements for the VEGNET were conducted at night. Some tests of the measurement process by VEGNET at night time indicated that at distances greater than 60 m or in areas larger than 3600 m² (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 0.1ha 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), 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

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510 laser distance measurement (d) assuming that the terrain is flat as describe *Culvenor et al.*
511 *(2014)*.

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

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

517 Consequently, the estimation of cumulative plant area index (PAI) by the conversion of
518 $P_{\text{gap}(z)}$ was performed using the following the equation (*Culvenor et al., 2014*):

$$PAI_{(z)} = -1.1 \times \ln(P_{\text{gap}(z)}) \quad (2)$$

522 From this calculation, the density of vegetation components at any level of z was
523 computed as the derivative of PAI with respect to h . This calculation is commonly referred
524 to as the plant area volume density (PAVD) (*Culvenor et al., 201*) described by:

$$PAVD_{(z)} = \delta PAI_{(z)} / \delta z \quad (3)$$

528 It is important to note that these calculations represent tridimensional variations (x , y ,
529 z) of the forest structure (*Culvenor et al., 2014*), because of this, in our statistical analysis
530 we used the maximum h estimated by the LiDAR per plot (H_{max}), the cumulative PAI as a
531 function of the canopy height (PAI), and the mean PAVD at different heights ($PAVD_{\text{mean}}$).

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533 These calculations were extracted using the “VEGNET Data Display and Export Version
 534 2.5” software developed by Environmental Sensing Systems Inc (Melbourne, Australia).
 535 Likewise, from the LiDAR measurements we also used shape metrics such as the
 536 centroid (C) and radius of gyration (RG) to understand how the vertical profile of the forest
 537 could change according to successional stages and liana abundance. The RG and the C are
 538 metrics that are mainly used in LiDAR waveforms to describe the motion of objects and the
 539 manner in which material is distributed around an axis (Muss *et al.*, 2013). We used a
 540 similar approach by calculating the C and the RG for the PAVD vertical profile of each plot.
 541 Specifically, C represents the geometric center of a two-dimensional (x and y) region (e.g.,
 542 the arithmetic mean position) of all the points (n) in the shape of the PAVD profile, while
 543 RG is the root mean square of the sum of the distances for all points on the PAVD vertical
 544 profile, which is described as:

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

547 This parameter can be visualized as the relationship between the total length of the
 548 PAVD vertical profile and its shape and position, which are determined using the sum of x
 549 or y coordinates divided by the total length of the profile (Muss *et al.*, 2013). In general, the
 550 RG captures the manner in which the PAVD profile is distributed around the centroid,
 551 making it a better descriptor of the vertical profile shape than just the centroid itself, and
 552 thus, more suitable for relating VEGNET measurements to forest structure (Muss *et al.*,
 553 2013; Culvenor *et al.*, 2014). Therefore, we used the RG to relate the shape of the PAVD
 554 profile to forest biomass at the footprint level. For a more detailed explanation on the
 555 functioning of the VEGNET in the field please refer to Portillo-Quintero *et al.* (2014) as

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587 well as *Culvenor et al. (2014)*. A single successful scan was performed during the wet
588 season using the VEGNET instrument at each site on clear nights.

589 **2.6 Hemispherical photographs**

591 Hemispherical photographs (HPs) were taken during the early morning in the middle of each
592 plot, using a digital camera (E4500, Nikon, Tokio, Japan) equipped with a fisheye lens of 35
593 mm focal length. The camera was leveled at 1.50 m by a tripod and orientated towards
594 magnetic north, in order to ensure photographic standardization.. The resulting pictures were
595 analyzed using the software Gap Light Analyzer version 2.0.4 (*Frazer et al., 1999*). This
596 analysis was performed by creating 340 sky sectors (36 azimuth classes and 9 elevation
597 angle classes) with a time series of 2 min along the solar track. The leaf area index (LAI)
598 and the canopy openness were subsequently extracted by this analysis; however, the LAI
599 was extracted using the “4 ring” which is a more accurate depiction of the site than using “5
600 rings” because the latter takes into account trees that are not immediately surrounding the
601 site, and which are found outside of the plot footprint.

603 **2.7 Statistical analysis**

604 This study compared the effect of the successional stages, the abundance of lianas, and their
605 interaction on the parameters of forest structure as well as VEGNET-HPs parameters using a
606 multivariate analysis of variance (MANOVA), in order to demonstrate that this study had
607 been conducted in contrasting environments. For each MANOVA we extracted the
608 univariate analysis of variance (ANOVA) to describe the multivariate effects of each
609 parameter. To show the potential of the VEGNET and HPs to predict variations in the

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614 structure of the dry forest, we applied a canonical correlation analysis (CCA) using the
615 VEGNET-HPs parameters as independent variables and the features of the forest stand as
616 dependent variables. Due to the CCAs sensitivity to the collinearity among variables (*Quinn
617 and Keought, 2002*), we only used RG, PAI, PAVD_{mean}, H_{max}, LAI, and canopy openness as
618 independent parameters. Specifically, the CCA was used to extract the canonical correlation
619 between VEGNET-HPs and forest structure (eigenvalues), the correlation between the
620 canonical variates and each matrix (eigenvectors), and the scores that describe the
621 multidimensional variation of each plot according to its correlation. To extract the statistical
622 significance of the canonical correlation coefficients, we computed an asymptotic test on the
623 first canonical dimensions to extract the *F*-approximations of Wilks' Lambda along with its
624 significance. This statistical significance was subsequently validated using a permutation
625 test on each dimension by 10000 iterations.

626 _____ After describing the potential of the VEGNET-HPs parameters to predict variations
627 in the structure of the dry forest, we were interested in demonstrating how the relative
628 abundance of lianas could affect the bias of prediction extracted from these sensors. In
629 ecological terms, it is a perceived expectation that during successional transitions increases
630 in basal area, height and vertical strata of the vegetation should be observed; consequently,
631 these transitions could be translated into increases in VEGNET-HPs parameters (except
632 canopy openness which is inverse). However, from hypothesis derived from previous
633 studies, it is possible that the abundance of lianas may actually arrest the forest succession
634 and reduce the biomass accumulation of woody vegetation (*Paul and Yavitt 2011; Schnitzer
635 et al., 2000*). If the above is true, correlations between descriptors of forest structure and
636 parameters extracted from VEGNET and HPs could be diffuse or stochastic in the dry forest.

637 and their application under the presence of lianas could prove ineffective. Under this
638 reasoning, we compare the parametric correlations of four parameters according to the
639 successional stages and the liana abundance, separately. The four parameters selected were
640 those with the two highest eigenvalues for the VEGNET-HPs matrix and the two parameters
641 with the highest eigenvalue for forest structure, determined by the first two canonical
642 dimensions described by the CCA. This comparison was conducted using an ordinary
643 resampling method to replicate the correlation 5000 times, in which the resampled values
644 were used to build density plots to describe the bias of prediction according to its overlap.

645 The previous analyses were conducted in R software version 3.3.1 (R Development
646 Core Team, 2016) using the “CCA” package (González and Déjean, 2015) to extract the
647 canonical correlations, the “CCP” package (Menzel, 2009) to extract the significance of the
648 CCA and its permutation, and the “boot” package (Canty and Ripley, 2016) to extract the
649 resampled values. When the normality of the data was not reached, each parameter was
650 previously transformed using the Box-Cox transformation for the analysis.

651

652 **3 Results**

653 **3.1 Forest structure**

654 According to the MANOVA the forest structure of the plots differed between successional
655 stages (Wilk’s $\Lambda_{(4,21)} = 0.51$; $p < 0.01$) and liana abundance (Wilk’s $\Lambda_{(4,21)} =$
656 0.58 ; $p < 0.05$), but without interaction between these categories (Wilk’s $\Lambda_{(4,21)} =$
657 0.76 ; $p = 0.20$) (Table 1). This analysis suggests that the DBH_{mean} and TBA were the only
658 parameters affected by the interaction between successional stages and liana abundance,
659 where *E* successional plots with LL and *I* plots with HL showed lower values of DBH_{mean}

660 and TBA than *E* and *I* plots with HL and LL, respectively. In terms of the effect of the liana
661 abundance, the univariate analysis suggests that plots with LL showed lower values of
662 L/TBA in comparison with HL plots.

663

664 **3.2 VEGNET-Hemispherical Photographs (HPs)**

665 The multivariate comparisons of the VEGNET-HPs parameters showed that the sensor
666 estimations did not differ between successional stages (Wilk's $\Lambda_{(8,17)} = 0.58$; $p =$
667 0.21), liana abundance (Wilk's $\Lambda_{(8,17)} = 0.62$; $p = 0.29$), and these categories did not
668 show an interaction (Wilk's $\Lambda_{(8,17)} = 0.53$; $p = 0.14$) (Table 2). Despite the absence of
669 a multivariate effect of the liana abundance, the univariate responses extracted from this
670 comparison suggest that the LAI and canopy openness differs between plots with HL and
671 LL, where LL plots showed lower values of LAI and higher values of canopy openness in
672 comparison with HL plots (Table 1). On the other hand, the univariate responses showed
673 that the canopy openness was affected by the successional stages, where *E* successional plots
674 showed higher values of canopy openness than *I* plots. Likewise, the univariate comparisons
675 suggest that C_x , PAI, and $PAVD_{mean}$ are affected by the interaction of the successional stages
676 and liana abundance, where *E* successional plots with LL and *I* plots with HL showed higher
677 values of C_x , PAI, and $PAVD_{mean}$ in comparison with *E* and *I* successional plots with HL and
678 LL, respectively.

679

680 **3.3 Canonical correspondence analysis**

681 The CCA showed that sensor parameters are strongly associated with the trends in forest
682 structure (Fig 2). In general, the first and second canonical dimension showed correlations of

683 0.81 (Wilk's Lambda_(24,64,01) = 0.13; $p < 0.01$) and 0.72 (Wilk's Lambda_(15,52,85) = 1.46; $p =$
684 0.16) between our sensors and forest structure. Specifically, the correlation between the
685 canonical variates in the first canonical dimension suggested that canopy openness and the
686 LAI have a great weight in the sensor matrix, while L/TBA and stem density had an
687 important effect on the forest structure (Fig 2a). Likewise, the correlation between the
688 canonical variates in the second canonical dimension showed that H_{\max} and PAVD_{mean} had a
689 strong correlation with the sensor parameters, while TBA and steam density had a strong
690 correlation on the forest structure. The scores that described the multidimensional variation
691 of each plot did not reflect a visual aggregation according to the successional stages and
692 liana abundance (Fig. 2b). In terms of the validation of the significance of the canonical
693 correlation coefficients, the permutations test showed that there is an important increase in
694 the significance of the first two canonical dimensions (Fig. 2c, 1d), where the first
695 dimension presented an increase of 0.21 points for the Wilks's statistic, while the second
696 dimension showed an increase of 0.25 points, which results in a significant effect.

697

698 **3.4 Comparison of correlations between successional stages and liana abundance**

699 The different trends of correlation showed that the successional stages and mainly the liana
700 abundance have an important effect in the prediction of the forest structure using VEGNET-
701 HPs parameters (Figure 3), but at the same time, these trends showed that some of these
702 parameters have the potential to predict the implication of the liana abundance on the forest
703 structure. Specifically, variation in the correlations of canopy openness on L/TBA (Figures
704 3a, b, c) and H_{\max} on TBA (Figures 3g, h, i) showed that the correlation trends between
705 successional stages are overlapped, while the correlations trends between liana abundance

706 are separated, in where low values of canopy openness and H_{max} are associated with high
707 values of L/TBA and TBA, and consequently with the discrimination of HL plots. Likewise,
708 variation in the correlation between LAI and L/TBA showed that the trends might not be
709 used to separate successional stages or liana abundance (Figures 3d, e, f). However, the
710 correlation between H_{max} and TBA suggest that H_{max} can not discriminate between different
711 successional stages, but can discriminate with different liana abundance (Figures 3j, k, l),
712 where high values of correlation are associated with intermediated and HL plots.

714 4. Discussion

715 Woody vines or lianas tend to proliferate in disturbed forest stands such as
716 regenerating forests (Paul and Yavitt, 2010). Much research on liana ecology, however, has
717 focused on old-growth forests despite that secondary forests currently cover a larger area
718 than old-growth forests and may become the dominant ecosystem in tropical regions
719 (Wright, 2005). Due to shorter stature and a higher variability of light in secondary forests,
720 lianas may be particularly abundant in these ecosystems, but little is understood about the
721 role of lianas in forest succession (Letcher and Chazdon, 2009). In this study, we used the
722 VEGNET, a terrestrial LiDAR system combined with HPs, to assess the impact of liana
723 abundance on forest succession. Our overall analysis first indicated that VEGNET
724 parameters in combination with HPs derived information was able to characterize changes in
725 forest structure at different successional stages. This finding in fact is not new, and it has
726 been demonstrated previously in the literature for other TDFs across the Americas including
727 the SRNP-EMSS (Sanchez-Azofeifa et al, 2009) when the effect of lianas is ignored. In fact,
728 it should be normal to expect some sort of correlation between forest succession and changes

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Deleted: 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 meters from the ground, with the highest biomass between 2-4 meters as measured by the VEGNET system (Figure 2). At the intermediate site (no lianas) PAVD is lower in the first 2-5 meters from the ground and reaches higher values between 6-12 meters, which corresponds, as expected, to the vertical distribution of canopy and subcanopy leaves and branches (Figure 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 (Figure 2). At the late successional stages (no lianas) PAVD values show two distinctive peaks (canopy and understorey, one occurring at the first 5 meters from the ground and the other one between 8 and 14 meters. At the late successional sites (with lianas, Figure 2), most PAVD is concentrated between 2-10 meters with no clear distinction between forest strata. PAVD was significantly higher ($H=7.2$, $P=0.02$.) in the late stages (1.64 ± 0.17) compared to the early stages (0.88 ± 0.5) in stands without lianas. ... [30]

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787 on structural parameters since many parameters such as biomass, LAI, Canopy Openess and
788 H_{max} will change as trees grow during the successional process. The fundamental difference
789 occurs when lianas are integrated into the successional system.

790 When we consider the bias of correlations between the forest structure and the
791 parameters extracted from our two sensors at different successional stages, as well as liana
792 abundance, our results suggest that this late variable has an important effect on the bias of
793 prediction for a given forest structure. The main reason is probably a result of lianas
794 introducing random tangles into the 3-dimensional space that is occupied by all forest
795 biomass at a given plot. In other words, lianas tend to randomize a space typically utilized
796 by trees, which in the absence of lianas would be occupied deterministically by trees. This
797 randomization of the 3D space occupied by trees and lianas is an element that has not been
798 considered as of today; since most studies do not consider the space occupied by lianas
799 because of a lack of TLS information.

800 This change in deterministic patterns of the forest structure is probably due to
801 competition between lianas and trees in forest stands, within a random 3D space. In
802 disturbed sites, such as secondary forests, lianas deploy leaves in the canopy, and create large
803 amounts of tangles in both the ground and mid canopy, in order to reduce the amount of
804 light available as well as the amount of incoming solar radiation available for photosynthesis
805 for other plant species (Graham et al., 2013). Moreover, in regenerating stands within
806 forests (e.g., treefall gaps), high densities of lianas can inhibit the regeneration of tree
807 species and reduce the abundance of shade-tolerant trees (Schnitzer et al., 2000), which in
808 turn can affect the 3D arrangement of species within a given area. These ecological
809 processes may cause a shift in forest structure, which is detected as a shift in the vertical

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861 structure signature by TLS in sites with high liana abundance. These differences in
862 structures have been confirmed in a recent study, which found that a liana-infested forest
863 had a more irregular canopy with canopy heights between 10 and 20 m, while the
864 surrounding forests had a significantly taller canopy between 25 and 35m along with a
865 denser canopy (*Tymen et al., 2016*).

866 The information provided in this paper is clear in the sense that some variations in
867 the TLS and hemispherical camera parameters can be used to estimate the impact of lianas
868 on forest structure along the path of succession, although not all of parameters were
869 significant. In other words, there is a strong need to carefully select which parameters should
870 be considered if we want to estimate changes in the forest structure as function of liana
871 abundance. One key example is the use of PAI as tool to evaluate the impact of liana
872 abundance on forest succession. PAI as a single measurement theoretically could provide
873 insights on the impact of liana abundance on successional stages. Theoretically we could
874 expect that PAI will increase as leaf and wood biomass increase during succession (*Quesada*
875 *et al., 2009*). It is surprising that we did not find differences in the PAI values between
876 stands that did and did not have. It is possible that PAI is not the best parameter to
877 differentiate between plots with and without liana presence, instead variables more related
878 with leaf components, such as leaf area index (LAI) may be more suitable for finding
879 differences in liana signature across sites, especially when the contribution of lianas to the
880 woody area index (WAI) to overall plot PAI is relatively small in comparison to the
881 allocation of WAI from trees (*Sanchez-Azofeifa et al., 2009*).

882 A recent study assessing the role of lianas on forest dynamics in the Amazon,
883 indicated that a liana-infested forest appeared to be in an arrested stage of ecological

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902 succession, due to the evidence provided by LiDAR surveys from 2007 to 2012 which
 903 showed that the overall extent of forest area had remained stable, with no notable net gain or
 904 loss over the surrounding forest (Tymen et al., 2016). It is possible that studying forest
 905 dynamics in forest stands across successional stages, with different levels of liana abundance
 906 integrated into the TLS and HPs parameters, may allow us in the future to provide stronger
 907 evidence as to whether lianas can arrest succession in dry forests as it appears to occur in
 908 humid forests (Schnitzer et al., 2000; Tymen et al., 2016).

910 5 Conclusions

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

922 Our study provides important insights on the contributions of lianas to the
 923 successional process, and highlights the potential that TLS has in monitoring liana presence
 924 in tropical dry forests environments. Lianas are increasing in density and biomass in tropical

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967 forests, but it is unknown whether this pattern is also found in secondary forests, which are
968 suitable for liana proliferation. TLS systems are capable of providing unbiased estimations
969 for the vertical structure of a given site, and thus constitute a powerful tool to monitor the
970 increases in liana density and biomass. Although, our study is limited to one single site in
971 Costa Rica, this is a first step on the development of more comprehensive approaches, which
972 take advantage of advanced technology to understand the effects of liana abundance on
973 tropical dry forest structure. The approach presented in this paper, presents important
974 contributions to efforts directed to estimate the potential effects of lianas on forest carbon in
975 secondary forests (*Durán and Sanchez-Azofeifa, 2015*), elements that seems not fully
976 considered yet in the tropical literature.

977 **Acknowledgements**

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983 **References**

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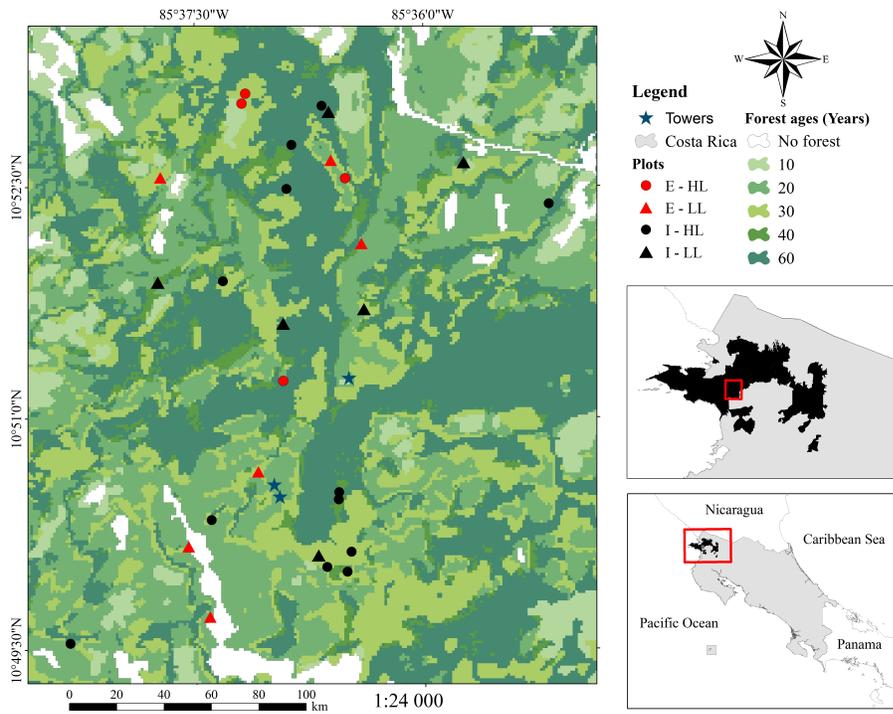
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Figure 1. Localization of the sampled forest stands in Santa Rosa National Park

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Environmental Monitoring Super Site, Guanacaste, Costa Rica, Where E-HL indicate Early

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successional stage with a high relative abundance of lianas; E-LL Early successional stage

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with a low relative abundance of lianas; I-HL, Intermediate successional stage with a high

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relative abundance of lianas; I-LL, Intermediate successional stage with a low relative

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abundance of lianas. In addition, forests ages refer to: 60, forests detected since 1956; 40,

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forests detected since 1979; 30, forests detected since 1986; 20, forests detected since 1997;

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10 forests detected since 2005, and no forest correspond to non-related to woodlands.

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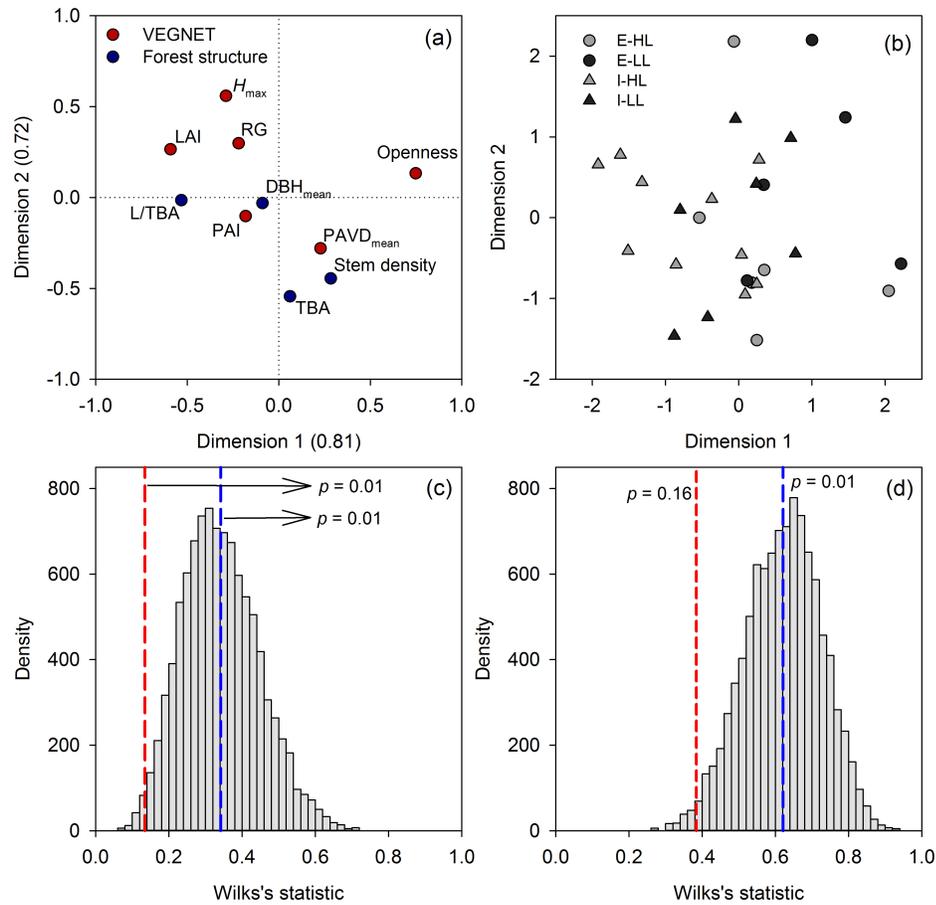
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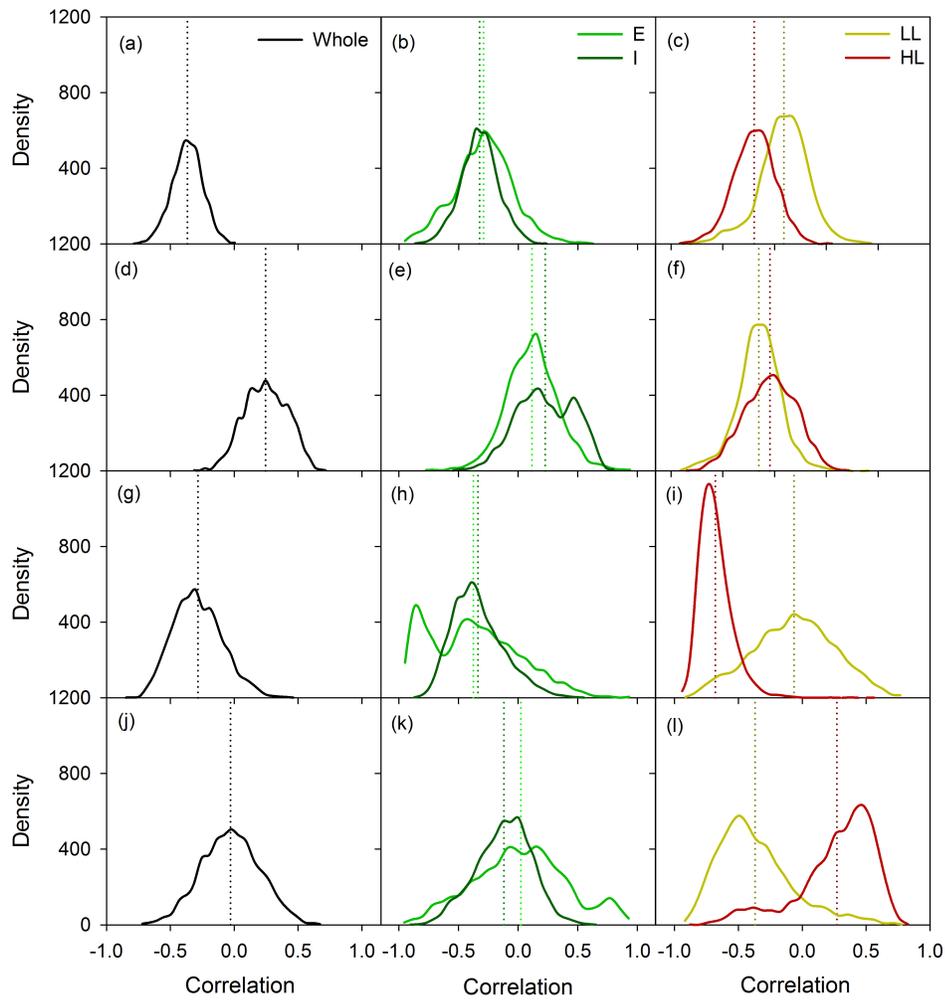


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1393 Figure 2. Canonical correspondence analysis to describe the association between the
 1394 parameters estimated by VEGNET system and the forest structure. a) VEGNET
 1395 coefficients are represented by red points, while forest structure coefficients are
 1396 represented by blue points. b) Individual scores of each plot of the canonical variates are
 1397 represented according to successional stages (E, early; I, intermediate) and relative liana
 1398 abundance (LL, low liana abundance; HL, high liana abundance). C and d represent the
 1399 permutation distribution of the Wilks' Lambda test to assign the statistical significance of

1400 canonical correlation coefficients considering 4 and 3 canonical correlations,
1401 respectively; the red line represent the original value Wilks' Lambda, while the blue line
1402 represent the mean value permutated.

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1405 Figure 3. Density distribution of the bootstrapped correlation coefficients without and
 1406 with distinction between successional stages (E, early; I, intermediate) and relative liana
 1407 abundance (LL, low liana abundance; HL, high liana abundance). a, b, and c correspond
 1408 to the correlation of canopy openness and the ratio of liana basal area (L) to total basal
 1409 area (TBA); d, e, f correspond to leaf area index-L/TBA correlation; g, h, and i

1410 | correspond to the maximum tree height-TBA correlation; j, k, and l correspond to plant
1411 | area volume density-TBA correlation.

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