Dear
Dr. Anja Rammig
Associate editor
Biogeosciences

We are very pleased to submit a revised version of the manuscript bg-2015-358 entitled "**Structural effects of liana presence in secondary tropical dry forests using ground LiDAR**". In preparing this revision we have considered all referee's comments and incorporated many of their suggestions. Below we provide the specific details for the changes of the previous version of the manuscript and responses to referees are in another color to facilitate follow-up of the changes in the current version. We greatly appreciate the time and effort spent in reviewing this manuscript by the referees and the associated editor, which have improved the final revised version of the manuscript.

Sincerely yours,

Arturo Sánchez

REVIEWER COMMENTS TO AUTHOR

Referee 1

Comments to the Author

In their Discussion paper Sánchez-Azofeifa et al. present a study on the effect of liana presence on forest structure in secondary dry forest in Costa Rica. They use the VEGNET ground LIDAR system to study the vegetation structure of forest stands (with and without lianas) along a successional gradient. The topic of the paper is important, the idea has merit and I believe that terrestrial LIDAR scanning has a lot of potential in this context. However, the study setup is rather limited, the methods and analysis are not well presented and some important information is missing. The analysis is too weak to support the conclusion that the authors make. I can therefore not recommend this manuscript for publication in Biogeosciences.

***Response**: We thank referee 1 for the comments. In effect LiDAR has a lot of potential to identify lianas and vegetation structure in forest of different stands, but few studies have been conducted assessing the potential of ground LiDAR to differentiate among stand ages or stands that differ in composition of functional groups such as woody vines, thus where the contribution of the paper lies.*

We believe our data shows solid evidence of the capabilities of LiDAR technology and its measured variables (PAI, RG) to detect and differentiate forest with lianas and forest with no lianas, over a successional gradient. This evidence has positive implications for the use of ground remote sensing platforms in long term forest monitoring, and for the use of airborne point cloud data to detect liana infestation over large areas in tropical dry forests.

*We have addressed the comments from referee 1 by providing clarifications about the methods and study set up in the new version of the manuscript (**lines 140-176**).*

Major comment 1

There is some important background information missing on the setup of the study. In the first place it is not clear why some stands have lianas and others not. Have they been artificially removed? Or has the presence/absence a natural cause? It is important to describe why lianas are present or absent. The factor that is determining the presence of lianas (e.g. the soil) might also influence the forest structure independently from the lianas… This would mean that the observed patterns might be caused by other factors than lianas.

***Response**: As we mentioned above, the study area and methods sections now provide more detail about the study area and plot description (**lines 130-176**). We also acknowledge in the discussion the reasons about liana presence in some stands (**lines 385-390**). There has not been artificial removal of lianas in the study area. The study area is part of a long-term project* *conducted by the tropi-dry network at Santa Rosa National Park (tropi-dry.eas.ualberta.ca). Thanks to our previous work there, we have been able to identify areas within the park with and without lianas that we were able to use for the current study. We do not have soil data on the plots sampled with the Vegnet to disentangle the different factors influencing the presence of liana in the region. However, whether soil structure is causing the differences across successional stages does not preclude the value of our paper, as our purpose is precisely to assess whether terrestrial scanning can detect differences in aboveground structure across plots. In the paper, we account for other factors aboveground that may be accounting for differences across plots, but we do not consider necessary to account for belowground variables to address our objectives.*

Major comment 2

- The stands in the study area have been classified in different age classes. This classification is done in a rather non-transparent way (page 17158, lines 14-23). Multiple criteria have been used for this classification, but it is not clear how much weight is given to each of the criteria. And in addition, forest structure appeared to be an important factor in determining the age classes! This is not really a good setup to test differences in forest structure afterwards.

***Response*: *The stands in the study area have been classified in a transparent way. We mentioned on page 17158 that sites were classified based on land use history, age since land abandonment, using remote sensing data and field inventories. We provided a brief description because the cited references provided a thorough explanation. Nonetheless, in the last version of the manuscript, thanks to reviewer's comments, we now have broadened this section to clarify the classification and characteristics of the different successional stages (**lines 130-176**). Here, it is important to highlight that the criteria for plot selection has been the same for sites with lianas and no lianas, so there should not be any biases for comparison across stand ages in that regard. Moreover, the selected plots and their characterization are the core elements of several papers already published, where specific information on previous land uses and past disturbances can be associated to each study plot (see Arroyo-Mora et al 2005; Kalacska et al. 2004, 2005; Sánchez-Azofeifa et al. 2009, & Castillo et al. 2012 in the references section).*

Major comment 3

The story needs more focus. Currently the results are describing both the impact of succession and the impact of lianas. However, none of both topics is well-developed. Maybe the authors should choose one of both topics to be developed in detail.

Response*:** *We disagree with the reviewer that the paper needs more focus. The paper deals with both succession and the impact of lianas. If the editor considered needed, we can increase this section, but we consider the scope of the paper is very clear, and the stated hypotheses. We are* *using our sampling design of plots with and without lianas to evaluate whether the liana presence, over a chronosequence, could be detected by the terrestrial laser scanning, and by doing that trying to get inferences about the potential role of lianas in secondary succession. There have not been many studies of lianas in secondary forests, but the few existing ones, in treefall gaps mostly, suggest that lianas may arrest secondary succession in tropical forests. Thus, studying lianas in the context of succession is relevant for forest ecology. Moreover, as mentioned in the introduction, lianas are considered a structural change in tropical forests, and they have increased in the last decades, which potential consequences for forest carbon dynamics* ***(lines 40-47)*. Thus, studies such as ours assessing the potential of remote sensing tools to monitor vegetation changes is applicable and pertinent to the current literature in tropical forests and secondary succession. Our method in the current manuscript attempts to get insights about the role of lianas in succession, by addressing some of the current concerns in the literature, specifically to evaluate whether lianas could be modifying the trajectory of succession in tropical forests as previously hypothesized by Schnitzer et al (2000), Paul &Yavitt (2011)* ***(lines 48-55).*** *This is another contribution of the study, as research on lianas in secondary forests is rather scarce (see Paul &Yavitt 2011, Duran & Sánchez-Azofeifa 2015).*

Major comment 4

- In that respect I also wonder if the number of studied stands is statistically sufficient to study both patterns (succession and liana presence) simultaneously. The studied stands differ in a lot of aspects (age, : : :), I doubt if they can be really considered as repetitions.

Response *We presume the referee meant to say replicates instead of repetitions, since to conduct statistical analysis replicates (as independent units) are more relevant than repetitions (not independent, and sampled more than once). Previous studies when plots were selected in the study area verified that the plots can be considered replicates as they are randomly distributed in the study area. Plot selection in the study area was conducted before 2004, and spatial analyses using the Ripley's function were conducted to verify that plots were not clustered or dispersed. A previous study when permanent plots were established verified that plots have a random spatial distribution at all scales between 0-5000 m (Kalacska et al. 2004). Thanks to the reviewer, we now have incorporated this information in methods section (****lines 130-139).***

Major comment 5

- Why are the VEGNET test measurements done at night? (page 17160, line 17) are the actual measurements also done at night? Why?

Response: *All measurements conducted by the Vegnet, are performed using a visible wavelength of 635 nm. Measurements must be conducted at night, in order to avoid sunlight irradiance interference at the same wavelength with the VegNET laser light. Night time measurements* *ensure an optimal environment for recording all returns and avoiding interference. We have clarified this on the paper (**lines 186-190**).*

Major comment 6

- The RG metric is introduced technically in detail. But for me it was not clear what the actual meaning of this metric is in terms of forest structure. It is not clear why the authors hypothesize that RG would increase with succession but not in case of liana presence. Is RG used here mainly a proxy of biomass or as a measure of vertical canopy structure? It would be interesting to relate the lidar data to actual biomass data (based on inventories) of the stands.

***Response**: The idea of conducting a linkage to the site biomass to the vertical profiles of the Lidar is very interesting but this is out of the scope of our paper. In the case of our scope and our data, Plant Area Volume density (PAVD) provides a measure of the area covered by photosynthetic and non-photosynthetic material present in a given forest height. The PAVD vertical profile (Figure 2) then describes the distribution of the plant volume in the forest. We then use RG as a single measure to describe the distance between all PAVD values and the centroid of the vertical profile. This single measure provides a proxy to general forest volume. The greater the overall height, stratification and biomass of the forest (as a function of succession), the larger the RG value. The relation between RG and succession is evident in the the RG values obtained in Early, Intermediate and Late sampling plots with no lianas (Table 1, Figure 3). The presence of lianas affect forest structure and this is registered in the distances between PAVD values and the centroid of the vertical profiles of liana infested plots, therefore affecting RG values. We have incorporated a broader explanation of this hypothesis and the meaning in the manuscript (**lines 245-260**).*

Major comment 7

- Related to the comment above, it is a bit confusing why PAI as a function of RG is studied in order to study successional trajectories (fig 3). Why where the indices not studied along an axis of stand age? What does the PAI-RG relation actually mean?

***Respons** On the manuscript (**lines 207-226**) there is a section where PAI is explained, and it is clarified what it represents in terms of forest structure in the context of the manuscript. Forest structure changes as a function of succession. PAVD and RG are proxys of forest structure. See explanation above, in the response to major comment 6.*

Major comment 8

- On page 17163 (line 17) the authors observe that there is no significant trends in fig 3 for stands with lianas. And that there is a trend for stands without lianas. However the liana stands are only available in intermediate and late succession: : : I suspects there will also not be a significant trend for the non-liana stands if you only consider the two oldest succession stages.

Response**:** *We assess the pathway by using all the available plots, and we found that the regression for the plots where lianas are absent show a statistically significant trend ($P < 0.05$), while the trend with plots where lianas are present do not show any significant trend. We have improved clarity in this point by adding the regression equation in the graph for the significant regression ($y = 1.68 \ln(x) - 5.67$, $P = 0.01$), and the equation for the plots with lianas ($y = -2.40 \ln(x) + 12.5$, $P = 0.29$.) has been added in the results (**lines 314-318**). What is interesting here is that for the plots with lianas despite the regression is not significant; the slope is negative, while for the plots without lianas the slope is positive and significant. We also included another figure with the distribution of RG across successional stages. In figure3 we can see that the RG median values show a positive and significant trend (see Table 1 for P-values), while the plots where lianas are present show no trend. We consider that by adding this figure we address the reviewer concern and provide clarity.*

Major comment 9

In the discussion the authors state that they "evaluated the role of VEGNET as a methodology to assess… However, the presented study is not an evaluation of the VEGNET tool. An evaluation of a tool should include a comparison with other methods, or at least one other method. And this is not the case in this study. The VEGNET methodology has probably been tested/evaluated in other studies, but this study should in my opinion not be presented as an evaluation of the VEGNET methodology.

Response**:** *We appreciate the comment. The reviewer is certain, and we are not assessing the VEGNET as a methodology, but instead we are assessing its utility to detect changes in vegetation structure among plots. We have re-phrased this section by stating that we used the VEGNET tool to assess differences in vertical structure, rather than assess the role of VEGNET as a tool (**lines 326-328**).*

Major comment 10

- The authors conclude on page 17165 (line 11) that their results suggest that lianas may be modifying the successional path for these forests. Although I believe that this phenomenon is very likely, the presented results are not strong enough and the setup is too limited to support this conclusion (see my comments above).

Response**:** *We acknowledge our small sample size, and the limitations of our study and that's why our conclusions in the manuscript are stated as suggestions and hypothesis. Moreover, we believe that now that we have included figure 3, it is easy to see the positive trend in stages without lianas, and how successional trajectories in stands with liana presence show no trend*

*(Figure 3, 4). We acknowledge that our study is a snapshot here and in our conclusions, but we consider the clarifications provided now about PAI, RG, and PAVD thanks to the referees, and the discussion about how vertical structure changes under liana presence (**lines 330-361**) provide enough information to suggest that lianas may be modifying the successional pathway. In this point, it is also important to mention that our conclusions are conservative, and we leave this as a hypothesis to be tested in other dry forests and more comprehensive studies (**lines 402-421**). It is also possible that temporal studies provide a clearer pattern to be able to confirm that lianas can arrest succession. A recent study with temporal LiDAR surveys found that liana-infested forests indeed have lower canopy height, supporting some of our result interpretation. We have included this reference in the manuscript and discuss the need for long-term studies using ground LiDAR in the discussion (**lines 372-400**).*

Minor comments:

- Also refer in the introduction to the recent paper of van der Heijden et al. 2015 inPNAS

Response:*Thanks for the suggestion; we have included this paper in the revised version of the manuscript*

Referee 2

We thank Referee No. 2 for his/her comments and suggestions. Some of the comments raised by referee 2 are similar to the ones provided by Referee No. 1 , so we will refer to our previous responses when appropriate.

General comments:

The authors have undertaken an interesting study of the structural effects of lianas intropical dry forests and the extent to which structural changes may be detected using ground based lidar at different stages of forest succession. Furthering our understanding of the role of lianas in forest successional processes is of great merit in terms offorest management in general and carbon accounting in particular. The use of ground based lidar (terrestrial laser scanning, TLS), as a structural measurement tool is reasonable in the context of the study. There are some aspects of the study which need to be improved to make the manuscript suitable for publication. These can be dividedintotwomaincategories:

Comment 1

1. Description of the lidar metric 'Radius of Gyration' (RG) as a means of describingforest structure. The authors have given a conceptual description, but I still have trouble understanding what it means, ecologically or structurally. For example, what would an'increase in RG' look like in the forest? On page 17165, line 5: ": : :Stands without

lianas showed a significant gradual increase in the RG. This is consistent with accumulation of basal area, vegetation material and biomass accumulation…”. How does an increase in RG relate to an increase in basal area? Some further descriptive words or illustrative (even simulated) examples of PAVD profiles with different RG values would help greatly.

***Response*:** *Thank you for the comments and we agree on the need to provide additional clarification. As described above, RG provides a proxy to general forest volume. The greater the overall height, stratification and biomass of the forest (as a function of succession), the larger the RG value. The relation between RG and succession is evident in the RG values obtained in Early, Intermediate and Late sampling plots with no lianas (Table 1). More basal area in a forest means more hits and returns registered in the laser scan, and higher PAVD values per forest height.*

*As explained in the response to Comment #6, and as inserted in **lines 245-260**, in a successional trajectory, basal area and tree height are low in an early stage forest, so RG is low as well. A PAVD profile will show a large concentration of biomass at lower heights in this case. If the forest increases in overall height and number of strata laser returns are received from greater distances and the distances between PAVD values and the centroid increase, and so the RG increases its value. So, basal area and tree height increases as trees increase their DBH towards a late stage forest, but since stem density decreases in the understory and a greater amount of hits and returns now come from branches located in the sub-canopy and the canopy, changes include not only an increase in RG value but also a change in the PAVD vertical profile where larger plant volumes can be observed in the canopy and subcanopy strata.*

The presence of lianas affect forest structure and this is registered in the distances between PAVD values and the centroid of the vertical profiles of liana infested plots, therefore affecting RG values.

Comment 2

2. Field plot selection and description. This is perhaps the biggest issue. A total of fifteen plots were sampled across three different forest successional stages: early, intermediate and late. Of these, 9 sites had lianas and 6 did not. A detailed description of these plots is critical as the basis for subsequent analyses. Specifically:

***Response*:** *We have tried to cover some of the points associated to this issue in the previous responses to the referee No. 1. We have added more details about the study setup and methods below and in the manuscript (**lines 130-176**).*

We defined successional stages as classified in previous studies for the same study area (see Arroyo-Mora et al. 2005). Successional stages as classified based on forest structure using and *age since land abandonment. Early successional stages comprise an area of sparse patches of woody vegetation and shrubs, and they only have a single stratum of tree crowns. The vegetation composition of this successional stage includes several species that lose most of their leaves during the dry season (Arroyo-Mora et al. 2005). The intermediate successional stage has 2 vegetation layers. The first one comprises fast growing deciduous tree species, shade-tolerant evergreen species and juveniles of tree species, which represent a second vegetation layer below the canopy. The late stage consists of 3 layers of vegetation. The upper layer consists of trees up to 30 m height, while the second layer consists of juveniles of all ages and heights, as well as a number of species that live entirely in the understory (Kalacska et al. 2004; Arroyo-Mora et al. 2005).*

Comment 3

a. Describe the inherent between-plot variance within succession classes without lianas. It is difficult to know whether statistically significant differences in PAI, PAVD orRG metrics could be observed between plots within the same succession class without lianas. This then makes it difficult to judge the significance of differences between plots with- and without-lianas.

Response**:** *The inherent between plot variance for the stands without lianas for PAI and RG has been already included in the manuscript on Table 1. Regarding RG, we have also included another figure where the between plot variation across stands with and without lianas can be seen (Figure 3). Regarding PAVD, we also conducted a Kruskal-Wallis and we found that PAVD was significantly higher in the late stages compared to early stages. These results are included in the manuscript (**lines 291-301**).*

Comment 4

b. What is relative location of the plots? It is interesting to note in Figure 2 that the intermediate-aged plots with lianas are approximately 4 meters taller that the intermediate plots without lianas. Is this caused by lianas or geographical differences related to climate, topography or soil. A map illustrating the plot locations would be useful.

Response**:** *Many thanks for this comment. A map with the location of the plots has been included in the text. Forest are more or less of the same age since abandonment and therefore regeneration started right after the Santa Rosa National Park was created in 1971, but we do not know why some plots lack of lianas. We have attempted to explain this in the discussion by considering some factors that influence liana abundance, but unfortunately we don't have soil data to test whether this could be a factor (**see lines 385-390**).*

Comment 5

c. In what way might the classification of age classes predetermine the observed differences in PAI, PAVD or RG metrics? Page 17158, line 15 mentions that the number of vertical strata" was one of the criteria used to differentiate age classes, a priori.

***Response*:** *Indeed, strata play a key role on the differentiation of succession as well as other elements such as LAI, PAI, canopy closure and species composition (all elements already described on several papers since 1998), but this is not what it is evaluated in the study Our interest is focused on the impact of liana presence on forest structure in successional stages and the ability of terrestrial LiDAR to detect the effect of liana presence.*

Comment 6

d. How does liana density vary between plots? Is there any way to quantify this in terms of stems-per-hectare of lianas or liana-affected trees within the plots? On page 17165, the last paragraph discusses the general lower density of lianas in late, compared to intermediate, successional stages. This naturally raises the question "how does liana density vary within and between age classes in the sampled plots"?

***Response*:** *We conducted a Kruskal-Wallis to compare the intermediate and late stages with lianas, and we did not find significant differences neither in the absolute number of lianas, neither in the number of lianas per hectare. We can add this information to the manuscript to illustrate the within-plot variation in sites where lianas are present.*

Detailed comments:

- p. 17154, line 18: ": : :distinction of vertical strata and the vertical height of accumulatedPAVD". Suggest changing this to "distinction of vertical strata and canopy height".

Response: *These changes have been made on the manuscript.*

- p. 17155, line 11: change "old growth forests" to "old growth tropical forests".

Response: *These changes have been made on the manuscript.*

- p. 17156, last paragraph.: "Ground LiDAR has demonstrated the capability to measurecanopy properties such as height and cover (Ramírez et al., 2013) and tree architecture(Lefsky et al., 2008), using terrestrial laser scanning systems (TLS): : :". Suggestremoving ": : :using terrestrial laser scanning systems (TLS)" as this is synonymouswith ground lidar in the context of this study.
  p. 17157, line 2: ": : :Laser 65 Scanners: : :". Check.

Response: *These changes have been made on the manuscript.*

- p. 17157, line 3: ": : :pulses emitted in the visible or near-infrared comes into contact with an object, part of that energy is reflected back toward the instrument: : :". Technically, other wavelengths are reflected too. Lidar systems operating in the short-wave infrared and even ultra-violet are common. Perhaps remove or qualify the wavelength specificity.

Response**:** *The wavelength has been specified in the manuscript (**line 180**).*

- p. 17157, line 23: "Significant increases in vertical structure with stand age (e.g., as aresult of increases in basal area, height and volume with stand age): : :". Despite the examples, I am a still confused by the terminology "increase in vertical structure". Do you mean "structural complexity"?

Response*: Yes, we agree with this suggestion. We have change the sentence to "Structural complexity" (**line 110-112**).*

- p. 17161, line 9: "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)". At the fixed scan zenith angle of 57.5 degrees the plot area is defined by the mean canopy height, as this dictates thehorizontal distance from the instrument when the laser exits the canopy. If the trees were all exactly the same height (h), the laser would exit the canopy at a distance of (h * tan (57.5 degrees)), or approximately 1.6h from the plot center. At h = 33 m the laserhas reached its maximum effective range of 60 m as defined on page 17160, line 17. Based on the PAVD profiles in Figure 2, the minimum and maximum canopy heights are approximately 10 m and 18 m, respectively. This translates to plot areas of 0.08 ha to 0.26 ha.

Response*: We were conservative before, but now we have inserted a calculation of the footprint in our study area using real height measurements from the instrument as suggested. The estimations now approximate what the reviewer suggested (see **lines 218-226**).*

- p. 17162, line 9: "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: : :".This is somewhat confusing. A change in what way?

Response**:** *The rationale for understanding this statement is explained in the response to the first reviewer in major comment 6 and 7, and clarification of this point has been included in the manuscript (**lines 245-260**).*

- p. 17162, line 14: “: : :the radius of gyration (RG) showed a significant increase alongin succession in plots with no lianas (Table 1): : :”. First, consider removing the words“along in succession”. Secondly, the RG metric increases in plots with no lianas in thelate successional stage plots only. In the intermediate age class the reverse seems to be true. Please clarify.

Response: *We will remove or rephrase the sentence. We disagree with the latter comment. Although an internal variation in RG values in successional stages exists, the increase in RG between successional stages is evident in Table 1 and Figure 3.*

- P. 17163, lines 14 & 15: Should the text refer to Figure 2?

Response: *These changes have been made on the manuscript.*

- p. 17166, line 12: The “vertical height of PAVD” is better described simply as “canopyheight”.

Response**:** *These changes have been made on the manuscript.*.

- p. 17174: The Figure 2 caption refers to a “Time-series” of PAVD, yet there is no timescale or differentiation of scan dates in the figure. Suggest removing the “timeseries”terminology and simply state “Figure 2. Plant Area Volume Density (PAVD)values calculated by: : :”

Response**:** *These changes have been made on the manuscript.*