

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

This article present results which seems interesting but its general organization make it difficult to appreciate. It seems to be a study with a high potential but it cannot be presented as it is now. I suggest major revisions before acceptance in BG.

R/. The comment is unclear. Without specific indication of where the “problem with the structure are”, it is difficult for us to modify specific areas of the manuscript. We have done a significant amount of modifications accepted some and rejecting some in order to improve the structure of the paper, these modifications were significant in the introduction and discussion of the paper. We hope that the changes are satisfactory.

You remove one question from the introduction but you are still discussing it. I think the ecological interpretation of your result is interesting but should be made with more detail or should be removed completely (as you seem to decide in the introduction).

R:/ Not really, our discussion focuses on the two questions at hand.

When answering the first question in the discussion (assessing “the potential of VEGNET and HPs to detect the vertical structure of forest stands at different successional stages”) you say : “This finding in fact is not new, and it has been demonstrated previously in the literature for other TDFs across the Americas including the SRNP-EMSS”. You should then change your question or precise it is just a confirmation. You can also consider removing the first question in the introduction and keep only the second one.

R/. We agree with the reviewer that this could be confusing. We have removed the sentence from the discussion. Our point fundamentally was that the changes on different forest structure variables have also been observed, using HP, in other tropical dry forests environments.

31 I think you should add at the end of the introduction a question on the ecological
32 significance of your results. You show some interesting changes of structure in the forest
33 due to liana presence and it should be discuss with more details. Then I think it should also
34 be announced in the introduction. You present the article as a methodological one while
35 interesting ecological interpretation might be made out of it.

36

37 R/. Although we appreciate the comment from the reviewer but we want to make it clear that
38 dealing with ecological aspects of liana presence, is not part of our goals. The ecological
39 significance can be very wide for interpretation, and can range from areas such as tree
40 recruitment, impacts on photosynthetic active radiation, fauna (specifically birds), mortality,
41 among many others. Expanding the paper in this are is not part of the goals of this
42 manuscript.

43

44 Results should be reorganize according to the questions of the introduction.

45

46 R/. We disagree. In the last paragraphs of introduction we say: “As such, in this paper we
47 first assess the potential of VEGNET and HPs to detect the vertical structure of forest stands
48 at different successional stages. Second, we examine how liana abundance could affect the
49 bias of prediction of VEGNET and HPs to detect the level of succession of a given forest
50 stand”. Because of this, we show first our results canonical correlation analysis and then the
51 univariate correlations. Obviously, before of these results we need to present first to the
52 readers the descriptive trends of forest structure, VEGNET, and HPs between the our factors
53 to reach our goals. We do not consider that we need to reorganize our results, not at this
54 state.

55

56 The discussion is too superficial.

57

58 R/. This is a very vague statement from the reviewer. Currently the discussion is three pages
59 long and without the standards of similar papers published by the journal. Having said that
60 we have added a new paragraph at the end of the discussion address the need of liana
61 information on global vegetation models.

62

63 Point(4) of the conclusion is not needed.

64

65 R/. We disagree, this is part of the outcome of our paper and we have made the decision to
66 keep it.

67

68 Line 48- 50 I don't understand the transition. First info might not be interesting or should be
69 explained in more detail.

70

71 R/. Thanks for the comments. We have made a modification to the first two paragraphs of
72 the introduction. Not we have a better transition.

73

74 Line 49 Cite (Phillips *et al.* 2005)

75

76 R/. We would like to cite it but there is no reference provided. We look into Phillips et al.
77 2005 and we assume that the suggested reference is

78

79 Phillips O.L et al. (2005) Large lianas are hyperdynamic elements of the tropical forest
80 canopy. Ecology

81

82 Line50 to 65 consider reorganizing to get a more relevant introduction

83

84 R/. Thank you for the suggestion. As a result of integrating Phillips et al (2005) we have
85 reorganized the first two paragraphs.

86

87 Line 63 don't understand the (?)

88

89 R/. We agree, this was corrected.

90

91 Line 90 Cite (Ledo *et al.* 2016)

92

93 R/. Again because of the lack of proper reference we have to guess on which publication the
94 reviewer is suggesting. This is making it very difficult to integrate since we have to guess
95 that the reviewer has in mind. We assume that the reference is Ledo et al. (2016) on the
96 Journal of Ecology.

97

98 Line 95 Lefsky TLS ?

99

100 R/. Correct, the reference is: Lefsky M., and McHale M.: Volumes estimates of trees with
101 complex architecture from terrestrial laser scanning. J Appl Remote Sens., 2, 023521, 2008.

102 We really do understand the “Really” comment from the reviewer.

103

104 Line 101 really biomass distribution ?

105

106 R/. Correct. New technologies as the reviewer is aware provide information on the vertical
107 and horisal distribution of biomass.

108

109 Line 105 hemispherical photographs instead of the first HPs

110

111 R/. We agree, this was corrected.

112

113 Line 163 repetition

114

115 R/. We agree, this was corrected.

116

117 Line 189 “more later” is not English

118

119 R/. We agree, this was corrected.

120

121 Line 190-192 I don't really understand

122

123 R/. The main reason for this information is because “late” tropical dry forests really do not
124 exist in Santa Rosa National Park. What we have are tropical moist forests associated to very
125 deep soils. Not the sentence reads “*We did not select “late forests” since they tend to reflect*
126 *the characteristics of tropical moist forests with structural characteristics that are very*
127 *different from true late tropical dry forests sites, “late” tropical dry forests at the SR-NP*
128 *EMSS are mostly tropical moist forests due to soil associations (Tosi, personal*
129 *communication).*” Late tropical dry forests do not exist at the SRNP as those present in
130 Chamela (Mexico) or Santa Cruz (Bolivia).

131
132 Line 195 over total number of stem

133
134 R/. We agree, this was corrected.

135
136 Line 203 you can remove “we used 11 E plots and 17 I plots, with 12 of those 203 plots
137 being LL and the other 16 plots being HL. Altogether,”

138
139 R/. We agree, this was removed.

140
141 Line 302-305 precise the angle from the vertical taken into account in the ring 4 OF THE
142 Gap Light analyzer

143
144 R/. We agree, a description of the zenith angles was included.

145
146 Line 357 (Table1) makes no sense here.

147
148 R/. We agree, the Table 1 was moved a sentence below.

149
150 Line 368 (Table2) makes no sense here.

151
152 R/. We agree, the Table 1 was moved a sentence below.

153

154 Line 360 – 362 “In terms of the effect of the liana abundance, the univariate analysis
155 suggests that plots with LL showed lower values of L/TBA in comparison with HL plots. »
156 Isn't it circular? I thought liana load was determined by L abundance and then L/TBA was
157 necessarily high in HL plot than in LL plots by definition.

158

159 R/. We disagree, this is not circular, but this could be correlated. This sentence is making a
160 reference about the relationship between abundance of lianas and its structure in terms of the
161 contribution of lianas to the total basal area. If we make an analogy with trees during the
162 successional trajectories, in early successional states we can found high abundance of trees
163 with low contribution of each individual to the total basal area, but in the intermediate or late
164 successional stages there is a shift in which we can found low abundance of trees but with
165 high contribution of each individual the total basal area; these trend could be expected also
166 during the successional trajectories of lianas. It is expected to have a correlation between
167 these two parameters but this correlation may not mean causality, because of this, we need
168 to highlight it.

169

170 Line 410-412 Unclear, do you suggest to use the strength of the correlation between Hmas
171 and TBA to distinguish between plot rich and poor in liana respectively? Is that true only for
172 intermediate stage of succession?

173

174 R/. We agree, this was corrected.

175

176 Line 444-447 Reformulate: “lianas deploy leaves in the canopy and create large amounts of
177 tangles in both the ground and mid canopy, in order to reduce the amount of light available
178 as well as the amount of incoming solar radiation available for photosynthesis for other plant
179 species”.

180 Stated like that it seems wrong or at least highly over-interpreted. There is no evidence of
181 intention in tangle constitution by lianas... Moreover liana leaves deployment is probably
182 linked with their role in energy supply for the liana itself.

183

184 R/. Agreed, now it reads *“In disturbed sites, such as secondary forests, lianas deploy leaves*
185 *in the canopy and create large amounts of tangles in both the ground and mid canopy, this*
186 *high density of tangles contribute to a reduction on the amount of available transmitted*
187 *incoming solar radiation available for photosynthesis at the understory (Sanchez-Azofeifa et*
188 *al. 2009, Graham et al., 2013).”*

189

190 Line 456-459 The sentence is not precise enough. You should mention which parameters
191 were useful and why. Hypotheses on why the other parameters did not provide relevant
192 information may also be interesting.

193

194 R/. Fully agree and we appreciate the comment. Now it reads *“Our observations from*
195 *changes on DBH_{mean}, TBA, LAI and canopy openness as function of liana abundance provide*
196 *evidence that these variables can be used to estimate the impact of lianas on forest structure*
197 *along the path of succession, although not all of parameters, such as stem density and*
198 *L/TBA, were significant.”*

199

200 Line 465 “It is surprising that we did not find differences in the PAI values between stands
201 that did and did not have” I don’t understand the sentence.

202

203 R/. Agreed, it is very confusing. Not it reads *“It is surprising that we did not find differences*
204 *in the PAI values between stands that did and did not have lianas.”*

205

206 **Table 1** Stem density should be mentioned with unity (stem/ha ?)

207

208 R/. We agree, the unit of stem density was included.

209

210 The two interesting result here are the interactions between liana abundance (condition if I
211 well understood) and stage for TBA and DBH.

212

213 R/. Correct and we address this in the results of our paper.

214

215 The lower TBA and DBH at intermediate stage with HL make me think of the condition of
216 an earlier succession. It could be interpreted using results from Schnitzer et al
217 (2000,2010,2011), van der Heijden et al (2013), Tymen et al (2016).

218

219 R/. Agreed but this will only make sense if we were thinking about a tropical rainforest or
220 moist forests sites; but the plots that represent our conditions at Santa Rosa (where the
221 precipitation gradient MAP ca. 1250 mm) are very different from those plots were Schnitzer
222 et al. and our other colleagues conduct their work, so the comparison/comment is not valid.
223 For example. Some of the provide references are from Barro Colorado Island in Panama and
224 other from the Brazilian Amazon (If we are correct) with totally different ecological and
225 biophysical conditions than our sites in Costa Rica which makes the observation not valid,
226 but having been on those sites we fully understand where the reviewer comes from.

227 Furthermore, the new work in tropical dry forests by Schnitzer et al. from the Azuero
228 Peninsula in Panama (which we could argue is close to our tropical dry forests in Santa Rosa
229 although with significant high level of degradation compared with our site) is only starting
230 to emerge, and it is the only site which we feel we could eventually make comparisons to
231 Santa Rosa, Costa Rica.

232

233 The higher TBA in early HL plots may come from a higher stem density, this could also be
234 discussed more deeply.

235

236 R/. We think that this is a good point; early Tropical Dry Forests (at least from our
237 observations in Mexico and Costa Rica) tend to have a significant large number of stems that
238 in turn will affect TBA but this is site specific since we do not observe this on our Brazil
239 sites. But we fail to see how the discussion will contribute to the goals of our paper therefore
240 we made the decision to expand on this aspect.

241

242 **Table 2**

243 High Liana abundance reduces canopy openness and increase LAI without direct relation on
244 PAI. How canopy openness can be reduce without increasing PAI?

245

246 R/. PAI is a combination of Plant Area Index (PAI), LAI and Woody Area Index (WAI). Not
247 just LAI alone, as such $PAI = LAI + WAI$. Therefore, if PAI remains the same and canopy
248 openness is reduced this is probably due to an increase of WAI (largest amount of liana
249 biomass from tangles in mid canopy as we are observing at this time with a higher resolution
250 LiDAR system which is allowing to map a vertical distribution of biomass). This is very
251 common in sites like Chamela and Santa Rosa but again not in Brazil, our Sanchez-Azofeifa
252 et al (2009) paper touches on this. Furthermore, it is unclear if lianas truly contribute to a
253 significant amount of leaves to a given canopy. Some authors suggest probably up to 5%,
254 therefore we cannot generalize with a broad statement such as “Liana abundance reduces
255 canopy openness and increase LAI without direct relationship to PAI.” Other factors such as
256 extremely high density of tangles can play a role.

257

258 PAI and PAVD decrease with succession in LL plots, that is very strange, it has to be
259 discussed

260 Cx variation should be interpreted.

261

262 R/. Thank you for your comment. We discussed this point in our discussion, specifically we
263 added the following comment: *“As lianas emerge along they path of succession they create
264 a more heterogenous space which is captured by the variability on C_x . C_x is affected by PAI
265 and $PAVD_{mean}$ as function of understory components (shurbs, grasses and also liana
266 tangles). A higher value of C_x may be interpreted on an E-LL as a high dominance of shubrs,
267 tall grasses and short trees; while a high value of C_x on a E-HL will mean a high
268 distribution of tangles combined with shurbs which make accessibility impossible to some
269 sites due to a high density of understory liana tangles.”*

270

271 **Figure 1**

272 Nice figure!

273

274 R/. Thank you.

275

276 **Figure 2**

277 The values of the first eigenvalues could be mentioned somewhere. Why did you choose to
278 take two?

279

280 R/. We partially agree. The four parameters selected were those with the two highest
281 correlation values for the VEGNET-HPs matrix and the two parameters with the highest
282 correlation values for forest structure, determined by the first two canonical dimensions
283 described by the CCA. Our selection was not based on eigenvalues, it was based on values
284 of correlation; sorry for the misunderstanding. However, those values of correlation can be
285 observed in the Figure 2a. Why did we choose to take two? Well we have 4 parameters for
286 forest structure and 8 parameters of VEGNET-HPs, if we make a correlation without and
287 with distinction between successional stages and the relative liana abundance between those
288 parameters we need to do 160 analyzes which is a huge number and many of those
289 correlations could not have an important logic of our line of reasoning. Because of this, we
290 selected those parameters with the highest values of correlation or the highest “importance”
291 to reduce the number of analyzes.

292 |

293
294
295
296
297
298
299
300
301
302
303
304
305
306
307
308
309
310

Can Terrestrial Laser Scanner (TLS) and hemispherical photographs predict Tropical Dry Forest Succession with liana abundance?

G. Arturo Sánchez-Azofeifa^{a*}, Mauricio Vega-Araya^b, J. Antonio Guzmán Q.^a, Carlos Campos-Vargas^a, Sandra M. Durán^a, Nikhil D’Souza^a, Thomas Gianoli^a, Carlos Portillo-Quintero^c, Iain Sharp^a

^a Center for Earth Observation Sciences (CEOS), Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

^b Laboratorio de Teledetección de Ecosistemas (LabTEc), INISEFOR-Universidad Nacional de Costa Rica, Heredia, Costa Rica, Central America

^c Department of Natural Resources Management, Texas Tech University, Lubbock, Texas, USA.

* Corresponding author. Tel. +1-780-4921822; E-mail address: gasanche@ualberta.ca

311 **Abstract**

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

332

333 1 Introduction

334 Lianas, woody vines, are a key structural component of tropical forests; they account
335 for 25–40% of the woody stems and more than 25% of the woody species (*Schnitzer and*
336 *Bongers, 2011*). Lianas are structural parasites that use trees to ascend to the forest canopies
337 and move from tree to tree. Lianas have been defined as hyper-dynamic elements of the
338 canopy structure (*Phillips et al. 2005, Sánchez-Azofeifa and Castro, 2006*). Lianas can be
339 detrimental to host trees by competing with them for above- and belowground resources
340 (*Chen et al., 2008*), reducing tree growth rates, and increasing tree mortality (*Schnitzer and*
341 *Carson 2010, van der Heijden et al., 2013*). ~~(*Durán and Gianoli, 2013; van der Heijden et*~~
342 ~~*al., 2015*).~~
343 ~~Lianas have been defined as hyper-dynamic elements of the canopy structure~~
344 ~~(*Sánchez-Azofeifa and Castro, 2006*).~~ In the last two decades lianas have increased in
345 density and biomass in old-growth forests (*Phillips et al., 2002; Schnitzer and Bongers,*
346 *2011*), and this increment is considered to be one of the major structural changes in tropical
347 forests (*Phillips and Lewis, 2014*). These structural changes mentioned above may have
348 potential negative effects on carbon stocks since they tend to reduce carbon storage and
349 uptake in old-growth tropical forests (*Durán and Gianoli, 2013; van der Heijden et al.,*
350 *2015*). Liana dynamics in secondary forests and their impact on forest structure, however,
351 are not yet understood despite the fact that secondary forests are becoming increasingly
352 dominant in tropical regions, and currently occupy more area than old-growth forests (*Durán*
353 *and Sánchez-Azofeifa, 2015; Wright, 2005*).

354 Lianas are considered light-loving plants, because they tend to respond positively to
355 disturbance and show high density in areas of secondary forest succession (*Paul and Yavitt,*

356 | 2011). Furthermore, secondary forests may promote liana abundance because they provide
357 | both high light availability and an abundance of trellises (*Schnitzer and Bongers, 2002*). As
358 | tree turnover increased gaps due to mortality, lianas can take advantage of this process and
359 | form dense tangles, which in turn reduce the amount of light reaching the forest understory
360 | (*Paul and Yavitt, 2011; Schnitzer et al., 2000*). These liana tangles can persist for long
361 | periods (up to 13 years) and alter the successional pathway stalled by liana abundance by
362 | inhibiting the regeneration, growth, and density of late successional species (*Schnitzer et al.,*
363 | *2000*).

364 | As of today, it is still unknown whether lianas can alter successional trajectories in
365 | secondary forests resulting from anthropogenic disturbance (*Durán and Sánchez-Azofeifa,*
366 | *2015*). Two studies in secondary wet forests have found an increment in liana density in the
367 | first 20 years of regeneration (age since land abandonment), with a subsequent decline
368 | (*DeWalt et al., 2000; Letcher and Chazdon, 2009*). This decline of lianas in wet forests
369 | appears to be related with reductions in light availability due to greater tree and shrub
370 | biomass at later stages of succession (*Letcher and Chazdon, 2009*). Nonetheless, it remains
371 | unclear whether this pattern holds true with more open forest types, and whether other
372 | factors such as structure, canopy openness, plant density and the volume of forest stands can
373 | also influence successional trajectories of lianas (*Durán and Sánchez-Azofeifa, 2015;*
374 | *Sánchez et al., 2009*).

375 | Despite the fact of the important effect of lianas on the biomass distribution within
376 | tropical forests (*Schnitzer and Bongers, 2011; Ledo et al. 2016*), and their potential role as
377 | fingerprints of climate change (*Phillips et al. 2005*), remote sensing tools aimed to measure
378 | their presence/absence as well as their distribution within tropical forests are limited (*Foster*

379 et al., 2008, Kalacksa et al. 2007a & b, Zhang et al. 2006). Current knowledge based on leaf
380 spectroscopy approaches provides two key messages regarding liana extent mapping: first
381 that lianas in tropical rainforests tend to confuse the spectral reflectance of their host trees
382 making it in many cases impossible to use remote sensing to create species maps (Castro-
383 Esau et al., 2004), and second that there is a higher degree of probability of success for
384 efforts aimed to map liana coverage in tropical dry forests than on rain forests environments
385 (Sanchez-Azofeifa et al., 2009b; Kalacska et al. 2007b).

386 Moreover, studying the impact of lianas on tropical dry forest structure, Sanchez-
387 Azofeifa et al. (2009) used hemispherical photography over a succession of tropical dry
388 forests in Mexico, Costa Rica and Brazil, found that lianas infested sites were significantly
389 different in both canopy openness and Woody Area Index (WAI). Findings associated to
390 WAI impacts were significant since this structural variable when associated to Leaf Area
391 Index (LAI), is used to defined the concept of Plant Area Index (PAI = LAI + WAI).

392 Initial attempts aimed to start untangling the effects that lianas have on remote
393 sensing observations may require data fusion techniques on which hyperspectral remote
394 sensing approaches (leaf spectroscopy finding) are merged with ground based forest
395 structure information derived from terrestrial laser scanners and hemispherical photography
396 (e.g. LAI, WAI and PAI). Terrestrial Laser Scanners (TLS) have demonstrated their capability
397 to measure canopy properties such as height and cover (Ramírez et al., 2013) and tree
398 architecture (Lefsky et al., 2008), (Dassot et al., 2011; Richardson et al., 2014). In the last
399 decade, there has been a rapid development in portable TLS (Dassot et al., 2011; Richardson
400 et al., 2014). When laser pulses emitted in the visible or near-infrared come into contact with
401 an object, part of that energy is reflected back toward the instrument which triggers the

402 recording of its distance and intensity (Beland *et al.*, 2014). TLS systems typically employ
403 vertical and horizontal scanning around a fixed point of observation, providing a
404 hemispherical representation of biomass distribution in the forest -leaves, branches and
405 trunks- which allows for the exploration of foliage angle distributions and clumping
406 (Clawges *et al.*, 2007; Jupp *et al.*, 2009; Strahler *et al.*, 2008).

407 | Until today, there has been no concrete evidence about how liana abundance can
408 | affect the prediction of the forest structure by TLS or [hemispherical photographs](#) (HPs),
409 | [which in turn can drive the development of better remote sensing techniques for mapping](#)
410 | [their extent](#). Because of this, the objective of this study was to evaluate the feasibility of a
411 | TLS named VEGNET in combination with HPs to assess changes in forest structure in
412 | secondary TDFs with different levels of lianas abundance. The VEGNET is a TLS that
413 | automatically scans a forest plot producing a vertical foliage density profile. Given its
414 | automated mode of operation and semi-permanent installation, the VEGNET instrument is
415 | described as an *in situ* Monitoring LiDAR (IML) (Culvernor *et al.*, 2014; Portillo-Quintero
416 | *et al.*, 2014).

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

423

424 **2 Methods**

425 2.1 Study Area

426 The study area is located in the Santa Rosa National Park Environmental Monitoring Super
427 Site (SRNP-EMSS), which is a part of the Guanacaste Conservation Area in Costa Rica
428 (10°48" N, 85°36" W) (Figure 1). This site covers an area of 50,000 ha, receives 1720 mm
429 of annual rainfall, has a mean annual temperature of 25°C and a 6-month dry season
430 (Dec–May) (Kalácska *et al.*, 2004). The SRNP-EMSS site has suffered intense deforestation
431 in the past 200 years due to the expansion of pasturelands (Calvo-Alvarado *et al.*, 2009).
432 Original land management practices in the park included pasture rotation between different
433 large corrals surrounded by life fences that can still be identified today. More recently (early
434 1970's) with the creation of Santa Rosa National Park, a process of secondary regeneration
435 has become the dominant land cover change force in the region. Today and after the creation
436 of SRNP, the uplands of the park are a mosaic of secondary forest in various stages of
437 regeneration and with different land use histories related to anthropogenic fires, intense
438 deforestation, and clearing for pasture lands (Kalácska *et al.*, 2004; Arroyo-Mora *et al.*,
439 2005a, Cao *et al.*, 2015).

440

441 2.2 Definition of forest cover and plot age.

442 A map of forest cover and forest cover ages was generated using aerial photographs
443 collected by the US Army in 1956 (Scale 1:24,000), a Multispectral Scanner (MSS) image
444 from 1979 (80 m spatial resolution); 4 Landsat Thematic Mapper [TM] images from 1986,
445 1997, 2000 and 2005 (28.5 m spatial resolution); one Spot Multispectral image from 2010
446 (20 m spatial resolution); and a Landsat 8 image from 2015. All images had less than 10%
447 cloud cover.

448 The 1986 image was georeferenced to 1:50,000 topographic maps from the Costa Rica
449 National Geographic Institute with a Root Mean Square Error (RSME) of 0.5 pixels or 14.25
450 m. We defined this as our master image in order to georeference all of the other images, as
451 such all other images were then geo-referenced to the 1986 image seeking a RMSE close to
452 0.5 pixels between the master and the target image. All images were then classified using a
453 supervised classification. Image accuracy was conducted for the 1997, 2000, 2005 and 2010
454 satellite images as part of independent validation efforts conducted by the Costa Rica's
455 National Forest Financing Fund (FONAFIFO). Overall accuracy for the forest/non-forest
456 images was 90%. Further information on image processing can be found in [Sánchez-](#)
457 [Azofeifa et al. \(2001\)](#).

458 Final quality controlled forest cover maps (forest non-forest) for 1956, 1979, 1986, 1997,
459 2000, 2005, 2010 and 2015 were cross referenced to produce a tropical dry forest age map.
460 Specifically, forest coverage with 60 years old correspond to woodlands which were being
461 observed in images since 1956; forests that were 40 years old were not detected in 1956 but
462 have been recognizing as forests since 1979; on the other hand, woodlands that were referred
463 to as being 10 years old have a minimum of 10 years as a discriminable forest coverage.

464 Based on [Arroyo-Mora et al. \(2005b\)](#) and [Kalascka et. al's \(2005a\)](#) studies the following
465 successional classification was developed: Ages 10 to 40 years (Early), and ages 40 to 60
466 (Intermediate). Figure 1 presents the final land cover and forest age map for our study area.

467

468 **2.3 Plots selection and description**

469 Based on Figure 1, twenty-eight randomly stratified 0.1ha plots were selected. The number
470 of plots chosen for each forest successional stage was based upon each stages total forest cover

471 area. Plot sizes of 0.1 ha follows convention used in tropical forest studies at this site (Kalascka
472 et al. 2005a). Fieldwork conducted in July 2016 was conducted in order to characterize
473 diameter at breast height (DBH), tree height, total biomass, VEGNET observations (canopy
474 vertical profiles) and hemispherical photos (Canopy openness and Leaf Area Index).

475 The characterization of successional stages was performed following previous approaches
476 for seasonally dry forests of Costa Rica (Arroyo-Mora et al., 2005b; Kalácska et al., 2005) and
477 adjusted according to the estimated forest ages (Figure 1). These approaches categorized the
478 secondary regeneration in different successional stages such as early and intermediate
479 successional stages (*E* and *I*, respectively) (Arroyo-Mora et al., 2005a). The *E* stage is a
480 forest area with patches of sparse woody vegetation composed of shrubs, small trees, and
481 saplings, with a thick herbaceous understory, and with a single stratum of tree crowns with a
482 maximum height of less than 10 m (Castillo et al., 2012). Some of the common species that
483 are characteristic of this early stage of succession includes *Genipa americana*,
484 *Cochlospermum vitifolium*, *Gliricidia sepium*, *Randia monantha* (Hilje et al., 2015;
485 Kalácska et al., 2004). In contrast, the *I* stage has two vegetation strata composed of
486 deciduous species of woody plants. The first strata is comprised of fast-growing deciduous
487 tree species that reach a maximum height of 10–15 m (e.g., *Cydista aequinoctialis*) and the
488 second stratum is represented by lianas and vines, adults of shade-tolerant and slow-growing
489 evergreen species as well as the juveniles of many species such as *Annona reticulata*,
490 *Ocotea veraguensis*, and *Hirtella racemosa* (Arroyo-Mora et al., 2005a; Kalácska et al.,
491 2004). No lianas were present in the early successional stage plots. Lianas in early forests
492 tend to be more present during the transition from early to intermediate stages. We did not
493 select “late forests” at our study site since they tend to reflect structural characteristics

494 | (DBH, three height and species composition) associated tropical moist forest (Tosi, personal
495 | communication).

496 | On the other hand, the characterization of the plots according to the liana abundance was
497 | based on the structure of plants that compose the tropical dry forest of SRNP-EMSS. In this
498 | way, we classified the 28 plots according to the relative abundance of stems of lianas over
499 | total number of stems, where plots with a relative abundance greater than 0.1 were
500 | categorized as plots having high liana abundance (HL), while plots with a relative
501 | abundance lower than 0.1 were categorized as having a low liana abundance (LL). Although
502 | this classification seems to be in-deterministic, this kind of classification represents an
503 | important ecological component which is very difficult to study as a continuum due to its
504 | spatial and temporal variation, and its categorization can help to improve the understanding
505 | of ecological processes as many other ecological categories.

506 | At the end of this characterization, our plots for the study consisted of 5 *E*-LL plots, 6
507 | *E*-HL plots, 7 *I*-LL plots, and 10 *I*-HL plots. In each of these plots we extracted the available
508 | information that described the complexity of the dry forest according to its structure, but at
509 | the same time deployed the ground LiDAR and hemispherical photograph measurements to
510 | predict and describe that complexity. Information about the parameters used and estimated
511 | according to the forest structure, ground LiDAR, and hemispherical photographs is
512 | described below.

513

514 | **2.4 Forest structure**

515 | Four parameters that characterize the forest structure were used in this study. These
516 | parameters were selected because these are easily obtained in any forest inventory, which

517 could help in the applicability of this study in other regions. Specifically, we selected the
518 stem density (stems/ha) as a parameter to describe the number of individuals per plot, the
519 mean diameter at breast height (1.3 m) (DBH_{mean} , cm) as a parameter that can describe the
520 mean size of the individuals, the total basal area (TBA, m^2) as a parameter that can describe
521 the biomass of each plot, and the ratio of liana basal area to TBA (L/TBA) as a parameter
522 that can describe the contribution of lianas biomass to the total biomass of each plot. Each of
523 these parameters was extracted from DBH measurements for lianas (>2.5 cm) and trees (>5
524 cm).

525

526 **2.5 Ground LiDAR measurements**

527 The VEGNET ground LiDAR system was deployed in the middle of each of the selected
528 plots, in which a single successful scan was performed between June 12th to June 27th, 2016.
529 The VEGNET IML instrument uses a phase-based laser rangefinder with a wavelength of
530 635 nm, in which a laser beam is directed at a rotating prism that reflects the laser at a fixed
531 angle of 57.5° zenith or the “hinge angle” (*Jupp et al., 2009*). The prism is designed to
532 perform full 360° azimuth rotations at this fixed zenith angle (no vertical scanning motion)
533 and has the capability to be programmed to obtain up to 7360 range measurements for a full
534 azimuth scan (an average of 20.6 measurements per azimuth degree) (*Culvenor et al., 2014*).
535 Because sunlight irradiance may cause interference with the VEGNET laser at the same
536 wavelength (*Culvenor et al., 2014, Portillo-Quintero et al., 2014*), measurements for the
537 VEGNET were conducted at night. Some tests of the measurement process by VEGNET at
538 night time indicated that at distances greater than 60 m or in areas larger than 3600 m^2 (0.36
539 ha) the laser beam does not provide reliable measurements (*Culvenor et al., 2014*). In a

540 tropical forest setting, data analysis and interpretation may be restrained to the footprint,
541 which is dependent on forest height at each site. Based on the forest heights of our study
542 sites, the effective footprint of LiDAR measurements was within 0.1ha of our original
543 sampling area.

544 From these measurements at night six parameters were estimated: the maximum tree
545 height (H_{\max}), the plant area index (PAI), plant area volume density (PAVD), the centroid of
546 x (C_x) and y (C_y), and the radius of gyration (RG). To estimate these parameters, the height
547 (h) was initially calculated as the cosine of the laser zenith angle (57.5°) multiplied by the
548 laser distance measurement (d) assuming that the terrain is flat as describe *Culvenor et al.*
549 (2014).

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

554

$$555 \quad P_{\text{gap}(z)} = [\#z_i < h] / N \quad (1)$$

556

557 Consequently, the estimation of cumulative plant area index (PAI) by the conversion of
558 $P_{\text{gap}(z)}$ was performed using the following the equation (*Culvenor et al., 2014*):

559

$$560 \quad \text{PAI}_{(z)} = -1.1 \times \ln(P_{\text{gap}(z)}) \quad (2)$$

561

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

$$565 \text{PAVD}_{(z)} = \delta \text{PAI}_{(z)} / \delta z \quad (3)$$

566
567
568 It is important to note that these calculations represent tridimensional variations (x , y ,
569 z) of the forest structure (*Culvenor et al., 2014*), because of this, in our statistical analysis
570 we used the maximum h estimated by the LiDAR per plot (H_{\max}), the cumulative PAI as a
571 function of the canopy height (PAI), and the mean PAVD at different heights (PAVD_{mean}).
572 These calculations were extracted using the “VEGNET Data Display and Export Version
573 2.5” software developed by Environmental Sensing Systems Inc (Melbourne, Australia).

574 Likewise, from the LiDAR measurements we also used shape metrics such as the
575 centroid (C) and radius of gyration (RG) to understand how the vertical profile of the forest
576 could change according to successional stages and liana abundance. The RG and the C are
577 metrics that are mainly used in LiDAR waveforms to describe the motion of objects and the
578 manner in which material is distributed around an axis (*Muss et al., 2013*). We used a
579 similar approach by calculating the C and the RG for the PAVD vertical profile of each plot.
580 Specifically, C represents the geometric center of a two-dimensional (x and y) region (e.g.,
581 the arithmetic mean position) of all the points (n) in the shape of the PAVD profile [and it](#)
582 [could, specially, be interpreted as the variability of PAI with height and it will change as a](#)
583 [function of understory changes along the path of succession \(grasses to shrubs to short](#)

584 | [trees](#)). [On the other hand](#), RG is the root mean square of the sum of the distances for all
585 | points on the PAVD vertical profile, which is described as:

586

$$587 \quad RG = \sqrt{\frac{\sum(x_i - c_x)^2 + \sum(y_i - c_y)^2}{n}} \quad (4)$$

588

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

600

601 | **2.6 Hemispherical photographs**

602 | Hemispherical photographs (HPs) were taken during the early morning in the middle of each
603 | plot, using a digital camera (E4500, Nikon, Tokio, Japan) equipped with a fisheye lens of 35
604 | mm focal length. The camera was leveled at 1.50 m by a tripod and orientated towards
605 | magnetic north, in order to ensure photographic standardization. The resulting pictures were
606 | analyzed using the software Gap Light Analyzer version 2.0.4 (*Frazer et al., 1999*). This

607 analysis was performed by creating 340 sky sectors (36 azimuth classes and 9 elevation
608 angle classes) with a time series of 2 min along the solar track. The leaf area index (LAI)
609 and the canopy openness were subsequently extracted by this analysis; however, the LAI
610 was extracted using the “4 ring” (with a zenith angle between 0 to 60°) which is a more
611 accurate depiction of the site than using “5 rings” because the latter takes into account trees
612 that are not immediately surrounding the site, and which are found outside of the plot
613 footprint.

614

615 **2.7 Statistical analysis**

616 This study compared the effect of the successional stages, the abundance of lianas, and their
617 interaction on the parameters of forest structure as well as VEGNET-HPs parameters using a
618 multivariate analysis of variance (MANOVA), in order to demonstrate that this study had
619 been conducted in contrasting environments. For each MANOVA we extracted the
620 univariate analysis of variance (ANOVA) to describe the multivariate effects of each
621 parameter. To show the potential of the VEGNET and HPs to predict variations in the
622 structure of the dry forest, we applied a canonical correlation analysis (CCA) using the
623 VEGNET-HPs parameters as independent variables and the features of the forest stand as
624 dependent variables. Due to the CCAs sensitivity to the collinearity among variables (*Quinn
625 and Keought, 2002*), we only used RG, PAI, PAVD_{mean}, H_{max} , LAI, and canopy openness as
626 independent parameters. Specifically, the CCA was used to extract the canonical correlation
627 between VEGNET-HPs and forest structure (eigenvalues), the correlation between the
628 canonical variates and each matrix (eigenvectors), and the scores that describe the
629 multidimensional variation of each plot according to its correlation. To extract the statistical

630 significance of the canonical correlation coefficients, we computed an asymptotic test on the
631 first canonical dimensions to extract the F -approximations of Wilks' Lambda along with its
632 significance. This statistical significance was subsequently validated using a permutation
633 test on each dimension by 10000 iterations.

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

652 values were used to build density plots to describe the bias of prediction according to its
653 overlap.

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

660

661 **3 Results**

662 **3.1 Changes on forest structure along the path of succession and liana abundance**

663 According to the MANOVA the forest structure of our plots differed between successional
664 stages (Wilk’s $\Lambda_{(4,21)} = 0.51; p < 0.01$) and liana abundance (Wilk’s $\Lambda_{(4,21)} =$
665 $0.58; p < 0.05$), but without interaction between these categories (Wilk’s $\Lambda_{(4,21)} =$
666 $0.76; p = 0.20$). This analysis suggests that the DBH_{mean} and TBA were the only parameters
667 affected by the interaction between successional stages and liana abundance, where E
668 successional plots with LL and I plots with HL showed lower values of DBH_{mean} and TBA
669 than E and I plots with HL and LL, respectively (Table 1). In terms of the effect of the liana
670 abundance, the univariate analysis suggests that plots with LL showed lower values of
671 L/TBA in comparison with HL plots.

672

673 **3.2 VEGNET-Hemispherical Photographs (HPs), forest succession, and liana** 674 **abundance**

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

689

690 | **3.3 Canonical correspondence analysis and trends of forest structure**

691 The CCA showed that sensor parameters are strongly associated with the trends in forest
692 structure (Fig 2). In general, the first and second canonical dimension showed correlations of
693 0.81 (Wilk's $\Lambda_{(24,64.01)} = 0.13$; $p < 0.01$) and 0.72 (Wilk's $\Lambda_{(15,52.85)} = 1.46$; $p =$
694 0.16) between our sensors and forest structure. Specifically, the correlation between the
695 canonical variates in the first canonical dimension suggested that canopy openness and the
696 LAI have a great weight in the sensor matrix, while L/TBA and stem density had an
697 important effect on the forest structure (Fig 2a). Likewise, the correlation between the

698 canonical variates in the second canonical dimension showed that H_{\max} and $PAVD_{\text{mean}}$ had a
699 strong correlation with the sensor parameters, while TBA and steam density had a strong
700 correlation on the forest structure. The scores that described the multidimensional variation
701 of each plot did not reflect a visual aggregation according to the successional stages and
702 liana abundance (Fig. 2b). In terms of the validation of the significance of the canonical
703 correlation coefficients, the permutations test showed that there is an important increase in
704 the significance of the first two canonical dimensions (Fig. 2c, 1d), where the first
705 dimension presented an increase of 0.21 points for the Wilks's statistic, while the second
706 dimension showed an increase of 0.25 points, which results in a significant effect.

707

708 **3.4 Comparison of correlations between successional stages and liana abundance**

709 The different trends of correlation showed that the successional stages and mainly the liana
710 abundance have an important effect in the prediction of the forest structure using VEGNET-
711 HPs parameters (Figure 3), but at the same time, these trends showed that some of these
712 parameters have the potential to predict the implication of the liana abundance on the forest
713 structure. Specifically, variation in the correlations of canopy openness on L/TBA (Figures
714 3a, b, c) and H_{\max} on TBA (Figures 3g, h, i) showed that the correlation trends between
715 successional stages are overlapped, while the correlations trends between liana abundance
716 are separated, in where low values of canopy openness and H_{\max} are associated with high
717 values of L/TBA and TBA, and consequently with the discrimination of HL plots. Likewise,
718 variation in the correlation between LAI and L/TBA showed that the trends might not be
719 used to separate successional stages or liana abundance (Figures 3d, e, f). However, the
720 correlation between H_{\max} and TBA suggest that H_{\max} can not discriminate between different

721 successional stages, but can discriminate with different liana abundance (Figures 3j, k, l),
722 where lower values of correlation are associated with HL plots.

723

724 **4 Discussion**

725 4.1 Potential of VEGNET and HPs to detect the vertical structure of forest stands at 726 different successional stages

727 Woody vines or lianas tend to proliferate in disturbed forest stands such as regenerating
728 forests (*Paul and Yavitt, 2010*). Much research on liana ecology, however, has focused on
729 old-growth forests despite that secondary forests currently cover a larger area than old-
730 growth forests and may become the dominant ecosystem in tropical regions (*Wright, 2005*).

731 Due to shorter stature and a higher variability of light in secondary forests, lianas may be
732 particularly abundant in these ecosystems, but little is understood about the role of lianas in
733 forest succession (*Letcher and Chazdon, 2009*). In this study, we used the VEGNET, a
734 terrestrial LiDAR system combined with HPs, to assess the impact of liana abundance on
735 forest succession. Our overall analysis indicated that VEGNET parameters, in combination
736 with HPs derived information, were able to characterize changes in forest structure at
737 different successional stages with and without lianas. Changes observed using HP, along the
738 successional gradient, we similar to those observed in other tropical dry forests
739 environments where parameters such as biomass, LAI, Canopy Openess and H_{\max} changed
740 as trees grow (*Sanchez-Azofeifa et al. 2009*). Our work using the TLS suggested also that
741 this technology can be also used to detect differences along the forest succession trajectory
742 when lianas are integrated into the analysis. In terms of the comparison of VEGNET
743 parameters between our categories, probably the effect of the interaction of the successional

744 stages and liana abundance on C_x , PAI and $PAVD_{mean}$ are some of the most revealing. As
745 lianas emerge along their path of succession they create a more heterogeneous space which is
746 captured by the variability on C_x . C_x is affected by PAI and $PAVD_{mean}$ as a function of
747 understory components (shrubs, grasses and also liana tangles). A higher value of C_x may be
748 interpreted on an E-LL as a high dominance of shrubs, tall grasses and short trees; while a
749 high value of C_x on an E-HL will mean a high distribution of tangles combined with shrubs
750 which make accessibility impossible to some sites due to a high density of understory liana
751 tangles.

752

753 4.2 How liana abundance could affect the bias of prediction of VEGNET and HPs to 754 detect the level of succession of a given forest stand?

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

764 This change in deterministic patterns of the forest structure is probably due to
765 competition between lianas and trees in forest stands within a random 3D space. In disturbed
766 sites, such as secondary forests, lianas deploy leaves in the canopy and create large amounts

767 of tangles in both the ground and mid canopy, this high density of tangles contribute to a
768 reduction on the amount of available transmitted incoming solar radiation available for
769 photosynthesis at the understory (Sanchez-Azofeifa et al. 2009, Graham et al., 2013).
770 Moreover, in regenerating stands within forests (e.g., treefall gaps), high densities of lianas
771 can inhibit the regeneration of tree species and reduce the abundance of shade-tolerant trees
772 (Schnitzer et al., 2000), which in turn can affect the 3D arrangement of species within a
773 given area. These ecological processes may cause a shift in forest structure, which is
774 detected as a shift in the vertical structure signature by TLS in sites with high liana
775 abundance. These differences in structures have been confirmed in a recent study, which
776 found that a liana-infested forest had a more irregular canopy with canopy heights between
777 10 and 20 m, while the surrounding forests had a significantly taller canopy between 25 and
778 35m along with a denser canopy (Tymen et al., 2016). Together, our results and Tymen et al.
779 (2016) observations could highlight the potential of entropy analysis of the forests to detect
780 the presence and the effect of lianas on the forest structure and the pathways of succession.

782 4.3 A cautionary tale associated to emergent TLS monitoring technologies applied to 783 liana-infested sites

784 Our observations from changes on DBH_{mean}, TBA, LAI and canopy openness as function of
785 liana abundance provide evidence that these variables can be used to estimate the impact of
786 lianas on forest structure along the path of succession, although not all of parameters, such
787 as stem density and L/TBA, were significant. In other words, there is a strong need to
788 carefully select which parameters should be considered if we want to estimate changes in the
789 forest structure as function of liana abundance. One key example is the use of PAI (PAI=

790 [LAI + WAI](#)) as tool to evaluate the impact of liana abundance on forest succession. PAI as a
791 single measurement theoretically could provide insights on the impact of liana abundance on
792 successional stages; [as such](#) we could expect that PAI will increase as leaf and wood biomass
793 increases during succession (*Quesada et al., 2009*). [Furthermore, PAI could be better](#)
794 [understood if specific measurements of TLS can be done during the dry season to quantify the](#)
795 [real value of WAI to PAI, tropical dry forests in contrast to tropical rainforests can provide](#)
796 [significant advantage on better understanding PAI \(Kalascka et al. 2005b\)](#). It is surprising that
797 we did not find differences in the PAI values between stands that did and did not have
798 [lianas](#). It is possible that PAI is not the best parameter to differentiate between plots with and
799 without liana presence, instead variables more related with leaf components, such as leaf
800 area index (LAI) [and Woody Area Index \(WAI\)](#) may be more suitable for finding
801 differences in liana signature across sites, especially when the contribution of lianas to the
802 woody area index (WAI) to overall plot PAI is relatively small in comparison to the
803 allocation of WAI from trees ([Kalascka et al. 2005b](#), *Sanchez-Azofeifa et al., 2009*).

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

813 Moreover, our work seeks to strength the argument for the inclusion of lianas on
814 global terrestrial vegetation models (Verbeek & Kearsley, 2016). We argue here that the first
815 step on the development of such models is to have a clear understanding of how lianas affect
816 ecosystem structure and composition, which in turn, will affect tree mortality/recruitment,
817 and carbon storage aboveground and belowground (Poulsen et al. 2016, Schnitzer et al.
818 2014). Furthermore, lianas because of their impact on the 3D structure of a given forest
819 space, may have the possibility of changing faunal diversity (e.g. birds) an impact that has
820 not fully documented as today. As such, our study also supports the arguments by Schnitzer
821 et al (2016) that calls for the need for developing a network of observational and
822 experimental sites that can provide insights on the impact of lianas at different ecological
823 levels.

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

829

830 **5 Conclusions**

831 This study evaluated the potential for TLS and hemispherical photos to observe differences
832 between successional stages of a tropical dry forest chrono-sequence and liana abundance.

833 Our work provided five main conclusions: (1) that TLS data combined with hemispherical
834 photography data can help to predict the forest structure of the tropical dry forest as

835 demonstrated before, (2) that these predictions get blurry when liana abundance is

836 considered, (3) that variations in TLS and HPs parameters can be used to predict the effect
837 of liana abundance on the successional path, (4) that not all the parameters could address the
838 effect of the presence or impact of lianas along a successional gradient, and (5) we suggest
839 that the impact of lianas on successional stages changes the deterministic nature of forest
840 structure, by randomizing the 3D space where they grow at given plot; the higher the
841 abundance of lianas the higher the randomization.

842 Our study provides important insights on the contributions of lianas to the
843 successional process, and highlights the potential that TLS has in monitoring liana presence
844 in tropical dry forests environments. Lianas are increasing in density and biomass in tropical
845 forests, but it is unknown whether this pattern is also found in secondary forests, which are
846 suitable for liana proliferation. TLS systems are capable of providing unbiased estimations
847 for the vertical structure of a given site, and thus constitute a powerful tool to monitor the
848 increases in liana density and biomass. Although, our study is limited to one single site in
849 Costa Rica, this is a first step on the development of more comprehensive approaches, which
850 take advantage of advanced technology to understand the effects of liana abundance on
851 tropical dry forest structure. The approach presented in this paper, presents important
852 contributions to efforts directed to estimate the potential effects of lianas on forest carbon in
853 secondary forests (*Durán and Sanchez-Azofeifa, 2015*), elements that seems not fully
854 considered yet in the tropical literature.

855

856 **Acknowledgements**

857 This work was carried out with the aid of a grant from the Inter-American Institute for
858 Global Change Research [IAI] CRN3 025 which is supported by the US National Science

859 | Foundation [Grant GEO-1128040], [and the Discovery Grant Program of the National](#)
860 | [Science and Engineering Research Council of Canada](#). We thank Ericka James her help
861 | during the process of data analysis. We thank also Dr. Stefan Schnitzer for comments on
862 | earlier versions of the manuscript [and the constructive comments from three anonymous](#)
863 | [reviewers](#).

864

865 | **References**

866 | Arroyo-Mora, J.P., Sánchez-Azofeifa, G.A, Kalacska, M., Rivard, B., Calvo-Alvarado, J.,
867 | and Janzen, D.: Secondary forest detection in a Neotropical dry forest landscape
868 | using Landsat 7 ETM+ and IKONOS Imagery. *Biotropica*, 37(4), 497-507, 2005[a](#).

869 | Arroyo-Mora, J. P., Sanchez-Asofeifa, G.A, Rivard, B., Calvo-Alvarado, J. C. and Janzen,
870 | D. H.: Dynamics in landscape structure and composition for the Chorotega region,
871 | Costa Rica from 1960 to 2000, *Agriculture, Ecosystems & Environment*, 106(1), 27–
872 | 39, 2005**b**.

873 | Beland, M., Baldocchi, D. D., Widlowski, J.-L., Fournier, R. A. and Verstraete, M. M.: On
874 | seeing the wood from the leaves and the role of voxel size in determining leaf area
875 | distribution of forests with terrestrial LiDAR, *Agriculture and Forest Meteorology*
876 | 184, 82–97, 2014.

877 | Calvo-Alvarado, J., B McLennan, GA Sánchez-Azofeifa, and T Garvin.: Deforestation and
878 | forest restoration in Guanacaste, Costa Rica: Putting conservation policies in context.
879 | [For. Ecol. Manage.](#), 258(6), 931-940, 2009.

880 | Canty, A. and Ripley B.: boot: bootstrap functions, available at: [https://cran.r-](https://cran.r-project.org/web/packages/boot/)
881 | [project.org/web/packages/boot/](https://cran.r-project.org/web/packages/boot/) (last access: September 30, 2016), 2016.

- 882 | [Cao, S., Yu, Q., Sanchez-Azofeifa, A., Feng, J., Rivard, B., & Gu, Z.: Mapping tropical dry](#)
883 | [forest succession using multiple criteria spectral mixture analysis. ISPRS Journal of](#)
884 | [Photogrammetry and Remote Sensing, 109, 17-29, 2015.](#)
- 885 Castillo, M., Rivard, B., Sánchez-Azofeifa, A., Calvo-Alvarado, J. and Dubayah, R.: LIDAR
886 remote sensing for secondary Tropical Dry Forest identification, *Remote Sens.*
887 *Environ.*, 121, 132–143, 2012.
- 888 Castro-Esau, K., Sánchez-Azofeifa, G.A. and Caelli, T.: Discrimination of lianas and trees
889 with leaf-level hyperspectral data, *Remote Sens. Environ.*, 90 (3), 353–372, 2004.
- 890 Chen, Y.-J., Bongers, F., Cao, K.-F. and Cai, Z.-Q.: Above- and below-ground competition
891 in high and low irradiance: tree seedling responses to a competing liana *Byttneria*
892 *grandifolia*. *J. Trop. Ecol.*, 24, 517–524, 2008.
- 893 Clawges, R., Vierling, L., Calhoun, M. and Toomey, M.: Use of a ground-based scanning
894 lidar for estimation of biophysical properties of western larch (*Larix occidentalis*),
895 *Int. J. Remote Sens.* 28 (19), 4331–4344, 2007.
- 896 Culvenor, D., Newnham, G., Mellor, A., Sims, N. and Haywood, A.: Automated In-Situ
897 Laser Scanner for Monitoring Forest Leaf Area Index, *Sensors*, 14(8), 14994–15008,
898 2014.
- 899 Dassot, M., Constant, T. and Fournier, M.: The use of terrestrial LiDAR technology in forest
900 science.: Application fields, benefits and challenges, *Ann. For. Sci.*, 68(5), 959–974,
901 2011.
- 902 Dewalt, S. J., Schnitzer, S. A. and Denslow, J. S.: Density and diversity of lianas along a
903 chronosequence in a central Panamanian lowland forest, *J. Trop. Ecol.*, 16(1), 1–19,
904 2000.

905 Durán, S.M. and Gianoli, E.: Carbon stocks in tropical forests decrease with liana density,
906 Biol. Lett., 3–6, 2013.

907 Durán, S. M. and Sánchez-Azofeifa.: Liana effects on carbon storage and uptake in mature
908 and secondary tropical forests, in: Biodiversity of lianas, edited by: Parthasarathy, N.,
909 pp. 43–55. Springer-Verlag, 2015.

910 Frazer, G.W., Canham, C.D., and Lertzman, K.P.: Gap light analyzer (GLA), Version 2.0:
911 Imaging software to extract canopy structure and gap light transmission indices from
912 true-colour fisheye photographs, users manual and program documentation. Simon
913 Fraser University, BC and the Institute of Ecosystem Studies, NY, 1999.

914 Foster, J. R., Townsend, P. A. and Zganjar, C. E.: Spatial and temporal patterns of gap
915 dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat
916 Thematic Mapper, Remote Sens. Environ., 112 (5), 2104–2117, 2008.

917 González, I. and Déjean S.: CCA: canonical correlation analysis, available at: [https://cran.r-](https://cran.r-project.org/web/packages/CCA/)
918 [project.org/web/packages/CCA/](https://cran.r-project.org/web/packages/CCA/) (last access: September 30, 2016), 2015.

919 Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G. and Wright, S. J.: Cloud cover
920 limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons.,
921 Proc. Natl. Acad. Sci. U. S. A., 100(2), 572–576, 2003.

922 van der Heijden, G.M.F, Schnitzer, S.A., Powers, J.S. and Phillips, O.L.: Liana Impacts on
923 Carbon Cycling, Storage and Sequestration in Tropical Forests. Biotropica 45, 682–
924 692, 2013.

925 van der Heijden, Powers, J.S., and Schnitzer, S.A.: Lianas reduce carbon accumulation and
926 storage in tropical forests. PNAS 112, 13267-13271, 2015.

927 Hilje, B., Calvo-alvarado, J., Jiménez-rodríguez, C., Sánchez-azofeifa, A., José, S., Rica, C.,
928 Forestal, E. D. I., Rica, T. D. C. and Rica, C.: Tree species composition, breeding
929 systems, and pollination and dispersal syndromes in three forest successional stages
930 in a tropical dry forest in Mesoamerica, *Trop. Conserv. Sci.*, 8(1), 76–94, 2015.

931 Jupp, D. L. B., Culvenor, D. S., Lovell, J. L., Newnham, G. J., Strahler, A. H. and
932 Woodcock, C. E.: Estimating forest LAI profiles and structural parameters using a
933 ground-based laser called “Echidna”., *Tree Physiol.*, 29(2), 171–81, 2009.

934 Kalacska, M.: Leaf area index measurements in a tropical moist forest: A case study from
935 Costa Rica, *Remote Sens. Environ.*, 91(2), 134–152, 2004.

936 [Kalacska, M., J Calvo, and GA Sánchez-Azofeifa: Assessment of seasonal changes in](#)
937 [species' leaf area in a tropical dry forest in different states of succession. *Tree*](#)
938 [*Physiology*. 25: 733-744. 2005a.](#)

939 Kalacska, M., Sánchez-Azofeifa, G. A., Calvo-Alvarado, J. C., Rivard, B. and Quesada, M.:
940 Effects of season and successional stage on leaf area index and spectral vegetation
941 indices in three mesoamerican tropical dry forests, *Biotropica*, 37(4), 486–496,
942 2005b.

943 [Kalacska, M., Sanchez-Azofeifa, G. A., Rivard, B., Caelli, T., White, H. P. and Calvo-](#)
944 [Alvarado, J. C.: Ecological fingerprinting of ecosystem succession: Estimating](#)
945 [secondary tropical dry forest structure and diversity using imaging spectroscopy,](#)
946 [*Remote Sens. Environ.*, 108, 82–96, 2007a.](#)

947 [Kalacska, M., Bohlman, S., Sanchez-Azofeifa, G. A., Castro-Esau, K. and Caelli, T.:](#)
948 [*Hyperspectral discrimination of tropical dry forest lianas and trees: Comparative data*](#)

949 | [reduction approaches at the leaf and canopy levels, Remote Sens. Environ., 109,](#)
950 | [406–415, 2007b.](#)

951 | [Ledo, A., Illian, J. B., Schnitzer, S. A., Wright, S. J., Dalling, J. W. and Burslem, D. F. R.](#)
952 | [P.: Lianas and soil nutrients predict fine-scale distribution of above-ground biomass](#)
953 | [in a tropical moist forest, J. Ecol., 104, 1819–1828, 2016.](#)

954 | Lefsky M., and McHale M.: Volumes estimates of trees with complex architecture from
955 | terrestrial laser scanning. J Appl Remote Sens., 2, 023521, 2008.

956 | Letcher, S. G. and Chazdon, R. L.: Lianas and self-supporting plants during tropical forest
957 | succession, For. Ecol. Manage., 257 (10), 2150–2156, 2009.

958 | Lovell, J. L., Jupp, D. L. B., Culvenor, D. S. and Coops, N. C.: Using airborne and ground-
959 | based ranging lidar to measure canopy structure in Australian forests, Can. J. Remote
960 | Sens., 29 (5), 607–622, 2014.

961 | Menzel, U.: CCP: Significance tests for canonical correlation analysis (CCA), available at:
962 | <https://cran.r-project.org/web/packages/CCP/> (last access: September 30, 2016),
963 | 2012.

964 | Muss, J. D., Aguilar-Amuchastegui, N., Mladenoff, D. J. and Henebry, G. M.: Analysis of
965 | Waveform Lidar Data Using Shape-Based Metrics, IEEE Geosci. Remote Sens. Lett.,
966 | 10 (1), 106–110, 2013.

967 | Paul, G. S. and Yavitt, J. B.: Tropical Vine Growth and the Effects on Forest Succession: A
968 | Review of the Ecology and Management of Tropical Climbing Plants, Bot. Rev., 77
969 | (1), 11–30, 2010.

970 | Phillips, O., Martínez, R., Arroyo, L. and Baker, T.: Increasing dominance of large lianas in
971 | Amazonian forests, Nature, 418, 770–774, 2002.

972 Phillips, O. L. and Lewis, S. L.: Recent changes in tropical forest biomass and dynamics,
973 For. Glob. Chang., 4, 77–108, 2014.

974 [Phillips, O. L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T. R. and Núñez](#)
975 [Vargas, P.: Large lianas are hyperdynamic elements of the tropical forest canopy,](#)
976 [Ecology, 86, 1250–1258, 2005.](#)

977 Portillo-Quintero, C., Sanchez-Azofeifa, A. and Culvenor, D.: Using VEGNET In-Situ
978 monitoring LiDAR (IML) to capture dynamics of plant area index, structure and
979 phenology in Aspen Parkland Forests in Alberta, Canada, Forests, 5 (5), 1053–1068,
980 2014.

981 [Poulsen, J. R., Koerner, S. E., Miao, Z., Medjibe, V. P., Banak, L. N. and White, L. J. T.:](#)
982 [Forest structure determines the abundance and distribution of large lianas in Gabon,](#)
983 [Glob. Ecol. Biogeogr., doi:10.1111/geb.12554, 2016.](#)

984 Quesada, M., Sanchez-Azofeifa, G. A., Alvarez-Añorve, M., Stoner, K. E., Avila-Cabadilla,
985 L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M. M., Fagundes, M., Fernandes,
986 G. W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L. P. C., Powers,
987 J. S., Neves, F. D. S., Rosas-Guerrero, V., Sayago, R. and Sanchez-Montoya, G.:
988 Succession and management of tropical dry forests in the Americas: Review and new
989 perspectives, For. Ecol. Manage., 258 (6), 2009.

990 Quinn, G. P. and Keough M. J.: Experimental design and data analysis for biologists.
991 Cambridge University Press, New York, 443-472, 2002.

992 R Development Core Team: R: a language and environment for statistical computing,
993 available at: <http://www.r-project.org> (last access: September 30, 2016), 2016.

994 Ramírez, F. A., Armitage, R. P. and Danson, F. M.: Testing the application of terrestrial
995 laser scanning to measure forest canopy gap fraction, *Remote Sens.*, 5 (6), 3037–
996 3056, 2013.

997 Richardson, J., Moskal, L. and Bakker, J.: Terrestrial Laser Scanning for Vegetation
998 Sampling, *Sensors*, 14 (11), 20304–20319, 2014.

999 Sánchez-Azofeifa, RC Harris, and DL Skole. Deforestation in Costa Rica: A quantitative
1000 analysis using remote sensing imagery. *Biotropica*. 33(3), 378-384, 2001.

1001 Sánchez-Azofeifa, G. A. and Castro-Esau, K.: Canopy observations on the hyperspectral
1002 properties of a community of tropical dry forest lianas and their host trees, *Int. J.*
1003 *Remote Sens.*, 27 (10), 2101–2109, 2006.

1004 | Sánchez-Azofeifa, G. A., Kalácska, M., Espírito-Santo, M. M. Do, Fernandes, G. W. and
1005 | Schnitzer, S.: Tropical dry forest succession and the contribution of lianas to wood
1006 | area index (WAI), *For. Ecol. Manage.*, 258 (6), 941–948, 2009.

1007 Schnitzer, S. A and Bongers, F.: Increasing liana abundance and biomass in tropical forests:
1008 emerging patterns and putative mechanisms., *Ecol. Lett.*, 14 (4), 2011.

1009 Schnitzer, S. A and Carson, W. P.: Lianas suppress tree regeneration and diversity in treefall
1010 gaps., *Ecol. Lett.*, 13 (7), 849–57, 2010.

1011 Schnitzer, S. A., Dalling, J. W. and Carson, W. P.: The impact of lianas on tree regeneration
1012 in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase
1013 regeneration, *J. Ecol.*, 88 (4), 655–666, 2000.

1014 | [Schnitzer, S., van der Heijden, G.M.F., and Powers, J.: Addressing the challenges of](#)
1015 | [including lianas in global vegetation models. PNAS, 113 \(1\), E6, 2016.](#)

1016 | [Schnitzer, S. A., van der Heijden, G., Mascaro, J. and Carson, W. P.: Lianas in gaps reduce](#)
1017 | [carbon accumulation in a tropical forest, Ecology, 95, 3008–3017, 2014.](#)

1018 | Strahler, A. H., Jupp, D. L. ., Woodcock, C. E., Schaaf, C. B., Yao, T., Zhao, F., Yang, X.,
1019 | Lovell, J., Culvenor, D., Newnham, G., Ni-Miester, W. and Boykin-Morris, W.:
1020 | Retrieval of forest structural parameters using a ground-based lidar instrument
1021 | (Echidna ®), Can. J. Remote Sens., 34 (sup2), S426–S440, 2014.

1022 | Tymen, B., Réjou-Méchain, M., Dalling, J. W., Fauset, S., Feldpausch, T. R., Norden, N.,
1023 | Phillips, O. L., Turner, B. L., Viers, J. and Chave, J. Evidence for arrested succession
1024 | in a liana-infested Amazonian forest. J. Ecol. 104 (1), 149-159. 2016_

1025 | [Verbeek, H., Kearsley, E.: The importance of including lianas in global vegetation models,](#)
1026 | [PNAS, 113 \(1\), E4, 2016.](#)

1027 | Wright, S. J.: Tropical forests in a changing environment, Trends Ecol. Evol., 20(10), 553–
1028 | 560, 2005.

1029 | [Zhang, J., Rivard, B., Sánchez-Azofeifa, A. and Castro-Esau, K.: Intra- and inter-class](#)
1030 | [spectral variability of tropical tree species at La Selva, Costa Rica: Implications for](#)
1031 | [species identification using HYDICE imagery, Remote Sens. Environ., 105, 129–141,](#)
1032 | [2006.](#)

1033

1034 Table 1. Mean (\pm SD) of parameters of forest structure extracted from plots with
 1035 different successional stages and different relative abundance of lianas in the dry forest
 1036 at Santa Rosa National Park, Costa Rica. Significant differences (*F-values* and their *p-*
 1037 *values*) according to the successional stages, relative abundance of lianas and their
 1038 interaction are represented by a posteriori ANOVA text extracted from MANOVA. Stem
 1039 density (stems/ha); DBH_{mean}, mean stem diameter at breast height (cm); TBA, total basal
 1040 area (m²); L/TBA, ratio of liana basal area to TBA.

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

1041 *, $p < 0.05$; ***, $p < 0.01$

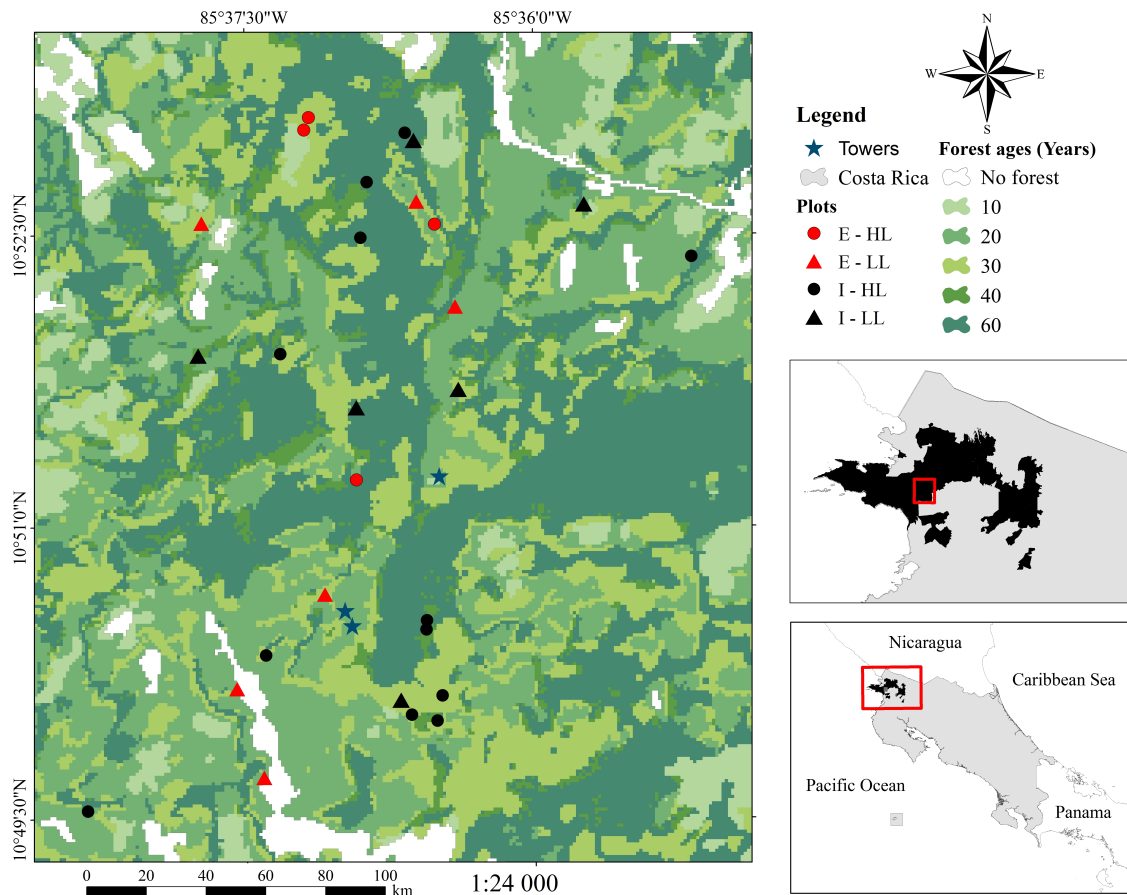
1042

1043 Table 2. Mean (\pm SD) of parameters calculated by VEGNET system and HPs in plots
 1044 with different successional stages and different relative abundance of lianas in the dry
 1045 forest at Santa Rosa National Park, Costa Rica. Significant differences (*F-values* and
 1046 their *p-values*) according to the successional stages, relative abundance of lianas and
 1047 their interaction are represented by a posteriori ANOVA text extracted from MANOVA.
 1048 RG, radius of gyration; PAI, plant area index; PAVD_{mean}, plant area volume density;
 1049 H_{max} , maximum tree height (m); LAI, leaf area index.

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

1050 *, $p < 0.05$

1051
1052



1053

1054 Figure 1. Localization of the sampled forest stands in Santa Rosa National Park

1055 Environmental Monitoring Super Site, Guanacaste, Costa Rica. Where E-HL indicate Early

1056 successional stage with a high relative abundance of lianas; E-LL Early successional stage

1057 with a low relative abundance of lianas; I-HL, Intermediate successional stage with a high

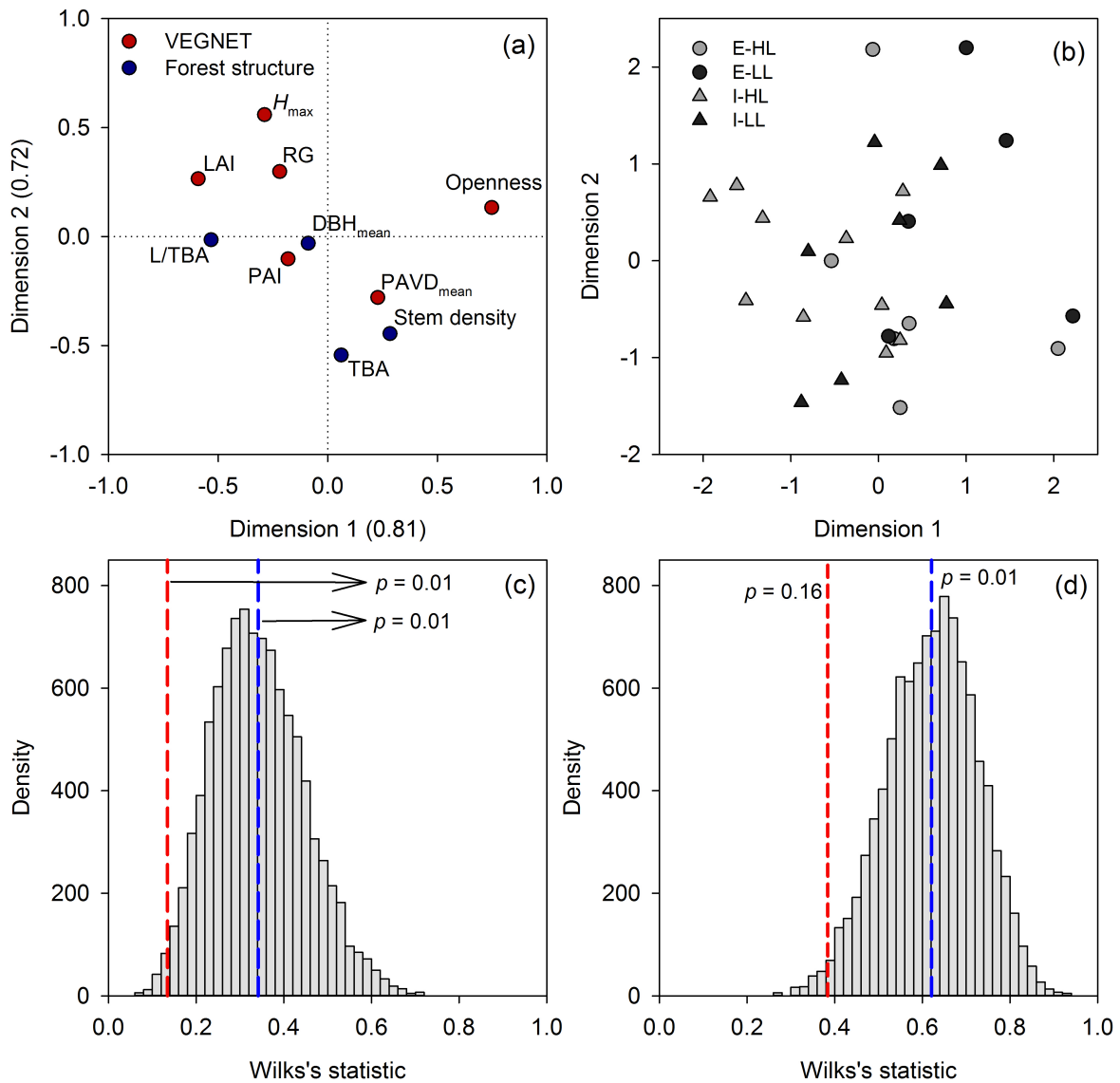
1058 relative abundance of lianas; I-LL, Intermediate successional stage with a low relative

1059 abundance of lianas. In addition, forests ages refer to: 60, forests detected since 1956; 40,

1060 forests detected since 1979; 30, forests detected since 1986; 20, forests detected since 1997;

1061 10 forests detected since 2005, and no forest correspond to non-related to woodlands.

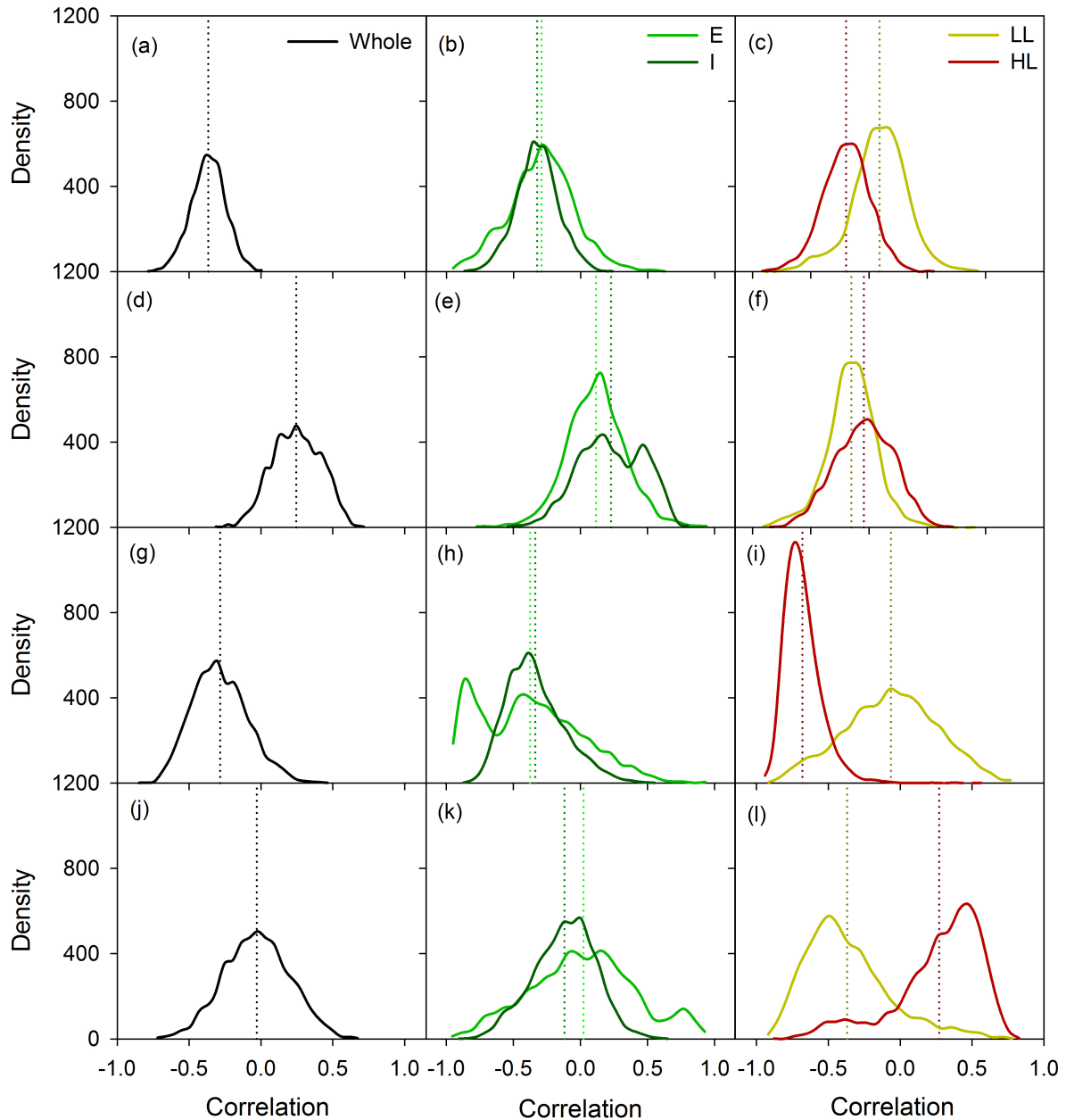
1062



1063

1064 Figure 2. Canonical correspondence analysis to describe the association between the
 1065 parameters estimated by VEGNET system [hemispherical photographs \(HPs\)](#) and the
 1066 forest structure. a) VEGNET-[HPs](#) coefficients are represented by red points, while forest
 1067 structure coefficients are represented by blue points. b) Individual scores of each plot of
 1068 the canonical variates are represented according to successional stages (E, early; I,
 1069 intermediate) and relative liana abundance (LL, low liana abundance; HL, high liana
 1070 abundance). C and d represent the permutation distribution of the Wilks' Lambda test to

1071 assign the statistical significance of canonical correlation coefficients considering 4 and
1072 3 canonical correlations, respectively; the red line represent the original value Wilks'
1073 Lambda, while the blue line represent the mean value permutated.
1074



1075

1076 Figure 3. Density distribution of the bootstrapped correlation coefficients without and
 1077 with distinction between successional stages (E, early; I, intermediate) and relative liana
 1078 abundance (LL, low liana abundance; HL, high liana abundance). a, b, and c correspond
 1079 to the correlation of canopy openness and the ratio of liana basal area (L) to total basal
 1080 area (TBA); d, e, f correspond to leaf area index-L/TBA correlation; g, h, and i

1081 correspond to the maximum tree height-TBA correlation; j, k, and l correspond to plant
1082 area volume density-TBA correlation.