1   January 24, 2017

2   Dear Editor,

3   Please find attaching our response to the comments from the reviewer. We hope that our

4   responses are now satisfactory. We look forward to the outcome of your decision.

5   Sincerely yours,

6   Arturo Sanchez-Azofeifa

7

8   **Explanation of how we dealt with the reviewers' or editor's comments**
9

10 **Introduction:**

11 Line 93: The following sentence might be removed: "Findings associated to WAI impacts

12 were significant since this structural variable when associated to Leaf Area Index (LAI), is

13 used to defined the concept of Plant Area Index (PAI = LAI + WAI)." I don't understand

14 what relevant information it brings.

15 **R/.** We agree, this was removed.

16

17 Line 121: If I well understand, according to the organisation of the result section, it appears

18 to me that you first assess the changes of forest structure du to liana presence and forest

19 succession. Then you assess the potential of VEGNET and HPs to detect the vertical

20 structure of forest stands at different successional stages. And third you reported how liana

21 abundance could affect the prediction the level of succession of a given forest stand from

22 VEGNET and HPs.

23 It might be clearer to state it like that in the introduction.

24 **R/.** We agree, this was clarified.

25

Material and methods:

Line 195: consider rephrasing: "Lianas in early forests tend to be more present during the transition from early to intermediate stages" in something like "Lianas abundance tends to increase in early forests during their transition to intermediate stages".

R/. We agree, this was rephrased.

31

Line 198 "with" seems to be missing.

R/. We agree, this was corrected.

Line 211: The sentence "In each of these plots we extracted the available information that described the complexity of the dry forest according to its structure" is unclear. Do you mean you extracted all the information available describing structural complexity of the forest? Why using the word complexity, how do you define it? I would remove it.

R/. We agree, this was removed.

39

Line 250 : Do Cx, Cy and RG relate to the PAVD or to the PAI distribution along height, or both ? Or didn't I understand what they are related to. If so I suggest a small piece of explanation in the text.

R/. We disagree. On the line 250 we are making an introduction to the six parameters that we extracted from LiDAR measurements. Between lines 280 and 305 there is an extended explanation to describe the meaning of these parameters and their significance in our study.

46

47   Line 329-330: The link between LAI and canopy openness (see my comment about Table 2)

48   wouldn't lead me to consider both variable in the CCA.

49   **R/.** We disagree. Despite that parameters come from the same measurement, both of them

50   represented different traits of the forest. In general, canopy openness is the percentage of the

51   total sky area that is found in canopy gaps for each sky region, while the LAI is the effective

52   leaf area index integrated over the zenith angles 0 to 60º which is based on Beer`s law as

53   applied to leaf canopies, with the assumption that the location of leaves are statistical

54   independent random variables with a uniform density function in the canopy. Although there

55   is a slight collinearity between both parameters, there is not a perfect relationship because

56   these are derived from different calculations that have different meaning as shown in the

57   following figure. Due to the later, we can consider both parameters in the CCA.
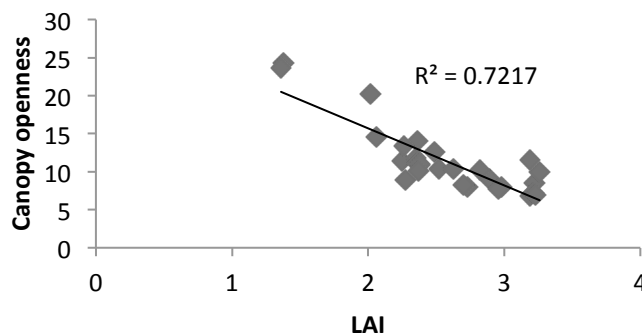
58

59   Line 367: a coma is missing after "MANOVA".

60   **R/.** We agree, this was corrected.

61

62   Line 425 "[…], but can discriminate with different liana abundance where lower values of

63   correlation are associated with HL plots" should be replace by something like "[…], but can

64   discriminate between different liana abundance since lower values of correlation are

65   associated with HL plots".

66   **R/.** We agree, this was rephrased.

67

68   Line 449: typo, "they" might be "the"

69   **R/.** We agree, this was corrected.

70

71   Line 452 & 453: "shubrs " and "shurbs" are probably "shrubs".

72   **R/.** We agree, this was corrected.

73

74   Line 453: "High distribution" might means "high density at low height" isn't it?.

75   **R/.** We agree, this was rephrased.

76

77   Line 454: makes.

78   **R/.** We agree, this was corrected.

79

80   **Table 2**

81   I still have a problem with the relation between PAI and canopy opennes.

82    $PAI(z) = -1.1 \times \ln(Pgap(z))$ from VEGENET. On the ground isn't Pgap equal to canopy

83   openness? I know it would be a canopy openness measured from TLS while in your study

84   LAI and canopy openness come from hemispherical photography. Why canopy openness

85   from gap light analyzer wouldn't take into account woody part of the vegetation?

86 **R/.** Yes, you are right, Pgap from VEGENET could be considering equal or similar to

87 canopy openness from HP; however, we are not using Pgap as a parameter that describes the

88 canopy openness, we are using Pgap to estimate other parameters, specifically PAI.

89

90 If I well understood, there is no distinction between leaves and wood in the Gap Light

91 Analyzer?

92 The effective LAI is computed following (Stenberg et al. 1994). Those author estimate

93 indeed LAI but in scots pine stands. We don't know if the LAI/WAI respective proportions

94 are the same in scots pine stands and dry tropical forest, then LAI estimation might not be

95 very trustable. Moreover with this way of calculation it is not possible to take into account

96 the potential modification of leaf/wood ratio according to liana abundance or forest

97 succession.

98 **R/.** We partially agree. We compute the LAI based on Stenberg's et al. (1994) method of 4-

99 ring via the Gap Light Analyzer (GLA). Like many other studies in boreal and tropical

100 regions (using broadleaves not needleaves), we consider that GLA just uses the range of

101 zenith angles published by Stenberg et al. (1994), and not their assumptions of clumping or

102 type of leaves for scots pine stands to make the calculations (in our case as presented by

103 Kalacska et al 2005a, the clump factor for the same plots is 1). Consequently, these

104 calculations do not make a modification of leaf/wood ratio according to liana abundance or

105 forest succession. In addition, our values of LAI match with the values of LAI previously

106 published by Kalàscska et al. (2005a,b) in the same place, and using the same categories of

107 forest succession. Moreover, the method that we used to estimate the LAI has been widely

108 applied in many other studies in tropical environments and in our case across several dry

109   forests (see. Kalacska et al 2005b). Despite the later, your comment gave us an idea; there

110   are not studies that highlight the assumptions of clumping or type of leaves for the

111   estimation of LAI by hemispherical photographs, and the implication of these assumptions

112   to estimate the LAI in environments with a high abundance of lianas. Therefore, in the

113   future, we will address this question trying to improve the classic approach. Thank you for

114   your comment.

115

116   By the way, if you compare PAI values obtained from VEGENET to LAI values from HP

117   you see that they overlap in every forest categories you have.

118   **R/.** Yes, that is true; however, that does not mean that our values are wrong. We deployed

119   two different systems in the field, so it is expected have an overlap between estimations that

120   could describe similar features. By the way, if you see the values of LAI previously

121   published by Kalàscska et al. (2005a) you will see that there is an overlap of LAI between

122   categories of forest succession; therefore the differences that we found between plots could

123   be attributed to the presence of lianas, as we discuss.

124

125   I then think the difference in LAI you find between HL and LL should be interpreted

126   (together with canopy openness difference) as PAI differences sensed by HP but no by

127   VEGENET. In the discussion on the ability for VEGENET to accurately measure forest

128   structure characteristics should maybe take into account this fact (I wouldn't necessarily

129   conclude that VEGENET is worse than HP).

130   **R/.** We disagree. As we found and discuss, it is expected to have a low contribution of lianas

131   to the woody area index (WAI), but a high contribution of lianas to the LAI. Therefore, our

132 differences in LAI between plots with high and low abundance of lianas can be discussed as

133 differences sensed by HP, as we did. In the manuscript, we state that "It is possible that PAI

134 is not the best parameter to differentiate between plots with and without liana presence,

135 instead variables more related to leaf components". On the other hand, we are concerned

136 about your comment "I wouldn't necessarily conclude that VEGENET is worse than HP"

137 because in our manuscript we never conclude which is the best method to describe the forest

138 structure and the implications of the liana abundance. We claim that *"there is a strong need*

139 *to carefully select which parameters should be considered if we want to estimate changes in*

140 *the forest structure as a function of liana abundance"*, but we never claim which is the best

141 parameter or the best method.

142

143 **Figure 2:**

144 I don't understand the p=0.01 and p=0.16 in the panels c and d. What do they stand for?

145 **R/.** These values represent the significance of Wilks' Lambda test, this was clarified.

146

147 **Figure 3:**

148 I think you should replace "the ratio of liana basal area (L) to total basal area (TBA)" by

149 "the ratio of liana basal area to total basal area (L/TBA)". More generally pay attention to

150 use always the same notation.

151 **R/.** We agree, this was replaced.

152

153 **References**

154   Kalascka, M., J Calvo, and GA Sánchez-Azofeifa: Assessment of seasonal changes in
155   species' leaf area in a tropical dry forest in different states of succession, Tree
156   Physiol., 25: 733-744. 2005a.

157   Kalacska, M., GA Sánchez-Azofeifa, M Quesada, and J Calvo. A comparison of Leaf Area
158   Index of three tropical dry forests environments. Biotropica. 37(4): 486-497. 2005b.

159

160   **Can Terrestrial Laser Scanner (TLS) and hemispherical photographs predict Tropical**

161   **Dry Forest Succession with liana abundance?**

162

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175

176   **Abstract**

177   Tropical Dry Forests (TDFs) are ecosystems with long drought periods, a mean temperature

178   of 25$^{\mathrm{o}}$C, a mean annual precipitation that ranges from 900 to 2000 mm, and that possess a

179   high abundance of deciduous species (trees and lianas). What remains of the original extent

180   of TDFs in the Americas remains highly fragmented and at different levels of ecological

181   succession. It is estimated that one of the main fingerprints left by global environmental and

182   climate change in tropical environments is an increase in liana coverage. Lianas are non-

183   structural elements of the forest canopy that eventually kill their host trees. In this paper we

184   evaluate the use of a Terrestrial Laser Scanner (TLS) in combination with hemispherical

185   photographs (HPs) to characterize changes in forest structure as a function of ecological

186   succession and liana abundance. We deployed a TLS and HP system in 28 plots throughout

187   secondary forests of different ages and with different levels of liana abundance. Using a

188   canonical correspondence analysis, we addressed how the VEGNET and HPs could predict

189   TDF structure. Likewise, using univariate analysis of correlations we show how the liana

190   abundance could affect the prediction of the forest structure. Our results suggest that TLS

191   and HPs can predict differences in the forest structure at different successional stages, but

192   that these differences disappear as liana abundance increases. Therefore, in well-known

193   ecosystems such as the tropical dry forest of Costa Rica, these biases of prediction could be

194   considered as structural effects of liana presence. This research contributes to the

195   understanding of the potential effects of lianas in secondary dry forests and highlights the

196   role of TLS combined with HPs to monitor structural changes in secondary TDFs.

197

1 Introduction

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

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

Lianas are considered light-loving plants, because they tend to respond positively to disturbance and show high density in areas of secondary forest succession (*Paul and Yavitt, 2011*). Furthermore, secondary forests may promote liana abundance because they provide both high light availability and an abundance of trellises (*Schnitzer and Bongers, 2002*). As

221   tree turnover increased gaps due to mortality, lianas can take advantage of this process and

222   form dense tangles, which in turn reduce the amount of light reaching the forest understory

223   (*Paul and Yavitt, 2011; Schnitzer et al., 2000*). These liana tangles can persist for long

224   periods (up to 13 years) and alter the successional pathway stalled by liana abundance by

225   inhibiting the regeneration, growth, and density of late successional species (*Schnitzer et al.,*

226   *2000*).

227   As of today, it is still unknown whether lianas can alter successional trajectories in

228   secondary forests resulting from anthropogenic disturbance (*Durán and Sánchez-Azofeifa,*

229   *2015*). Two studies in secondary wet forests have found an increment in liana density in the

230   first 20 years of regeneration (age since land abandonment), with a subsequent decline

231   (*DeWalt et al., 2000; Letcher and Chazdon, 2009*). This decline of lianas in wet forests

232   appears to be related with reductions in light availability due to greater tree and shrub

233   biomass at later stages of succession (*Letcher and Chazdon, 2009*). Nonetheless, it remains

234   unclear whether this pattern holds true with more open forest types, and whether other

235   factors such as structure, canopy openness, plant density and the volume of forest stands can

236   also influence successional trajectories of lianas (*Durán and Sánchez-Azofeifa, 2015;*

237   *Sánchez et al., 2009*).

238   Despite the fact of the important effect of lianas on the biomass distribution within

239   tropical forests (*Schnitzer and Bongers, 2011; Ledo et al. 2016*), and their potential role as

240   fingerprints of climate change (*Phillips et al. 2005*), remote sensing tools aimed to measure

241   their presence/absence as well as their distribution within tropical forests are limited (*Foster*

242   *et al., 2008, Kalacksa et al. 2007a & b, Zhang et al. 2006*). Current knowledge based on leaf

243   spectroscopy approaches provides two key messages regarding liana extent mapping: first

244   that lianas in tropical rainforests tend to confuse the spectral reflectance of their host trees

245   making it in many cases impossible to use remote sensing to create species maps (*Castro-*

246   *Esau et al., 2004)*, and second that there is a higher degree of probability of success for

247   efforts aimed to map liana coverage in tropical dry forests than on rain forests environments

248   (*Sanchez-Azofeifa et al., 2009b; Kalacska et al. 2007b)*. Moreover, studying the impact of

249   lianas on tropical dry forest structure, *Sanchez-Azofeifa et al*. (*2009*) used hemispherical

250   photography over a succession of tropical dry forests in Mexico, Costa Rica and Brazil,

251   found that lianas infested sites were significantly different in both canopy openness and

252   Woody Area Index (WAI).

253   Initial attempts aimed to start untangling the effects that lianas have on remote

254   sensing observations may require data fusion techniques on which hyperspectral remote

255   sensing approaches (leaf spectroscopy finding) are mergered with ground based forest

256   structure information derived from terrestrial laser scanners and hemispherical photography

257   (e.g. LAI, WAI and PAI). Terrestrial Laser Scanners (TLS) have demonstrated their

258   capability to measure canopy properties such as height and cover (*Ramírez et al., 2013*) and

259   tree architecture (*Lefsky et al., 2008*), (*Dassot et al., 2011*; *Richardson et al., 2014*). In the

260   last decade, there has been a rapid development in portable TLS (*Dassot et al., 2011;*

261   *Richardson et al., 2014*). When laser pulses emitted in the visible or near-infrared come into

262   contact with an object, part of that energy is reflected back toward the instrument which

263   triggers the recording of its distance and intensity (*Beland et al., 2014*). TLS systems

264   typically employ vertical and horizontal scanning around a fixed point of observation,

265   providing a hemispherical representation of biomass distribution in the forest -leaves,

266   branches and trunks- which allows for the exploration of foliage angle distributions and

267   clumping (*Clawges et al., 2007; Jupp et al., 2009; Strahler et al., 2008*).

268   Until today, there has been no concrete evidence about how liana abundance can

269   affect the prediction of the forest structure by TLS or hemispherical photographs (HPs),

270   which in turn can drive the development of better remote sensing techniques for mapping

271   their extent. Because of this, the objective of this study was to evaluate the feasibility of a

272   TLS named VEGNET in combination with HPs to assess changes in forest structure in

273   secondary TDFs with different levels of lianas abundance. The VEGNET is a TLS that

274   automatically scans a forest plot producing a vertical foliage density profile. Given its

275   automated mode of operation and semi-permanent installation, the VEGNET instrument is

276   described as an *in situ* Monitoring LiDAR (IML) (*Culvernor et al., 2014; Portillo-Quintero*

277   *et al., 2014*).

278   As such, in this paper we first assess the changes of tropical dry forests structure due

279   to liana presence and forest succession. Second, we analyze the potential of VEGNET and

280   HPs to detect the vertical structure of forest stands at different successional stages. Finally,

281   we examine how liana abundance could affect the bias of prediction of VEGNET and HPs to

282   detect the level of succession of a given forest stand. Therefore, in well-known ecosystems

283   such as the tropical dry forest of Costa Rica, this bias of prediction could be considered as

284   the effect of liana presence on forest structure.

285

286   **2 Methods**

287   **2.1 Study Area**

14

288   The study area is located in the Santa Rosa National Park Environmental Monitoring Super

289   Site (SRNP-EMSS), which is a part of the Guanacaste Conservation Area in Costa Rica

290   (10°48" N, 85°36" W) (Figure 1). This site covers an area of 50,000 ha, receives 1720 mm

291   of annual rainfall, has a mean annual temperature of 25°C and a 6-month dry season

292   (Dec–May) (*Kalácska et al.,2004*). The SRNP-EMSS site has suffered intense deforestation

293   in the past 200 years due to the expansion of pasturelands (*Calvo-Alvarado et al., 2009*).

294   Original land management practices in the park included pasture rotation between different

295   large corrals surrounded by life fences that can still be identified today. More recently (early

296   1970's) with the creation of Santa Rosa National Park, a process of secondary regeneration

297   has become the dominant land cover change force in the region. Today and after the creation

298   of SRNP, the uplands of the park are a mosaic of secondary forest in various stages of

299   regeneration and with different land use histories related with anthropogenic fires, intense

300   deforestation, and clearing for pasture lands (*Kalácska et al., 2004; Arroyo-Mora et al.,*

301   *2005a, Cao et al, 2015*).

302

303   **2.2 Definition of forest cover and plot age.**

304   　　A map of forest cover and forest cover ages was generated using aerial photographs

305   collected by the US Army in 1956 (Scale 1:24,000), a Multispectral Scanner (MSS) image

306   from 1979 (80 m spatial resolution); 4 Landsat Thematic Mapper [TM] images from 1986,

307   1997, 2000 and 2005 (28.5 m spatial resolution); one Spot Multispectral image from 2010

308   (20 m spatial resolution); and a Landsat 8 image from 2015. All images had less than 10%

309   cloud cover.

310   The 1986 image was georeferenced to 1:50,000 topographic maps from the Costa Rica

311   National Geographic Institute with a Root Mean Square Error (RSME) of 0.5 pixels or 14.25

312   m. We defined this as our master image in order to georeference all of the other images, as

313   such all other images were then geo-referenced to the 1986 image seeking a RMSE close to

314   0.5 pixels between the master and the target image. All images where then classified using a

315   supervised classification. Image accuracy was conducted for the 1997, 2000, 2005 and 2010

316   satellite images as part of independent validation efforts conducted by the Costa Rica's

317   National Forest Financing Fund (FONAFIFO). Overall accuracy for the forest/non-forest

318   images was 90%. Further information on image processing can be found in Sánchez-

319   Azofeifa et al. (2001).

320   Final quality controlled forest cover maps (forest non-forest) for 1956, 1979, 1986, 1997,

321   2000, 2005, 2010 and 2015 were cross referenced to produce a tropical dry forest age map.

322   Specifically, forest coverage with 60 years old correspond to woodlands which were being

323   observed in images since 1956; forests that were 40 years old were not detected in 1956 but

324   have been recognizing as forests since 1979; on the other hand, woodlands that were referred

325   to as being 10 years old have a minimum of 10 years as a discriminable forest coverage.

326   Based on Arroyo-Mora et al. (2005b) and Kalascka et. al's (2005a) studies the following

327   successional classification was developed: Ages 10 to 40 years (Early), and ages 40 to 60

328   (Intermediate). Figure 1 presents the final land cover and forest age map for our study area.

329

330   **2.3 Plots selection and description**

331   Based on Figure 1, twenty-eight randomly stratified 0.1ha plots were selected. The number

332   of plots chosen for each forest successional stage was based upon each stages total forest cover

333   area. Plot sizes of 0.1 ha follows convention used in tropical forest studies at this site (Kalascka

334   et al. 2005a). Fieldwork conducted in July 2016 was conducted in order to characterize

335   diameter at breast height (DBH), tree height, total biomass, VEGNET observations (canopy

336   vertical profiles) and hemispherical photos (Canopy openness and Leaf Area Index).

337   The characterization of successional stages was performed following previous approaches

338   for seasonally dry forests of Costa Rica (*Arroyo-Mora et al., 2005b; Kalácska et al., 2005*) and

339   adjusted according to the estimated forest ages (Figure 1). These approaches categorized the

340   secondary regeneration in different successional stages such as early and intermediate

341   successional stages (*E* and *I*, respectively) (*Arroyo-Mora et al., 2005a*). The *E* stage is a

342   forest area with patches of sparse woody vegetation composed of shrubs, small trees, and

343   saplings, with a thick herbaceous understory, and with a single stratum of tree crowns with a

344   maximum height of less than 10 m (*Castillo et al., 2012*). Some of the common species that

345   are characteristic of this early stage of succession includes *Genipa americana*,

346   *Cochlospermum vitifolium*, *Gliricidia sepium*, *Randia monantha* (*Hilje et al., 2015;*

347   *Kalácska et al., 2004*). In contrast, the *I* stage has two vegetation strata composed of

348   deciduous species of woody plants. The first strata is comprised of fast-growing deciduous

349   tree species that reach a maximum height of 10−15 m (e.g., *Cydista aequinoctialis*) and the

350   second stratum is represented by lianas and vines, adults of shade-tolerant and slow-growing

351   evergreen species as well as the juveniles of many species such as *Annona reticulata*,

352   *Ocotea veraguensis*, and *Hirtella racemosa* (*Arroyo-Mora et al., 2005a; Kalácska et al.,*

353   *2004*). No lianas were present in the early successional stage plots. Lianas abundance tends

354   to increase in early forests during their transition to intermediate stages. We did not select

355   "late forests" at our study site since they tend to reflect structural characteristics (DBH, three

356   height and species composition) associated with tropical moist forest (Tosi, personal

357   communication).

358   On the other hand, the characterization of the plots according to the liana abundance was

359   based on the structure of plants that compose the tropical dry forest of SRNP-EMSS. In this

360   way, we classified the 28 plots according to the relative abundance of stems of lianas over

361   total number of stems, where plots with a relative abundance greater than 0.1 were

362   categorized as plots having high liana abundance (HL), while plots with a relative

363   abundance lower than 0.1 were categorized as having a low liana abundance (LL). Although

364   this classification seems to be in-deterministic, this kind of classification represents an

365   important ecological component which is very difficult to study as a continuum due to its

366   spatial and temporal variation, and its categorization can help to improve the understanding

367   of ecological processes as many other ecological categories.

368   At the end of this characterization, ours plots for the study consisted of 5 *E*-LL plots, 6

369   *E*-HL plots, 7 *I*-LL plots, and 10 *I*-HL plots. In each of these plots we extracted all the

370   information available to describe the dry forest according to its structure, but at the same

371   time deployed the ground LiDAR and hemispherical photograph measurements to predict

372   and describe that structure. Information about the parameters used and estimated according

373   to the forest structure, ground LiDAR, and hemispherical photographs is described below.

374

375   **2.4 Forest structure**

376   Four parameters that characterize the forest structure were used in this study. These

377   parameters were selected because these are easily obtained in any forest inventory, which

378   could help in the applicability of this study in other regions. Specifically, we selected the

379   stem density (stems/ha) as a parameter to describe the number of individuals per plot, the

380   mean diameter at breast height (1.3 m) (DBH_{mean}, cm) as a parameter that can describe the

381   mean size of the individuals, the total basal area (TBA, m^2) as a parameter that can describe

382   the biomass of each plot, and the ratio of liana basal area to TBA (L/TBA) as a parameter

383   that can describe the contribution of lianas biomass to the total biomass of each plot. Each of

384   these parameters was extracted from DBH measurements for lianas (>2.5 cm) and trees (>5

385   cm).

386

387   **2.5 Ground LiDAR measurements**

388   The VEGNET ground LiDAR system was deployed in the middle of each of the selected

389   plots, in which a single successful scan was performed between June 12th to June 27th, 2016.

390   The VEGNET IML instrument uses a phase-based laser rangefinder with a wavelength of

391   635 nm, in which a laser beam is directed at a rotating prism that reflects the laser at a fixed

392   angle of 57.5° zenith or the "hinge angle" (*Jupp et al., 2009*). The prism is designed to

393   perform full 360° azimuth rotations at this fixed zenith angle (no vertical scanning motion)

394   and has the capability to be programmed to obtain up to 7360 range measurements for a full

395   azimuth scan (an average of 20.6 measurements per azimuth degree) (*Culvenor et al., 2014*).

396   Because sunlight irradiance may cause interference with the VEGNET laser at the same

397   wavelength (*Culvenor et al*., 2014, *Portilllo-Quintero et al*., 2014), measurements for the

398   VEGNET were conducted at night. Some tests of the measurement process by VEGNET at

399   night time indicated that at distances greater than 60 m or in areas larger than 3600 m^2 (0.36

400   ha) the laser beam does not provide reliable measurements (*Culvenor et al., 2014*). In a

401   tropical forest setting, data analysis and interpretation may be restrained to the footprint,

402   which is dependent on forest height at each site. Based on the forest heights of our study

403   sites, the effective footprint of LiDAR measurements was within 0.1ha of our original

404   sampling area.

405   From these measurements at night six parameters were estimated: the maximum tree

406   height (H_{max}), the plant area index (PAI), plant area volume density (PAVD), the centroid of

407   x (C_x) and y (C_y), and the radius of gyration (RG). To estimate these parameters, the height

408   (h) was initially calculated as the cosine of the laser zenith angle (57.5°) multiplied by the

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

410   (*2014*).

411   On the other hand, canopy "hits" and "gaps" were recorded to enable the calculation

412   of angular gap fraction or gap probability (P_{gap}) at each h where a leaf, trunk or branch was

413   hit by the laser (*Lovell et al., 2003*). P_{gap} at a given h is the ratio of the number of valid

414   returns below z ($\#z_i < h$) to the total number of laser shots (N) (*Culvenor et al., 2014*):

415

416                           $$P_{gap(z)} = [\#z_i < h\,]\,/\,N \qquad\qquad (1)$$

417

418   Consequently, the estimation of cumulative plant area index (PAI) by the conversion of

419   $P_{gap(z)}$ was performed using the following the equation (*Culvenor et al., 2014*):

420

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

422

423   From this calculation, the density of vegetation components at any level of z was

424   computed as the derivative of PAI with respect to h. This calculation is commonly referred

425   to as the plant area volume density (PAVD) (*Culvenor et al., 2014*) described by:

426

427                               $$PAVD_{(z)} = \delta\ PAI_{(z)}\ /\ \delta_z \tag{3}$$

428

429   It is important to note that these calculations represent tridimensional variations (x, y,

430   z) of the forest structure (*Culvenor et al., 2014*), because of this, in our statistical analysis

431   we used the maximum h estimated by the LiDAR per plot (H_{max}), the cumulative PAI as a

432   function of the canopy height (PAI), and the mean PAVD at different heights ($PAVD_{mean}$).

433   These calculations were extracted using the "VEGNET Data Display and Export Version

434   2.5" software developed by Environmental Sensing Systems Inc (Melbourne, Australia).

435   Likewise, from the LiDAR measurements we also used shape metrics such as the

436   centroid (C) and radius of gyration (RG) to understand how the vertical profile of the forest

437   could change according to successional stages and liana abundance. The RG and the C are

438   metrics that are mainly used in LiDAR waveforms to describe the motion of objects and the

439   manner in which material is distributed around an axis (*Muss et al., 2013*). We used a

440   similar approach by calculating the C and the RG for the PAVD vertical profile of each plot.

441   Specifically, C represents the geometric center of a two-dimensional (x and y) region (e.g.,

442   the arithmetic mean position) of all the points (n) in the shape of the PAVD profile and it

443   could, specially, be interpreted as the variability of PAI with height and it will change as a

444   function of understory changes along the path of succession (grasses to shrubs to short

21

445   trees). On the other hand, RG is the root mean square of the sum of the distances for all

446   points on the PAVD vertical profile, which is described as:

447

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

449

450   This parameter can be visualized as the relationship between the total length of the PAVD

451   vertical profile and its shape and position, which are determined using the sum of x or y

452   coordinates divided by the total length of the profile (*Muss et al., 2013*). In general, the RG

453   captures the manner in which the PAVD profile is distributed around the centroid, making it

454   a better descriptor of the vertical profile shape than just the centroid itself, and thus, more

455   suitable for relating VEGNET measurements to forest structure (*Muss et al., 2013; Culvenor*

456   *et al., 2014*). Therefore, we used the RG to relate the shape of the PAVD profile to forest

457   biomass at the footprint level For a more detailed explanation on the functioning of the

458   VEGNET in the field please refer to *Portillo-Quintero et al.* (*2014*) as well as *Culvenor et*

459   *al.* (*2014*). A single successful scan was performed during the wet season using the

460   VEGNET instrument at each site on clear nights.

461

462   **2.6 Hemispherical photographs**

463   Hemispherical photographs (HPs) were taken during the early morning in the middle of each

464   plot, using a digital camera (E4500, Nikon, Tokio, Japan) equipped with a fisheye lens of 35

465   mm focal length. The camera was leveled at 1.50 m by a tripod and orientated towards

466   magnetic north, in order to ensure photographic standardization. The resulting pictures were

467   analyzed using the software Gap Light Analyzer version 2.0.4 (*Frazer et al., 1999*). This

468 analysis was performed by creating 340 sky sectors (36 azimuth classes and 9 elevation

469 angle classes) with a time series of 2 min along the solar track. The leaf area index (LAI)

470 and the canopy openness were subsequently extracted by this analysis; however, the LAI

471 was extracted using the "4 ring" (with a zenith angle between 0 to 60º) which is a more

472 accurate depiction of the site than using "5 rings" because the latter takes into account trees

473 that are not immediately surrounding the site, and which are found outside of the plot

474 footprint.

475

476 **2.7 Statistical analysis**

477 This study compared the effect of the successional stages, the abundance of lianas, and their

478 interaction on the parameters of forest structure as well as VEGNET-HPs parameters using a

479 multivariate analysis of variance (MANOVA), in order to demonstrate that this study had

480 been conducted in contrasting environments. For each MANOVA we extracted the

481 univariate analysis of variance (ANOVA) to describe the multivariate effects of each

482 parameter. To show the potential of the VEGNET and HPs to predict variations in the

483 structure of the dry forest, we applied a canonical correlation analysis (CCA) using the

484 VEGNET-HPs parameters as independent variables and the features of the forest stand as

485 dependent variables. Due to the CCAs sensitivity to the collinearity among variables (*Quinn*

486 *and Keought, 2002*), we only used RG, PAI, $PAVD_{mean}$, H_{max}, LAI, and canopy openness as

487 independent parameters. Specifically, the CCA was used to extract the canonical correlation

488 between VEGNET-HPs and forest structure (eigenvalues), the correlation between the

489 canonical variates and each matrix (eigenvectors), and the scores that describe the

490 multidimensional variation of each plot according to its correlation. To extract the statistical

491   significance of the canonical correlation coefficients, we computed an asymptotic test on the

492   first canonical dimensions to extract the *F*-approximations of Wilks' Lambda along with its

493   significance. This statistical significance was subsequently validated using a permutation

494   test on each dimension by 10000 iterations.

495   After describing the potential of the VEGNET-HPs parameters to predict variations

496   in the structure of the dry forest, we were interested in demonstrating how the relative

497   abundance of lianas could affect the bias of prediction extracted from these sensors. In

498   ecological terms, it is a perceived expectation that during successional transitions increases

499   in basal area, height and vertical strata of the vegetation should be observed; consequently,

500   these transitions could be translated into increases in VEGNET-HPs parameters (except

501   canopy openness which is inverse). However, from hypothesis derived from previous

502   studies, it is possible that the abundance of lianas may actually arrest the forest succession

503   and reduce the biomass accumulation of woody vegetation (*Paul and Yavitt 2011; Schnitzer*

504   *et al., 2000*). If the above is true, correlations between descriptors of forest structure and

505   parameters extracted from VEGNET and HPs could be diffuse or stochastic in the dry forest,

506   and their application under the presence of lianas could prove ineffective. Under this

507   reasoning, we compare the parametric correlations of four parameters according to the

508   successional stages and the liana abundance, separately. The four parameters selected were

509   those with the two highest correlation values for the VEGNET-HPs matrix and the two

510   parameters with the highest correlation values for forest structure, determined by the first

511   two canonical dimensions described by the CCA. This comparison was conducted using an

512   ordinary resampling method to replicate the correlation 5000 times, in which the resampled

513 values were used to build density plots to describe the bias of prediction according to its

514 overlap.

515   The previous analyses were conducted in R software version 3.3.1 (R Development

516 Core Team, 2016) using the "CCA" package (*González and Déjean, 2015*) to extract the

517 canonical correlations, the "CCP" package (*Menzel, 2009*) to extract the significance of the

518 CCA and its permutation, and the "boot" package (*Canty and Ripley, 2016*) to extract the

519 resampled values. When the normality of the data was not reached, each parameter was

520 previously transformed using the Box-Cox transformation for the analysis.

521

522 **3 Results**

523 **3.1 Changes on forest structure along the path of succession and liana abundance**

524 According to the MANOVA, the forest structure of our plots differed between successional

525 stages (Wilk's Lambda$_{(4,21)}$ = 0.51; $p < 0.01$) and liana abundance (Wilk's Lambda $_{(4,21)}$ =

526 0.58; $p < 0.05$), but without interaction between these categories (Wilk's Lambda$_{(4,21)}$ =

527 0.76; $p = 0.20$). This analysis suggests that the DBH$_{mean}$ and TBA were the only parameters

528 affected by the interaction between successional stages and liana abundance, where *E*

529 successional plots with LL and *I* plots with HL showed lower values of DBH$_{mean}$ and TBA

530 than *E* and *I* plots with HL and LL, respectively (Table 1). In terms of the effect of the liana

531 abundance, the univariate analysis suggests that plots with LL showed lower values of

532 L/TBA in comparison with HL plots.

533

534 **3.2 VEGNET-Hemispherical Photographs (HPs), forest succession, and liana**

535 **abundance**

536   The multivariate comparisons of the VEGNET-HPs parameters showed that the sensor

537   estimations did not differ between successional stages (Wilk's Lambda$_{(8,17)}$ = 0.58; p =

538   0.21), liana abundance (Wilk's Lambda$_{(8,17)}$ = 0.62; p = 0.29), and these categories did not

539   show an interaction (Wilk's Lambda$_{(8,17)}$ = 0.53; p = 0.14). Despite the absence of a

540   multivariate effect of the liana abundance, the univariate responses extracted from this

541   comparison suggest that the LAI and canopy openness differs between plots with HL and

542   LL, where LL plots showed lower values of LAI and higher values of canopy openness in

543   comparison with HL plots (Table 2). On the other hand, the univariate responses showed

544   that the canopy openness was affected by the successional stages, where E successional plots

545   showed higher values of canopy openness than I plots. Likewise, the univariate comparisons

546   suggest that C_x, PAI, and PAVD$_{mean}$ are affected by the interaction of the successional stages

547   and liana abundance, where E successional plots with LL and I plots with HL showed higher

548   values of C_x, PAI, and PAVD$_{mean}$ in comparison with E and I successional plots with HL and

549   LL, respectively.

550

551   **3.3 Canonical correspondence analysis and trends of forest structure**

552   The CCA showed that sensor parameters are strongly associated with the trends in forest

553   structure (Fig 2). In general, the first and second canonical dimension showed correlations of

554   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 =

555   0.16) between our sensors and forest structure. Specifically, the correlation between the

556   canonical variates in the first canonical dimension suggested that canopy openness and the

557   LAI have a great weight in the sensor matrix, while L/TBA and stem density had an

558   important effect on the forest structure (Fig 2a). Likewise, the correlation between the

559   canonical variates in the second canonical dimension showed that H_{max} and $PAVD_{mean}$ had a

560   strong correlation with the sensor parameters, while TBA and steam density had a strong

561   correlation on the forest structure. The scores that described the multidimensional variation

562   of each plot did not reflect a visual aggregation according to the successional stages and

563   liana abundance (Fig. 2b). In terms of the validation of the significance of the canonical

564   correlation coefficients, the permutations test showed that there is an important increase in

565   the significance of the first two canonical dimensions (Fig. 2c, 1d), where the first

566   dimension presented an increase of 0.21 points for the Wilks's statistic, while the second

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

568

569   **3.4 Comparison of correlations between successional stages and liana abundance**

570   The different trends of correlation showed that the successional stages and mainly the liana

571   abundance have an important effect in the prediction of the forest structure using VEGNET-

572   HPs parameters (Figure 3), but at the same time, these trends showed that some of these

573   parameters have the potential to predict the implication of the liana abundance on the forest

574   structure. Specifically, variation in the correlations of canopy openness on L/TBA (Figures

575   3a, b, c) and H_{max} on TBA (Figures 3g, h, i) showed that the correlation trends between

576   successional stages are overlapped, while the correlations trends between liana abundance

577   are separated, in where low values of canopy openness and H_{max} are associated with high

578   values of L/TBA and TBA, and consequently with the discrimination of HL plots. Likewise,

579   variation in the correlation between LAI and L/TBA showed that the trends might not be

580   used to separate successional stages or liana abundance (Figures 3d, e, f). However, the

581   correlation between H_{max} and TBA suggest that H_{max} can not discriminate between different

582 successional stages, but can discriminate different liana abundance since lower values of

583 correlation are associated with HL plots (Figures 3j, k, l).

584

585 **4 Discussion**

586 **4.1 Potential of VEGNET and HPs to detect the vertical structure of forest stands at**

587 **different successional stages**

588 Woody vines or lianas tend to proliferate in disturbed forest stands such as regenerating

589 forests (*Paul and Yavitt, 2010*). Much research on liana ecology, however, has focused on

590 old-growth forests despite that secondary forests currently cover a larger area than old-

591 growth forests and may become the dominant ecosystem in tropical regions (*Wright, 2005*).

592 Due to shorter stature and a higher variability of light in secondary forests, lianas may be

593 particularly abundant in these ecosystems, but little is understood about the role of lianas in

594 forest succession (*Letcher and Chazdon, 2009*). In this study, we used the VEGNET, a

595 terrestrial LiDAR system combined with HPs, to assess the impact of liana abundance on

596 forest succession. Our overall analysis indicated that VEGNET parameters, in combination

597 with HPs derived information, were able to characterize changes in forest structure at

598 different successional stages with and without lianas. Changes observed using HP, along the

599 successional gradient, we similar to those observed in other tropical dry forests

600 environments where parameters such as biomass, LAI, canopy openness and H_{max} changed

601 as trees grow (*Sanchez-Azofeifa et al. 2009*). Our work using the TLS suggested also that

602 this technology can be also used to detect differences along the forest succession trajectory

603 when lianas are integrated into the analysis. In terms of the comparison of VEGNET

604 parameters between our categories, probably the effect of the interaction of the successional

605   stages and liana abundance on C_x, PAI and $PAVD_{mean}$ are some of the most reveling. As

606   lianas emerge along the path of succession they create a more heterogeneous space which is

607   captured by the variability on C_x. C_x is affected by PAI and $PAVD_{mean}$ as function of

608   understory components (shrubs, grasses and also liana tangles). A higher value of C_x may be

609   interpreted on an E-LL as a high dominance of shrubs, tall grasses and short trees; while a

610   high value of C_x on a E-HL will mean a high density at low height of tangles combined with

611   shrubs which makes accessibility impossible to some sites due to a high density of

612   understory liana tangles.

613

614   **4.2 How liana abundance could affect the bias of prediction of VEGNET and HPs to**

615   **detect the level of succession of a given forest stand?**

616   When we consider the bias of correlations between the forest structure and the parameters

617   extracted from our two sensors at different successional stages, as well as liana abundance,

618   our results suggest that this latter variable has an important effect on the bias of prediction

619   for a given forest structure. The main reason is probably a result of lianas introducing

620   random tangles into the 3-dimensional space that is occupied by all forest biomass at a given

621   plot. In other words, lianas tend to randomize or reduce the degree of organization of the

622   natural space which is typically utilized by trees. This randomization of the 3D space

623   occupied by trees and lianas is an element that has not been considered as of today; since

624   most studies do not consider the space occupied by lianas because of a lack of TLS

625   information.

626   This change in deterministic patterns of the forest structure is probably due to

627   competition between lianas and trees in forest stands within a random 3D space. In disturbed

628   sites, such as secondary forests, lianas deploy leaves in the canopy and create large amounts

629   of tangles in both the ground and mid canopy, this high density of tangles contribute to a

630   reduction on the amount of available transmitted incoming solar radiation available for

631   photosynthesis at the understory (*Sanchez-Azofeifa et al. 2009, Graham et al., 2013*).

632   Moreover, in regenerating stands within forests (e.g., treefall gaps), high densities of lianas

633   can inhibit the regeneration of tree species and reduce the abundance of shade-tolerant trees

634   (*Schnitzer et al., 2000*), which in turn can affect the 3D arrangement of species within a

635   given area. These ecological processes may cause a shift in forest structure, which is

636   detected as a shift in the vertical structure signature by TLS or even HPs in sites with high

637   liana abundance. These differences in structures have been confirmed in a recent study,

638   which found that a liana-infested forest had a more irregular canopy with canopy heights

639   between 10 and 20 m, while the surrounding forests had a significantly taller canopy

640   between 25 and 35m along with a denser canopy (*Tymen et al., 2016*). Together, our results

641   and Tymen et al. (2016) observations could highlight the potential of entropy analysis of the

642   forests to detect the presence and the effect of lianas on the forest structure and the pathways

643   of succession.

644

645   **4.3 A cautionary tale associated to emergent TLS and HPs monitoring technologies**

646   **applied to liana-infested sites**

647   Our observations from changes on DBH_{mean}, TBA, PAI, $PAVD_{mean,}$ LAI and canopy

648   openness as function of liana abundance provide evidence that these variables can be used to

649   estimate the impact of lianas on forest structure along the path of succession, although not

650   all of parameters, such as stem density and L/TBA, were significant. In other words, there is

651   a strong need to carefully select which parameters should be considered if we want to

652   estimate changes in the forest structure as function of liana abundance. One key example is

653   the use of PAI (PAI= LAI + Woody Area Index (WAI)) as tool to evaluate the impact of

654   liana abundance on forest succession. PAI as a single measurement theoretically could

655   provide insights on the impact of liana abundance on successional stages; as such we could

656   expect that PAI will increase as leaf and wood biomass increases during succession (*Quesada*

657   *et al., 2009*). Furthermore, PAI could be better understood if specific measurements of TLS

658   can be done during the dry season to quantify the real value of WAI to PAI, tropical dry forests

659   in contrast to tropical rainforests can provide significant advantage on better understanding PAI

660   (Kalascka et al. 2005b). It is surprising that we did not find differences in the PAI values

661   between stands that did and did not have lianas. It is possible that PAI is not the best

662   parameter to differentiate between plots with and without liana presence, instead variables

663   more related with leaf components, such as LAI and WAI may be more suitable for finding

664   differences in liana signature across sites, especially when the contribution of lianas to the

665   WAI to overall plot PAI is relatively small in comparison to the allocation of WAI from

666   trees (*Kalascka et al. 2005b, Sanchez-Azofeifa et al., 2009*).

667   A recent study assessing the role of lianas on forest dynamics in the Amazon,

668   indicated that a liana-infested forest appeared to be in an arrested stage of ecological

669   succession, due to the evidence provided by LiDAR surveys from 2007 to 2012 which

670   showed that the overall extent of forest area had remained stable, with no notable net gain or

671   loss over the surrounding forest (*Tymen et al., 2016*). It is possible that studying forest

672   dynamics in forest stands across successional stages, with different levels of liana abundance

673   integrated into the TLS and HPs parameters, may allow us in the future to provide stronger

674   evidence as to whether lianas can arrest succession in dry forests as it appears to occur in

675   humid forests (*Schnitzer et al., 2000; Tymen et al., 2016*).

676   Moreover, our work seeks to strength the argument for the inclusion of lianas on

677   global terrestrial vegetation models (*Verbeek & Kearsley, 2016*). We argue here that the first

678   step on the development of such models is to have a clear understanding of how lianas affect

679   ecosystem structure and composition, which in turn, will affect tree mortality/recruitment,

680   and carbon storage aboveground and belowground (*Poulsen et al. 2016, Schnitzer et al.*

681   *2014*). Furthermore, lianas because of their impact on the 3D structure of a given forest

682   space, may have the possibility of changing faunal diversity (e.g. birds) an impact that has

683   not fully documented as today. As such, our study also supports the arguments by Schnitzer

684   et al (2016) that calls for the need for developing a network of observational and

685   experimental sites that can provide insights on the impact of lianas at different ecological

686   levels.

687   We extend the previous argument to remote sensing studies as well. Since lianas

688   represent a significant ecological component of tropical ecosystems (with stronger presence

689   on intermediate stages than early or late successional stages), we also argue that the

690   development of more robust global vegetation models must start from understanding liana

691   impact of forest structure which in turn will drive other components of those models.

692

693   **5 Conclusions**

694   This study evaluated the potential for TLS and hemispherical photos to observe differences

695   between successional stages of a tropical dry forest chrono-sequence and liana abundance.

696   Our work provided five main conclusions: (1) that TLS data combined with hemispherical

697 photography data can help to predict the forest structure of the tropical dry forest as

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

699 considered, (3) that variations in TLS and HPs parameters can be used to predict the effect

700 of liana abundance on the successional path, (4) that not all the parameters could address the

701 effect of the presence or impact of lianas along a successional gradient, and (5) we suggest

702 that the impact of lianas on successional stages changes the deterministic nature of forest

703 structure, by randomizing the 3D space where they grow at given plot; the higher the

704 abundance of lianas the higher the randomization.

705   Our study provides important insights on the contributions of lianas to the

706 successional process, and highlights the potential that TLS and HPs have in monitoring liana

707 presence in tropical dry forests environments. Lianas are increasing in density and biomass

708 in tropical forests, but it is unknown whether this pattern is also found in secondary forests,

709 which are suitable for liana proliferation. TLS systems, and to a lesser extent HPs are

710 capable of providing unbiased estimations for the vertical structure of a given site, and thus

711 constitute powerful tools to monitor the increases in liana density and biomass. Although,

712 our study is limited to one single site in Costa Rica, this is a first step on the development of

713 more comprehensive approaches, which take advantage of advanced technology to

714 understand the effects of liana abundance on tropical dry forest structure. The approach

715 presented in this paper, presents important contributions to efforts directed to estimate the

716 potential effects of lianas on forest carbon in secondary forests (*Durán and Sanchez-*

717 *Azofeifa, 2015*), elements that seems not fully considered yet in the tropical literature.

718

719 **Acknowledgements**

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895

896   Table 1. Mean (± SD) of parameters of forest structure extracted from plots with

897   different successional stages and different relative abundance of lianas in the dry forest

898   at Santa Rosa National Park, Costa Rica. Significant differences (*F-values* and their *p-*

899   *values*) according to the successional stages, relative abundance of lianas and their

900   interaction are represented by a posteriori ANOVA text extracted from MANOVA. Stem

901   density (stems/ha); DBH_{mean}, mean stem diameter at breast height (cm); TBA, total basal

902   area (m^2); L/TBA, ratio of liana basal area to TBA.

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

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

904

905 Table 2. Mean (± SD) of parameters calculated by VEGNET system and HPs in plots

906 with different successional stages and different relative abundance of lianas in the dry

907 forest at Santa Rosa National Park, Costa Rica. Significant differences (*F-values* and

908 their *p-values*) according to the successional stages, relative abundance of lianas and

909 their interaction are represented by a posteriori ANOVA text extracted from MANOVA.

910 RG, radius of gyration; PAI, plant area index; $PAVD_{mean}$, plant area volume density;

911 H_{max}, maximum tree height (m); LAI, leaf area index.

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

912 *, $p < 0.05$

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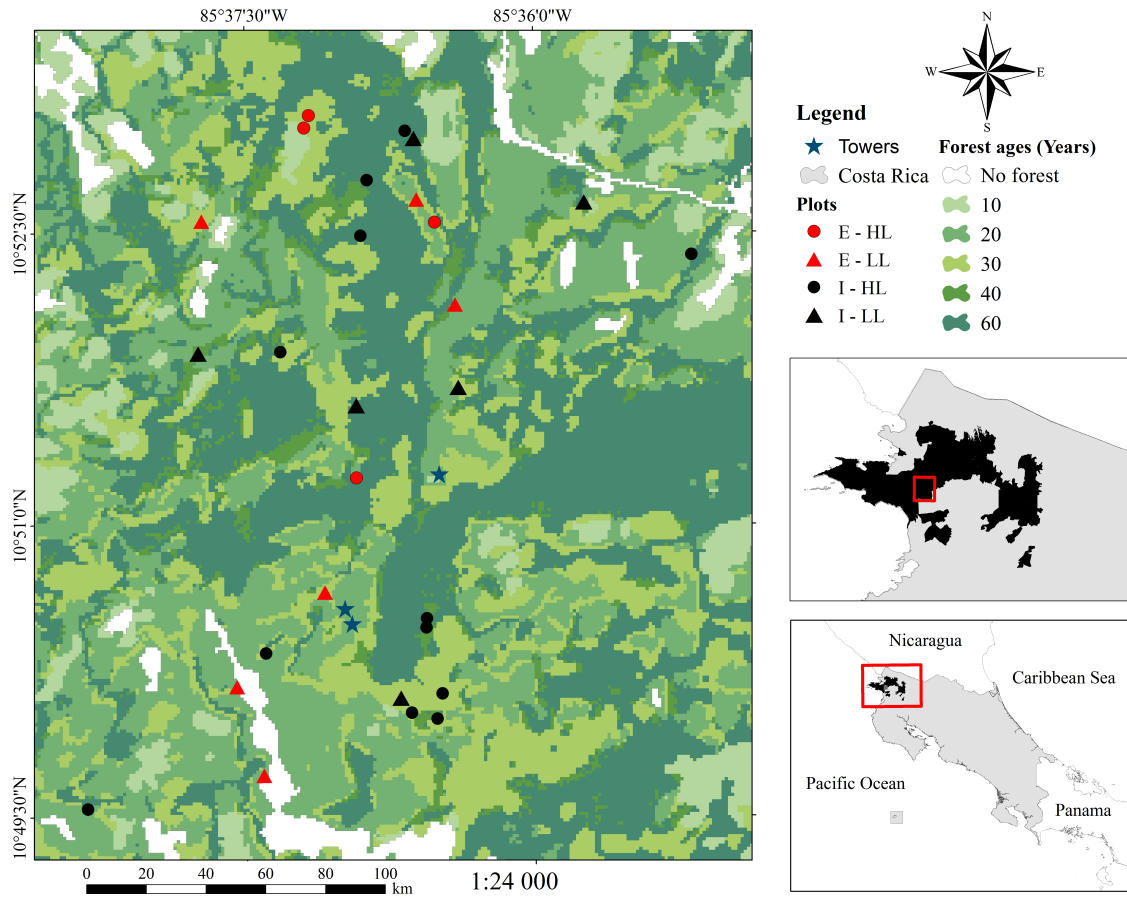
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917 Figure 1. Location of the sampled forest plots at the Santa Rosa National Park

918 Environmental Monitoring Super Site, Guanacaste, Costa Rica. Where E-HL indicates

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

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

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

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

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

924 10 forests detected since 2005, and no forest correspond to non-related to woodlands.

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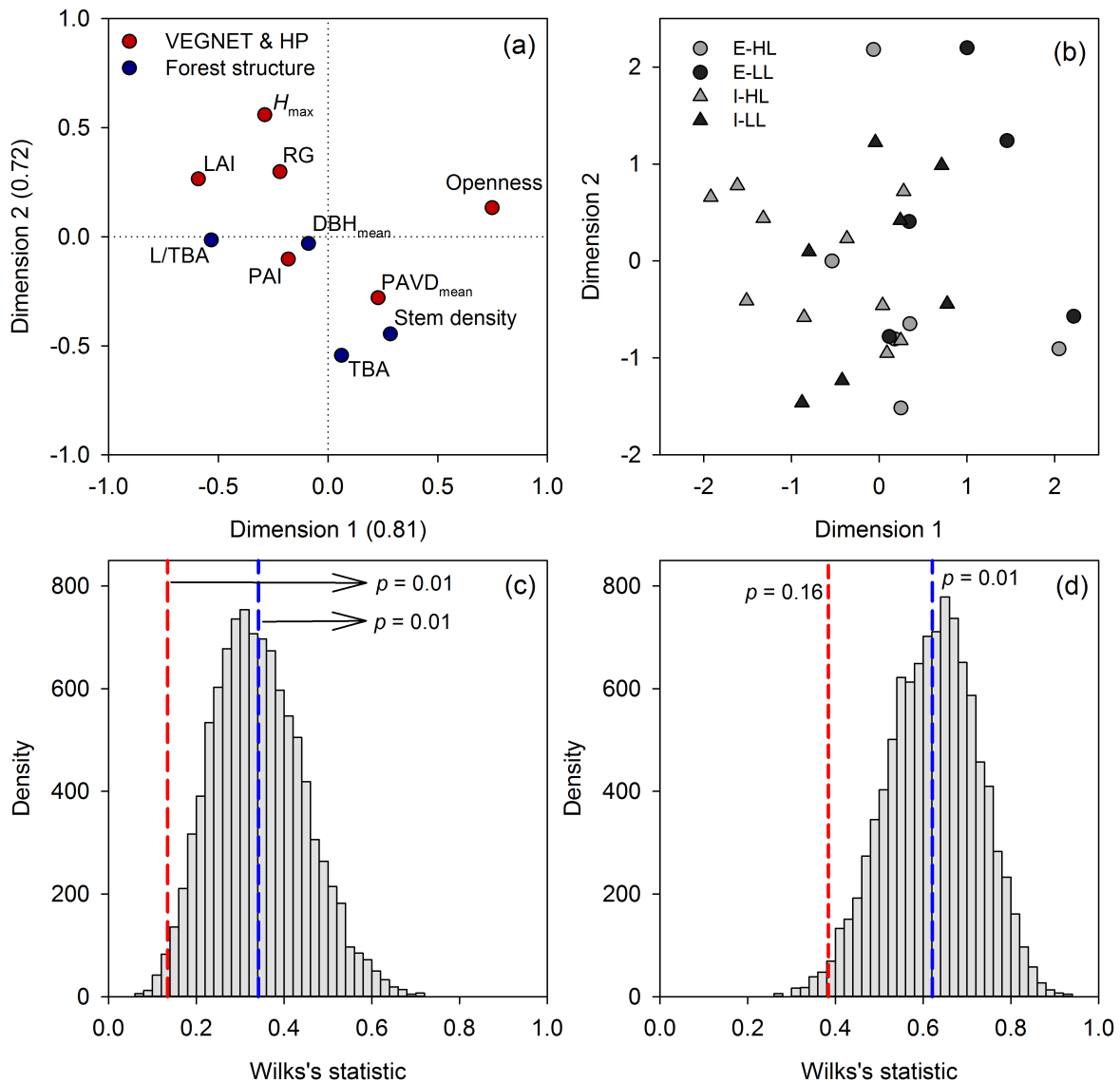
Figure 2. Canonical correspondence analysis to describe the association between the

parameters estimated by VEGNET system-hemispherical photographs (HPs) and the

forest structure. a) VEGNET-HPs coefficients are represented by red points, while forest

structure coefficients are represented by blue points. b) Individual scores of each plot of

the canonical variates are represented according to successional stages (E, early; I,

intermediate) and relative liana abundance (LL, low liana abundance; HL, high liana

abundance). C and d represent the permutation distribution of the Wilks' Lambda test to

934   assign the statistical significance of canonical correlation coefficients considering 4 and

935   3 canonical correlations, respectively; the red line represent the original value Wilks'

936   Lambda, while the blue line represent the mean value permutated. The p values next to

937   each line represent the significance of the Wilks' Lambda test.

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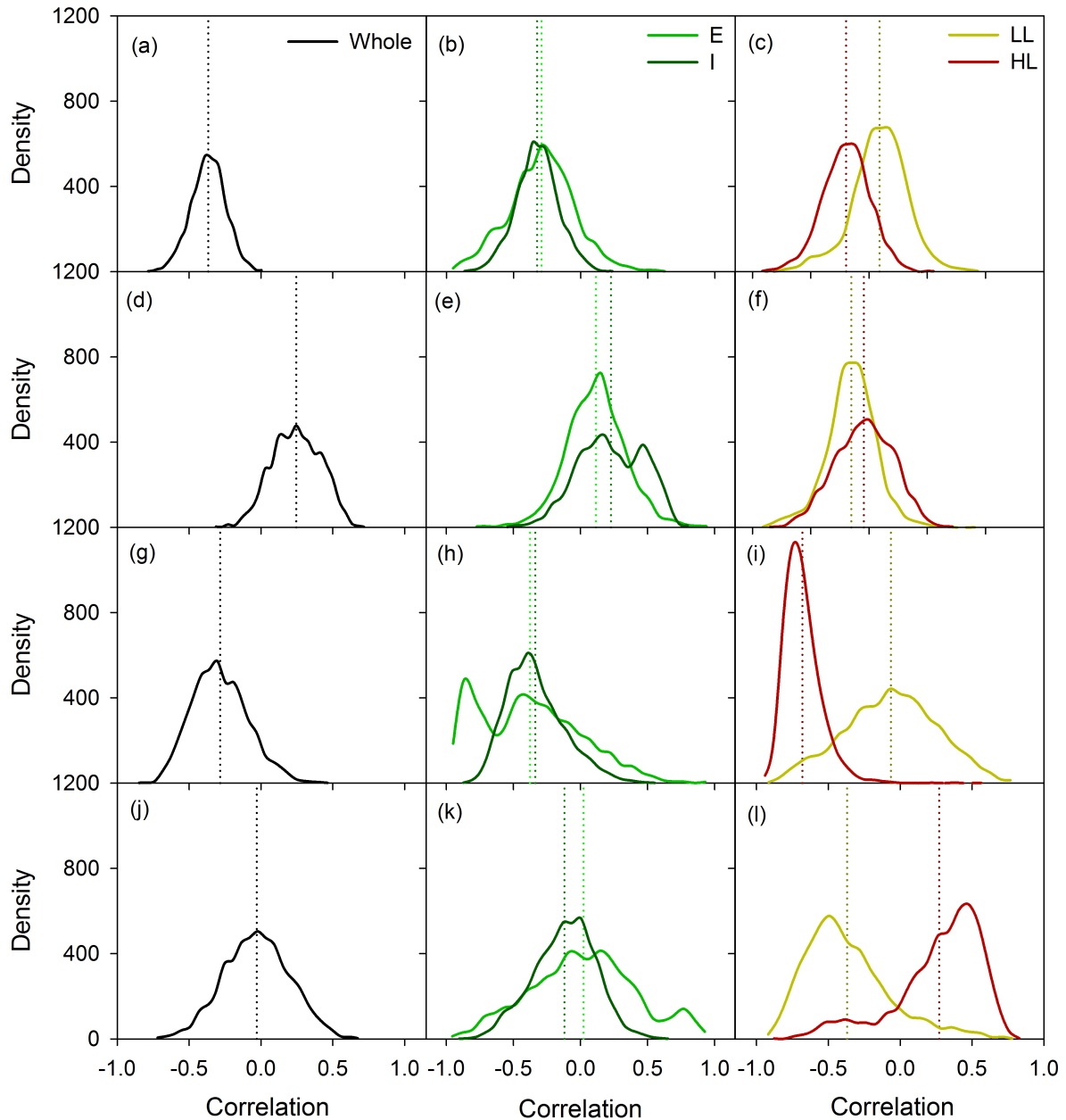
Figure 3. Density distribution of the bootstrapped correlation coefficients without and with distinction between successional stages (E, early; I, intermediate) and relative liana abundance (LL, low liana abundance; HL, high liana abundance). a, b, and c correspond to the correlation of canopy openness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

946   density-TBA correlation. Each dotted line represents the mean value of the bootstrapped

947   correlation.