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Running head: AMAZONIAN LIANA ABUNDANCE

## LONG-TERM CHANGES IN LIANA ABUNDANCE AND FOREST DYNAMICS IN UNDISTURBED AMAZONIAN FORESTS

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### ABSTRACT

Lianas (climbing woody vines) are important structural parasites of tropical trees and may be increasing in abundance in response to global-change drivers. We assessed long-term (~14-year) changes in liana abundance and forest dynamics within 36 1-ha permanent plots spanning ~600 km<sup>2</sup> of undisturbed rainforest in central Amazonia. Within each plot, we counted each liana stem ( $\geq 2$  cm diameter) and measured its diameter at 1.3 m height, and then used these data to estimate liana aboveground biomass. An initial liana survey was completed in 1997-99 and then repeated in 2012, using identical methods.

Liana abundance in the plots increased by an average of  $1.00 \pm 0.88\%$  yr<sup>-1</sup>, leading to a highly significant ( $t=6.58$ ,  $df=35$ ,  $P<0.00001$ ) increase in liana stem numbers. Liana biomass rose more slowly over time ( $0.32 \pm 1.37\%$  yr<sup>-1</sup>) and the mean difference between the two sampling intervals was nonsignificant ( $t=1.46$ ,  $df=35$ ,  $P=0.15$ ; paired  $t$ -tests). Liana size-distributions shifted significantly ( $\chi^2=191$ ,  $df=8$ ,  $P<0.0001$ ; Chi-square test for independence) between censuses, mainly as a result of a nearly 40% increase in the number of smaller (2-3 cm diameter) lianas, suggesting that lianas recruited rapidly during the study.

We used long-term data on rainfall and forest dynamics from our study site to test hypotheses about potential drivers of change in liana communities. Lianas generally increase with rainfall seasonality but we found no significant trends over time (1997-2012) in five rainfall parameters (total annual rainfall, dry-season rainfall, wet-season rainfall, the number of very dry months, and the CV of monthly rainfall). However, rates of tree mortality and recruitment have increased significantly over time in our plots, and general linear mixed-effect models suggested that lianas were more abundant at sites with higher tree mortality and flatter topography. Rising concentrations of atmospheric CO<sub>2</sub>, which may stimulate liana growth, might also have promoted liana increases.

Our findings clearly support the view that lianas are increasing in abundance in old-growth tropical forests, possibly in response to accelerating forest dynamics and rising CO<sub>2</sub> concentrations. The aboveground biomass of trees was lowest in plots with abundant lianas, suggesting that lianas could reduce forest carbon storage and potentially alter forest dynamics if they continue to proliferate.

**Key words:** *Amazon; biomass; carbon storage; CO<sub>2</sub> fertilization; forest disturbance; forest dynamics; lianas; tree infestation; tree mortality; undisturbed forest; woody vines.*

50

51

## INTRODUCTION

52 Lianas (climbing woody vines) are a major feature of tropical rainforests. They constitute  
53 from 10-45% of all woody plants and species (Schnitzer and Bongers 2002) and produce up  
54 to 40% of the leaves in the forest (Kato et al. 1978, Putz 1983). Occasionally growing to >50  
55 cm in diameter and several hundred meters in length (Schnitzer et al. 2012), lianas exploit  
56 trees for physical support in order to reach the forest canopy. By creating structural stresses  
57 on trees and competing for light, nutrients, and water, liana infestations can reduce tree  
58 growth, fecundity, survival, and recruitment (Putz 1984, Stevens 1987, Schnitzer et al. 2000,  
59 Schnitzer and Carson 2010, Yorke et al. 2013). As a result, they can have a considerable  
60 impact on forest dynamics, tree-species composition, and carbon storage (Schnitzer and  
61 Bongers 2002, 2011, Körner 2004).

62 Most liana species are light loving and increase markedly in abundance in forests  
63 disturbed by windstorms (Webb 1958), logging (Appanah and Putz 1983), and habitat  
64 fragmentation (Laurance et al. 2001). They may also be increasing even in undisturbed  
65 forests. Liana abundances have been reported to have risen over time in old-growth forests in  
66 western Amazonia (Phillips et al. 2002, Foster et al. 2008), the Guianas (Chave et al. 2008),  
67 and Central America (Wright et al. 2004, Ingwell et al. 2010, Schnitzer et al. 2012, Yorke et  
68 al. 2013). Liana seedlings were also observed to proliferate in central Amazonia (by ~500%  
69 over 6.5 years), although this involved the colonization of small experimental clearings  
70 (Benítez-Malvido and Martínez-Ramos 2003) where liana recruitment might be favored.

71 Three main hypotheses have been proposed to explain the apparent increase in liana  
72 abundances in undisturbed old-growth forests (Schnitzer and Bongers 2011). First, seasonal  
73 droughts may be increasing in some tropical regions, such as the southern Amazon (Fu et al.  
74 2013), possibly as a result of regional or global climate change (Lewis et al. 2011, Brodie et  
75 al. 2012). Droughts would likely benefit lianas (Ingwell et al. 2010, Enquist and Enquist  
76 2011), which are more resilient and grow faster than do trees under dry conditions (Schnitzer  
77 2005, Cai et al. 2009). Second, elevated atmospheric CO<sub>2</sub> may increase liana growth and  
78 fecundity (Hättenschwiler and Körner 2003, Mohan et al. 2006, Körner 2009), especially in  
79 the deep shade of the forest understory (Granados and Körner 2002, Zotz et al. 2006).  
80 Finally, rates of tree mortality and turnover appear to be increasing in many tropical forests,  
81 possibly because forests are becoming more productive and competitive as a result of rising  
82 CO<sub>2</sub> fertilization (Phillips and Gentry 1994, Laurance et al. 2004, 2009, Lewis et al. 2004a).  
83 Such elevated forest dynamics would produce more treefall gaps, where lianas proliferate in  
84 stem number and diversity (Putz 1984, Schnitzer and Carson 2001, Dalling et al. 2012,  
85 Schnitzer et al. 2012). These three mechanisms are not mutually exclusive and might operate  
86 in concert or even synergistically (Schnitzer and Bongers 2011).

87 Here we assess long-term (~14-year) changes in liana abundance and biomass in  
88 undisturbed, old-growth forests of central Amazonia, which overlay nutrient-poor soils  
89 typical of much of the Amazon basin (Bravard and Righi 1989). Our network of 36  
90 permanent 1-ha plots spans an extensive geographic area (~600 km<sup>2</sup>) and also provides long-  
91 term data on forest dynamics, tree-stand attributes, topography, and soil features (e.g.  
92 Laurance et al. 1997, 1999, 2000, 2006). When combined with local weather records, these  
93 data allow us to test leading hypotheses about the potential drivers and ecological  
94 consequences of changing liana abundance.

95

## METHODS

96

### *Study area*

97 This study was conducted in old-growth rainforests of the Biological Dynamics of Forest  
 98 Fragments Project (28° 30' S, 60° W), a large-scale experimental study of habitat  
 99 fragmentation located 70 km north of Manaus, Brazil (Lovejoy et al. 1986). The 36  
 100 permanent, 1-ha plots in the study span an area of about 15 x 40 km and range from 60-100 m  
 101 elevation. All plots were located  $\geq 150$  m from the nearest forest-pasture margin to minimize  
 102 edge effects (Laurance et al. 2002, 2011) and exhibited no evidence of anthropogenic  
 103 disturbances such as selective logging, fires, or past agriculture (Laurance et al. 2004, 2005).

104 The forests of the study area are among the most diverse in the world (averaging  $\sim 260$   
 105 tree species of  $\geq 10$  cm diameter-at-breast-height [DBH]  $\text{ha}^{-1}$ ) with a typical canopy height of  
 106 37-40 m (Laurance et al. 2010). The dominant soils in the study area are xanthic ferralsols  
 107 (Fearnside and Leal Filho 2001), which are heavily weathered and nutrient poor (Beinroth  
 108 1975). In this region, clay-rich plateaus are frequently dissected by steep stream gullies,  
 109 which have higher sand contents and lower concentrations of most soil nutrients (Chauvel et  
 110 al. 1987). Rainfall ranges from 1900-3500 annually with a moderately strong dry season from  
 111 June-October (Laurance 2001).

#### 112 *Data collected*

113  
 114 The 36 permanent plots we studied were established in the early-mid 1980s, with an initial  
 115 focus on tree-community dynamics and forest-carbon storage (Laurance et al. 1997, 1998,  
 116 2006a, 2006b). Within each plot, all trees ( $\geq 10$  cm DBH) were measured at 1.3 m height or  
 117 above any buttresses, mapped, and tagged, with sterile or fertile material collected to  
 118 facilitate species identification. Each plot was recensused at a nominal interval of  $\sim 5$  years to  
 119 record any dead, damaged, or newly recruited trees, with the most recent tree census in 2009.  
 120 Annualized rates of tree mortality were estimated using a logarithmic model (Sheil et al.  
 121 1995), corrected for variation in census interval (Lewis et al. 2004b). The aboveground dry  
 122 biomass (AGBM) of live trees was estimated for each plot and census using an allometric  
 123 formula based on destructively sampling 315 trees in nearby rainforests (Chambers et al.  
 124 2001).

125 Liana data in all but three of our plots were initially collected in 1997-99 (Laurance et  
 126 al. 2001), with the remaining three plots censused for lianas in early 2001. All plots were  
 127 resampled, using identical methods, in 2012, for a mean resampling interval of  $13.6 \pm 0.7$   
 128 years. Within each plot, all lianas ( $\geq 2$  cm diameter) were counted and measured at 1.3 m  
 129 height, following established protocols for enumerating liana stems (Putz 1984, Schnitzer et  
 130 al. 2006). As is typical, no attempt was made to distinguish liana ramets and genets. Liana  
 131 stems were not individually tagged during the initial survey. Estimates of liana aboveground  
 132 dry biomass (AGBM) were derived with an allometric model using liana stem-diameter data  
 133 ( $D$ ) from many different studies (Schnitzer et al. 2006), as follows:

$$134 \text{ AGBM} = \exp[-1.484 + 2.657 \ln(D)] \quad (1)$$

135  
 136  
 137 The only exception from established protocols was that in 1997-99 we measured the diameter  
 138 of non-circular liana stems (which constituted just 1.4% of all stems) with a DBH tape, rather  
 139 than averaging their length and width, as is now recommended (Schnitzer et al. 2006). For the  
 140 sake of consistency we retained this method in 2012, but found it had little impact on our  
 141 estimates of liana AGBM (using 2012 data, AGBM values for each plot calculated using the  
 142 two methods differed by just 0.5% on average).

143 Mean slope was determined for each plot with a clinometer, by dividing the plot into  
 144 25 subplots (each 20 x 20 m), determining the maximum slope within each subplot, and then  
 145 averaging these values. In our study area, mean slope is a good proxy for soil texture and  
 146 nutrient status; the major gradient is between clay-rich soils in flatter areas with higher C, N,

147 cation exchange capacity, and exchangeable bases, and sandy, nutrient-starved soils in  
148 steeper sites with greater aluminum toxicity (Laurance et al. 1999, 2001, 2010).

149 Monthly rainfall data were collected from the Brazilian National Institute for  
150 Meteorology weather station in Manaus, from 1997-2012 (<http://www.inmet.gov.br>). These  
151 data were used to generate five annual weather parameters: total rainfall, dry-season rainfall  
152 (May-October), wet-season rainfall (November-April), the coefficient of variation (CV) in  
153 monthly rainfall, and the number of 'very dry' months (those with <50 mm of rainfall).  
154 Monthly rainfall in Manaus and the study area are strongly correlated but the latter tends to  
155 be somewhat wetter on average, especially in the dry season (Laurance 2001). Daily rainfall  
156 data were recorded in the study area from 1988-1998 but records have been inconsistent since  
157 then.

158

159

#### *Data analysis*

160 We assessed changes in liana abundance and biomass over time in our 36 plots using paired *t*-  
161 tests. Data were log-transformed prior to analysis if differences between paired samples  
162 deviated significantly from normality. Changes over time in liana size-distributions were  
163 assessed with a Chi-square test for independence.

164 We tested effects of three possible predictors on liana abundance in 1997-99 and in  
165 2012. Our possible predictors were (1) mean number of trees per plot, (2) mean rate of tree  
166 turnover (the average of annualized rates of tree mortality and recruitment, a commonly used  
167 index of forest dynamics; Philips and Gentry 1994), and (3) mean slope of the plot. To do this  
168 we fitted general linear mixed models (GLMM) with Gaussian error distributions and identity  
169 link functions, using function *glmmadmb* in R's *glmmADMB* package (Bolker et al. 2012).  
170 Plots in the study area occur in three relatively discrete blocks (Laurance et al. 1998), and  
171 hence block was included as a random variable to account for the possible non-independence  
172 of samples within the same block. All variables were included in the general model because,  
173 in previous tests for collinearity, the variance-inflation factors for all variables were <3 (Zuur  
174 et al. 2009). Logarithmic and arcsine-squareroot transformations were used to improve the  
175 linear fits of tree mortality and slope data, respectively. All potential predictors were  
176 standardized prior to analysis so their effect sizes could be compared directly.

177

178

## RESULTS

179

### *Liana abundance and size distributions*

180 In our 36 plots, we recorded a total of 13,544 lianas in 1997-99, and 15,549 lianas in 2012.  
181 The increase in mean liana abundance over time (Fig. 1), from  $376 \pm 107$  (range: 200-637) to  
182  $428 \pm 118$  (range: 224-682) stems  $\text{ha}^{-1}$ , was highly significant ( $t=6.58$ ,  $\text{df}=35$ ,  $P<0.00001$ ;  
183 paired *t*-test with log-transformed data). On average, liana stems increased on each plot by  
184  $1.00 \pm 0.88$  %  $\text{yr}^{-1}$ .

185 The size distributions of lianas (Fig. 2) exhibited a highly significant shift over time  
186 ( $\chi^2=190.9$ ,  $\text{df}=8$ ,  $P<0.00001$ ; Chi-square test for independence). This shift mainly resulted  
187 from a nearly 40% increase in the number of small (2-3 cm diameter) lianas, from  $136 \pm 43$   
188 stems  $\text{ha}^{-1}$  in 1997-99 to  $190 \pm 56$  stems  $\text{ha}^{-1}$  in 2012. Lianas in most of the larger size-classes  
189 also increased over time, but the proportional differences were mostly minor (Fig. 2).

190

191

192

### *Liana biomass*

193 The estimated mean biomass of lianas also rose over time, from  $7.7 \pm 2.3$  tonnes  $\text{ha}^{-1}$  in 1997-  
194 99 to  $8.0 \pm 2.2$  tonnes  $\text{ha}^{-1}$  in 2012, but this difference was nonsignificant ( $t=1.46$ ,  $\text{df}=35$ ,  
195  $P=0.15$ ; paired *t*-test with log-transformed biomass data). In annualized terms, biomass  
196 increased by  $0.32 \pm 1.37$  %  $\text{yr}^{-1}$ . Results were similar for liana basal area, which rose from

197 0.717±0.194 to 0.748±0.186 m<sup>2</sup> ha<sup>-1</sup> on average, between 1997-99 and 2012. This difference  
198 was marginally nonsignificant ( $t=1.90$ ,  $df=35$ ,  $P=0.065$ ; paired  $t$ -test).

199 Estimates of liana biomass for each plot were heavily influenced by a few large  
200 lianas. In 2012, large (>10 cm diameter) lianas constituted just 2.7% of all recorded stems but  
201 40.9% of estimated biomass. The number of large lianas per plot explained much of the  
202 variation in liana biomass ( $F_{1,34}=53.78$ ,  $R^2=61.3\%$ ,  $P<0.0001$ ; linear regression). Patterns  
203 were similar in 1997-99.

204 Plots with many large lianas in 1997-99 tended to have many large lianas in 2012  
205 ( $r=0.729$ ,  $P<0.0001$ ). Likewise, plots with many smaller ( $\leq 10$  cm) lianas in 1997-99 had  
206 many smaller lianas in 2012 ( $r=0.898$ ,  $P<0.0001$ ). There was no significant correlation  
207 between the number of large and smaller lianas per plot in either 1997-99 ( $r=0.149$ ,  $P=0.39$ )  
208 or 2012 ( $r=0.055$ ,  $P=0.75$ ). However, in both 1997-99 ( $r= -0.553$ ,  $P=0.0005$ ) and 2012 ( $r= -$   
209  $0.509$ ,  $P=0.0015$ ), large lianas became relatively less frequent (comprising a smaller  
210 percentage of all liana stems) as the number of lianas per plot increased (all Pearson  
211 correlations with  $df=34$ ).

212

213

#### *Predicting liana abundance*

214 The GLMM analyses suggested that two variables, mean slope and our index of forest  
215 dynamics (mean tree-turnover rate), were moderately useful predictors of liana abundance in  
216 1997-99 and again in 2012 (Table 1). Lianas were generally more abundant on flatter sites  
217 with greater forest dynamics. Effect sizes for the two predictors were similar in 1997-99,  
218 whereas slope had a somewhat stronger influence on lianas in 2012.

219 Notably, forest dynamics have generally increased over time in our plots. Using  
220 available data for 33 of the plots, we contrasted mean mortality and recruitment rates of trees  
221 between two largely non-overlapping intervals: the early-mid 1980s to late 1997, versus early  
222 1998 to late 2009 (Fig. 3). Tree mortality increased modestly but significantly over time  
223 ( $t=2.19$ ,  $P=0.036$ ), from 1.33±0.64 to 1.46±0.36 % yr<sup>-1</sup>. Tree recruitment rose more  
224 markedly, from 1.15±0.32 to 1.46±0.53% yr<sup>-1</sup>, a highly significant difference ( $t=3.19$ ,  
225  $P=0.0031$ ; paired  $t$ -tests with  $df=32$  and log-transformed data).

226

227

#### *Rainfall*

228 We found no evidence of changing rainfall trends that might influence liana abundance.  
229 Using Pearson correlations between the year and annual weather variables from 1997 to  
230 2012, there were no significant trends in total rainfall ( $r=0.158$ ,  $P=0.56$ ), dry-season rainfall  
231 ( $r= -0.151$ ,  $P=0.58$ ), wet-season rainfall ( $r=0.253$ ,  $P=0.34$ ), the number of very dry months  
232 ( $r= -0.236$ ,  $P=0.38$ ), and the CV of monthly rainfall ( $r= -0.034$ ,  $P=0.90$ ). Analyses with  
233 Spearman rank correlations, which are insensitive to nonlinear trends, were similar.

234

235

## DISCUSSION

236

#### *Increasing liana abundance*

237 Our large-scale study suggests that in central Amazonian forests, lianas are progressively  
238 increasing in abundance—at a mean rate of ~1% per year over the past 14 years (Fig. 1). The  
239 forests of our study area overlay heavily weathered, infertile soils, which typify much of the  
240 vast Amazon Basin. Our findings accord with several other studies, most of which are  
241 smaller-scale or shorter-term in nature, which suggest that lianas are increasing in old-growth  
242 Neotropical forests (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright  
243 et al. 2004, Foster et al. 2008, Ingwell et al. 2010, Schnitzer et al. 2012, Yorke et al. 2013).

244 The proliferation of lianas we observed largely resulted from increases in smaller-  
245 sized lianas (Fig. 2), suggesting that liana recruitment was high during the course of our study  
246 (1997-2012). Most smaller (2-3 cm diameter) lianas have already reached the forest canopy

247 (Kurzel et al. 2006), indicating that they are potentially important ecologically even at that  
 248 limited size. Liana biomass rose only slightly (from an average of 7.7 to 8.0 tonnes ha<sup>-1</sup>) and  
 249 was highly variable among plots as a result of the patchy distribution of large ( $\geq 10$  cm  
 250 diameter), heavy lianas. Our findings are consistent with those of Benítez-Malvido and  
 251 Martínez-Ramos (2003), who observed a striking increase in numbers of liana seedlings  
 252 (~500% over 6.5 years) in our same study area. However, the degree to which their study  
 253 reflects reality is uncertain, because it measured seedling recruitment within small (1-m<sup>2</sup>),  
 254 artificial clearings that might not reflect actual recruitment processes. Most lianas favor gap  
 255 and edge environments and are adept at colonizing clearings, via both seed dispersal and  
 256 especially clonal growth (Putz 1984, Schnitzer et al. 2000, 2012, Dalling et al. 2012, Yorke et  
 257 al. 2013).

#### 258 *Potential drivers of liana increases*

259 Lianas are known to increase at the expense of trees under conditions of increasing rainfall  
 260 seasonality and declining total rainfall (Schnitzer and Bongers 2002, 2011). However, we  
 261 found no evidence for any such trends during the course of our study (1997-2012), suggesting  
 262 that the liana increases we observed did not result from changing weather conditions.

263 Our findings are, however, broadly consistent with the notion that lianas, which favor  
 264 disturbed forests, might be increasing in response to accelerating forest dynamics. In our  
 265 study area, lianas tended to be abundant in plots with high tree turnover (Table 1), and rates  
 266 of tree mortality and recruitment have both increased significantly in recent decades (Fig. 3).  
 267 Similar trends have recently been detected in a single 50-ha plot on Barro Colorado Island,  
 268 Panama (Dalling et al. 2012, Schnitzer et al. 2012). These increases have several potential  
 269 explanations (Laurance et al. 2004, 2009), including the possibility that rising concentrations  
 270 of atmospheric CO<sub>2</sub> are fertilizing plants and thereby accelerating forest productivity and  
 271 plant growth (Phillips and Gentry 1994, Lewis et al. 2004a). Accelerated growth, in turn,  
 272 might be expected to increase plant competition and thereby lead to more rapid tree mortality  
 273 and recruitment, as well as faster tree senescence. Notably, the large majority of tree genera  
 274 in our study area have exhibited accelerating growth rates over time (Laurance et al. 2004),  
 275 which suggests that forest productivity has indeed increased.

276 In addition, CO<sub>2</sub> increases might fertilize lianas to a greater extent than trees (Würth  
 277 et al. 1998, Hättenschwiler and Körner 2003, Schnitzer and Bongers 2011), leading to liana  
 278 increases. This difference might be attributable to the proportionately greater leaf area of  
 279 lianas, which could allow them to fix more carbon and grow more rapidly than do trees under  
 280 elevated CO<sub>2</sub> conditions (Cai et al. 2009). Additional attributes of lianas, such as their high  
 281 photosynthetic rates, N and P use efficiencies, and tolerance of drought stress, might also  
 282 enhance their response to CO<sub>2</sub> enrichment beyond that experienced by trees (Zhu and Cao  
 283 2010). If CO<sub>2</sub> fertilization of lianas is marked, then it would presumably also translate into  
 284 increased liana fecundity and recruitment, which could produce the major increase in smaller  
 285 lianas observed in this study (Fig. 2). Notably, CO<sub>2</sub> concentrations rose rapidly during the  
 286 course of our study, from 363 ppm in 1997 to 394 ppm in 2012  
 287 ([http://ftp.cmdl.noaa.gov/ccg/co2/trends/co2\\_annmean\\_mlo.txt](http://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_annmean_mlo.txt)).  
 288

#### 289 *Implications of liana increases*

290 Given their antagonistic relationships with trees, it has been suggested that increasing liana  
 291 abundances could have a number of impacts on tropical forest communities. Tree species  
 292 differ in their susceptibility to lianas, with slower-growing, shade-tolerant species being  
 293 particularly vulnerable and pioneer species far less so (Putz 1984, Ingwell et al. 2010,  
 294 Schnitzer and Carson 2010). Lianas thus have the potential to alter the composition and  
 295



296 dynamics of tree communities, especially where they are abundant (Appanah and Putz 1984,  
297 Putz 1984, Schnitzer and Bongers 2002, 2011).

298 Beyond this, lianas could potentially have a sizeable impact on forest carbon storage,  
299 by reducing tree growth and survival, especially for shade-tolerant species, which have high  
300 wood densities and thus high carbon storage (Laurance et al. 2001, 2006a, Körner 2004). For  
301 instance, in our old-growth forest plots, we found that lianas had a strong negative  
302 relationship with aboveground tree biomass (Fig. 4). It is difficult to separate cause and effect  
303 because lianas might either have suppressed tree biomass or have increased where extrinsic  
304 mortality events, such as droughts, windstorms, or disease outbreaks, had previously  
305 damaged forests. Nevertheless, these data clearly suggest that abundant lianas have the  
306 potential to reduce forest carbon storage, especially if they increase further in the future  
307 (Schnitzer and Bongers 2011, Fearnside 2013). In addition, lianas generally have low wood  
308 density and invariably invest far less in woody tissue than do trees (Putz 1984). Hence, even  
309 where hyper-abundant, lianas are unlikely to replace more than a small fraction of the tree  
310 biomass that they kill or suppress.

311 It has been assumed in recent studies that likely consequences of increasing  
312 atmospheric CO<sub>2</sub> concentrations on old-growth tropical forests will be increasing forest-  
313 carbon storage and drought resistance (Cox et al. 2013, Huntingford et al. 2013). However,  
314 the effects of proliferating lianas documented here and in other recent studies (see Ingwell et  
315 al. 2010, Schnitzer and Bongers 2011, Fearnside 2013) should temper the assumption that all  
316 potential effects of rising CO<sub>2</sub> will reduce emissions from these forests.

317

318

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514 Table 1. Potential predictors of liana abundance in 1997-99 and 2012 within 36 1-ha plots in  
 515 undisturbed Amazonian forest, using general linear mixed-effects models. The effect size of  
 516 each predictor is proportional to the absolute value of its Estimate value, with negative values  
 517 indicating a negative slope.

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519 **Number of liana stems in 1997-99**

<u>Predictor</u>	<u>Estimate</u>	<u>S.E.</u>	<u>Z</u>	<u>P</u>
Intercept	376.2	16.2	23.29	<0.0001
Tree turnover rate <sup>a</sup>	30.7	17.2	1.78	0.075
Number of tree stems	11.3	17.2	0.66	0.51
Slope <sup>b</sup>	-33.2	16.8	-1.97	0.048

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521 **Number of liana stems in 2012**

<u>Predictor</u>	<u>Estimate</u>	<u>S.E.</u>	<u>Z</u>	<u>P</u>
Intercept	428.2	17.3	24.79	<0.0001
Tree turnover rate <sup>a</sup>	30.4	18.4	1.65	0.098
Number of tree stems	12.8	18.3	0.70	0.49
Slope <sup>b</sup>	-47.7	18.0	-2.65	0.008

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523 <sup>a</sup>Data log<sub>10</sub>-transformed524 <sup>b</sup>Data arcsine-squareroot-transformed

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**FIGURE CAPTIONS**

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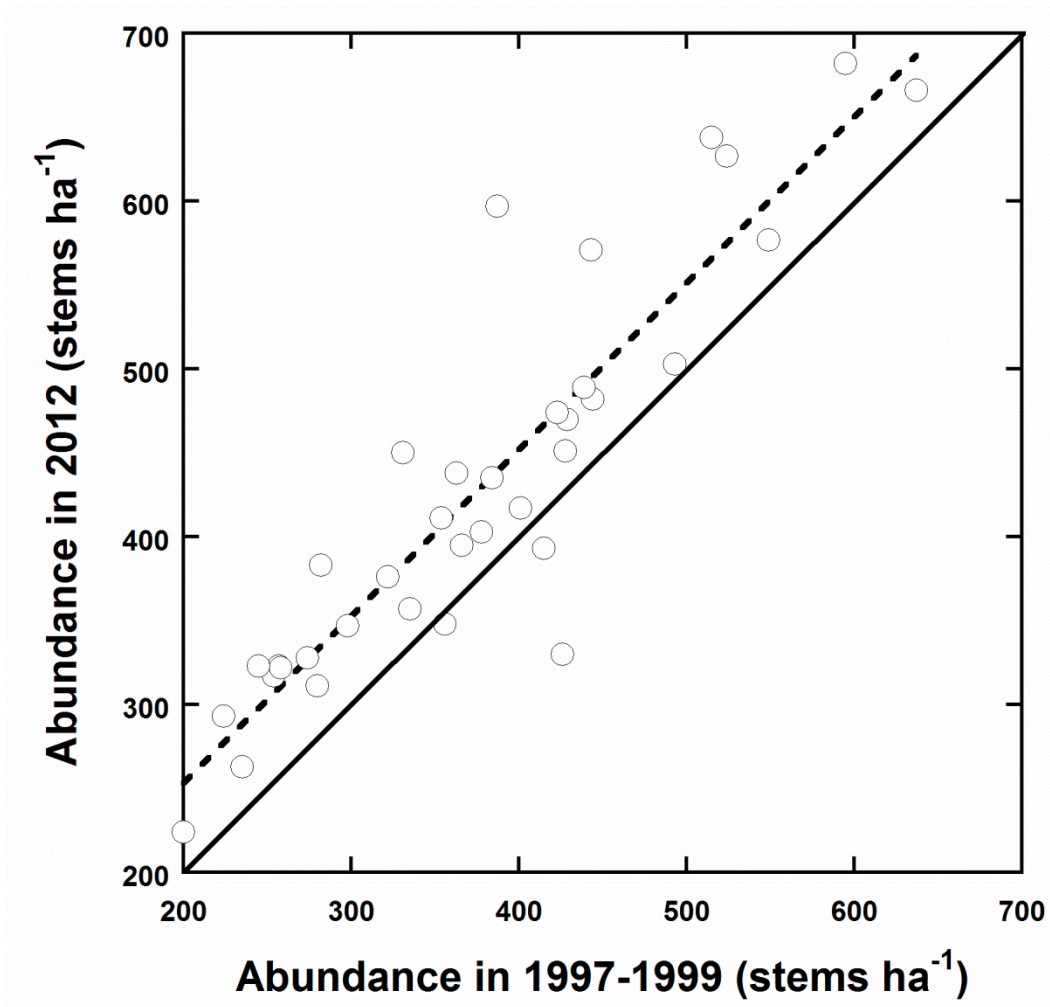
Fig. 1. Comparison of liana abundance (stems  $\geq 2$  cm diameter) between 1997-1999 and 2012 for 36 1-ha plots in undisturbed Amazonian forests. The solid line shows  $Y=X$  whereas the dotted line shows a fitted linear regression between liana abundances during the two time-periods.

Fig. 2. Mean number ( $\pm$ SD) of liana stems in different diameter classes recorded within 36 1-ha plots in central Amazonia in 1997-1999 ( $n=13,544$ ) and 2012 ( $n=15,549$ ).

Fig. 3. Mean annualized rates ( $\pm$ SD) of tree mortality and recruitment in 33 1-ha plots in undisturbed Amazonian forests, contrasted between interval 1 (early-mid 1980s to late 1997) and interval 2 (early 1998 to late 2009). Rates are based on 5-8 standardized censuses of trees ( $\geq 10$  cm diameter-at-breast-height) within each plot.

Fig. 4. Relationship between liana abundance in 2012 and mean aboveground tree biomass for 33 1-ha plots in undisturbed Amazonian forests.

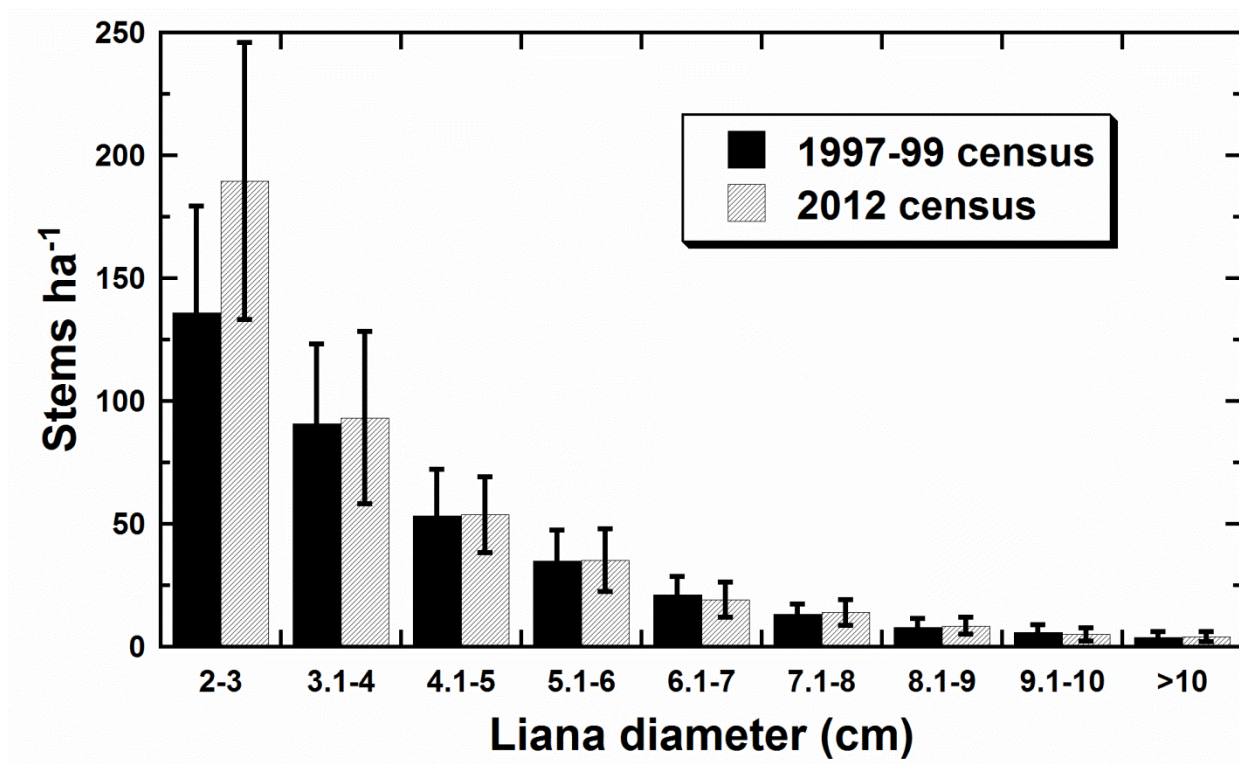
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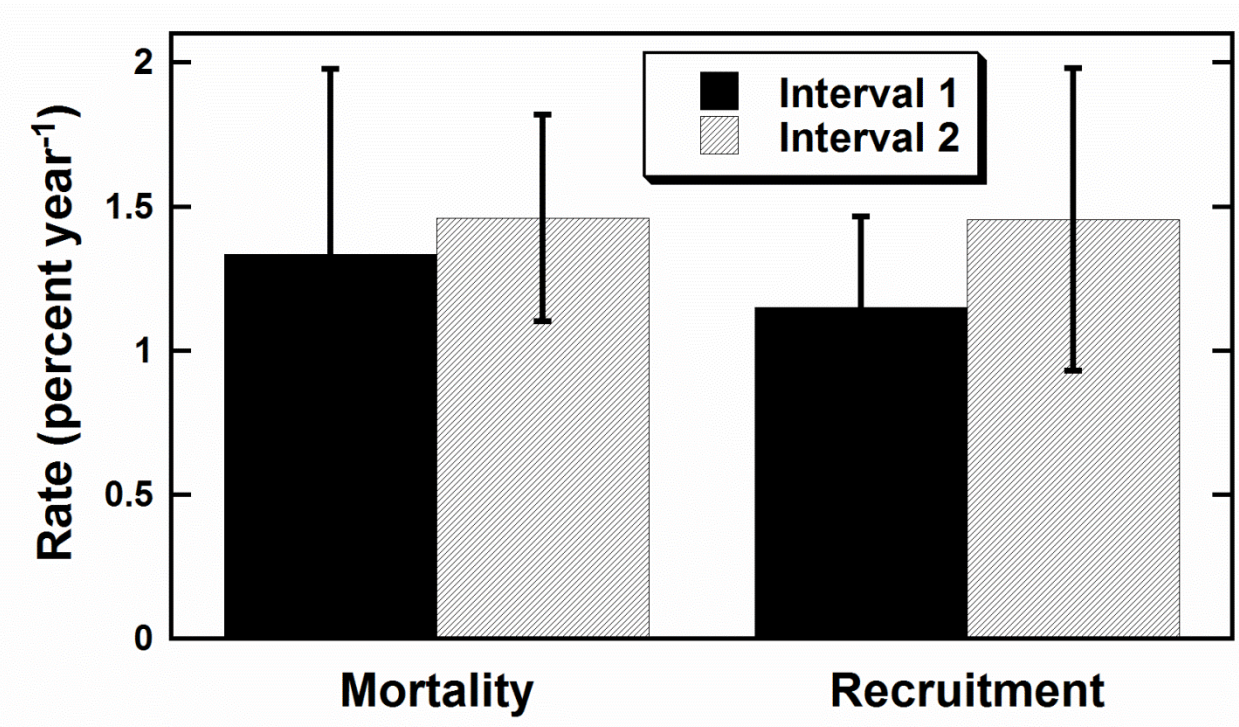


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557 Fig. 3

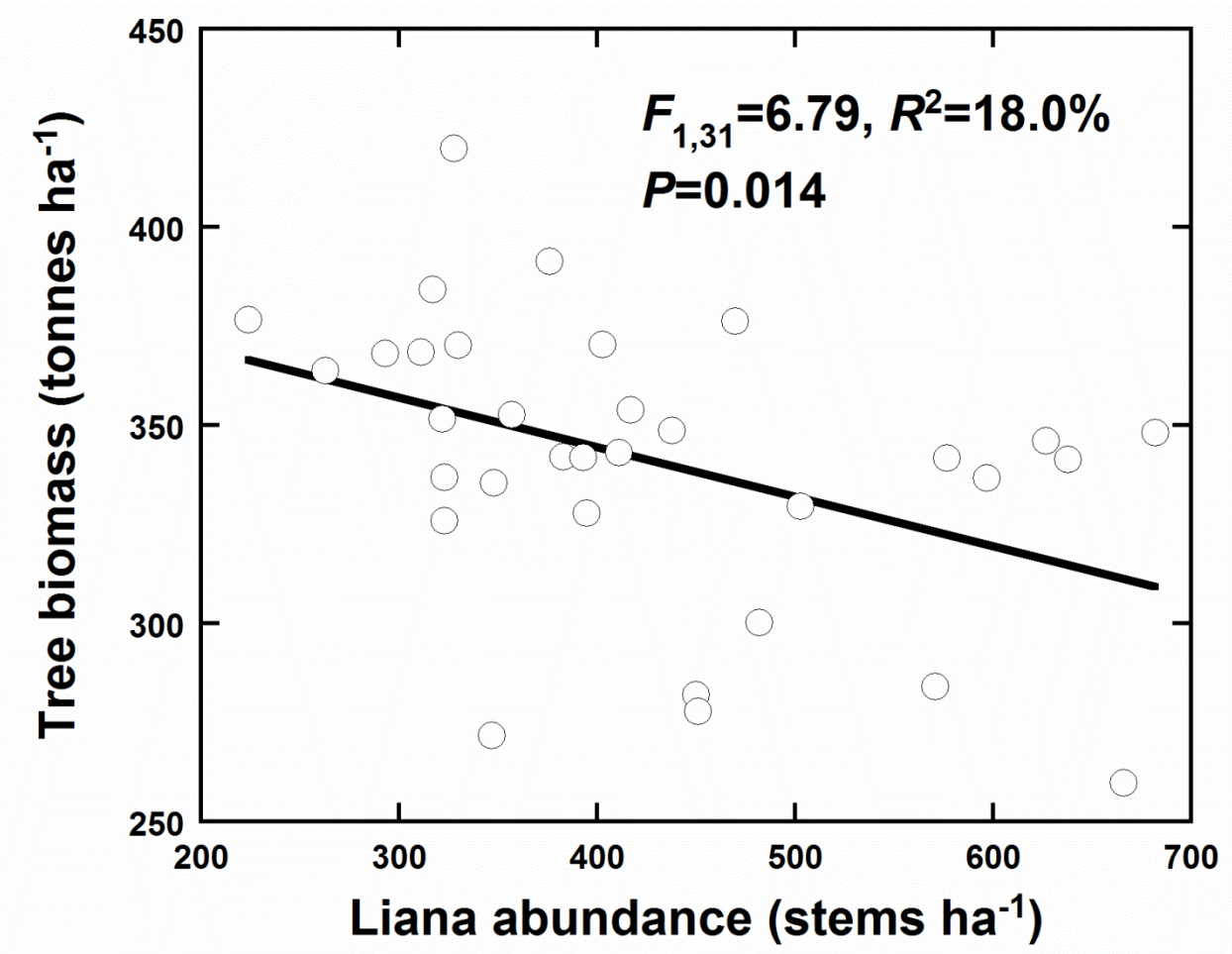


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560 Fig. 4

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