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2

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13

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Lianas decelerate tropical forest thinning during succession

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54 **Abstract**

55 The well-established pattern of forest thinning during succession predicts an increase in mean
56 tree biomass with decreasing tree density. The forest thinning pattern is commonly assumed to
57 be driven solely by tree-tree competition. The presence of non-tree competitors could alter
58 thinning trajectories, thus altering the rate of forest succession and carbon uptake. We used a
59 large-scale liana removal experiment over 7 years in a 60-to-70-year-old Panamanian forest to
60 test the hypothesis that lianas reduce the rate of forest thinning during succession. We found
61 that lianas slowed forest thinning by reducing tree growth, not by altering tree recruitment or
62 mortality. Without lianas, trees grew and presumably competed more, ultimately reducing tree
63 density while increasing mean tree biomass. Our findings challenge the assumption that forest
64 thinning is driven solely by tree-tree interactions; instead, they demonstrate that competition
65 from other growth forms, such as lianas, slow forest thinning and ultimately delay forest
66 succession.

67

68 **Introduction**

69 The successional development of ecosystems following disturbance is a foundational process in
70 ecology (Clements 1916; Gleason 1917). Following disturbance, there is an initial pulse of tree
71 recruitment, after which landscape-level biomass increases rapidly as trees grow in the high-
72 resource environment (Brown & Lugo 1990; Finegan 1996). As trees grow, however,
73 competition for increasingly scarce resources (e.g., light, water, nutrients) results in greater tree
74 mortality and a decrease in tree density, ultimately resulting in a forest dominated by large
75 survivors (Peet & Christensen 1987; Finegan 1996; Rees *et al.* 2001; Rozendaal & Chazdon

76 2015). The inverse relationship between mean tree size (mass) and density is commonly known
77 as self-thinning (Reineke 1933; Yoda 1963; White 1981; Pickard 1984; Westoby 1984).
78
79 The process of self-thinning dependably describes forest stand dynamics during succession; it
80 has been used to identify forest biomass accumulation with the decrease in tree density and it
81 is generally accepted as an intrinsic process to many managed and unmanaged plant
82 communities (Guo & Rundel 1998; van Breugel *et al.* 2006; Chazdon *et al.* 2007; Sea & Hanan
83 2012; Liu *et al.* 2019; Estrada-Villegas *et al.* 2020a). The concept of self-thinning was originally
84 applied to intraspecific competition among similar-sized tree cohorts during the development
85 of monodominant temperate forest stands (Reineke 1933; Yoda 1963; Harper 1967; Westoby
86 1984; Puntieri 1993; Pretzsch 2006). When the (log) mean tree biomass is plotted against the
87 (log) tree density, there is an upper boundary for populations undergoing density-dependent
88 mortality that represents the maximum achievable packing of trees on a surface at specific
89 densities (Reineke 1933; Yoda 1963). This boundary has been traditionally characterized by a
90 power-law with an exponent of $-3/2$ (Yoda 1963). More recent studies on ecological scaling,
91 focusing on how individuals use resources as a function of their size and including a mix of tree
92 sizes, ages, and species, suggest that a slope of $-4/3$ is more appropriate than a slope of $-3/2$,
93 which is based purely on geometrical considerations (Enquist *et al.* 1998; Enquist & Niklas
94 2002). The process of self-thinning has been largely criticized when applied to natural
95 communities (see Weller 1989; Midgley 2001; Reynolds & Ford 2005), where interspecific
96 competition, or “alien thinning”, also takes place (Harper 1967). Nevertheless, whether the
97 slope of the thinning line is close to $-3/2$ or $-4/3$, the thinning process affects most plant

98 communities (Harper 1967; Bazzaz & Harper 1976; Cousens & Hutchings 1983; Rivoire & Le
99 Moguedec 2012; Sea & Hanan 2012). Based on the scope of our study, we hereinafter refer to
100 the natural (i.e., unmanaged) process of self-thinning (or alien thinning) in natural communities
101 as forest thinning.

102

103 Most studies of thinning in natural forests have focused on competition among trees as the
104 main cause of the thinning pattern, ignoring other strong competitors. However, any factor that
105 reduces tree growth and survival (i.e., competition, stress or disturbance (Grime 1977)) could
106 alter tree forest-thinning trajectories, potentially reducing the slope of the thinning relationship
107 and thus the rate at which forests mature and sequester carbon (Morris 2003; Deng *et al.* 2006;
108 Zhang *et al.* 2011).

109

110 In tropical forests, lianas dramatically reduce tree growth and biomass accumulation (van der
111 Heijden *et al.* 2013) and thus may alter the thinning slope attributed to tree-tree competition.
112 Since trees comprise the majority of the biomass in tropical forest ecosystems (Putz 1983;
113 Gerwing & Farias 2000; Schnitzer *et al.* 2011), the reduction in tree growth will substantially
114 slow landscape-level biomass accumulation (van der Heijden *et al.* 2013, 2015). Lianas are
115 particularly abundant in secondary tropical forests (Schnitzer & Bongers 2002), where they tend
116 to accumulate early in succession (Dewalt *et al.* 2000; Barry *et al.* 2015). While trees invest in
117 the development of large, high-biomass trunks to support their massive crowns, lianas use
118 those trees for support and access to the forest canopy, and thus lianas have relatively thin,
119 low-biomass stems (van der Heijden *et al.* 2013; Schnitzer *et al.* 2014). Nonetheless, lianas

120 place their leaves above those of their host canopy trees and compete intensively with trees for
121 light (Putz 1984; Rodríguez-Ronderos *et al.* 2016; Medina-Vega *et al.* 2021), as well as for
122 below-ground resources (Dillenburg *et al.* 1995; Schnitzer 2005; Johnson *et al.* 2013).
123 Competition from lianas constrains tree recruitment, growth, reproduction and survival
124 (Schnitzer & Carson 2010; Estrada-Villegas & Schnitzer 2018; García León *et al.* 2018; Visser *et*
125 *al.* 2018); however, lianas themselves cannot sequester the quantity of carbon that they
126 displace in their tree hosts (e.g., van der Heijden *et al.* 2013; Schnitzer *et al.* 2014).

127
128 Determining whether competition from lianas alters the rate of forest thinning is critical to
129 understanding the processes governing forest recovery and succession, as well as the capacity
130 of secondary tropical forests to uptake and store carbon. Additionally, lianas are increasing in
131 relative abundance in tropical forests (Phillips *et al.* 2002; Laurance *et al.* 2014; Schnitzer *et al.*
132 2020, 2021), which may further alter forest thinning. Because tropical forests contain more
133 than half of the earth's aboveground terrestrial carbon stocks (Xu *et al.* 2021), and secondary
134 forests now contribute more than one-third of all tropical forest area (e.g., Chazdon *et al.*
135 2016), understanding the interacting factors that control the magnitude and direction of
136 biomass accretion during secondary tropical forest succession is of critical importance to global
137 carbon dynamics.

138
139 We used a 7-year liana removal study in a 60-to-70-year-old Panamanian secondary forest to
140 assess whether lianas alter the thinning process in forest communities. Specifically, we tested
141 the hypothesis that lianas reduce the slope of the thinning trajectory in tropical forests. We

142 predicted that in the presence of lianas, the relationship between mean tree biomass and
143 density will be shallower (i.e., less negative) compared to liana removal plots because lianas
144 reduce tree growth rates, which reduces tree competitive effects on each other and thus limit
145 the ability of trees to displace one another. By contrast, in the absence of lianas, trees will grow
146 faster and thus compete more intensely, ultimately displacing each other faster, which would
147 increase the negative slope of the thinning relationship between mean tree biomass and
148 density (i.e., more negative). Because lianas can also influence tree recruitment and survival
149 (e.g., Perez-Salicrup 2001; Martínez-Izquierdo *et al.* 2016) we also quantified the separate
150 contribution of tree recruitment and survival with and without lianas.

151

152 **Methods**

153 **Study sites**

154 We conducted this study in a 60-to-70-year-old secondary forest on Gigante Peninsula, part of
155 the Barro Colorado Natural Monument (BCNM) in central Panama. Gigante Peninsula receives
156 ca. 2600 mm precipitation annually and has a strong dry season from January to May (Schnitzer
157 & van der Heijden 2019). The forest is classified as a semi-deciduous, seasonally moist forest
158 (Leigh 1999). In 2008, we established sixteen 80 x 80 m plots, and we measured the diameter,
159 tagged, identified to species, and spatially mapped all trees ≥ 1 cm diameter in the central 60 x
160 60 m of each plot. Each 60 x 60 m plot was divided into nine 20 x 20 m quadrats. In 2011, we
161 surveyed the trees again (as well as the lianas ≥ 1 cm diameter) in all 16 plots and then we
162 removed all lianas in eight randomly selected liana-removal plots, while the other eight plots
163 were left unmanipulated as controls. We cut lianas near the forest floor with machetes and

164 liana stems were left in the site to avoid damaging tree crowns (follows Schnitzer & Carson
165 2010). Liana-removal plots were kept free from lianas by subsequent cutting of resprouting and
166 recruiting liana stems. We conducted additional censuses in the dry seasons of 2014 and 2018.
167 For each census, we quantified tree growth, mortality, and the recruitment of trees ≥ 1 cm.

168

169 **Calculation of tree biomass**

170 We measured the stem diameter of each individual with either a caliper (stems < 5 cm
171 diameter) or a fabric diameter tape (stems ≥ 5 cm diameter) at 1.3 m along the stem from the
172 rooting point on the forest floor (follows liana-specific sampling protocols by Gerwing *et al.*
173 (2006) and Schnitzer *et al.* (2008). Diameter measurements were collected at the beginning of
174 the dry season for each census year and at the same point on the stem, which we marked with
175 orange paint. We converted the DBH measurements for each tree per census year to AGB
176 (above-ground biomass) using a regression equation derived by Chave *et al.* (2014) (See
177 Appendix S1: Equation 1 in Supporting Information; see Appendix S1.2. for a summary of the
178 estimated mean AGB).

179

180 **Forest thinning**

181 We fitted thinning lines to the census data of mean tree diameter (converted to AGB kg C) and
182 tree density per quadrat (400 m²) per survey year (2011, 2014, and 2018) and treatment (liana
183 removal versus control). We modeled the log-transformed (base 10) AGB as a function of the
184 log-transformed (base 10) tree density, treatment (i.e., liana removal vs. control), and their
185 interaction using a linear mixed-effects model assuming a Gaussian error structure (Appendix

186 S1: Equation 2). We considered all living trees (including new recruits and excluding dead
187 individuals at each surveyed year) during the seven years of manipulation, from 2011 to 2018.
188 We also fitted independent thinning lines for each census year to assess the changes in the
189 slopes and intercepts between treatments among censuses. There is a long-standing debate
190 about fitting a straight line to logarithmic transformations of the original bivariate data (see
191 Packard *et al.* 2011; Mascaro *et al.* 2014; Niklas & Hammond 2014). The debate is related to an
192 incorrect implementation of the logarithmic transformation. Sometimes the transformation
193 fails to linearize the observations, leading to non-log-linear allometry (Packard 2012), and an
194 incorrect inference (Packard 2014). We checked for these potential issues with our data
195 (Appendix S1.4) and also constructed a model on the original data using a lognormal error
196 structure.

197

198 **Biomass gain from tree growth and recruitment versus biomass loss from tree mortality**

199 The change in AGB incorporates the growth of standing trees, biomass gain from tree
200 recruitment, and biomass loss from tree mortality. Lianas may influence tree recruitment and
201 survival in addition to tree growth. We assessed whether a liana-induced change in the forest
202 thinning relationship was due to differences in standing tree biomass from growth, recruitment,
203 or mortality by fitting three independent linear mixed-effects models to the log (base 10)
204 transformed AGB and assuming a Gaussian error structure (Appendix S1: Equation 3). Biomass
205 loss from mortality can be biased towards larger stems that have the highest biomass
206 (Nascimento *et al.* 2007; Rozendaal & Chazdon 2015). Furthermore, lianas may negatively affect
207 larger trees more than smaller trees because lianas tend to be in the larger trees that comprise

208 the forest canopy (Lai *et al.* 2017; Estrada-Villegas *et al.* 2020b), which could lead to increasing
209 large tree mortality. To test whether mortality varied ontogenetically between the treatments,
210 we assessed the number of dead trees as a function of size-class and treatment by fitting a
211 generalized linear mixed-effect model (GLMM) assuming a negative binomial error structure
212 (Appendix S1: Equation 4). We defined three size classes: (1) ‘small’ (i.e., trees in the range $1 \text{ cm} \leq \text{DBH} < 5 \text{ cm}$), (2) ‘medium’ (i.e., trees in the range $5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$) and (3) ‘large’ (i.e.,
213 trees with a $\text{DBH} \geq 10 \text{ cm}$), and included the log-transformed (base e) total number of trees per
214 observation period as an offset (i.e., exposure variable) to adjust for the amount of opportunity
215 for tree death.

217

218 **Statistical analyses**

219 We fitted all models in the probabilistic programming language ‘Stan’ (Carpenter *et al.* 2017) via
220 the package ‘brms’ (version 2.16.1, Bürkner 2018) and ‘cmdstanr’ (version 0.4.0, Gabry &
221 Češnovar 2021) in ‘R’ (version 4.1.2, R Core Team 2021). See Appendix S2 for the description
222 and the sensitivity assessment of the priors used in the analyses. We estimated the coefficients
223 of each model using four Markov chains and a number of iterations that varied per model
224 (Appendix S2.2). We monitored Markov chain mixing properties and checked parameter
225 convergence graphically via trace plots of the estimated coefficients (Appendix S3.1-8) and by
226 checking the Rhat metric (Gelman *et al.* 2013). The goodness-of-fit for each model was then
227 inspected via posterior predictive model checks (Conn *et al.* 2018; Gabry *et al.* 2019), where
228 simulation predictions from the best-fitted models are compared to the observed data
229 (Appendix S3.9). This process allowed us to assess any obvious discrepancies between the final

230 model and the observed data before reporting. Parameter values are presented using the
231 median of the posterior distribution and the uncertainty in the estimates was summarized using
232 the 95% credible intervals (CI's) computed using the highest density interval (HDI) of posterior
233 distributions, which favors probable over central values and is recommended for non-
234 symmetric posterior distributions (Kruschke 2014).

235

236 **Results**

237 **Forest thinning**

238 Both treatments (liana-removal and control plots) showed a strong power-law relationship
239 between mean tree biomass and tree density (Fig. 1; Appendix S4: Table S1, model A). The
240 negative slopes indicate that increments in mean tree AGB for both treatments (liana removal
241 and control) were associated with reductions in the number of trees, consistent with the
242 process of forest thinning. For the liana removal plots, the mean slope of the thinning line was -
243 1.15 [-1.38, -0.91]. By contrast, the mean slope of the thinning relationship for the control plots,
244 where lianas were present, was flatter (+0.44 [+0.11, +0.79]; Appendix S4: Table S1), indicating
245 that lianas reduced the increase in mean tree biomass with forest thinning, which ultimately
246 constrained the speed of forest-level biomass accumulation (Fig. 1). Forest thinning derived
247 equations for liana removal and control plots are $\log_{10} W = 4.18 - 1.15 \log_{10} N$ and $\log_{10} W =$
248 $3.14 - 0.71 \log_{10} N$, respectively, where W is the mean weight of trees and N is tree density. The
249 model explained 96% of the variation in the data (Conditional $R^2 = 0.96$ and Marginal $R^2 = 0.26$).
250 A model using a lognormal error structure for the original data used to construct thinning lines
251 showed similar results (Appendix S4: Table S3 and Figure S1).

252

253 The forest thinning relationship (i.e., the slope coefficient) was unequivocally different between
254 treatments when all data were combined (Appendix S4: Table S1, model A, and Figure 1).

255 Within censuses, the slope of thinning relationship did not differ between treatments, but the
256 y-intercept was higher in the liana-removal plots in years 2014 (Appendix S4: Table S1, model C)
257 and 2018 (Appendix S4: Table S1, model D), indicating that in the absence of lianas, mean tree
258 AGB was increasingly greater at the same tree density than in the control plots (Appendix S4:
259 Figure S2). There was no pre-treatment (year 2011) difference in the slope coefficient or mean
260 tree AGB per tree density (the y-intercept) between treatments (Appendix S4: Table S1, model
261 B, and Figure S2a). These findings indicate that lianas reduce tree biomass accumulation for a
262 given tree density and the effects appeared to strengthen with time.

263

264 **Standing tree biomass, biomass recruitment and biomass mortality**

265 Lianas constrained biomass accumulation in control plots by reducing the growth of living trees,
266 not by their effects on recruitment biomass nor mortality biomass (Fig. 2). For standing
267 biomass, trees in control plots had lower median biomass than trees in liana-removal plots in
268 years three (year 2014) and seven (year 2018) following the liana removal manipulation (2011)
269 (Fig. 2a; Appendix S4: Table S4, model A). The model explained 95% of the variation in the data
270 (Conditional $R_2 = 0.95$ and Marginal $R_2 = 0.05$). We did not find any differences in the gain in
271 tree biomass from recruitment (Fig. 2b; Appendix S4: Table S4, model B), the loss in tree
272 biomass from mortality (Fig. 2c; Appendix S4: Table S4, model C), or the number of dead trees
273 per size-class between treatments (Appendix S4: Table S4, model D). Nevertheless, we

274 observed higher mortality of trees in the smaller size class in both treatments (Appendix S4: Fig.
275 S3). The models for tree biomass recruitment and tree biomass mortality explained 74%
276 (Conditional $R_2 = 0.74$ and Marginal $R_2 = 0.69$) and 23% (Conditional $R_2 = 0.23$ and Marginal $R_2 =$
277 0.22) of the variation in the data, respectively. The model that assessed the number of dead
278 trees per size class and treatment explained 82% (Conditional $R_2 = 0.82$ and Marginal $R_2 = 0.68$)
279 of the variation in the data.

280

281 **Discussion**

282 A fundamental assumption in ecology is that the pattern of tree thinning in a forest is driven by
283 tree-tree competition, which predicts that tree density decreases as trees increase in size
284 during forest development (Reineke 1933; Yoda 1963; White 1981; Pickard 1984; Westoby
285 1984). That is, as trees grow, they compete intensely, ultimately displacing each other, and
286 surviving trees increase in biomass after the loss of neighboring trees. In the absence of lianas,
287 we found that trees maintain high rates of thinning, demonstrating that, indeed, tree-tree
288 competition during succession leads to a predictable loss in tree density with a commensurate
289 increase in mean tree biomass.

290

291 However, intense competition from lianas reduced the tree thinning slope, presumably by
292 changing competition from solely tree-vs-tree to liana-vs-tree-vs-tree. The addition of intense
293 competition from lianas reduced tree growth (this study) and biomass uptake (van der Heijden
294 *et al.* 2015, 2019), which slowed tree-vs-tree competition. Lianas alter the rate at which trees
295 grow and thus displace each other, ultimately changing thinning rates in tropical forests. Our

296 findings are consistent with previous studies that have used liana removal experiments to
297 demonstrate that, regardless of forest type, age, or geographic location, lianas have
298 detrimental effects on tree growth (Villegas *et al.* 2009; Toledo-Aceves 2015; Marshall *et al.*
299 2017; Estrada-Villegas & Schnitzer 2018; Mills *et al.* 2019), and thus we believe that the ability
300 of lianas to slow forest thinning and thus delay forest succession is broadly applicable to
301 tropical forests.

302

303 Our findings challenge the assumption that forest thinning is driven solely by tree-vs-tree
304 interactions. Instead, we show that liana competition changes tree thinning trajectories. Lianas
305 slow forest thinning by reducing tree growth, but not by altering tree recruitment or mortality;
306 we did not find evidence for variations in forest thinning trajectories resulting from liana-
307 induced changes in tree recruitment or mortality. The primary importance of growth to the
308 thinning pattern is consistent with observations in Costa Rica and Mexico, where tree basal
309 area accumulation was mostly associated with tree growth rates but not with changes in stem
310 density resulting from recruitment and mortality (Chazdon *et al.* 2007, 2010). Therefore, the
311 negative effect of lianas on tree growth influenced the thinning relationship between tree
312 density and mean tree biomass.

313

314 ***Liana-specific negative effects on tropical tree growth and forest thinning***

315 The strong negative effects of lianas on tree growth and biomass increment were likely due to
316 competition for shared resources. Both growth forms utilize the same set of resources (e.g.,
317 light, soil water and nutrients). In addition, lianas use the tree's architecture for support and

318 access to high light positions on the forest canopy. Once in the forest canopy, lianas place their
319 leaves over those of their host trees and access the most exposed light conditions (Avalos *et al.*
320 2007; Rodríguez-Ronderos *et al.* 2016; Medina-Vega *et al.* 2021). This interaction between
321 lianas and trees results in strong competition for light. However, lianas can also compete
322 intensely for belowground resources (Perez-Salicrup & Barker 2000; Perez-Salicrup *et al.* 2001;
323 Schnitzer 2005; Schnitzer *et al.* 2005), suggesting that there may be a similar overlap between
324 liana and tree roots.

325

326 In liana-dominated landscapes, weaker competition between trees due to the negative effects
327 of lianas on tree growth may result in relatively slow thinning rates and thus slower forest
328 succession (e.g., Fig. 1). By slowing tree-vs-tree interactions, lianas may delay the displacement
329 of early successional tree species by later-successional tree species, and thus may maintain a
330 larger number of tree species in tropical forests. Alternatively, because the strength of the
331 negative effect of lianas varies with tree species identity (e.g., Visser *et al.* 2018), lianas may
332 displace some species faster than others during succession, which could hasten the loss of tree
333 species diversity during succession. Competition from other growth forms, such as shrubs or
334 herbs, may also alter tree recruitment, but this effect appears to be temporary (Duncan &
335 Chapman 2003; Frappier *et al.* 2004), and it may not alter the thinning trajectory of a forest
336 undergoing density-dependent mortality. Although lianas are a key component of tropical and
337 temperate forests around the world, their contribution to forest dynamics, composition, and
338 structure is most substantial in the tropics (Gentry 1992; Schnitzer & Bongers 2002, 2011),

339 suggesting important differences in forest succession and forest thinning between tropical and
340 temperate forests.

341

342 ***Pervasive negative effects of lianas on secondary forest carbon accumulation***

343 By reducing the slope of forest thinning, lianas reduce the capacity for regenerating secondary
344 forests to accumulate carbon. Our experimental findings are consistent with other studies. For
345 secondary tropical forests in Panama, lianas reduced forest level carbon accumulation up to c.
346 22% (Lai *et al.* 2017; Estrada-Villegas *et al.* 2020b) and up to 76% for trees larger than 10 cm
347 DBH (van der Heijden *et al.* 2015). Lianas themselves contributed very little to the carbon they
348 displaced (van der Heijden *et al.* 2015; Lai *et al.* 2017; Estrada-Villegas *et al.* 2020b). The
349 relatively small contribution of lianas to forest-level carbon results from their low stem volume
350 (Schnitzer *et al.* 2012, 2021), slow accumulation of biomass (Letcher & Chazdon 2009), and their
351 greater allocation of above-ground biomass to leaves than to the stem than similar-sized trees,
352 which lowers their capacity to store carbon (Putz 1983; Gerwing & Farias 2000; Chave *et al.*
353 2001).

354

355 Lianas are particularly abundant early in forest succession, and the observed negative effects of
356 lianas on forest thinning have important ramifications for carbon uptake in regenerating
357 tropical forests. Most regenerating tropical forests have faster growth and higher net carbon
358 uptake than old-growth forests (Chazdon *et al.* 2016; Poorter *et al.* 2016). These young forests
359 are characterized by the vigorous growth of the many light-demanding trees (Finegan 1996).
360 Regenerating tropical forests also have fast biomass accumulation, high tree species diversity

361 and high tree species composition relative to late-successional forests (Poorter *et al.* 2021).
362 Because of the high productivity of regenerating tropical forests and the increasing loss of old-
363 growth tropical forests worldwide, secondary forests are expected to play an important role in
364 the global carbon dynamics (Grace *et al.* 2014; Chazdon *et al.* 2016). However, high liana
365 abundance in young forests (e.g., 40 years and younger) (Dewalt *et al.* 2000; Schnitzer *et al.*
366 2012, 2021; Barry *et al.* 2015) reduce tree growth and biomass accumulation (Estrada-Villegas
367 *et al.* 2020b). Therefore, the negative effects of lianas on tree-tree competition and forest
368 thinning may be particularly important in the early stages of forest succession, where lianas
369 likely reduce the potential of secondary forests to sequester carbon (Poorter *et al.* 2016).

370

371 ***Implications of increasing liana abundance for forest succession***

372 The contribution of lianas to forest structure and dynamics appears to be increasing in tropical
373 forests (Schnitzer & Bongers 2011), which may further slow tree thinning and, concomitantly,
374 reduce forest biomass uptake. Multiple long-term studies in the neotropics and one study in
375 South India (Pandian & Parthasarathy 2016) reported an increase in liana density and biomass
376 in both absolute terms and relative to trees (Phillips *et al.* 2002; Wright *et al.* 2004; Chave *et al.*
377 2008; Ingwell *et al.* 2010; Laurance *et al.* 2014; Schnitzer *et al.* 2020, 2021). The increase in
378 lianas relative to trees in tropical forests suggests a greater role of these non-tree competitors
379 in future forest succession and thinning. Moreover, among tropical forests, the negative effects
380 of lianas on forest succession and thinning may not be homogeneous but vary with liana
381 gradients and may become even stronger in forests where lianas are naturally more abundant

382 or in forests that are experiencing greater increases in liana abundance (Schnitzer & Bongers
383 2011).

384

385 Among tropical forests, liana abundance and diversity peak in highly seasonal forests and
386 decrease with increasing mean annual precipitation, increasing soil moisture availability (e.g.,
387 Manzané-Pinzón *et al.* 2018), and decreasing strength of seasonal drought (Swaine & Grace
388 2007; DeWalt *et al.* 2010; Parolari *et al.* 2020). This unique distribution of lianas is thought to be
389 driven by a greater ability to benefit from high dry season light availability than trees, thus
390 resulting in higher rates of growth and survival, and ultimately greater liana abundance
391 (Schnitzer 2005, 2018). In the context of our results and the unique distribution of lianas, we
392 hypothesize that forests with relatively strong seasonality of rainfall, where lianas are most
393 abundant, may experience slower rates of thinning than forests with higher precipitation and
394 lower seasonality. In wet, aseasonal tropical forests, where lianas are less abundant, forest
395 thinning trajectories may be steeper due to less liana-tree competition and thus more intense
396 tree-tree competition.

397

398 **Conclusions**

399 Lianas alter forest thinning trajectories in secondary tropical forests by decreasing tree growth.
400 The pervasive negative effects of lianas on tree growth appeared to decrease tree-tree
401 competition and thus slowed the ability of trees to displace one another, even as individual
402 trees grew to large sizes. Without lianas, tree growth rates were significantly higher, resulting in
403 greater tree-tree competition and thus a greater ability of trees to suppress and displace

404 weaker neighbors. Moreover, biomass accumulation in liana-free plots was particularly high
405 because surviving trees more rapidly compensated for the biomass loss of dead trees. The
406 slower accumulation of carbon that resulted from the effect of lianas on tree thinning could
407 have substantial negative effects on tropical forest succession and the global carbon cycle, since
408 secondary forests are a critical component of the tropical carbon budget.

409

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414

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667

668 **Figure 1.** Thinning lines for liana removal and control plots in Gigante Peninsula, Panama. The
669 vertical axis indicates the log-transformed (base 10) AGB and the horizontal axis indicates the
670 log-transformed (base 10) tree density (or the number of trees per 400 m² [20 x 20 m
671 quadrats]). Green points were used for the liana removal plots and orange for the control plots.
672 Individual points indicate subplot or quadrat-level observations per year (shape of the point)
673 and the lines linking the points indicate the repeated observations per subplot. The thick
674 orange and green lines indicate the predicted medians for the liana-removal and control plots
675 calculated from 200 draws from the posterior predictive distributions, which were represented
676 by light orange and light green lines that run parallel to the medians.

677

678 **Figure 2.** Predicted tree (a) standing biomass, (b) biomass gain from recruitment, and (c)
679 biomass loss from mortality for control (orange) and liana removal plots (green) on Gigante
680 Peninsula, Panama. The vertical axes indicate the census years (panel a) and inter-census
681 periods (panels b and c). The horizontal axes indicate the predicted log-transformed (base 10)
682 total AGB (kg) per 400 m² (20 x 20 m). The black interval bar indicates the median (at the circle),

683 and the 50% and 95% credible intervals calculated from 200 draws from the posterior
684 predictive distribution.