

1

2 Received Date:

3 Revised Date:

4 Accepted Date:

5 Article Type: Articles

6 Running Head: Drought and liana seedling survival

7 **Dry conditions and disturbance promote liana seedling survival and abundance**

8

9 María Natalia Umaña<sup>1,2\*</sup>, Jimena Forero-Montaña<sup>3</sup>, Christopher J. Nytech<sup>3</sup>, Jill  
10 Thompson<sup>4</sup>, María Uriarte<sup>6</sup>, Jess Zimmerman<sup>3,7</sup> and Nathan G. Swenson<sup>1,5</sup>

11

12 <sup>1</sup> *Department of Ecology and Evolutionary Biology, University of Michigan, Ann*  
13 *Arbor 48109.*

14 <sup>2</sup> *Department of Biology, University of Maryland, College Park, Maryland 20742,*  
15 *USA.*

16 <sup>3</sup> *Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931,*  
17 *USA.*

18 <sup>4</sup> *Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB,*  
19 *UK.*

20 <sup>5</sup> *Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical*  
21 *Garden, Chinese Academy of Sciences, Kunming, China.*

22 <sup>6</sup> *Department of Ecology, Evolution & Environmental Biology, Columbia University*  
23 *New York, NY 10027, USA.*

24 <sup>7</sup> *Department of Environmental Sciences, University of Puerto Rico, Río Piedras,*  
25 *Puerto Rico 00936, USA.*

26

27 \* **Corresponding Author:** maumana@gmail.com

28

29 **ABSTRACT**

30 Species composition and community structure in neotropical forests have been  
31 severely affected by increases in climate change and disturbance. Among the most  
32 conspicuous changes is the proliferation of lianas. These increases have affected not  
**This is the author manuscript accepted for publication and has undergone full peer  
review but has not been through the copyediting, typesetting, pagination and  
proofreading process, which may lead to differences between this version and the  
Version of Record. Please cite this article as [doi: 10.1002/ecy.2556](https://doi.org/10.1002/ecy.2556)**

33 only the carbon storage capacity of forests but also tree dynamics by reducing tree  
34 growth and increasing mortality. Despite the importance of lianas in neotropical  
35 forests, most of the studies on lianas have focused on adult stages, ignoring dynamics  
36 at the seedlings stage. Here, we asked whether observed increases in liana abundance  
37 are associated with a demographic advantage that emerges early in liana ontogeny and  
38 with decreased precipitation and increased disturbance. To test this, we compared  
39 patterns of growth and survival between liana seedlings and tree seedlings using a  
40 long-term dataset of seedling plots from a subtropical wet forest in Puerto Rico. Then,  
41 we examined the effect of precipitation and land use history on these demographic  
42 variables. We found evidence for liana seedling survival advantage over trees, but no  
43 growth advantages. This survival advantage exhibited significant temporal variation  
44 linked with patterns of rainfall, as well as differences associated with land-use history  
45 in the study area. Furthermore, we found that neighborhood density has a negative  
46 effect on liana survival and growth. Our results indicate that liana proliferation is  
47 likely related to a survival advantage that emerges in early stages, and is influenced  
48 by climatic conditions and past disturbance. Predicted climatic changes in rainfall  
49 patterns, including more frequent and severe droughts, together with increases in  
50 disturbance, could have a significant effect on seedling tropical communities by  
51 favoring lianas.

52 **KEY WORDS:** Community dynamics, growth, land use history, precipitation,  
53 seedlings crowding, survival, neotropical forest.

#### 54 **INTRODUCTION**

55 The high levels of species diversity found in tropical plant communities are in part  
56 represented by a high number of liana species that reach their peak diversity in  
57 tropical regions (Gentry 1992). During the last few decades, the proportion of lianas  
58 has increased in the tropics, especially in the Americas (Phillips et al. 2002, Wright et  
59 al. 2004, 2015b, Schnitzer and Bongers 2011, Schnitzer 2015) (but see Smith et al.  
60 2017 for small-sized trees) resulting in alterations of forests structure and composition  
61 as well as reductions in carbon storage capacity of the forests (Chave et al. 2008,  
62 Ingwell et al. 2010, Schnitzer and Bongers 2011, van der Heijden et al. 2015, Lai et al.  
63 2017). Despite the evident changes that tropical plant communities have been  
64 experiencing related to liana proliferation, explanations for the relative success of  
65 lianas in these environments remain unclear.

66 Previous studies have suggested that the success of lianas is caused by their  
67 superior competitive ability that reduces the recruitment and survival of adult trees  
68 (Schnitzer and Bongers 2002, Schnitzer 2005, Schnitzer and Carson 2010, Tobin et al.  
69 2012). Given that lianas are structural parasites of trees (Stevens 1987), they do not  
70 need to invest in structure to support the main stem. Instead, lianas may invest more  
71 in photosynthetic and vascular tissues that improve their water and nutrient uptake  
72 efficiency (Putz 1983, Schnitzer 2005). In adult stages, leaves of lianas easily invade  
73 the canopy by extending long branches laterally that take advantage of the good light  
74 conditions in the canopy (Schnitzer and Bongers 2002). In addition, it has been  
75 suggested that lianas may suffer less from water stress and thus grow better than trees  
76 during dry periods (Schnitzer 2005). Although the majority of the studies assessing  
77 the negative effects of lianas and their demographic success have been focused on  
78 adult stages of lianas (Schnitzer and Carson 2010, Wright et al. 2015a), we still have  
79 little evidence on whether the demographic advantage of lianas is evident even at their  
80 earliest stages of ontogeny (but see Wright et al. 2004; Hogan et al. 2017) .

81 Since lianas are freestanding individuals during early ontogeny, biomass  
82 allocation for self-supporting structures is necessary and the observed advantages at  
83 adult stages may not be reflected at seedling stages. However, lianas may still have  
84 physiological traits, such as large and wide vessels accompanied with thick xylem  
85 walls, and greater stomatal control compared to trees, that would provide advantages  
86 for water-uptake strategies independently of the ontogenetic stage (Ewers 1985,  
87 Ewers et al. 1990, Angyalossy et al. 2015). These physiological traits might benefit  
88 liana species over trees during dry periods, and in areas of high disturbance that are  
89 usually drier and sunnier than the shaded understory (Bazzaz and Wayne 1994,  
90 Laurance et al. 2001, Wright et al. 2004, Schnitzer and Bongers 2011), allowing  
91 higher growth and survival rates even at early stages of development. Indeed,  
92 previous studies have found that (adult) liana abundance increases in disturbed areas  
93 (Perez-Salicrup et al. 1998, Dewalt et al. 2000, Letcher and Chazdon 2009), yet, no  
94 studies have shown this for early ontogenetic stages.

95 At the local scale, individual crowding might also affect seedling performance.  
96 Previous studies have shown that density of neighboring seedlings influences  
97 individual performance (Packer and Clay, 2003, Comita et al. 2014, Kobe and  
98 Vriesendorp, 2011), and this effect could vary across species depending on their life-  
99 history strategies. For instance, large-seeded species are less negatively affected by

100 high density of conspecific neighbors than smaller-seeded species (Lebrija-Trejos et  
101 al. 2016). Given that lianas exhibit a set of strategies that are different from trees  
102 (Ewers 1985, Ewers et al. 1990, Angyalossy et al. 2015), the use of resources may  
103 overlap more among liana individuals than between lianas and trees. This greater  
104 overlap in resource use could result in lower performance of liana seedlings where  
105 higher densities of liana neighbors are present (Wright et al. 2015a).

106 In this study, we compared seedling performance between lianas and tree  
107 species in a subtropical wet forest in Puerto Rico and linked it to biotic and climatic  
108 factors. We combined a ten-year demographic inventory of seedling plots with local  
109 rainfall data and neighborhood crowding to investigate the following questions: (i) Do  
110 lianas have advantageous demographic performance (i.e., growth and survival)  
111 relative to trees at the seedling stage? (ii) Are liana seedlings responding differentially  
112 to abiotic factors such as local climatic conditions and land-use history? (iii) How is  
113 this potential advantage related with local neighborhood crowding? We predict that  
114 demographic advantages for lianas should emerge at early ontogenetic stages, likely  
115 associated with physiological characteristics that allow them a more efficient use of  
116 resources (i.e., water availability). The variability in climatic and local abiotic  
117 conditions should favor liana seedlings over tree seedlings in dry and disturbed  
118 conditions. In addition, we expect a negative neighborhood density effect on liana  
119 survival and growth.

120

## 121 **METHODS**

### 122 **Study site**

123 We compiled seedling information data from the 16-ha Luquillo Forest Dynamic Plot  
124 (LFDP) (18°20'N, 65°49'W) located in northeastern Puerto Rico, which is part of  
125 the Smithsonian's Forest-GEO network. This forest is classified as a subtropical wet  
126 forest with a mean annual temperature of 25.2 °C, mean annual rainfall of 3,500 mm  
127 year<sup>-1</sup>, and elevation from 333 to 428 m.a.s.l (Thompson et al. 2004). In the past, the  
128 plot was affected by natural (hurricanes) and human disturbances that severely altered  
129 species composition and dynamics. Two major hurricanes that impacted the island  
130 during the study period were Hurricane Hugo in September 1989, some months  
131 before the establishment of the LFDP, and hurricane Georges in 1998 (Brokaw and  
132 Gear 1991, Zimmerman et al. 1994, Thompson et al. 2004). In addition, in the early  
133 1900s, the north portion of the plot was greatly affected by agriculture based on

134 coffee and fruit plantations that were later abandoned after the hurricane San Felipe II  
135 1928, while selective logging was practiced on the south portion of the plot until 1944  
136 (Thompson et al. 2002). Based on aerial photographs taken in 1936 (Foster et al. 1999,  
137 Thompson et al. 2002), we classified the 16-ha plot in two categories: low-intensity  
138 land use ( $\geq 80\%$  of canopy cover) and high-intensity land use ( $< 80\%$  of canopy  
139 cover) to examine the role of past disturbance on liana seedling survival.

140

#### 141 **Seedling censuses**

142 We used information from 120 seedling-plot stations distributed along the LFDP.  
143 Each station consisted of three seedling plots of 1 x 1 m established at a distance of  
144  $\sim 2$  m from each other. From 2007 to 2016 (starting in January), all the seedling plots  
145 were annually monitored for growth, recruitment, and survival. All freestanding  
146 seedlings ( $>0$  to 100 cm in height) were tagged, identified, and measured. When plots  
147 had new recruits, these individuals were included in the new census following the  
148 same methodology previously explained. We classified all individual seedlings across  
149 the entire census according to their habit as liana or tree. We found a total of 15 liana  
150 species (*Cissampelos pareira* L., Menispermaceae; *Cissus verticillata* (L.) Nicolson &  
151 C.E. Jarvis, Vitaceae; *Dioscorea alata* L., Dioscoreaceae; *Dioscorea polygonoides*  
152 *Humb & Bonpl. Ex Willd.*, Dioscoreaceae; *Hippocratea volubilis* L., Celastraceae;  
153 *Heteropterys laurifolia* (L.) A. Juss, Malpighiaceae; *Ipomoea repanda* Jacq.,  
154 Convolvulaceae; *Marcgravia rectiflora* Triana & Planch, Marcgraviaceae; *Paullinia*  
155 *pinnata* L., Sapindaceae; *Pinzonia coriacea* Mart. & Zucc., Dilleniaceae; *Rourea*  
156 *surinamensis* Miq., Connaraceae; *Schlegelia brachyantha* Griseb., Schlegeliaceae;  
157 *Securidaca virgate* Sw., Polygonaceae; *Smilax coriacea* Spreng., Smilacaceae; *Smilax*  
158 *domingensis* Willd., Smilacaceae) and 77 species of trees (Appendix S1: Table S1).  
159 For the analyses, we combined seedling information at the station level, and our  
160 sample size was 120.

161

#### 162 **Climatic data**

163 We used information about local daily precipitation that has been measured at the El  
164 Verde meteorological station from 1974 to 2014. This station is situated less than 0.5  
165 km to the south of the LFDP. Our analyses used annual precipitation values that were

166 computed from daily precipitation data from 2007 to 2014. These data were obtained  
167 from the LTER website (<http://luq.lter.network/>).

168

### 169 **Data analyses**

170 We recorded annual seedling survival across the 120 stations and calculated relative  
171 growth rates for each individual seedling as  $\frac{\log(H_{t+\Delta t}) - \log(H_t)}{\Delta t}$ , where H indicates  
172 seedling height at successive time steps  $t$ . Then, we assessed the proportion of liana  
173 and tree seedlings that survived at each station.

174 In order to compare annual seedling survival between lianas and trees, we  
175 built a null model, in which we shuffled the habit (i.e., liana or tree) of all the  
176 individuals within one station (three seedling plots), keeping the total number of  
177 lianas and trees for each station constant. Next, we recalculated the proportion of  
178 surviving lianas. Because the local conditions within each station may change from  
179 site to site we restricted randomizations to each station. In total, we used 999  
180 randomizations such that at the end we had 999 null estimates of the proportion of  
181 surviving lianas in each station for each year. We estimated the standardized effect  
182 size (SES) for the proportion of liana survival by subtracting the mean values of the  
183 null distribution from the observed values and dividing by the standard deviation of  
184 the null distribution. Positive SES values indicate a higher proportion of liana survival  
185 over trees, given observed individuals of lianas and trees, whereas negative values  
186 indicate the opposite.

187 We used a similar null model to test whether the relative growth rate of liana  
188 seedlings was significantly higher than tree seedlings. We randomized the habit (liana  
189 or tree) for all individuals within each plot 999 times and then we estimated mean  
190 relative growth rates for lianas. Next, we calculated SES mean relative growth rates  
191 for lianas in the same way it was described above, and the meaning of positive and  
192 negative values remain the same as well.

193 To explore the role of temporal variability in precipitation and land-use effects  
194 on liana seedling survival and growth advantage, we fit models for SES survival and  
195 SES growth, respectively, which included as fixed effects the mean annual rainfall  
196 from the year prior to the census, and the land-use category at the station level.  
197 Station was modeled as a random effect to account for spatial variation. The data used  
198 for these analyses span the period between 2007 and 2014, given that rainfall

199 information is only available for these years. To facilitate interpretation, the mean  
200 annual rainfall variable was centered at its average and divided by its standard  
201 deviation.

202         Considering that local neighborhood might influence the demographic  
203 performance of seedlings we evaluated whether the density of neighbor individuals  
204 had a significant effect on liana seedling survival and growth. To accomplish this, we  
205 fit models in which SES liana survival and SES liana growth were modeled as a  
206 function of liana seedling density or total density including tree and liana seedlings.  
207 To account for spatial variation, the variable station was modeled as a random effect.  
208 Census was also modeled as a random effect. All models were fit by implementing  
209 linear mixed-effects models with normal-distributed errors by using the *lme4* package  
210 (Bates et al. 2015) in R 3.4.0 (R Development Core Team, 2017). Confidence  
211 intervals for each parameter were computed by bootstrap.

212

## 213 **RESULTS**

### 214 **Comparing survival and growth between lianas and trees**

215 We found that during 2007-2016 the total number of seedlings (lianas and trees)  
216 increased from about 7,000 to 11,500 across the 120 stations. In addition, the  
217 proportion of liana seedlings increased from ~0.4 to more than 0.6 (Fig. 1). Liana  
218 survival was significantly higher than tree survival during the first two-year intervals  
219 (2007-2008 and 2008-2009), in 2012-2013, and in the last two-year intervals (2014-  
220 2015 and 2015-2016), marginally significant in 2009-2010, non-significant in 2013-  
221 2014, and significantly lower than trees in 2010-2011 and 2011-2012 (Fig. 2). On the  
222 other hand, seedling growth rates were in general no different for lianas and trees,  
223 except in the time intervals of 2008-2009 and 2010-2011 where growth rates were  
224 significantly lower for lianas than trees (Fig. 2).

225

### 226 **Effects of climate and land-use history on liana seedling survival**

227 We examined whether the variation in SES liana survival and SES growth were  
228 influenced by mean annual precipitation from 2007 to 2014 and land-use history. We  
229 found that SES liana survival was significant and negatively associated with mean  
230 annual precipitation (Fig. 3). In addition, we found that SES liana survival was  
231 significantly lower in the portion of the plot with high-intensity land use than in the  
232 area that experienced low-intensity land use (Fig. 4, Appendix S1: Table S2). Similar

233 analyses for SES liana growth showed a non-significant effect of annual mean  
234 precipitation and land use (Appendix S1: Table S3).

235

### 236 **Effects of neighborhood crowding on liana seedling demography**

237 To evaluate whether variation in tree and liana seedling demography was associated  
238 with neighborhood density, we examined the relationship between SES liana values  
239 of growth and survival with the total density of neighbors and the density of liana  
240 neighbors. We found that the density of lianas had a significant negative effect on  
241 liana survival, while the effect of total density was not significant (Fig. 5; Appendix  
242 S1: Tables S4 and S5). For the analyses considering growth rates and neighborhood  
243 density effects, we found that high density of seedlings and high density of lianas  
244 were negatively correlated with liana growth rates (Fig. 5, Appendix S1: Tables S6  
245 and S7).

246

## 247 **DISCUSSION**

248 An increasing number of studies have shown that tropical forests are experiencing  
249 remarkable changes in structure and dynamics (Phillips and Gentry 1994, Condit  
250 1998, Allen et al. 2010, Enquist and Enquist 2011), which includes an outstanding  
251 proliferation of lianas in the Neotropics (Phillips et al. 2002, Schnitzer and Bongers  
252 2011, Delgado et al. 2016, Hogan et al. 2017). Determining whether these changes are  
253 also present in earlier ontogenetic stages and linked to abiotic and biotic factors is a  
254 central goal in ecology and conservation biology. In this study, we sought to  
255 investigate whether lianas exhibit a demographic advantage during seedling stages,  
256 thereby helping to further elucidate the drivers of the increasing abundance of lianas  
257 in Neotropical forests. Our findings suggest that liana seedlings exhibit a survival  
258 advantage associated with dry years and high-intensity land-use portions of the forest.  
259 These results have important implications for forest structure, diversity, and dynamics  
260 in the context of global climate change, wherein more severe and frequent extreme  
261 drought events are predicted to occur in tropical environments (IPCC 2013).

262

### 263 *Liana seedlings are increasing over time*

264 By looking at the general patterns that describe the changes in seedling number and  
265 proportion of liana individuals over time (Fig. 1), a clear feature of the seedling  
266 community in Puerto Rico is a high and increasing proportion of liana individuals.



267 This trend is consistent with patterns of adult lianas in other Neotropical forests  
268 (Phillips et al. 2002, Schnitzer and Bongers 2011), and with a previous study in the  
269 same site examining the recruitment success for some liana and tree species from  
270 2008 to 2010 (Muscarella et al. 2013). The proportion of lianas during 2007 to 2016  
271 ranged from approximately 40% to more than 60%, almost three times the proportion  
272 of lianas found in Barro Colorado Island (BCI), Panama during eight years of  
273 monitoring (1994 to 2002) (Wright et al. 2004). This first result highlights, then, that  
274 lianas represent an increasingly important component of the seedling community in  
275 this forest.

276

277 *Temporal and spatial variability in liana seedlings demography is associated with*  
278 *rainfall and disturbance*

279 The observed increase in liana seedlings is likely associated with a survival advantage  
280 that was evidenced in our results (Fig. 2). This pattern, however, was not consistently  
281 found across the whole study period. There was important inter-annual variation in  
282 liana demographic success associated with temporal seasonality related to local  
283 climatic conditions, in which liana-seedling survival was enhanced during periods of  
284 low annual precipitation (Fig. 3). Although, for seedling stages, drought is perhaps  
285 one of the key causes of plant mortality in tropical forests (Bunker and Carson 2005,  
286 Nepstad et al. 2007, Engelbrecht et al. 2007, Kraft et al. 2011, Saatchi et al. 2012,  
287 Comita and Engelbrecht 2014, O'Brien et al. 2017), our results suggest that liana  
288 seedlings are less affected by dry conditions. This demographic advantage of lianas  
289 during dry periods has been also reported in a recent analysis using a subset of species  
290 of the seedling community in the LFDP (Uriarte et al. 2017), and in other tropical  
291 forests for adult lianas (Swaine and Grace 2007). Further, Wright et al. (2004) found  
292 high variation in seedling densities in Barro Colorado Island related to dry and warm  
293 periods associated with ENSO events, where higher recruitment occurred during the  
294 ENSO years. In our study, ENSO occurred during 2009-2010 and 2014-2015,  
295 coinciding with the years when survival advantage was detected for liana seedlings  
296 and when precipitation was particularly low (Fig 3). Nevertheless, longer time series  
297 would be needed to thoroughly test the link between liana seedling advantages and  
298 ENSO events in Puerto Rico.

299 The observed superior survival of liana seedlings relative to trees suggests that  
300 lianas might exhibit physiological and ecological characteristics that allow them to

301 attain better performance than trees at early ontogenetic stages. For example, recent  
302 studies have shown that lianas have a greater stomatal control that helps to regulate  
303 water loss under low water conditions (Cai and Bongers 2007, Cai et al. 2009). Other  
304 studies have found that lianas are deep-rooted, which enables them to access water at  
305 great depths during dry periods (Restom and Nepstad 2004, discussed by Schnitzer  
306 2005, Swaine and Grace 2007). Lianas are also equipped with the largest and widest  
307 vessels among the vascular plant species, which allow great conductivity. This same  
308 attribute also contributes to enhanced vulnerability (Ewers 1985, Ewers et al. 1990,  
309 Angyalossy et al. 2015); however, lianas have also thick xylem walls that help avoid  
310 water transport failure (Masrahi 2014). These characteristics are likely developed  
311 during early stages and provide physiological benefits that allow liana seedlings to  
312 perform better under drought conditions (Schnitzer 2005).

313 Another potential factor that influences the success of lianas in Puerto Rico is  
314 related to the history of human and natural disturbances. Many studies have suggested  
315 that adult lianas benefit from disturbance (Perez-Salicrup et al. 1998, Laurance et al.  
316 2001, Schnitzer and Bongers 2002) and are linked to successional processes (Letcher  
317 and Chazdon 2009, Alves et al. 2012, Hogan et al. 2017). Currently, the plant  
318 community in the LFDP is recovering from past disturbance after hurricanes Hugo  
319 and Georges (Zimmerman et al. 1994, Thompson et al. 2002, 2004, Uriarte et al.  
320 2009) and varied land-use history that occurred before 1934. We evaluated the  
321 response of liana seedlings to land-use and hurricane effects by integrating land-use  
322 information based on aerial canopy photographs taken two years after human  
323 activities ceased in the plot. The results suggest that the spatial variation in liana  
324 seedling survival throughout the LFDP is explained by differences in past disturbance  
325 (Fig. 4), emphasizing the variable roles of hurricanes and anthropogenic influences on  
326 the current proliferation of liana seedlings in this forest. In agreement with these  
327 findings, Hogan et al. (2017) found that abundance of adult lianas and liana seed rain  
328 increased after 2001, especially in the high land-use intensity portion of the LFDP.  
329 Our results, therefore, indicate that the positive effect of disturbance on lianas is also  
330 evidenced during early ontogenetic stages.

331 Our study also shows that growth and seedling survival are not necessarily  
332 coupled. Overall, significant differences in survival between trees and lianas were  
333 more frequent than differences in growth. One potential explanation for these results  
334 is that differences in growth may occur at shorter temporal scales. For example,

335 Schnitzer (2005) showed intra-annual variability in growth, where liana species tend  
336 to exhibit faster growth than trees during the dry season compared with the wet  
337 season. Another explanation might simply be that growth rates are noisier than  
338 survival rates.

339

#### 340 *Crowding effects on liana seedlings*

341 The demographic advantages of liana seedlings observed during dry years are  
342 sensitive to liana crowding effects, which decrease liana density after years of high  
343 recruitment (Fig. 5). When analyzing the role of neighborhood density on liana  
344 survival, we found that liana seedling survival is negatively related to the total  
345 number of liana neighbors (Fig. 5). For growth, the results showed that not only the  
346 liana density but also the density of all neighbors have negative effects on liana  
347 growth. These negative crowding effects are likely associated with years of high  
348 recruitment that are followed by periods of high mortality (Appendix S1: Fig. S1).

349

#### 350 *Conclusion*

351 Our study indicates that lianas exhibit a demographic advantage that starts early in  
352 ontogeny and is associated with past disturbance and drought. Predicted increases in  
353 anthropogenic activities and natural disturbances, together with more frequent severe  
354 droughts in tropical forests, are likely to drive compositional changes in plant  
355 communities (Woods 1989, Enquist and Enquist 2011, Esquivel-Muelbert et al. 2016)  
356 and potentially lead to continued increases in liana abundances. The integration of  
357 long-term information that considers fluctuations in climatic phenomena is key to  
358 predict alterations in structure and composition of tropical seedling communities in  
359 response to environmental change. Future studies should include analyses of relevant  
360 functional traits to provide additional insights into the underlying physiological  
361 mechanisms.

362

#### 363 **ACKNOWLEDGMENTS**

364 We thank several field assistants and staff involved in recording the data on seedling  
365 census during these past years. Masha van der Sande, Michael O'Brien, and an  
366 anonymous reviewer provided helpful comments on earlier versions of the manuscript.  
367 Financial support was provided by two grants from the National Science Foundation,  
368 DEB-0614658 and DEB-1122325. Additional support was provided by grants DEB-

369 0620910, DEB-129764, and DEB-1546686 from NSF to the Department of  
370 Environmental Science, University of Puerto Rico, and to the International Institute of  
371 Tropical Forestry USDA Forest Service, as part of the Luquillo Long-Term  
372 Ecological Research Program. The U.S. Forest Service (Dept. of Agriculture) and the  
373 University of Puerto Rico gave additional support.

374

375

376

377

378

379

380

381 **LITERATURE CITED**

- 382 Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M.  
383 Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez,  
384 R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W.  
385 Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and  
386 heat-induced tree mortality reveals emerging climate change risks for forests.  
387 *Forest Ecology and Management* 259:660–684.
- 388 Alves, L. F., M. A. Assis, J. van Melis, A. L. S. Barros, S. A. Vieira, F. R. Martins, A.  
389 Martinelli, Luiz, and C. A. Joly. 2012. Variation in liana abundance and biomass  
390 along an elevational gradient in the tropical Atlantic Forest (Brazil). *Ecological*  
391 *Research* 27:323–332.
- 392 Angyalossy, V., M. R. Pace, and A. C. Lima. 2015. Liana anatomy: a broad  
393 perspective on structural evolution of the vascular system. Pages 251–287 *in* S.  
394 A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. *Ecology of*  
395 *Lianas*. John Wiley & Sons, LTD.
- 396 Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-  
397 effects models using lme4. *Journal of Statistical Software* 67:1–48.
- 398 Bazzaz, F. A., and P. M. Wayne. 1994. Coping with environmental heterogeneity: the  
399 physiological ecology of tree seedling regeneration across the gap – understory  
400 continuum. Pages 349–390 *in* M. M. Caldwell and R. W. Pearcy, editors.  
401 *Physiological Ecology: A Series of Monographs, Texts, and Treatises*.  
402 *Exploitation of Environmental Heterogeneity by Plants*. Ecophysiological

- 403 Processes Above- and Belowground. Academic Press, San Diego, CA.
- 404 Brokaw, N. V. L., and J. S. Grear. 1991. Forest structure before and after hurricane  
405 Hugo at three elevations in the Luquillo mountains, Puerto Rico. *Biotropica*  
406 23:386–392.
- 407 Bunker, D. E., and W. P. Carson. 2005. Drought stress and tropical forest woody  
408 seedlings: effect on community structure and composition. *Journal of Ecology*  
409 93:794–806.
- 410 Cai, Z., and F. Bongers. 2007. Contrasting nitrogen and phosphorus resorption  
411 efficiencies in trees and lianas from a tropical montane rain forest in  
412 Xishuangbanna, south-west China. *Journal of Tropical Ecology* 23:115.
- 413 Cai, Z. Q., S. A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level  
414 physiology give lianas a competitive advantage over trees in a tropical seasonal  
415 forest. *Oecologia* 161:25–33.
- 416 Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J.  
417 Twery. 2006. Neighborhood analyses of canopy tree competition along  
418 environmental gradients in New England forests. *Ecological Applications*  
419 16:540–54.
- 420 Chave, J., J. Olivier, F. Bongers, P. Chatelet, P. Forget, P. van der Meer, N. Norden,  
421 B. Riera, and P. Charles-Dominique. 2008. Above-ground biomass and  
422 productivity in a rain forest of eastern South America. *Journal of Tropical*  
423 *Ecology* 24:355–366.
- 424 Comita, L. S., and B. M. J. Engelbrecht. 2014. Drought as a driver of tropical tree  
425 species regeneration dynamics and distribution patterns. Pages 261–308 *in* D. A.  
426 Coomes, D. F. R. Burslem, and W. D. Simonson, editors. *Forests and Global*  
427 *Change*. Cambridge University Press.
- 428 Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric  
429 density dependence shapes species abundances in a tropical tree community.  
430 *Science* 329:330–332.
- 431 Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas,  
432 N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell  
433 hypothesis: A meta-analysis of experimental evidence for distance- and density-  
434 dependent seed and seedling survival. *Journal of Ecology* 102:845–856.
- 435 Condit, R. 1998. Ecological implications of changes in drought patterns: Shifts in  
436 forest composition in Panama. *Climatic Change* 39:413–427.

- 437 Delgado, D. L., J. Figueroa, and C. Restrepo. 2016. Using multiple traits to assess the  
438 potential of introduced and native vines to proliferate in a tropical region.  
439 Ecology and Evolution 6:8832–8845.
- 440 Dewalt, S. J., S. A. Schnitzer, and J. S. Denslow. 2000. Density and diversity of lianas  
441 along a chronosequence in a central Panamanian lowland forest. Journal of  
442 Tropical Ecology 16:1–19.
- 443 Engelbrecht, B. M. J., L. S. Comita, R. S. Condit, T. a Kursar, M. T. Tyree, B. L.  
444 Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution  
445 patterns in tropical forests. Nature 447:80–82.
- 446 Enquist, B. J., and C. A. F. Enquist. 2011. Long-term change within a Neotropical  
447 forest: Assessing differential functional and floristic responses to disturbance and  
448 drought. Global Change Biology 17:1408–1424.
- 449 Esquivel-Muelbert, A., T. R. Baker, K. G. Dexter, S. L. Lewis, H. ter Steege, G.  
450 Lopez-Gonzalez, A. Monteagudo Mendoza, R. Brienen, T. R. Feldpausch, N.  
451 Pitman, A. Alonso, G. van der Heijden, M. Peña-Claros, M. Ahuite, M.  
452 Alexiades, E. Álvarez Dávila, A. A. Murakami, L. Arroyo, M. Aulestia, H.  
453 Balslev, J. Barroso, R. Boot, A. Cano, V. Chama Moscoso, J. A. Comiskey, F.  
454 Cornejo, F. Dallmeier, D. C. Daly, N. Dávila, J. F. Duivenvoorden, A. J. Duque  
455 Montoya, T. Erwin, A. Di Fiore, T. Fredericksen, A. Fuentes, R. García-  
456 Villacorta, T. Gonzales, J. E. Guevara Andino, E. N. Honorio Coronado, I.  
457 Huamantupa-Chuquimaco, T. J. Killeen, Y. Malhi, C. Mendoza, H. Mogollón, P.  
458 M. Jørgensen, J. C. Montero, B. Mostacedo, W. Nauray, D. Neill, P. N. Vargas,  
459 S. Palacios, W. Palacios Cuenca, N. C. Pallqui Camacho, J. Peacock, J. F.  
460 Phillips, G. Pickavance, C. A. Quesada, H. Ramírez-Angulo, Z. Restrepo, C.  
461 Reynel Rodriguez, M. R. Paredes, R. Sierra, M. Silveira, P. Stevenson, J. Stropp,  
462 J. Terborgh, M. Tirado, M. Toledo, A. Torres-Lezama, M. N. Umaña, L. E.  
463 Urrego, R. Vasquez Martinez, L. V. Gamarra, C. I. A. Vela, E. Vilanova Torre,  
464 V. Vos, P. von Hildebrand, C. Vriesendorp, O. Wang, K. R. Young, C. E.  
465 Zartman, and O. L. Phillips. 2016. Seasonal drought limits tree species across the  
466 Neotropics. Ecography:618–629.
- 467 Ewers, F. W. 1985. Xylem structure and water conduction in conifer trees, dicot trees,  
468 and lianas. IAWA Bulletin 6:309–317.
- 469 Ewers, F. W., J. B. Fisher, and S. T. Chiu. 1990. A survey of vessel dimensions in  
470 stems of tropical lianas and other growth forms. Oecologia 84:544–552.

- 471 Gentry, A. H. 1992. The distribution and evolution of climbing plants. Pages 3–49 in  
472 F. E. Putz and H. A. Mooney, editors. In *The Biology of Vines*. Cambridge  
473 University Press.
- 474 van der Heijden, G. M. F., J. S. Powers, and S. A. Schnitzer. 2015. Lianas reduce  
475 carbon accumulation and storage in tropical forests. *Proceedings of the National  
476 Academy of Sciences* 112:13267–13271.
- 477 Hogan, J. A., S. Mayorquín, K. Rice, J. Thompson, J. K. Zimmerman, and N.  
478 Brokaw. 2017. Liana dynamics reflect land-use history and hurricane response in  
479 a Puerto Rican forest. *Journal of Tropical Ecology* 33:155–164.
- 480 Ingwell, L. L., S. Joseph Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer.  
481 2010. The impact of lianas on 10 years of tree growth and mortality on Barro  
482 Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- 483 Kobe, R. K., and C. F. Vriesendorp. 2011. Conspecific density dependence in  
484 seedlings varies with species shade tolerance in a wet tropical forest. *Ecology  
485 Letters* 14:503–10.
- 486 Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist,  
487 J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V Cornell, K. F. Davies,  
488 A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. a Myers. 2011.  
489 Disentangling the drivers of  $\beta$  diversity along latitudinal and elevational  
490 gradients. *Science (New York, N.Y.)* 333:1755–8.
- 491 Lai, H. R., J. S. Hall, B. L. Turner, and M. van Breugel. 2017. Liana effects on  
492 biomass dynamics strengthen during secondary forest succession. *Ecology  
493* 98:1062–1070.
- 494 Laurance, W. F., D. R. Perez-Salicrup, P. Delamonica, P. Fearnside, S. D'Angelo, A.  
495 Jerozolinski, L. Pohl, and T. Lovejoy. 2001. Rain forest fragmentation and the  
496 structure of Amazonian liana communities. *Ecology* 82:105–116.
- 497 Letcher, S. G., and R. L. Chazdon. 2009. Lianas and self-supporting plants during  
498 tropical forest succession. *Forest Ecology and Management* 257:2150–2156.
- 499 Masrahi, Y. S. 2014. Ecological significance of wood anatomy in two lianas from arid  
500 southwestern Saudi Arabia. *Saudi Journal of Biological Sciences* 21:334–341.
- 501 Muscarella, R., M. Uriarte, J. Forero-Montaña, L. S. Comita, N. G. Swenson, J.  
502 Thompson, C. J. Nytch, I. Jonckheere, and J. K. Zimmerman. 2013. Life-history  
503 trade-offs during the seed-to-seedling transition in a subtropical wet forest  
504 community. *Journal of Ecology* 101:171–182.

505 Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Gardinot. 2007. Mortality  
506 of large trees and lianas following experimental drought in an amazon forest.  
507 Ecology 88:2259–2269.

508 O’Brien, M. J., R. Ong, and G. Reynolds. 2017. Intra-annual plasticity of growth  
509 mediates drought resilience over multiple years in tropical seedling communities.  
510 Global Change Biology 23:4235–4244.

511 Packer, A., and K. Clay. 2003. Soil pathogens and *Prunus serotina* seedling and  
512 sapling growth near conspecific trees. Ecology 84:108–119.

513 Perez-Salicrup, D. R., V. L. Sork, and F. E. Putz. 1998. Lianas and trees in a liana  
514 forest of Amazonian Bolivia. Biotropica 33:34–47.

515 Phillips, O. L., and A. H. Gentry. 1994. Increasing Turnover through time in tropical  
516 forests. Science 263:954–958.

517 Phillips, O. L., R. Vásquez Martínez, L. Arroyo, T. R. Baker, T. Killeen, S. L. Lewis,  
518 Y. Malhi, A. Monteagudo Mendoza, D. Neill, P. Núñez Vargas, M. Alexiades,  
519 C. Cerón, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B.  
520 Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests.  
521 Nature 418:770–774.

522 Putz, F. E. 1983. Liana biomass and leaf area of a “Tierra Firme” forest in the Rio  
523 Negro basin, Venezuela. Biotropica 15:185–189.

524 R Development Core Team. 2017. R: A language and environment for statistical  
525 computing R Development Core Team. R Foundation for Statistical Computing.

526 Restom, T. G., and D. C. Nepstad. 2004. Seedling growth dynamics of a deeply  
527 rooting liana in a secondary forest in eastern Amazonia. Forest Ecology and  
528 Management 190:109–118.

529 Saatchi, S., S. Ase, Y. Malhi, L. E. O. C. Aragão, and L. O. Anderson. 2012.  
530 Persistent effects of a severe drought on Amazonian forest canopy. Proceedings  
531 of the National Academy of Science 110:2000–2009.

532 Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana  
533 abundance and distribution. The American Naturalist 166:262–276.

534 Schnitzer, S. A. 2015. Ecology of Lianas. Page (S. A. Schnitzer, F. Bongers, R. J.  
535 Burnham, and F. E. Putz, Eds.). John Wiley. John Wiley & Sons Ltd, Oxford,  
536 UK.

537 Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests.  
538 Trends in Ecology & Evolution 17:223–230.



- 539 Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in  
540 tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters*  
541 14:397–406.
- 542 Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and  
543 diversity in treefall gaps. *Ecology Letters* 13:849–57.
- 544 Smith, J. R., S. A. Queenborough, P. Alvia, H. Romero-Saltos, and R. Valencia. 2017.  
545 No strong evidence for increasing liana abundance in the Myristicaceae of a  
546 Neotropical aseasonal rain forest. *Ecology* 98:456–466.
- 547 Stevens, G. C. 1987. Lianas as structural parasites: The *Bursera simaruba* example.  
548 *Ecology* 68:77–81.
- 549 Swaine, M. D., and J. Grace. 2007. Lianas may be favoured by low rainfall: Evidence  
550 from Ghana. *Plant Ecology* 192:271–276.
- 551 Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. I. Everham, and D.  
552 A. Schaefer. 2004. Luquillo forest dynamics plot, Puerto Rico, United States.
- 553 Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J.  
554 Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history,  
555 environment, and tree composition in a tropical forest. *Ecological Applications*  
556 12:1344–1363.
- 557 Tobin, M. F., A. J. Wright, S. A. Mangan, and S. A. Schnitzer. 2012. Lianas have a  
558 greater competitive effect than trees of similar biomass on tropical canopy trees.  
559 *Ecosphere* 3:1–11.
- 560 Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat,  
561 N. Fetcher, and B. L. Haines. 2009. Natural disturbance and human land use as  
562 determinants of tropical forest dynamics: results from a forest simulator.  
563 *Ecological Monographs* 79:423–443.
- 564 Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2017. Environmental heterogeneity  
565 and biotic interactions mediate climate impacts on tropical forest regeneration.  
566 *Global Change Biology*:1–13.
- 567 Woods, P. 1989. Effects of logging, drought, and fire on structure and composition  
568 of tropical forests in Sabah, Malaysia. *Biotropica* 21:290–298.
- 569 Wright, A., M. Tobin, S. Mangan, and S. A. Schnitzer. 2015a. Unique competitive  
570 effects of lianas and trees in a tropical forest understory. *Oecologia* 177:561–  
571 569.
- 572 Wright, S. J., O. Calderón, A. Hernández, and S. Paton. 2004. Are lianas increasing in

573 importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–  
574 489.

575 Wright, S. J., I. F. Sun, M. Pickering, C. D. Fletcher, and Y. Y. Chen. 2015b. Long-  
576 term changes in liana loads and tree dynamics in a Malaysian forest. *Ecology*  
577 96:2748–2757.

578 Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N.  
579 V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical  
580 wet forest in Puerto Rico - Implications for tropical tree life-histories. *Journal of*  
581 *Ecology* 82:911–922.

582

583

584

585

586

587

588

#### DATA AVAILABILITY

589 The data used in this study are archived at the Luquillo LTER data repository:

590 <https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569>

591

#### 592 FIGURE LEGENDS

593 **Fig. 1.** Bar-plot showing changes in the total number of seedlings across 120 sites in  
594 LFDP, Puerto Rico from 2007 to 2016. The gray line represents changes in the  
595 proportion of lianas over time.

596

597 **Fig. 2.** Standardized effect size of the proportion of liana seedling survival and liana  
598 relative growth rates relative to trees in seedling communities over ten years. White  
599 boxplots show the results based on survival and dark-gray boxplots show the results  
600 based on relative growth rates. The two light-gray boxplots in the top figure show  
601 ENSO events that occurred during the study period. Positive SES values indicate  
602 higher growth rates or higher proportion of liana seedling survival over trees given  
603 observed individuals of lianas and trees, whereas negative values indicate the opposite.  
604 The values on top of the boxplot indicate the level of significance of Wilcoxon  
605 signed-rank test where \*\*\* for  $p < 0.001$ , \*\* for  $p < 0.01$  and \* for  $p < 0.05$ .

606

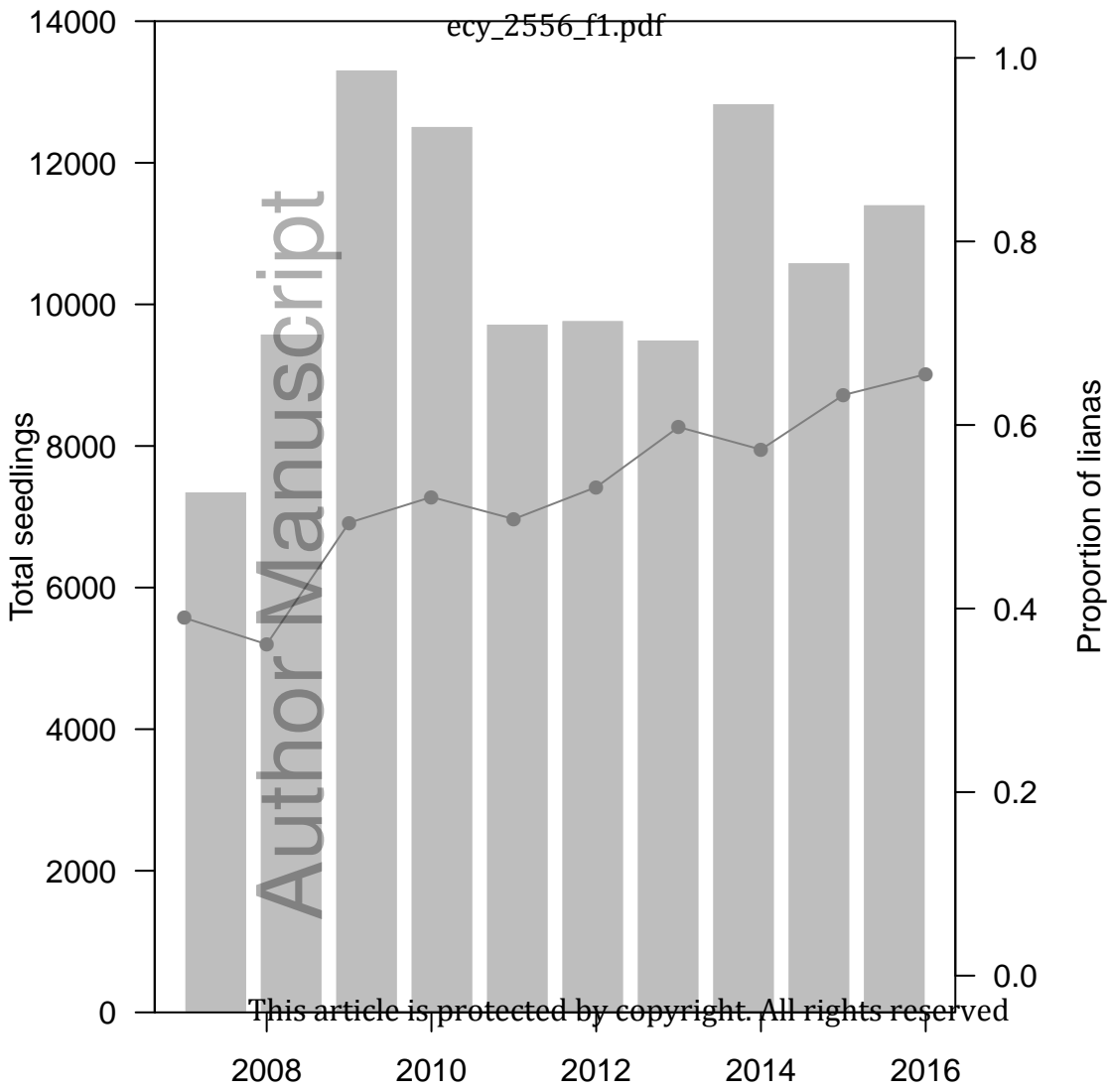
607 **Fig. 3.** Relationship between mean annual precipitation at El Verde Field Station and  
608 SES liana survival. The gray line shows the variation in scaled annual precipitation  
609 from 2007 to 2014. The black dashed line shows the temporal variation in mean  
610 annual SES liana survival at intervals from 2007-2008 to 2014-2015. The plot at the  
611 right shows the result of the model testing for the relationship between mean annual  
612 precipitation (MAP) and SES liana survival. Each point represents a station.

613

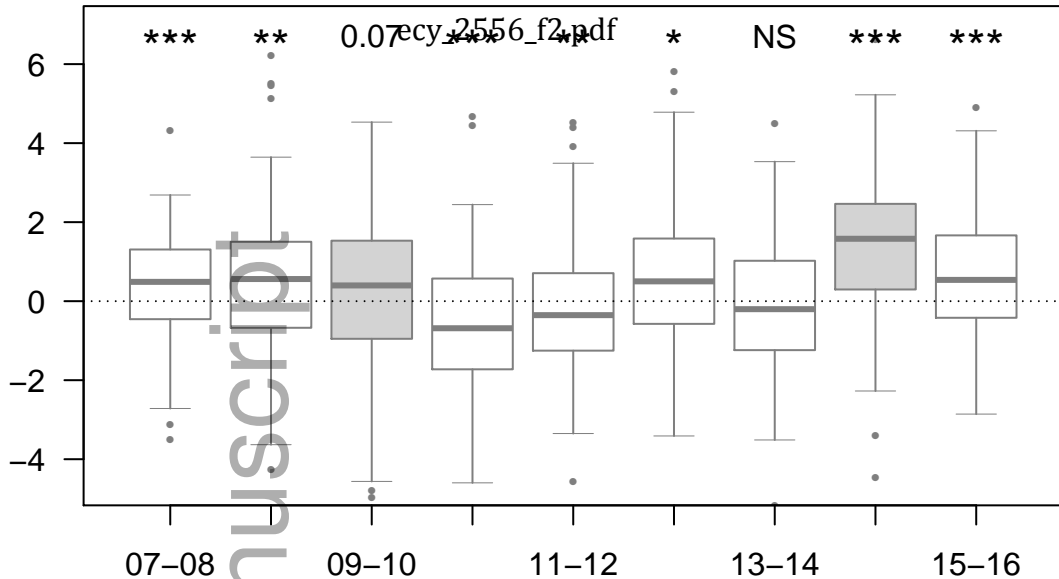
614 **Fig. 4.** Land use effect on SES liana survival. Dots indicate seedling stations, the  
615 black line represents the mean estimate and the shaded gray area shows the 95%  
616 credible intervals. Values for this covariate are summarized in Appendix S1: Table S2.

617

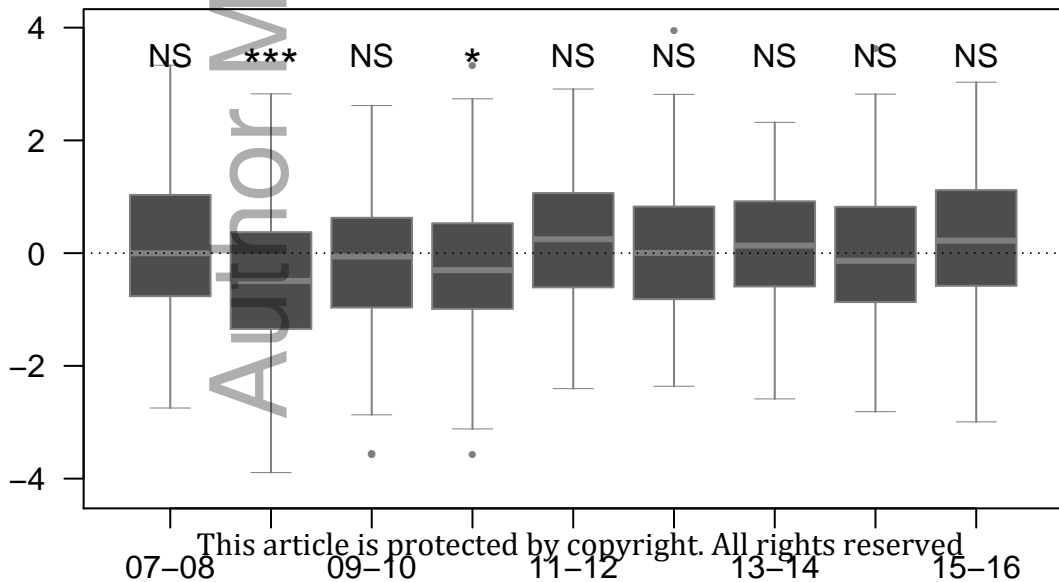
618 **Fig. 5.** Crowding effect on liana demography. Top plots with gray dots show  
619 relationships using SES liana survival. Bottom plots with black points show  
620 relationships using SES liana relative growth rate. Black lines show significant  
621 relationships, the dashed line shows a non-significant relationship.



SES Liana Survival



SES Liana Relative Growth Rate



Time interval

