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9 **Long-term dynamics of liana seedlings suggest decelerating increases in liana relative**  
10 **abundance over time**

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21 **ABSTRACT**

- 22 1. Over the past decades, tropical forests have experienced both compositional and  
23 structural changes. In the Neotropics, researchers at multiple sites have observed  
24 significant increases in the abundance and biomass of lianas (i.e. woody vines)  
25 relative to trees. However, the role of dynamics at early life stages in contributing to  
26 increasing liana abundance remains unclear.
- 27 2. We took advantage of a unique dataset on seedling dynamics over 16 years in  
28 ~20,000 1-m<sup>2</sup> plots in a tropical forest in Panama to examine temporal and spatial  
29 trends in liana and tree seedling abundance.
- 30 3. We found that the relative abundance of liana seedlings increased across the study  
31 period, from 0.18 in 2001 to 0.24 in 2017. However, increases in liana seedling  
32 relative abundance appear to have leveled off in more recent years. The observed

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33 increases in liana relative abundance appear to be the result of both higher survival  
34 and higher recruitment rates of liana seedlings compared to tree seedlings.

35 4. Increasing liana abundance in the seedling layer was not explained by annual  
36 variation in dry season length, total rainfall, or the proportion of area occupied by  
37 canopy gaps. In addition, liana seedlings did not exhibit a demographic advantage  
38 (i.e., higher recruitment or survival) over tree seedlings in dry habitats.

39 5. *Synthesis:* Our results reveal that seedling communities experienced important  
40 compositional changes in the past, but liana seedling relative abundance may have  
41 stabilized in recent years. Longer-term monitoring is needed to determine whether  
42 tropical forests will continue to experience compositional changes that may alter  
43 forest structure and ecosystem function.

44

45 **Keywords:** Barro Colorado Island, forest structure, light gaps, precipitation, Panama,  
46 regeneration dynamics, topographic habitat.

47

#### 48 **ABSTRACT IN SPANISH**

49 1. En las últimas décadas los bosques tropicales han experimentado cambios en  
50 estructura y composición. En el Neotrópico, investigadores en múltiples sitios han  
51 observado incrementos significativos en la abundancia y biomasa de lianas  
52 comparado con árboles. Sin embargo, nuestro entendimiento de cómo estas dinámicas  
53 contribuyen a la abundancia de lianas en etapas tempranas del ciclo de vida de las  
54 plantas es limitado.

55 2. Nuestro estudio tomó ventaja de una serie de datos únicos que incluyen información  
56 de dinámicas de plántulas a lo largo de 16 años en ~ 20,000 parcelas de 1- m<sup>2</sup>  
57 establecidas en un bosque tropical en Panamá para examinar las variación temporal y  
58 espacial de la abundancia de plántulas de árboles y lianas.

59 3. Encontramos que la abundancia relativa de plántulas de lianas incrementó a los largo  
60 del periodo de estudio desde 0.18 en el 2001 hasta 0.24 en el 2017. Sin embargo, este  
61 aumento parece haberse estabilizado en los últimos años. El aumento en plántulas de  
62 liana es probablemente el resultado de tasas de supervivencia y reclutamiento  
63 mayores comparadas con plántulas de árboles.

64 4. Los incrementos en la abundancia de lianas en el estrato de plántulas no fueron  
65 explicados por la variación en la longitud de la estación seca. precipitación anual total  
66 o por la proporción de área ocupada por claros. Además, en hábitats secos las

67 plántulas de lianas no mostraron una ventaja demográfica (i.e., aumento en el  
68 reclutamiento o supervivencia) comparado con plántulas de árboles.

69 5. *Síntesis*: Nuestros resultados muestran que las comunidades de plántulas  
70 experimentaron importantes cambios de composición en el pasado reciente, pero la  
71 abundancia relativa de plántulas de liana parece haberse estabilizado en los últimos  
72 años. El monitoreo de comunidades a largo plazo es necesario para determinar si los  
73 bosques tropicales continuarán experimentando cambios en composición que podrían  
74 alterar la estructura del bosque y la función del ecosistema.

75

## 76 INTRODUCTION

77 Lianas are important structural components of tropical forests, occupying about 50% of the  
78 canopy cover (Putz 1984). During the last two decades, a number of studies have documented  
79 significant increases in the density and biomass of adult lianas in Neotropical forests (Phillips  
80 et al., 2002; Schnitzer & Bongers, 2011, but see, Smith *et al.* 2017), yet causes of this  
81 proliferation are largely unknown. The observed proliferation of adult lianas should also  
82 generate increases in lianas at earlier ontogenetic stages, such as higher production of liana  
83 seeds and higher liana seedling recruitment. Indeed, Umaña *et al.* (2019) reported an increase  
84 in the relative abundance of liana seedlings for a tropical forest in Puerto Rico from 2007 to  
85 2017. In contrast, while Wright *et al.* 2004 found increases in liana leaf litter production,  
86 liana seed production (over 14 years) and seedling proportion (over 8 years) fluctuated over  
87 time. If the same conditions that promote increases at the adult stage are also favorable for  
88 liana seedlings, we should see higher survival of liana seedlings over time and increasing  
89 relative abundance of liana species. However, compared to the recent spate of studies focused  
90 on increasing abundance of adult lianas, relatively little is known about changing dynamics  
91 of lianas at earlier ontogenetic stages. Examining changes in seedling community  
92 composition can provide insights into not only the processes underlying liana increases, but  
93 also whether increases in liana relative abundance will continue unabated into the future.

94 Increasing abundance of lianas in the seedling layer could result from either declines  
95 in seedling mortality rates, increases in seedling recruitment rates, or both. Seedling  
96 recruitment is highly dependent on seed production, as well as on favorable conditions that  
97 allow the successful establishment of seedlings. Once established, seedling mortality is  
98 driven by biotic (e.g., pathogens, herbivores) and abiotic factors (e.g., limited light, moisture)  
99 that impair seedling performance (Augsburger, 1984; Clark & Clark, 1985; Johnson, Condit,  
100 Hubbell, & Comita, 2017; Uriarte, Muscarella, & Zimmerman, 2018). Demographic rates of

101 both tree and liana species appear to be constrained by similar life history trade-offs (between  
102 growth and survival rates) at the seedling stage (Gilbert *et al.* 2006). However, studies have  
103 also found key differences in liana vs. tree responses to biotic and abiotic variables at early  
104 life stage (Muscarella *et al.* 2013; Uriarte *et al.* 2018; Umaña *et al.* 2019). For example, for  
105 seedling communities in a subtropical forest in Puerto Rico, lianas survived better than trees  
106 during drier years and in areas that experienced intense land-use history (Uriarte *et al.* 2018;  
107 Umaña *et al.* 2019). Thus, shifting conditions in tropical forests may differentially impact  
108 liana and tree seedling dynamics, leading to changes in relative abundance of lianas in the  
109 understory. Such changes at the seedling stage are likely to influence later stages, since early  
110 life stages tend to be demographic bottlenecks and processes occurring at early stages play a  
111 significant role in shaping community composition and maintaining diversity in plant  
112 communities (Harper 1977).

113 Multiple mechanisms have been hypothesized to explain observed increases in liana  
114 abundance (reviewed by Schnitzer and Bongers 2011), several of which would likely  
115 influence recruitment and mortality at the seedling stage. First, Schnitzer (2005) suggested  
116 increasing liana abundance and biomass relative to trees could be due to increasing  
117 evapotranspirative demand (as a result of increased temperature and/or drought severity)  
118 because lianas are thought to have a demographic advantage (i.e., higher survival or  
119 recruitment) over trees under drier conditions. Previous studies on adult lianas have  
120 supported this hypothesis (Swaine & Grace 2007; Chen *et al.* 2015; van der Sande *et al.*  
121 2019). Therefore, we would similarly expect liana seedlings to have a survival advantage  
122 over trees in drier habitats and in years with more severe droughts. An additional factor that  
123 could promote the proliferation of lianas is increased light availability due to disturbance  
124 (i.e., tree fall gaps) (Schnitzer 2005, 2018). Previous studies have shown that canopy gaps  
125 and highly disturbed areas accumulate higher abundance and diversity of adult and seedling  
126 lianas (Dalling *et al.* 2012; Ledo & Schnitzer 2014; Umaña *et al.* 2019). Thus, increases in  
127 the relative abundance of lianas may result from increases in the total area of canopy gaps  
128 within a forest.

129 We examined woody seedling dynamics across 16 years in a Neotropical lowland  
130 moist forest and compared liana and tree seedling dynamics, as well as changes in the relative  
131 abundance of these two growth forms over the study period. Using data on 396 species  
132 collected every 1 to 2 years between 2001 and 2017 in ~20,000 1-m<sup>2</sup> seedling plots, we  
133 asked the following questions: (1) Are liana seedlings increasing in relative abundance in this  
134 tropical forest and are such changes constant over time? (2) Are observed changes in liana

135 seedling relative abundance driven by lower mortality, higher recruitment, or both? (3) Do  
136 liana seedlings outperform tree seedlings specifically in drier habitats, in drier years or in  
137 years that had a higher proportion of area open due to canopy gaps?  
138

## 139 **METHODS**

### 140 **Study site**

141 The study was conducted on Barro Colorado Island (BCI), Panama (9°10' N, 79°51' W). The  
142 forest is classified as tropical moist forest according to Holdridge life zones. Average annual  
143 temperature is 25.9°C and average annual precipitation is 2,600 mm, the majority of which  
144 occurs during the wet season between May and December (Paton 2016). During the study  
145 period, a strong ENSO event resulted in severe drought conditions during the 2015-2016 dry  
146 season. Between 1980 and 1982, a 50-ha permanent plot was established to monitor the  
147 dynamics of woody trees  $\geq 1$  cm diameter at 1.3 m above ground (DBH) (Hubbell & Foster  
148 1983). The plot is predominantly old growth ( $>500$  years), with a 2-ha area of secondary  
149 forest in the north-east corner of the plot. Although the island was affected in the past by  
150 anthropogenic activities, the old growth forest has not been cleared for agriculture in the last  
151 1500 years (Piperno 1990).

### 152 **Seedling census**

153 In 2001, a 1 x 1 m seedling plot was established in the center of each 5 x 5 m subplot within  
154 the 50-ha plot, for a total of 20,000 plots used to monitor dynamics of early life stages. In the  
155 initial census in 2001, all free-standing woody individuals  $\geq 20$  cm tall and  $< 1$  cm DBH were  
156 tagged, identified to species, and measured for height (Comita, Condit & Hubbell 2007). The  
157 seedling census included shrubs and trees (hereafter referred to simply as 'trees'), but palm  
158 seedlings were excluded. Typically, lianas start life as free-standing seedlings in the forest  
159 understory before eventually using a host tree to climb for access to the canopy (but see  
160 Letcher & Chazdon 2012). Liana seedlings were therefore included in the seedling census if  
161 they were  $\geq 20$  cm tall and not yet twining or climbing on other plants. Seedling plots were re-  
162 censused annually from 2002 to 2017, except for in 2005, 2007, 2010, and 2015 (for  
163 logistical reasons).  
164

### 165 **Proportion of area in gaps**

166 To assess light conditions in the understory we used data from annual canopy censuses  
167 conducted between 2003 and 2012 (Hubbell *et al.* 2014). In each year, for every 5 x 5 m  
168

169 quadrat within the 50-ha plot, the presence/absence of vegetation was recorded at different  
170 height classes: 0-1 m, 1-2 m, 2-5 m, 5-10 m, 10-20 m, 20-30 m, and >30 m above ground.  
171 Using these data, we estimated the proportion of plot area with no vegetation (i.e. canopy  
172 gaps) above 1 m, 2m, and 5m for each year.

173

#### 174 **Analyses**

175 For our analyses, we used data on free-standing woody seedlings that were  $\geq 20$  and  $\leq 100$  cm  
176 tall, because taller liana seedlings usually start twining on other individuals (and thus were  
177 not captured by the seedling census).

178 We checked for temporal trends in liana vs. tree seedling abundances in the BCI  
179 forest in several ways. First, we calculated the relative abundance of lianas in each seedling  
180 census (i.e. proportion of all woody seedlings that belonged to liana species) and plotted liana  
181 relative abundance over time. In addition, we calculated the population growth rate ( $\lambda$ )  
182 between 2001 and 2017 of liana and tree seedlings separately within each 1-ha quadrat  
183 (100x100m; 400 seedling plots per ha) of the 50-ha plot, using the formula:  $(\lambda) = \frac{\ln n_t - \ln n_0}{\Delta t}$   
184 , where  $\Delta t$  is the census interval,  $n_t$  and  $n_0$  is the population size at time t and time zero  
185 respectively. We then tested for a difference between liana and tree seedlings in population  
186 growth rate using a paired t-test after testing for normality using a Shapiro-Wilk test ( $P >$   
187 0.05).

188 To check if the proportion of species exhibiting shifts in overall population growth  
189 rates was different between lianas and trees, we performed a Chi-squared test in which we  
190 examined whether the portion of species that increased or decreased in abundance across the  
191 study period (2001 to 2017) was different between lianas and trees. For this test, we only  
192 used species with  $>20$  individuals in the initial census to avoid any spurious effect caused by  
193 small changes in abundance of rare species.

194 To examine whether changes in population size were related to recruitment, mortality  
195 or both, we divided the dataset into four non-overlapping intervals, each three-years long  
196 (2001-2004, 2006-2009, 2011-2014, 2014-2017), and calculated recruitment and mortality  
197 rates for lianas and trees separately in each 1-ha quadrat in each 3-yr interval. We calculated  
198 mortality ( $m$ ) as:  $m = \frac{\ln n_0 - \ln S_t}{\Delta t}$ , where the  $S_t$  is the number of survivors at time  $t$ . We  
199 calculated recruitment ( $r$ ) as,  $r = \frac{\ln n_t - \ln S_t}{\Delta t}$  (Hubbell, Condit & Foster 1990). Next, we  
200 performed a paired t-test to examine differences between liana and tree seedlings in mortality

201 or recruitment rates for each interval at each plot, correcting for multiple comparisons using  
202 the false discovery rate method (Benjamini & Hochberg 1995).

203 To examine whether changes in the relative abundance of lianas over the study period  
204 were related to rainfall patterns, dry season length and/or light availability, we calculated the  
205 change in relative abundance of lianas per census interval (Ch RA) and related it to annual  
206 precipitation (AP, mm), length of the dry season (LDS, days) and proportion of area in gaps  
207 (PG). We used a single model to test the effect of AP and LDS, and a separate model to test  
208 the effects of PG because data on gap area were only available for 2003-2012. For models of  
209 gap area effects, we ran separate models using gap area above 1 m, 2 m, and 5 m. However,  
210 results were qualitatively similar for all height cutoffs, and so we only present results using  
211 area of gaps above 1 m. Because community-level responses to abiotic variables do not occur  
212 instantaneously, we compared the change in relative abundance of lianas to abiotic data from  
213 the previous year (e.g. the change in relative abundance between 2008 and 2009 was linked  
214 to data on annual rainfall, dry season length and gap area from 2007). For the four census  
215 intervals that were two years long, we used the average abiotic information for the years prior  
216 to each year in the interval (e.g. for the interval 2014-16, annual rainfall was averaged for  
217 2013 and 2014). In addition, we calculated the change in proportion of recruits and change in  
218 proportion of survivors per census interval and fit the same models. To examine changes in  
219 raw abundances of liana vs. tree seedlings in response to the abiotic variables, we also ran  
220 similar models but instead of using the change in relative abundance of lianas we calculated  
221 the change in absolute (log-transformed) abundance of liana and tree seedlings per census  
222 interval (Ch AB). The models had the following form:  $Ch\ AB \sim \beta_0 + \beta_1 \times GF \times AB$ . GF  
223 refers to growth form (i.e., liana or tree), and AB refers to the abiotic variable (i.e., either AP,  
224 LDS or PG).

225 To examine whether liana seedlings were better able to tolerate drier habitats  
226 compared to tree seedlings, we used the habitat classification of Harms *et al.* (2001), which  
227 assigned each 20 x 20 m subplot in the BCI 50-ha plot to one of seven habitat types: high  
228 plateau, low plateau, slope, stream, swamp, young (secondary forest), or mixed (i.e. more  
229 than one habitat type). For our analyses, subplots classified as *high plateau* and *low plateau*  
230 were assigned as “dry” habitats and *slope* and *stream* subplots were assigned as “wet”  
231 habitats, based on their soil moisture availability (Becker *et al.* 1988; Grandgirard *et al.* 2002;  
232 Comita & Engelbrecht 2009, 2014). Previous studies have found effects of these habitat types  
233 on plant community composition, species distributions, and tree seedling survival in the BCI

234 50-ha plot (Engelbrecht *et al.* 2007; Comita & Engelbrecht 2009, 2014; Murphy, Salpeter &  
235 Comita 2016). *Swamp*, *Mixed*, and *Young* habitat types were removed from the analyses  
236 because of their low representation in the 50-ha plot. We then examined the differences in  
237 mortality rates (from 2001 to 2017) between lianas and trees per 20x20 m subplot as a  
238 function of habitat, life form and the interaction of both using a linear mixed-effects model.  
239 Subplot was included as a random effect. The linear mixed model was conducted by using  
240 the “lmer” function from the package “lme4” in R (Bates *et al.* 2015).

241 All analyses were performed in R version 3.4.4 (R Development Core Team 2017).

242

## 243 RESULTS

244 Between 2001 and 2017, 37,445 liana seedlings of 151 species and 139,835 tree seedlings of  
245 257 species (including morpho-species) were tagged and monitored in the seedling census.  
246 Liana seedlings increased in relative abundance over the study period (Fig 1A), and the  
247 population growth rate of liana seedlings was significantly higher than tree seedlings between  
248 2001 and 2017 ( $t=7.7$ ,  $P<0.001$ , Fig. S1). Increases in liana relative abundance were steepest  
249 in the first few years of the study (2001 to 2003) and continued to increase until 2014 when  
250 the values leveled off (Fig. 1A). Changes in absolute abundance over time were similar for  
251 liana and tree seedlings, with both groups showing increases in seedling numbers between  
252 2002 and 2008, and then a pronounced decline between 2008 and 2016, before a small uptick  
253 between 2016 and 2017 (Fig. 1B). Despite the similarity in temporal trends in absolute  
254 abundance, increases were greater and declines were less for liana seedlings compared to tree  
255 seedlings, leading to increasing liana relative abundance in the seedling layer over the study  
256 period. We also found that the proportion of species that increased in seedling abundance was  
257 greater for liana species compared to tree species (Chi-squared test,  $\chi^2 = 3.92$ ,  $P = 0.04$ ) (Fig.  
258 S2).

259 Liana seedlings had significantly lower mortality and higher recruitment rates  
260 compared to tree seedlings for intervals 1 and 2, but not for intervals 3 and 4 (Fig. 2).

261 Graphs of annual variation in total rainfall, dry season length, and proportion of area  
262 in gap clearly show that temporal trends in these abiotic factors do not mirror the observed  
263 increases over time in liana seedling abundance during the study period (Fig. 1C-E).

264 Consistent with this, none of these abiotic variables had significant effects in models of  
265 changes in liana relative abundance or in models of changes in absolute abundances of tree  
266 and liana seedlings (Table 1). Results comparing the effect of habitat type between lianas and



267 trees showed no significant effect of habitat on mortality or recruitment, nor any significant  
268 interaction between habitat and growth form (Fig. 3 and Table S1).

269

## 270 **DISCUSSION**

271 Using our extensive, long-term data on tropical seedling dynamics, we found that the relative  
272 abundance of lianas in the seedling layer increased in the BCI forest dynamics plot over the  
273 16-year period spanning 2001-2017. This pattern does not appear to be driven by one or a  
274 handful of species, but rather reflects a more general trend at the community level (Fig. S2).

275 The proliferation of lianas appears to be driven by both higher survival and higher  
276 recruitment of lianas compared to trees, particularly in the first eight years of the study.

277 Higher recruitment could reflect a past increase in liana seed production, while both higher  
278 recruitment and survival likely reflect a potential physiological advantage that allows liana  
279 seedlings to establish and survive better than tree seedlings (van der Sande *et al.* 2019).

280 Despite the hypothesized effects of water availability and canopy gaps in driving the  
281 increasing prevalence of lianas, we did not find differences in demography between liana and  
282 tree seedlings related to habitat type, nor any relationship between changes in liana seedling  
283 relative abundance and annual rainfall, dry season length or proportion of area in gaps.

284 Overall, our results indicate that the seedling layer is mirroring patterns found for adult stages  
285 in other Neotropical forests (Phillips *et al.* 2002; Schnitzer & Bongers 2011), where lianas  
286 have been shown to be increasing in relative abundance compared to trees. Interestingly,  
287 however, our results show that these increases in liana seedling relative abundance appear to  
288 have leveled off in recent years, suggesting that there may be some limit to the increases in  
289 liana abundance observed in Neotropical forests. These results have important implications  
290 for understanding and predicting future changes in forest structure, species composition, and  
291 carbon balance.

292 Our finding of increasing abundance of lianas over trees in the seedling layer agrees  
293 with a recently published long-term study from Puerto Rico that showed higher increases in  
294 liana seedling abundance relative to trees over a 10-year period (Umaña *et al.* 2019).

295 However, additional studies focused on the seedlings stage are needed to determine whether  
296 this pattern extends to other tropical forests. Even within a single forest, temporal patterns of  
297 liana relative abundance may depend both on the time period and size classes examined. For  
298 example, a previous study at our study site in Panama showed more variable patterns in the  
299 proportion of liana seedlings during an earlier time period (i.e., 1994 to 2002) (Wright *et al.*  
300 2004). That study by Wright *et al.* (2004) included seedlings smaller than our minimum size

301 cut-off (20 cm tall). Younger seedlings tend to fluctuate more in abundance than older,  
302 established seedlings given that their dynamics are highly determined by seed production  
303 pulses followed by high mortality rates of seeds and young seedlings.

304 Our results also indicate that rates of liana proliferation varied over time. During the  
305 first nine years of our study, both lianas and trees increased in absolute abundance, with  
306 lianas showing higher rates of increase than trees; however, after 2008, the seedling  
307 community, both lianas and trees, experienced substantial declines. The most striking  
308 differences between liana and tree seedling dynamics during the first part of the study were  
309 the result of lower mortality and higher recruitment rates of lianas compared to trees during  
310 the first two intervals examined (2001-2004, 2006-2009). However, the rate of increase of  
311 liana relative abundance tended to decelerate over the later years of the study (Fig. 1A), and  
312 the differences in demographic rates between lianas and trees were not significant in later  
313 census intervals (Fig. 2). Observed temporal trends in demographic success of liana seedlings  
314 have been attributed to variation in precipitation, which has shown significant relationships  
315 with liana seedlings dynamics in previous studies in Neotropical forests (Wright *et al.* 2004;  
316 Umaña *et al.* 2019). In particular, lianas are hypothesized to benefit over trees when water is  
317 limited because of special physiological characteristics, such as good stomatal control, that  
318 allow them to exploit water more efficiently (Schnitzer 2005). However, in our study, dry  
319 season length and total annual rainfall on BCI during the 16-year study period were not  
320 significantly related to shifts in relative abundance of liana seedlings in the BCI forest or  
321 proportion of liana recruits or survivors (Table 1). We may have failed to detect trends  
322 related to annual climate fluctuations because four of the 12 census intervals included in our  
323 study spanned two years rather than one, and multiyear census intervals can obscure climatic  
324 signals in forest dynamics (Clark & Clark 2011). However, visual inspection of annual  
325 variation in rainfall and dry season length (Fig. 1C & D) suggest that it is unlikely that these  
326 variables explain the trend of increasing liana relative abundance over the course of the study.  
327 In addition, our study spanned a severe El Niño event in 2015-16 that resulted in a  
328 particularly long dry season in 2016. However, liana seedling relative abundance showed  
329 only a small increase from 2016 to 2017, especially compared to the much larger increases in  
330 liana relative abundance observed earlier in the study in years with shorter dry seasons (Fig.  
331 1A). Thus, while several studies have shown that lianas have physiological advantages over  
332 trees under dry conditions (van der Sande *et al.* 2019), we found no evidence that lianas  
333 benefited over trees in dry years, at least at the seedling stage. However, we cannot rule out  
334 the possibility that increasing liana seedling relative abundance is a result of combined,

335 interactive effects of multiple climatic variables (e.g. drought severity and night-time  
336 temperature). We also examined the potential positive effects of proportion of area in gaps on  
337 shifts in liana seedling abundance, but found no significant effect (Table 1). A potential  
338 explanation for this null result is that the study site is a relatively well-preserved forest that is  
339 not subject to frequent severe disturbances (e.g. hurricanes), and thus has a low proportion of  
340 disturbed areas at any given time (at the height of 1 m, the average proportion of area in gaps  
341 from 2003 to 2012 was 0.003, Table S2). Interestingly, the proportion of area in gaps above 2  
342 and 5 m was particularly high initially (i.e., 2003 and 2004), and then declined (Fig. 1E).  
343 These areas with gaps above 2 or 5 m are likely older gaps that are beginning to fill in. Thus,  
344 we cannot rule out the possibility that the initial steep increases in liana relative abundance  
345 we observed were partly due to a delayed response to higher gap formation in the years just  
346 prior to the start of the seedling census, perhaps due to increased seed production of adult  
347 lianas leading to higher liana seedling recruitment. Future studies examining canopy gap  
348 dynamics prior to 2003, as well as spatially-explicit analyses of liana seedling dynamics in  
349 gap vs. non-gap areas of the 50-ha plot, would shed light on the potential role of canopy gaps  
350 in driving liana proliferation.

351 At regional scales, liana abundance has been shown to increase markedly with  
352 decreasing precipitation, increasing seasonality, and in soils with low water-holding capacity  
353 (Swaine & Grace 2007; Manzané-Pinzón, Goldstein & Schnitzer 2018), leading to the  
354 hypothesis that lianas have a competitive advantage in drier, more seasonal environments and  
355 will increase in abundance with higher evapotranspirative demand (Schnitzer 2005; Schnitzer  
356 & Bongers 2011). We tested for a demographic advantage of lianas over trees under drier  
357 conditions by examining differences in mortality and recruitment between lianas and trees in  
358 topographic habitat types that differ in water availability (Hubbell & Foster 1983; Condit  
359 1998). This topographic variation in soil moisture in the BCI plot drives significant habitat  
360 associations for both tree and liana species at the adult stage (Dalling *et al.* 2012). At the  
361 seedling stage, variation in water availability across these habitats has been shown to drive  
362 interspecific differences in tree seedling survival across habitats in the BCI forest (Comita &  
363 Engelbrecht 2009). However, we found that tree and liana seedlings did not differ in  
364 mortality or recruitment responses to habitat. Thus, our results suggest that drier habitats do  
365 not favor lianas over trees at the seedling stage in this forest, although we cannot rule out  
366 differential responses to water availability at later life stages. Indeed, Dalling *et al.* (2012)  
367 found a high abundance of adult lianas in drier plateau habitats relative to wetter slope  
368 habitats in the BCI plot.

369           Increasing liana relative abundance has also been attributed to differences in dispersal  
370 strategy in the Neotropics: lianas tend to be dispersed by abiotic means (e.g. wind), while a  
371 larger proportion of tree species rely on animal dispersers, which have suffered large declines  
372 in many tropical forests (Wright, Hernández & Condit 2007; Wright *et al.* 2015). However,  
373 hunting is not permitted on BCI, and the forest there is well protected from poachers by park  
374 guards (Wright *et al.* 2007). Although bird inventories on BCI have found population  
375 decreases and in some cases complete extinctions, the guilds that experienced more  
376 pronounced declines were nectarivores and insectivores (Karr 1982). Therefore, the seed  
377 disperser community appears to be largely intact on BCI, which has likely contributed to  
378 maintaining effective dispersion for tree species dependent on animals (Jansen *et al.* 2012).  
379 Consistent with this, shifts in abundances of liana and tree seedlings between 2001 and 2017  
380 were unrelated to species' dispersal strategy (Table S3). The observed increases in liana  
381 seedling relative abundance over time, despite the intact seed disperser community, indicates  
382 that other factors must have promoted the success of liana over tree seedlings in the BCI  
383 forest across our study period.

384           In conclusion, we show that the BCI seedling community experienced substantial  
385 increases in the relative abundance of lianas over a 16-year period. These increases were  
386 driven by both lower seedling mortality and higher recruitment of lianas compared to trees,  
387 but do not appear to result from differences between the growth forms in response to water or  
388 light availability. Although these two mechanisms cannot be ruled out at larger geographical  
389 scales, at the local scale, in our study, their effect on seedling community dynamics appears  
390 to be negligible. These results have implications for forest dynamics in the short and long  
391 run, where the observed shifts not only imply changes in structure and composition of current  
392 seedling communities, but also indicate potential shifts in the carbon dynamics of the forest  
393 as well as arrested succession in disturbed areas that are dominated by lianas. Previous  
394 studies have shown that proliferation of adult lianas in tropical forests reduce forest-level  
395 carbon uptake and storage capacities (Durán, Gianoli & Dura 2013; van der Heijden, Powers  
396 & Schnitzer 2015). Observed changes in the seedling layer may be counteracted by processes  
397 at later life stages. However, if observed dynamics of earlier stages reflect dynamics of the  
398 future adult layer, tropical forests will likely face substantial alteration in their carbon  
399 dynamics. At the same time, our study also demonstrates that the increase in liana relative  
400 abundance in the seedling layer has leveled off in recent years. Whether increases in adult  
401 liana abundance and biomass in Neotropical forests will follow a similar trend remains to be  
402 seen. Continued long-term monitoring of tropical forests is needed to understand and predict

403 how these ecologically and economically valuable ecosystems will be altered in a changing  
404 world.

405

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413

#### 414 **AUTHORS' CONTRIBUTIONS**

415 MNU, EMP and LSC designed the study. EMP and LSC collected the data. MNU analyzed  
416 the data. MNU, EMP and LSC wrote the manuscript.

417

#### 418 **DATA ACCESSIBILITY**

419 Seedling census data are available from Dryad Digital Repository (DOI:  
420 <https://doi.org/10.5061/dryad.fm654>) for years 2001-2012 and Dryad DOI pending for years  
421 2013-2017. Canopy census data are available from  
422 <https://repository.si.edu/handle/10088/21929>, and climate data are available from  
423 [https://biogeodb.stri.si.edu/physical\\_monitoring/research/barrocolorado](https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado).

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546 TABLES

547 **Table 1.** Coefficients of total annual rainfall, length of dry season, and proportion of area in  
 548 gaps from models of annual changes in (1) relative abundance of lianas (2) proportion of  
 549 liana recruits, (3) proportion of liana survivors, and from models of (4) log-transformed (raw)  
 550 abundances of liana and tree seedlings per census interval in the BCI forest. Data on total  
 551 rainfall and dry season length were available for all census intervals. Information on  
 552 proportion of area in gaps was only available for the period between 2003 and 2012.

Dependent variable		Std.		t value	P value
		Estimate	Error		
Change in relative abundance of lianas	(Intercept)	0.01	0.01	1.24	0.25
	Total rainfall	3.5E-06	2.7E-06	1.26	0.24
	Length dry season	-1.5E-04	7.7E-05	-1.90	0.09
	(Intercept)	0.01	1.7E-03	3.33	0.02
	Gap area	-0.04	0.05	-0.87	0.43
Change in proportion of liana recruits	(Intercept)	9.65E-03	1.17E-02	0.82	0.44
	Total rainfall	4.23E-06	2.70E-06	1.57	0.16
	Length dry season	-1.24E-04	7.55E-05	-1.65	0.14
	(Intercept)	0.008	0.002	3.68	0.01
	Gap area	-0.093	0.060	-1.55	0.18
Change in the proportion of liana survivors	(Intercept)	0.12	7.37E-02	1.66	0.14
	Total rainfall	-9.85E-06	1.64E-06	-0.60	0.57

	06	05		
Length dry	-6.71E-	4.58E-		
season	04	04	-1.47	0.19
(Intercept)	0.01	0.01	0.99	0.37
Gap area	-0.23	0.38	-0.60	0.57
(Intercept)	0.01	0.16	0.04	0.97
Liana	-0.02	0.23	-0.08	0.94
Total rainfall	-1.4E-05	5.9E-05	-0.24	0.81
Liana:Total				
rainfall	1.9E-05	8.4E-05	0.23	0.82
(Intercept)	-0.02	0.22	-0.07	0.95
Liana	0.16	0.32	0.51	0.61
Length dry				
season	-1.3E-04	1.6E-03	-0.08	0.94
Liana:Length				
dry season	-9.6E-04	2.3E-03	-0.41	0.68
(Intercept)	-0.02	0.05	-0.41	0.69
Liana	0.04	0.07	0.56	0.59
Gap area	-0.22	1.38	-0.16	0.88
Liana:Gap area	6.9E-04	1.95	0.03	0.97

Change in log-transformed  
abundance

553

554 FIGURE LEGENDS

555

556 **Figure 1.** Temporal variation in the seedling community, precipitation and proportion of area  
557 in gaps in Barro Colorado Island (BCI), Panama. Plot A shows shifts in relative abundance of  
558 lianas during the study period at 50-ha forest plot. Plot B shows shifts in liana and tree  
559 seedling numbers in the 50-ha plot seedling census. Plot C shows total yearly rainfall and plot  
560 D shows length of the dry season for the period between 2000 and 2016. Plot E shows  
561 proportion of area in gaps for the period between 2003 and 2012. The dashed vertical lines  
562 indicate the years where seedling censuses were conducted. Note that y-axes do not include  
563 zero for plots A-D.

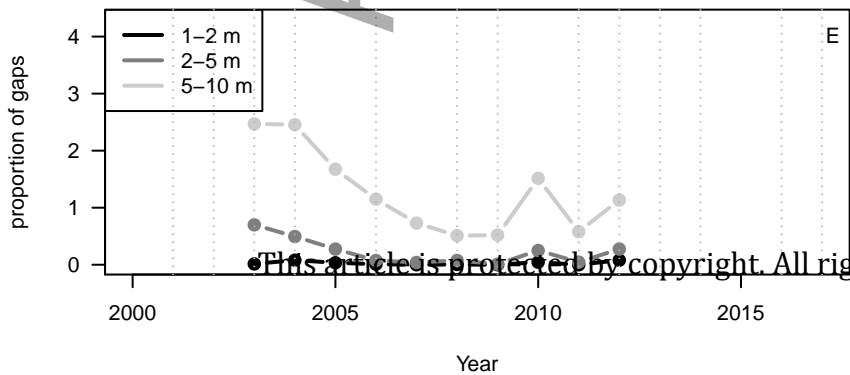
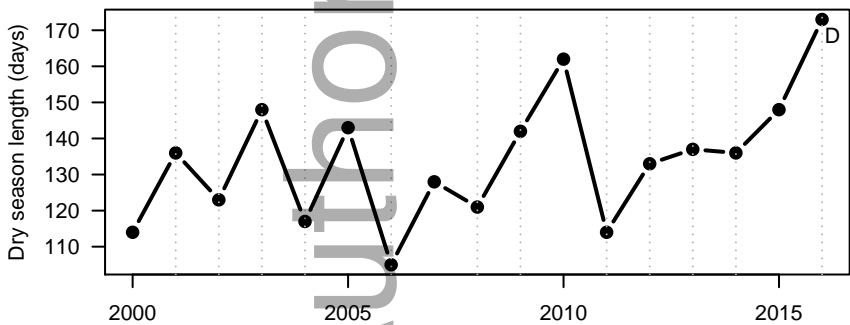
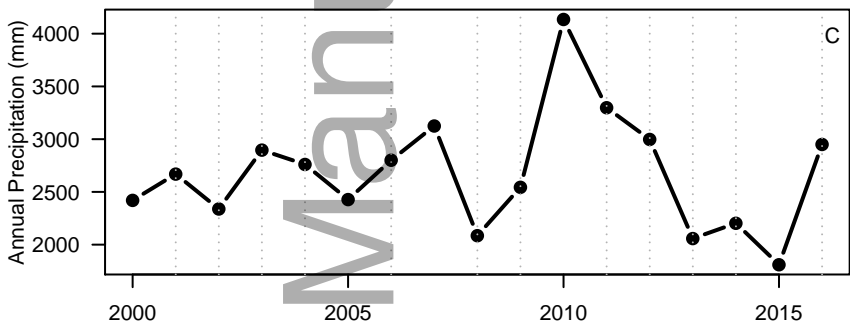
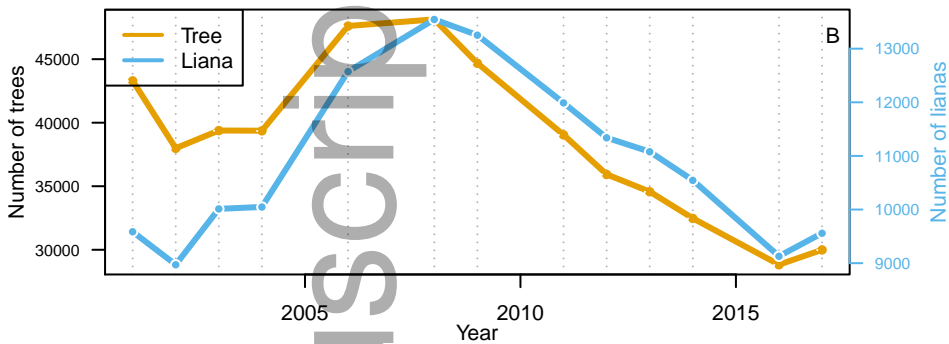
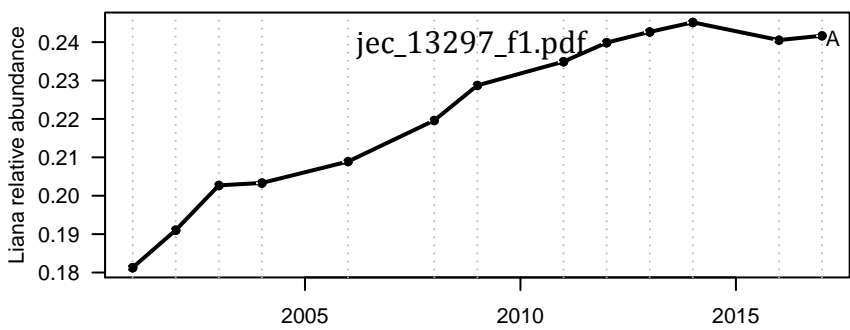
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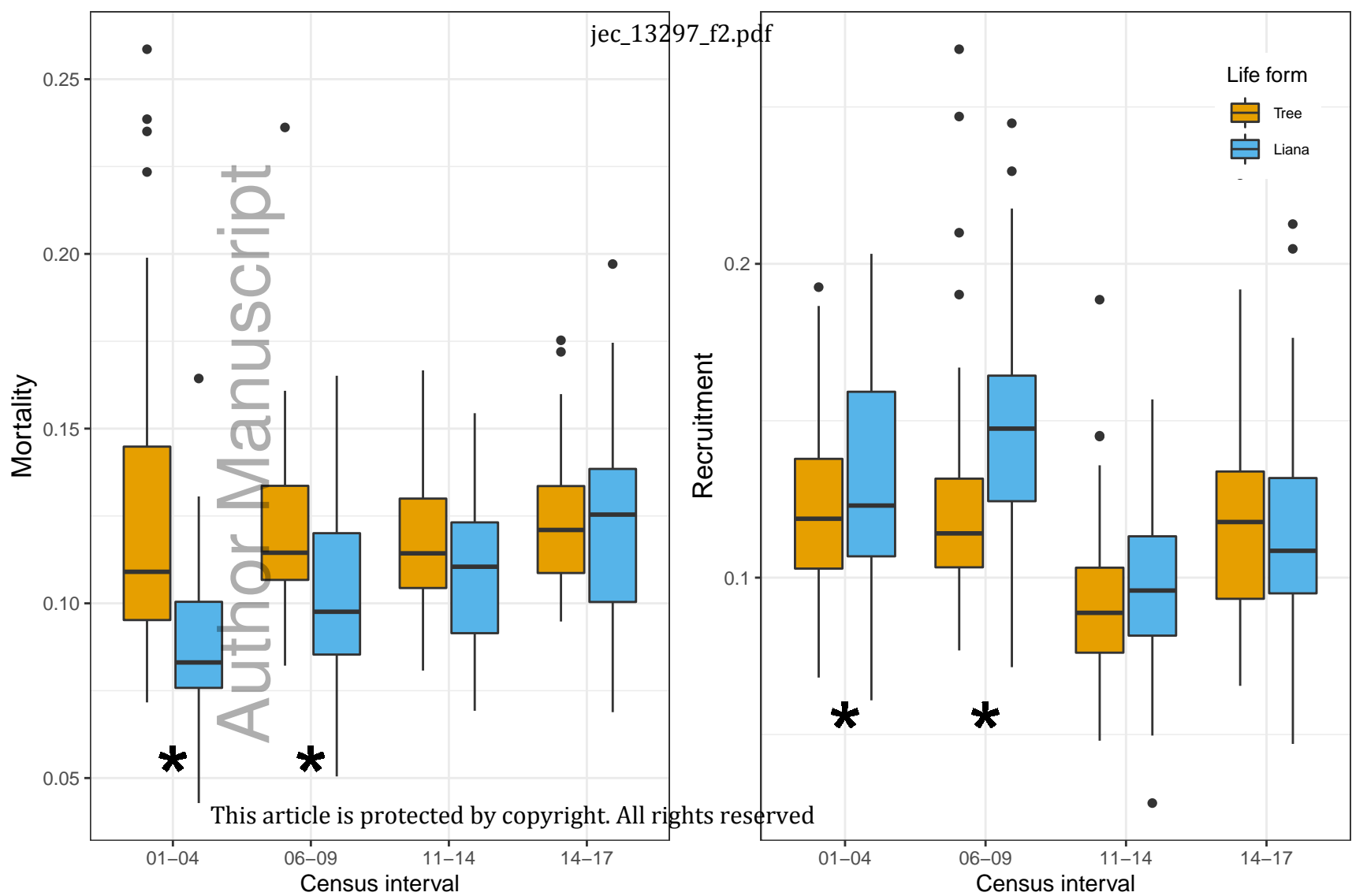
565 **Figure 2.** Boxplot showing mortality and recruitment rates of liana seedlings vs. tree  
566 seedlings across four-time intervals calculated in 1-ha blocks of the Barro Colorado Island  
567 50-ha forest plot, Panama. Asterisks indicate significant differences ( $P < 0.05$ ) between lianas  
568 and trees for each interval.

569

570 **Figure 3.** Mortality and recruitment rates of liana and tree seedlings in dry plateau vs. wet  
571 habitats in the Barro Colorado Island 50-ha plot, Panama. Differences between lianas and  
572 trees in responses to habitat type were not significant ( $P < 0.05$ ).

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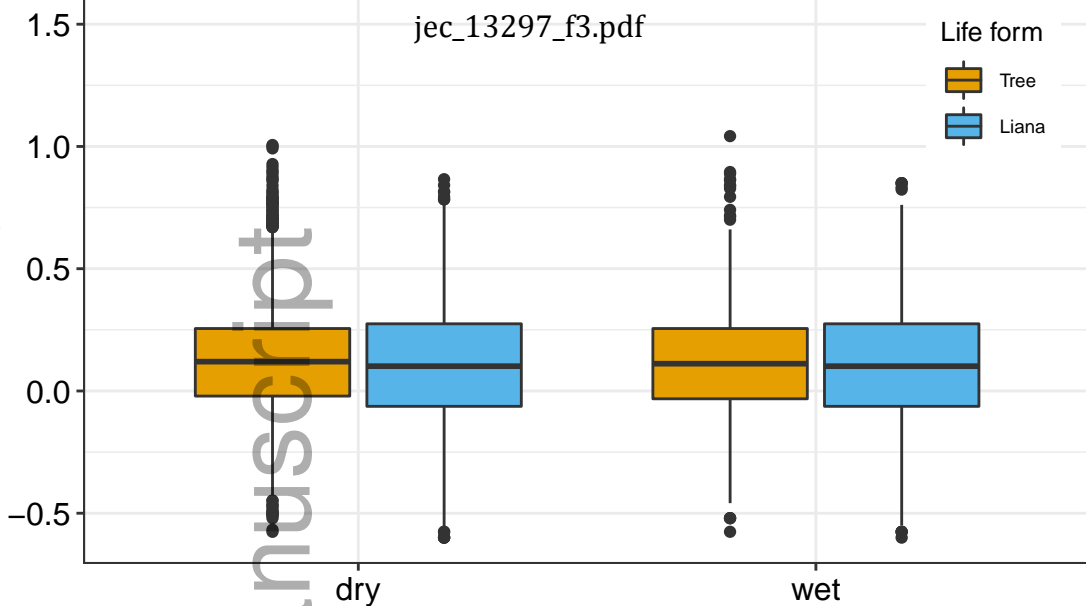


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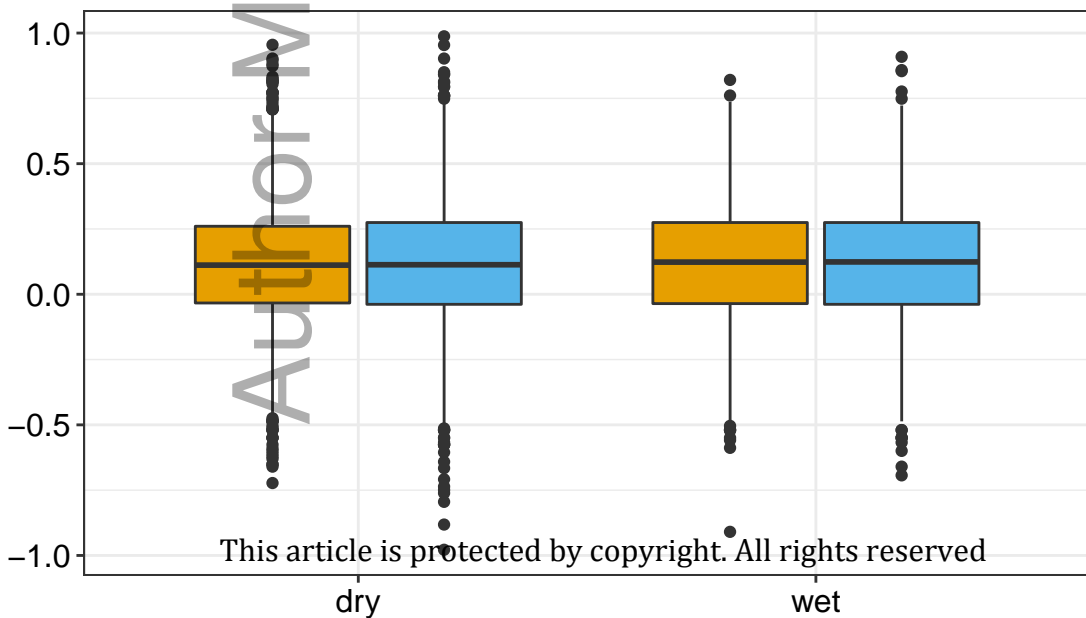
Life form



Mortality



Recruitment



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