



## Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall gradient

Weissflog, Anita; Markesteijn, Lars; Lewis, Owen T.; Comita, Liza S.; Engelbrecht, Bettina M. J.

### **Biotropica**

DOI:  
[10.1111/btp.12513](https://doi.org/10.1111/btp.12513)

Published: 01/03/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*  
Weissflog, A., Markesteijn, L., Lewis, O. T., Comita, L. S., & Engelbrecht, B. M. J. (2018). Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall gradient. *Biotropica*, 50(2), 302-311. <https://doi.org/10.1111/btp.12513>

#### **Hawliau Cyffredinol / General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

#### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23

LRH: Weissflog et al.

RRH: Herbivory and Predation across Rainfall Gradient

**Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall gradient**

Anita Weissflog<sup>1,2</sup>, Lars Markesteijn<sup>3,4,5</sup>, Owen T. Lewis<sup>5</sup>, Liza S. Comita<sup>3,6</sup>, Bettina M.J. Engelbrecht<sup>2,3</sup>

<sup>1</sup> Corresponding author: Anita1.Weissflog@uni-bayreuth.de; +49 30 4744950

<sup>2</sup> Department of Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), 95440 Bayreuth, Germany

<sup>3</sup> Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, República de Panama

<sup>4</sup> School of Environment, Natural Resources and Geography, Bangor University, Bangor, Gwynedd LL57 2DG, UK

<sup>5</sup> Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

<sup>6</sup> School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, U.S.A.

Received ; revision accepted .

24 One explanation for the extraordinarily high tree diversity of tropical lowland forests is that it is  
25 maintained by specialized natural enemies such as insect herbivores, which cause distance- and  
26 density-dependent mortality. Insect herbivory could also explain the positive correlation between  
27 tree species richness and rainfall if herbivory increases with rainfall, is higher on locally  
28 abundant versus rare species, and is not limited by predation pressure at wet sites. To test these  
29 predictions, insect herbivory and predation pressure on insect herbivores were quantified across a  
30 neotropical rainfall and tree species richness gradient, and herbivory was investigated in relation  
31 to local tree abundances. Insect herbivory on leaves (folivory) decreased strongly and  
32 significantly with rainfall, while predation pressure was significantly higher at the wetter site.  
33 Herbivores were more likely to attack abundant tree species, but herbivore damage levels were  
34 not related to tree species abundance. Insect folivores might contribute to local tree species  
35 coexistence in our system, but seem unlikely to drive the positive correlation between tree  
36 species richness and rainfall. The unexpected and contrasting patterns of herbivory and predation  
37 we observed support the need for a multi-trophic perspective to understand fully the processes  
38 contributing to diversity and ecosystem functioning.

39

40 Una explicación para la extraordinaria elevada diversidad de los árboles en los bosques  
41 tropicales de tierras bajas es que esta mantenida por enemigos naturales especializados como  
42 insectos herbívoros, los cuales causan mortalidad dependiente a la densidad y a la distancia. La  
43 herbivoría de los insectos podría explicar también la correlación positiva entre la riqueza de  
44 especies arbóreas y la precipitación, si la herbivoría se incrementa con la precipitación, es mayor  
45 en especies con alta abundancia local *versus* las especies poco comunes, y no está limitado por la  
46 presión de la predación en lugares húmedos. Para comprobar estas predicciones, la herbívora por

47 insectos y la presión de la predación en insectos herbívoros fueron cuantificadas, a lo largo de un  
48 gradiente de precipitación neotropical y de riqueza de especies, y a su vez herbivoría fue  
49 relacionada con las abundancias locales de 42 especies arbóreas de enfoque. La herbivoría de  
50 insectos en las hojas (folivoria) decrece considerable y significativamente con la precipitación,  
51 mientras que la presión por predación fue significativamente mayor en el sitio más húmedo. Con  
52 una mayor probabilidad los herbívoros atacaron las especies más abundantes, pero el nivel de  
53 daño por herbivoría no estaba relacionado con la abundancia de las especies arbóreas. En nuestro  
54 sistema, los insectos folívoros podrían contribuir a la coexistencia de las especies de árboles  
55 locales, pero parece improbable llevar a la correlación positiva entre la riqueza de especies y la  
56 precipitación. Los patrones inesperados y opuestos que se observaron de la herbivoría y la  
57 predación apoyan la necesidad de un punto de vista multitrófico para entender completamente el  
58 proceso que contribuye a la diversidad y funcionamiento del ecosistema.

59

60 **Key words:** community compensatory trend; Janzen-Connell; Panama; precipitation; species  
61 coexistence

62

63 **Tweetable abstract:** Climate alters herbivory: in wetter rainforests, insects cause less damage  
64 and have higher risk of predation

65 TROPICAL TREE SPECIES RICHNESS VARIES ENORMOUSLY ALONG ENVIRONMENTAL GRADIENTS  
66 (Pyke *et al.* 2001; Leigh *et al.* 2004; Davidar *et al.* 2005). Understanding how abiotic and biotic  
67 factors interact in shaping and maintaining gradients in tree species richness, composition, and  
68 ultimately ecosystem functioning is crucial to predict the susceptibility of forests to climate  
69 change and to mitigate socio-economic consequences of forest degradation.

70 One of the most prominent large-scale patterns in tropical plant diversity is the tendency  
71 for tree species richness to increase with rainfall and decrease with seasonality (Givnish 1999;  
72 Leigh *et al.* 2004; Davidar *et al.* 2005). Enhanced density- and distance-dependent insect  
73 herbivory in less seasonal and more humid forests has been suggested to contribute to this  
74 pattern (Janzen 1970; Connell 1971; Coley & Barone 1996; Leigh *et al.* 2004; Baltzer & Davies  
75 2012).

76 Specialized natural enemies such as insects can reduce the fitness of tree offspring  
77 growing close to conspecific adults, which serve as reservoirs for natural enemies, or at high  
78 conspecific offspring densities, which attract enemies via spatial resource concentration (Janzen  
79 1970; Connell 1971; Root 1973). Conspecific negative density dependence (CNDD) has been  
80 widely documented in tropical forests (Peters 2003; Comita *et al.* 2010, 2014; Paine *et al.* 2012;  
81 Bagchi *et al.* 2014) and is regarded as an important mechanism contributing to the maintenance  
82 of high alpha-diversity in tropical forests (Janzen 1970; Connell 1971; Paine *et al.* 2012; Bagchi  
83 *et al.* 2014).

84 An increase in insect herbivore pressure with rainfall has been suggested to explain  
85 higher tree species richness in wet than in dry tropical forests (Janzen 1970; Connell 1971; Coley  
86 & Barone 1996; Leigh *et al.* 2004; Baltzer & Davies 2012). Insect herbivores, as the most  
87 important primary consumers in tropical forests, consume up to ~70 percent of total leaf area

88 (Coley & Barone 1996) and have been proposed as major agents of distance- and density-  
89 dependent effects on plant species (Leigh *et al.* 2004; Brenes-Arguedas *et al.* 2009). Drier and  
90 more seasonal conditions could reduce insect abundance by increasing desiccation risk (Coley &  
91 Barone 1996; Givnish 1999; Connahs *et al.* 2011) and by causing resource limitation through  
92 decreased plant productivity (Coley & Barone 1996; Leigh *et al.* 2004; Richards & Coley 2007;  
93 Connahs *et al.* 2011). The hypothesized tendency for insect abundance to be higher in wetter,  
94 less seasonal forests is likely to translate into higher herbivory. However, empirical evidence is  
95 scarce and contradictory: insect abundance and herbivory have been shown to be higher (Brenes-  
96 Arguedas *et al.* 2009; Rodríguez-Castañeda 2013), lower (Coley & Barone 1996; Leigh *et al.*  
97 2004; Dirzo & Boege 2008) or similar (Baltzer & Davies 2012) in wet compared to dry tropical  
98 forests. Thus, it remains unclear whether insect herbivore pressure and CNDD do indeed  
99 increase with rainfall, and whether such a trend explains higher plant diversity in wetter tropical  
100 forests. In a recent meta-analysis, the strength of negative density- and distance-dependence was  
101 found to increase with increasing mean annual rainfall, suggesting that CNDD may contribute to  
102 increases in plant diversity along rainfall gradients (Comita *et al.* 2014). However, the degree to  
103 which this pattern is driven by insect herbivores or other mechanisms (e.g. pathogens,  
104 intraspecific competition) remains unknown.

105         The impact of CNDD may vary with the local abundance of tree species. Abundant  
106 species contribute more individuals per unit area, resulting in higher conspecific densities  
107 compared to rare species. Thus, natural enemies should have a higher chance to encounter, attack  
108 and build up populations if interacting with locally abundant species (Root 1973; Castagneyrol *et*  
109 *al.* 2014). In contrast, rare species that experience less herbivore damage would profit from a  
110 competitive advantage against abundant species, promoting species coexistence via a community

111 compensatory trend (Leigh *et al.* 2004; Norghauer *et al.* 2006). In order for insects to contribute  
112 to maintaining the high tree alpha-diversity of tropical forests via CNDD, the impact of insect  
113 herbivory must increase with tree species abundance in a community.

114         The effects of insect herbivores on plants can be moderated by their predators, which can  
115 effectively reduce insect herbivore populations (Purcell & Avilés 2008) and herbivory (Mazia *et*  
116 *al.* 2004; Stireman *et al.* 2005; Rodríguez-Castañeda 2013). Top-down control of herbivores has  
117 been suggested to increase from dry to wet tropical forests (Root 1973; Oksanen *et al.* 1981;  
118 Richards & Coley 2007). Higher plant productivity and species richness in wet, aseasonal forests  
119 may improve the fitness of predators by providing more complementary food and shelter options  
120 (Root 1973; Russell 1989). However, high predation pressure and the resulting lower abundance  
121 of insect herbivores in wetter forests would counter any tendency for more pronounced  
122 herbivore-imposed CNDD to act as a mechanism increasing tree species richness with rainfall.  
123 Despite the long-standing recognition of the impact of predators on herbivory (Coley & Barone  
124 1996), few studies have measured predation pressure across tropical rainfall gradients (Stireman  
125 *et al.* 2005; Connahs *et al.* 2011), and we are unaware of studies documenting trends in  
126 herbivory and predation simultaneously across multiple sites.

127         Overall, insect herbivory could explain the increase of tree species richness towards  
128 wetter tropical forests, if it increases with rainfall, is higher on locally abundant versus rare  
129 species, and is not limited by predation pressure at wet sites. Working in a network of sites  
130 across a steep gradient of rainfall and tree diversity in Panama, Central America, we quantified  
131 insect herbivory of tree saplings in six natural forest sites in relation to the local abundances of a  
132 total set of 42 focal tree species. At the same time, predation pressure on insect herbivores was  
133 assessed in one dry and one wetter forest along the same gradient. We tested the hypotheses that

134 (1) insect herbivory increases with rainfall, (2) insect herbivory increases with local tree and  
135 sapling abundance, and (3) predation pressure remains unchanged with rainfall.

136

## 137 **METHODS**

138

139 **FIELD SITES.** – The study was performed in forests in Central Panama, along a steep rainfall  
140 gradient. Within just 65 km, mean annual rainfall increases from the semi-deciduous forests at  
141 the Pacific side with ~1600 mm/ yr and a pronounced dry season from December to April (~129  
142 d), to the evergreen forests at the Caribbean side with ~ 4000 mm/ yr and a ~ 27 d shorter dry  
143 season (Engelbrecht *et al.* 2007). Tree richness ranges from 49 to 165 species per forest hectare  
144 along the gradient and is positively correlated with rainfall (Pyke *et al.* 2001). This study was  
145 conducted in six lowland 1-ha (100x100 m) forest sites, spanning almost the full range of  
146 variation in rainfall and tree species richness (Table 1). Adult trees and large saplings ( $\geq 1$  cm  
147 diameter at breast height, dbh), hereafter referred to as 'trees', were censused throughout each site  
148 (Condit 1998b, this study) and seedlings and small saplings ( $\geq 20$  cm tall and  $< 1$  cm dbh),  
149 hereafter 'saplings', in 400 1x1 m plots per 1-ha site (Comita *et al.* 2007 for census methods).  
150 Herbivory and predation pressure were assessed between late May and August 2014 during the  
151 rainy season, when insect abundance (Coley & Barone 1996) and predation pressure on insects  
152 (Molleman *et al.* 2016) is highest. Mean annual rainfall was calculated based on 20 – 80 year  
153 rainfall records in a network of rainfall stations (Steve Paton, pers. comm.).

154

155 **FOCAL SPECIES AND PLANT MATERIAL.** – We focused on shade-tolerant tree species, which  
156 contribute the majority of species and stems at these sites (Welden *et al.* 1991), to avoid

157 conflicting impacts of plant life history strategies and growth form. Species were selected to  
158 cover a wide range of abundances (based on census data from Condit 1998b and this study). The  
159 very rarest species, often represented by only one individual per hectare, were excluded to allow  
160 replication within sites. Specifically, species were included only if at least three saplings (50-200  
161 cm tall,  $\leq 1$  cm dbh) could be found in the understory (i.e. excluding tree-fall gaps) of a 1-ha site.  
162 We did not sample saplings located in conspecific clusters, i.e. more than three conspecific  
163 saplings standing in close proximity, to match scales of herbivory and abundance data. With  
164 these criteria, we selected 42 focal species (representing 35 genera, 21 families, and 12 orders;  
165 Table S1), of which some were sampled in more than one site amounting to 56 species-by-site  
166 combinations. Due to rapid species turnover across the gradient (Condit 1998a), focal species  
167 differed among sites. Only one species, *Lacistema aggregatum* P.J.Bergius (Rusby)  
168 (Malpighiales: Lacistemataceae), could be included in all six sites allowing for assessment of  
169 intraspecific variation in herbivory across the gradient. We measured 5-11 species per site with  
170 3-18 individuals per species (mean 11.54; Table S1), and a total of 680 saplings across all sites.

171

172 HERBIVORY MEASUREMENTS. – We focused on folivory and did not investigate more cryptic  
173 forms of insect herbivory (e.g., stem-boring, root-feeding). Five fully expanded, young, healthy,  
174 shaded and undamaged leaves per sapling were haphazardly chosen and tagged with numbered  
175 aluminum rings around the petioles. We focused on fully expanded leaves because herbivory on  
176 mature leaves can affect seedling survival negatively (Eichhorn *et al.* 2010). In contrast, plant  
177 mortality has been found to be unaffected by herbivory on young leaves (Eichhorn *et al.* 2010),  
178 although it is higher than herbivory on mature leaves (Coley & Barone 1996). Leaves with low  
179 levels of previous damage ( $< 2\%$  of leaf area) were included in cases where too few undamaged

180 leaves were found. Prior damage was measured with a millimeter grid. Leaves were collected to  
181 analyze herbivore damage about 50 days after tagging (minimum 46 d, maximum 58 d),  
182 alternating between drier and wetter sites. Missing leaves (3.29 % of all leaves) were not  
183 considered, as the cause of leaf loss could not be determined. Overall, 3209 leaves (3-5 leaves  
184 per sapling, mean 4.7) were collected.

185 Herbivory was assessed as the percentage leaf area removed relative to estimated total  
186 leaf area. Brown areas were considered as secondary damage and not included in the herbivory  
187 measurements. No damage of leaf miners or gall formers occurred on the tagged leaves during  
188 our sampling period. Leaves were covered and flattened with non-reflecting glass on a white  
189 background and photographed next to a 1 mm scale with a Nikon Coolpix P5000 camera.  
190 Photographs were analyzed for remaining and estimated total leaf area using ImageJ 1.46r  
191 (Rasband 2006). In the few cases where large parts of the leaf were missing and the original leaf  
192 outline could not be resolved, the median leaf area of all conspecific leaves was used as an  
193 estimate of the initial total leaf area. Any damage registered prior to the observation period was  
194 subtracted from the measured herbivory.

195

196 PREDATION PRESSURE. – Predation pressure was assessed in two of our sites (Metropolitano,  
197 Charco) in July 2014 using artificial caterpillars (hereafter 'caterpillars'; Howe *et al.* 2009). The  
198 caterpillars (30 x 2.5 mm, dark green color, Lewis Newplast) were odorless and non-toxic, and  
199 resembled undefended geometrid caterpillars. Members of the family Geometridae feed on  
200 woody plants and are among the most commonly observed caterpillars in forests worldwide,  
201 including our Metropolitano site (Connahs *et al.* 2011).

202 In each site, 100 caterpillars were placed individually on shaded tree recruits  $\leq 100$  cm

203 tall,  $\geq 100$  cm apart, with similar sized, entire, single leaves. Tree recruits were not identical to  
204 the saplings used for herbivory observations. Caterpillars were attached to the upper side of  
205 leaves with a small amount of quick-setting glue (Loctite Super Glue, Henkel) and examined for  
206 predator marks after 24 h, 48 h and 96 h ( $\pm 2$  h). Attacked caterpillars were collected. Fallen  
207 caterpillars without predator marks were reattached. The caterpillars and the experimental setup  
208 followed the protocols of a global citizen science project (Roslin *et al.* 2017).

209 Predator marks were clearly visible (Fig. S1) and classified into attacks by ants, birds,  
210 mammals, lizards, snails and slugs, and unidentified predators using reference pictures from the  
211 literature (e.g. Howe *et al.* 2009). Caterpillars showing several types of marks were scored as  
212 attacked caterpillars for each of the relevant predator groups. We excluded caterpillars that only  
213 showed marks by snails and slugs (which are not predators on real caterpillars) or unidentified  
214 marks (Charco: 34% of caterpillars, Metropolitano: 33%), and missing caterpillars (Charco 2%,  
215 Metropolitano 1%). Very high occurrence of snail and slug attacks (70%) required the exclusion  
216 of a third, high rainfall site (San Lorenzo), initially included in the study.

217

218 STATISTICAL ANALYSES. – Individual sapling herbivory was assessed as median herbivory of  
219 three to five leaves, because leaf herbivory data were heavily zero-inflated and non-normally  
220 distributed. For each sapling, we analyzed two measures of herbivory. First, we analyzed the  
221 probability of being attacked by herbivores by transforming sapling herbivory values into binary  
222 data (presence or absence of herbivory). Second, we quantified the amount of herbivory  
223 occurring on damaged individuals, including only saplings with a median herbivory greater than  
224 zero. We then tested whether the probability and amount of herbivory were significantly related  
225 to mean annual rainfall across sites, and to species' abundance within sites.

226 Abundance was analyzed separately for trees and saplings to test for potentially different  
227 effects of conspecific trees versus conspecific saplings on herbivory. We assessed species'  
228 abundances in three ways: (1) using counts of tree and sapling conspecifics within each 1-ha site;  
229 (2) transforming the counts of tree and sapling conspecifics within each 1-ha site into abundance  
230 ranks to account for variation in the total number of tree stems among sites. Abundance ranks  
231 were assigned across all tree species within a site, including non-focal species. The rarest species  
232 at each site, i.e. with fewest individuals within the respective 1-ha site, was assigned the lowest  
233 rank (=1); and (3) to improve comparability across our six sites and create a consistent  
234 abundance scale ranging from 0.01 (rare) to 1 (the most abundant species in each site), we  
235 standardized abundance ranks by dividing species' ranks by the total number of ranks per site.  
236 All three analyses yielded qualitatively similar results (Table S2, Fig. S2&3). We therefore  
237 present only the third abundance measure, which improves across-site comparability by  
238 controlling for absolute abundance, in the text.

239 We fitted a generalized linear model with logit link function to analyze the relationship of  
240 the probability of herbivory with mean annual rainfall. The relationships of the probability of  
241 herbivory with tree abundance and with sapling abundance were analyzed with separate  
242 generalized linear mixed-effects models with logit link function. Field site was included as a  
243 random effect.

244 We then analyzed the amount of herbivory occurring on damaged individuals. Species  
245 with fewer than three attacked individuals per site were excluded from analyses to ensure reliable  
246 median values. The correlation of species' median herbivory with mean annual rainfall, tree  
247 abundance, and sapling abundance was tested using non-parametric Spearman rank sum tests,  
248 while controlling for the effect of field site for the two latter correlations by calculating partial

249 correlation coefficients using the 'ppcor' package in R (Kim 2015).

250         Additionally, we analyzed how the probability and amount of herbivory varied with tree  
251 and sapling abundance within each site to check whether across-gradient patterns were mirrored  
252 in within-site patterns. We used generalized linear models with logit link function for probability  
253 of herbivory, and Spearman rank sum tests for amount of herbivory.

254         For *L. aggregatum*, the only species found at all six sites, we analyzed the probability of  
255 herbivory and individual median amount of herbivory as a function of mean annual rainfall, tree  
256 abundance, and sapling abundance (for the results of all three abundance methods see Table S2,  
257 Fig. S4&5), separately, as described above. Herbivory data from all six sites were considered in  
258 the binary analysis; in the continuous analysis, the wettest site was excluded, since only one  
259 individual showed a median herbivory above zero.

260         Predation pressure was calculated as the proportion of caterpillars attacked and compared  
261 between the two sites with an equal proportions test. We also compared predation pressure of  
262 each predator group separately between the sites, using generalized linear models with binomial  
263 errors and cloglog link to model the probability of a caterpillar showing a particular attack mark  
264 (e.g., characteristic of ants or birds). Since caterpillars were removed from the forest after the  
265 first sign of attack by any predator, we included a log(time) offset in the models to adjust for  
266 differences in the length of exposure to predators. All statistical analyses were performed using  
267 R v3.1.2 (R Core Team 2015).

268

## 269 **RESULTS**

270

271 The overall amount of leaf area removed by insect herbivores over the course of the study was

272 low (mean 1.06%, minimum 0%, maximum 85.53%; Table S1). Extrapolating mean annual  
273 herbivory (dividing mean herbivory by the days of exposure and multiplying the result by the  
274 365 days of a year), corresponds to a mean herbivory of about eight percent per year. In total,  
275 26.8 percent of the leaves (861 of 3209), and 61 percent of the saplings (416 of 680) experienced  
276 herbivory during our study.

277

278 HERBIVORY ACROSS THE GRADIENT. – Counter to our hypothesis, the probability of herbivory  
279 (Fig. 1A) and the amount of herbivory (Fig. 1C) decreased significantly with rainfall. For  
280 example, mean probability and median amount of herbivory were ~1.5 and 4.4 times higher,  
281 respectively, at the driest compared to the wettest site (Panama Pacifico: probability = 0.61,  
282 amount = 0.31%; San Lorenzo: probability = 0.42; amount = 0.07%).

283

284 HERBIVORY AND ABUNDANCE. – Our hypothesis of an increase in herbivory with tree species  
285 abundance was only partially supported. Analyzing all sites together, the probability of herbivory  
286 increased significantly with sapling abundance, but not with tree abundance (Fig. 2A&B).  
287 Moreover, the amount of herbivory was not related to either tree or sapling abundance (Fig.  
288 2C&D). Analyzing each site separately, we did not find a consistent relationship between species  
289 abundance and the probability or the amount of herbivory within each site, and in most cases  
290 there was no significant relationship (Table S3).

291

292 INTRASPECIFIC VARIATION IN HERBIVORY. – In *L. aggregatum*, neither the probability of  
293 herbivory (Fig. 1B), nor the amount of herbivory (Fig. 1D) were related to rainfall. The amount  
294 of herbivory was highest at a site with intermediate rainfall (Charco; Fig. 1D), in contrast to the

295 negative relationship between herbivory and rainfall observed across all species. The probability  
296 of herbivory was significantly positively related to the abundance of *L. aggregatum* saplings, but  
297 not trees across sites (Fig. 3A&B). The amount of herbivory of *L. aggregatum* was not  
298 significantly related to either tree or sapling abundance (Fig. 3C&D).

299

300 PREDATION PRESSURE. – Predation pressure, i.e. the overall proportion of attacked caterpillars  
301 after 4 days, was higher in the wetter site than in the dry site (wet: 54.7%, 35 of 64 caterpillars;  
302 dry: 22.7%, 15 of 66; Fig. 4A). Attack marks mainly originated from ants, birds, and mammals  
303 in descending frequency (Fig. 4B). For these different predator groups, the probability of attack  
304 was significantly higher in the wetter site than the dry site (Fig. 4B), for attack by ants (glm:  $z = -$   
305  $2.96$ ,  $P = 0.003$ ), with a similar, but non-significant, trend for attacks by birds ( $z = -1.896$ ,  $P =$   
306  $0.058$ ) and mammals ( $z = -1.915$ ,  $P = 0.055$ ). Only one caterpillar was attacked by a lizard.

307

## 308 **DISCUSSION**

309

310 Herbivory was overall low, equivalent to eight percent per year and comparable to values  
311 reported for tropical forests in some previous studies (Eichhorn *et al.* 2010; Baltzer & Davies  
312 2012; Table S1). Studies reporting higher herbivory rates usually defined herbivory more  
313 broadly, e.g. including lost leaves (e.g. Brenes-Arguedas *et al.* 2009) or discolored parts of the  
314 leaf (e.g. Plath *et al.* 2012), or used means instead of more conservative medians of individual  
315 herbivore damage levels (e.g. Plath *et al.* 2012). Nevertheless, even small amounts of herbivory  
316 on mature leaves can increase tree recruit mortality (Eichhorn *et al.* 2010) and reduce sapling  
317 growth, thereby delaying the age of first reproduction and enhancing the risk of mortality

318 (Marquis 1984; Sullivan 2003).

319

320 HERBIVORY ACROSS THE GRADIENT. – Counter to our prediction, both the probability and the  
321 amount of herbivory were lower in wetter forests (Fig. 1A&C). Insect herbivory can be  
322 suppressed at low annual rainfall (Brenes-Arguedas *et al.* 2009), a pattern hypothesized to result  
323 from insects experiencing an increased risk of desiccation, and/ or seasonal resource shortages in  
324 drier tropical forests (Givnish 1999). With ~1750 mm/ yr, the driest forest in our study was still  
325 relatively humid, with a dry season that may be too short to suppress herbivore pressure  
326 substantially. Nonetheless, the decreasing herbivory with increasing rainfall we report here  
327 agrees with several other studies showing higher herbivory rates on shade-tolerant plants in dry  
328 than in wet tropical forests (Coley & Barone 1996; Leigh *et al.* 2004; Dirzo & Boege 2008).  
329 Along the same gradient, Gaviria and Engelbrecht (2015) found evidence for a stronger impact  
330 of herbivory on plant establishment in a dry than a wet forest. Further support is provided by  
331 Novotny (2009), who questioned the idea of insect limitation through increased desiccation risk  
332 and presented evidence that insects have wider environmental tolerances than previously  
333 assumed.

334 Four main processes may contribute to higher herbivory in dry compared to wet sites.

335 First, more intense and more frequent rainfall events in wet forests may constrain insect  
336 abundance and activity simply through the physical force of heavy rain (Wirth & Leal 2001;  
337 Purcell & Avilés 2008). Second, a higher predation pressure, i.e. top-down control, on herbivores  
338 in wetter forests, as indicated by our results (Fig. 4A&B) and several other studies (Stireman *et*  
339 *al.* 2005; Richards & Coley 2007; Purcell & Avilés 2008) may decrease insect herbivore  
340 abundance (Richards & Coley 2007) and feeding activity (Mazía *et al.* 2004; Stireman *et al.*

341 2005; Rodríguez-Castañeda 2013) in wet forests (see below). Third, anti-herbivore defense of  
342 leaves may be more pronounced in wet forest tree species and may effectively deter insect  
343 herbivores (Coley & Barone 1996; Julian Gaviria & Bettina M.J. Engelbrecht, pers. comm.).  
344 Deciduous, dry forest trees produce short-lived leaves (Santiago *et al.*, 2004), which can easily  
345 be replaced due to lower light limitation and therefore do not need high chemical or mechanical  
346 protection against herbivores. In contrast, wet-forest trees invest more in their long-lived leaves,  
347 arming them with stronger structural defenses (Santiago *et al.*, 2004). Lastly, the Panamanian  
348 rainfall gradient is accompanied by an increase in tree species richness, which may decrease  
349 herbivory in wetter forests via the higher number of different plant stimuli in more diverse plant  
350 communities that may hinder host recognition for specialized herbivores (Tahvanainen & Root  
351 1972; Jactel & Brockerhoff 2007; Castagneyrol *et al.* 2014). Peters (2003) has shown that at a  
352 given density of conspecific trees, negative density dependent mortality decreased with the  
353 number of heterospecific trees in a tropical forest, attributing this effect to herd immunity.

354         Despite the relatively low number of leaves measured per species per site, our study is, to  
355 our knowledge, the most comprehensive analysis of insect herbivory in forest ecosystems across  
356 a rainfall gradient. While our data apply only to folivores, our results, together with earlier  
357 studies (Leigh *et al.* 2004; Mazía *et al.* 2004; Dirzo & Boege 2008), run counter to the theoretical  
358 prediction that insect herbivory increases with rainfall and is therefore a more important  
359 determinant of plant population dynamics and community composition in wetter tropical forests  
360 (Connell 1971; Givnish 1999; Leigh *et al.* 2004). CNDD may nevertheless contribute to high tree  
361 alpha-diversity via mechanisms other than herbivory, such as mortality from pathogens (Bagchi  
362 *et al.* 2014) or intraspecific competition for resources, or by acting more strongly on other life-  
363 stages (Zhu *et al.* 2015).

364

365 HERBIVORY AND ABUNDANCE. – The probability of herbivory increased with higher conspecific  
366 sapling abundance (Fig. 2B). However, the probability of herbivory was not related to tree  
367 abundance (Fig. 2A), and the amount of herbivory did not increase with abundance (Fig. 2C&D).  
368 In addition, when analyzing sites separately, we did not find a consistent relationship between  
369 abundance and herbivory (Table S3). Insect herbivores may respond to host leaf biomass rather  
370 than tree number. However, it is unlikely that in all our sites the rarest species had a similar or  
371 higher leaf biomass, i.e. larger and/ or more leaves, than the abundant species and such effects  
372 are therefore unlikely to have biased our results. We may have underestimated herbivory –  
373 abundance relationships, if insects respond to tree density at very small scales, because we  
374 avoided conspecific plant clusters in our sampling protocol. Nevertheless, our results indicate  
375 that the relationship between local plant abundance and insect herbivory is complex.

376         The higher probability of herbivory in tree species with higher sapling abundance  
377 supports our hypothesis and is in line with a rare species advantage facilitating species  
378 coexistence (Connell 1984). In abundant tree species, shorter distances between conspecific  
379 saplings may favor host-switching from one sapling to another, which has been suggested to  
380 benefit insect herbivores via intraspecific diet mixing (Plath *et al.* 2012; Hambäck *et al.* 2014). In  
381 contrast, saplings of rare species are likely to be more isolated from conspecifics, reducing the  
382 encounter rate and the probability of herbivory. Additionally, the diversity of cues emitted by  
383 plant species in tropical forests may cause a chemical masking of isolated tree individuals,  
384 further complicating host-finding for herbivores of rare species (Tahvanainen & Root 1972).  
385 Thus, a higher distance between individual plants combined with insect dispersal limitation may  
386 explain our result of the reduced probability of herbivory in rare species.

387           The lack of an increase in the amount of herbivory across abundance was, in contrast,  
388 unexpected and may seem at odds with a rare species advantage. A lower probability of  
389 herbivory in rare species alone may nevertheless allow the persistence of rare species within a  
390 community, if the saplings of rare species benefit enough from escape of herbivore attack to gain  
391 a competitive advantage compared to abundant species. The results thus point towards more  
392 complex processes influencing the relationship between host abundance and herbivory than  
393 expected.

394

395 INTRASPECIFIC VARIATION IN HERBIVORY. – In the one species studied across all six forest sites,  
396 *L. aggregatum*, the probability of herbivory increased with conspecific sapling abundance across  
397 sites, but was not related to conspecific tree abundance (Fig. 3A&B). Further, the amount of  
398 herbivory was not related to either tree or sapling abundance. Thus, the relationship of herbivory  
399 with abundance in *L. aggregatum* was similar to the pattern found in our across-species analyses.  
400 However, neither the probability nor the amount (Fig. 1B&D) of herbivory in *L. aggregatum* was  
401 related to rainfall, in contrast to the across-species pattern of decreasing herbivory with rainfall.  
402 A recent study of seed predation by insects across the same set of field sites in Panama also  
403 found no significant association between rainfall and levels of insect attack on fifteen focal plant  
404 species (Jeffs *et al.*, in revision). The divergent herbivory patterns in *L. aggregatum* imply that  
405 tree species may differ substantially in the relation of herbivory to rainfall. In addition to rainfall,  
406 other abiotic (e.g. nutrients, light) and biotic conditions (herbivore and plant community  
407 composition) vary across sites and, depending on species-specific ecological optima for plant  
408 and associated herbivore species, may strongly impact plant-insect interactions (Loranger *et al.*  
409 2013; Hambäck *et al.* 2014). These results indicate that studies focusing on single plant species

410 are unlikely to yield representative results and highlight the need for community level studies.

411

412 PREDATION PRESSURE. – The overall predation pressure and the probability of attack by each of  
413 the three main predator groups (ants, birds, mammals) were higher in the wetter than in the dry  
414 site (Fig. 4A&B). This trend is consistent with a previous study showing increasing predation  
415 with rainfall (Stireman *et al.* 2005), and with the notion that ants and birds are the most  
416 important predators of tropical insect herbivores (Tvardikova & Novotny 2012; Sam *et al.* 2015).  
417 Nevertheless, with only two sites, our results should be interpreted cautiously since the sites may  
418 differ in other ways that could influence predation rates (e.g., our drier site is located within an  
419 urbanized area, which may reduce predator abundances).

420         The relative importance of predator-imposed, top-down control compared to bottom-up  
421 regulation of herbivores has been hypothesized to increase with stability of climatic factors  
422 regulating ecosystem productivity, such as rainfall (enemies hypothesis; Root 1973; Oksanen *et*  
423 *al.* 1981). High and stable primary productivity is proposed to result in high and stable herbivore  
424 abundance throughout the year, which may result in a higher number of predators. In line with  
425 this prediction, Ferger *et al.* (2014) found that higher precipitation indirectly increases African  
426 insectivore bird richness, possibly mediated by an increase in vegetation complexity and biomass  
427 of invertebrates. Higher tree species richness in wetter forests may enhance the supply of  
428 alternative and complementary food sources, such as nectar, which may stabilize predator  
429 populations and improve their fitness (Russell 1989). Further, predators may be less sensitive to  
430 the physical effects of rainfall than herbivores due to their larger size and greater robustness.

431         Predation on larval stages poses a substantial mortality risk for herbivores and can  
432 additionally lead to behavioral changes, causing insect herbivores to spend relatively less time

433 feeding and more time sheltering (Mazía *et al.* 2004; Tvardikova & Novotny 2012). In  
434 combination, lethal and behavioral effects of predators have been shown to halve herbivory  
435 (Mazía *et al.* 2004). Increased predation pressure towards wetter forests is therefore likely to  
436 contribute to the unexpected decrease of herbivory with rainfall that we observed.

437

438 **CONCLUSION.** – To the best of our knowledge, our analysis based on data from six forest sites  
439 represents the most comprehensive investigation of insect herbivory in forest ecosystems across  
440 a rainfall gradient. Our data suggest that the increase in the probability of herbivory with local  
441 sapling abundance could facilitate tree species co-existence. It remains to be tested, however,  
442 whether the lower probability of herbivory in rare tree species is indeed translated into a  
443 competitive advantage.

444         We did not find support for the prediction that higher insect herbivory contributes to the  
445 increase in tree species richness with rainfall across the Isthmus of Panama. Rather, herbivory  
446 strongly decreased with rainfall, which may be at least partly explained by higher predation  
447 pressure in wetter forests. Our study highlights the need to incorporate multiple trophic levels  
448 when assessing the factors contributing to patterns of species richness.

449

450 **Acknowledgements:** We thank David Brassfield, Blexein Conteras, Carlos Green, and Roni  
451 Saenz for help with sapling identification in the field. Anna Pike, Tom Lewis, Lily Lewis, and  
452 Joe Lewis assisted with caterpillar predation fieldwork. We thank the Spatial Foodweb Ecology  
453 Group from the University of Helsinki for providing standardized artificial caterpillars. The  
454 Smithsonian Tropical Research Institute (STRI) provided logistical support for the study, and the  
455 Autoridad Nacional de Ambiente (ANAM) granted research permits for fieldwork. We thank

456 Agencia Panamá Pacífico (APP) and David Roubik for special permission to work in their  
457 forests (private properties), and the Center for Tropical Forest Science of the Smithsonian  
458 Tropical Research Institute for providing data on tree abundances. Set up and censuses of the  
459 forest sites were supported by the Ohio State University, Yale University, and the UK National  
460 Environment Research Council (standard grant NE/J011169/1 to OTL).

461

462 **Conflict of Interest:** The authors declare that they have no conflict of interest.

463

464 **Data availability:** The data used in this study are archived at the Dryad Digital Repository ().

465

466 **Literature cited:**

467 BAGCHI, R., GALLERY, R.E., GRIPENBERG, S., GURR, S.J., NARAYAN, L., ADDIS, C.E.,  
468 FRECKLETON, R.P., LEWIS, O.T. 2014. Pathogens and insect herbivores drive rainforest  
469 plant diversity and composition. *Nature* 506: 85-88. doi: [10.1038/nature12911](https://doi.org/10.1038/nature12911)

470 BALTZER, J.L., DAVIES, S.J. 2012. Rainfall seasonality and pest pressure as determinants of  
471 tropical tree species' distributions. *Ecol Evol* 2: 2682-2694. doi: [10.1002/ece3.383](https://doi.org/10.1002/ece3.383)

472 BONEBRAKE, T.C., BOGGS, C.L., MCNALLY, J.M., RANGANATHAN, J., EHRLICH, P.R. 2010.

473 Oviposition behavior and offspring performance in herbivorous insects: consequences of  
474 climatic and habitat heterogeneity. *Oikos* 119: 927-934. doi: [10.1111/j.1600-  
475 0706.2009.17759.x](https://doi.org/10.1111/j.1600-0706.2009.17759.x)

476 BRENES-ARGUEDAS, T., COLEY, P.D., KURSAR, T.A. 2009. Pests vs. drought as determinants of  
477 plant distribution along a tropical rainfall gradient. *Ecology* 90: 1751-1761. doi:  
478 [10.1890/08-1271.1](https://doi.org/10.1890/08-1271.1)

479 CASTAGNEYROL, B., JACTEL, H., VACHER, C., BROCKERHOFF, E.G., KORICHEVA, J. 2014. Effects  
480 of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J App*  
481 *Ecol* 51: 134-141. doi: [10.1111/1365-2664.12175](https://doi.org/10.1111/1365-2664.12175)

482 COLEY, P.D., BARONE, J.A. 1996. Herbivory and plant defenses in tropical forests. *Ann Rev Ecol*  
483 *Syst* 27: 305-335. doi: [10.2307/1942495](https://doi.org/10.2307/1942495)

484 COMITA, L.S., AGUILAR, S., PÉREZ, R., LAO, S., HUBBELL, S.P. 2007. Patterns of woody plant  
485 species abundance and diversity in the seedling layer of a tropical forest. *J Veg Sci* 18:  
486 163-174.

487 COMITA, L.S., ENGELBRECHT, B.M.J. 2014. Drought as a driver of tropical tree species  
488 regeneration dynamics and distribution patterns. *In* Coomes, D.A., Burslem, D.R.F.P.,  
489 Simonson, W. (Eds.) *Forests and Global Change*. Cambridge University Press.

490 COMITA, L.S., MULLER-LANDAU, H.C., AGUILAR, S., HUBBELL, S.P. 2010. Asymmetric density  
491 dependence shapes species abundances in a tropical tree community. *Science* 329:  
492 330-329. doi: [10.1126/science.1190772](https://doi.org/10.1126/science.1190772)

493 COMITA, L.S., QUEENBOROUGH, S.A., MURPHY, S.J., ECK, J.L., XU, K., KRISHNADAS, M.,  
494 BECKMAN, N., ZHU, Y. 2014. Testing predictions of the Janzen-Connell hypothesis: a  
495 meta-analysis of experimental evidence for distance- and density-dependent seed and  
496 seedling survival. *J Ecol* 102: 845-856. doi: [10.1111/1365-2745.12232](https://doi.org/10.1111/1365-2745.12232)

497 CONDIT, R. 1998a. Ecological implications of changes in drought patterns: shifts in forest  
498 composition in Panama. *Clim Chang* 39: 413-427. doi: [10.1023/A:1005395806800](https://doi.org/10.1023/A:1005395806800)

499 CONDIT, R. 1998b. Part 2. Field methods for a large forest plot. *In* Condit, R. (Ed.) *Tropical*  
500 *forest census plots*, pp. 15-99. Springer, Berlin.

501 CONNAHS, H., AIELLO, A., VAN BAELE, S., RODRÍGUEZ-CASTAÑEDA, G. 2011. Caterpillar

502 abundance and parasitism in a seasonally dry versus wet tropical forest of Panama. *J*  
503 *Trop Ecol* 27: 51-58. doi: [10.1017/S0266467410000568](https://doi.org/10.1017/S0266467410000568)

504 CONNELL, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in  
505 some marine animals and in rain forest trees. *In* Den Boer, P.J., Gradwell, G.R. (Eds.)  
506 *Dynamics of Population*, pp. 298-312. Pudoc, Wageningen.

507 CONNELL, J.H., TRACEY, J.G., WEBB, L.J. 1984. Compensatory recruitment, growth, and  
508 mortality as factors maintaining rain forest tree diversity. *Ecol Monogr* 54: 141-164. doi:  
509 [10.2307/1942659](https://doi.org/10.2307/1942659)

510 DAVIDAR, P., PUYRAVAUD, J.P., LEIGH, E.G. 2005. Changes in rain forest tree diversity,  
511 dominance and rarity across a seasonality gradient in the Western Ghats, India. *J*  
512 *Biogeogr* 32: 493-501. doi: [10.1111/j.1365-2699.2005.01165.x](https://doi.org/10.1111/j.1365-2699.2005.01165.x)

513 DIRZO, R., BOEGE, K. 2008. Patterns of herbivory and defense in tropical dry and rain forests. *In*  
514 Carson, W., Schnitzer, A. (Eds.) *Tropical Forest Community Ecology*, pp 63-78.  
515 Blackwell Science, West Sussex.

516 EICHHORN, M.P., NILUS, R., COMPTON, S.G., HARTLEY, S.E., BURSLEM, D.F.R.P. 2010.  
517 Herbivory of tropical forest tree seedlings correlates with future mortality. *Ecology* 91: 1092-  
518 1101. doi: [10.1890/09-0300.1](https://doi.org/10.1890/09-0300.1)

519 ENGELBRECHT, B.M.J., COMITA, L.S., CONDIT, R., KURSAR, T.A., TYREE, M.T., TURNER, B.L.,  
520 HUBBELL, S.P. 2007. Drought sensitivity shaped species distribution patterns in tropical  
521 forests. *Nature* 447: 80-82. doi: [10.1038/nature05747](https://doi.org/10.1038/nature05747)

522 FERGER, S.W., SCHLEUNING, M., HEMP, A., HOWELL, K.M., BÖHNING-GAESE, K. 2014. Food  
523 resources and vegetation structure mediate climatic effects on species richness of birds.  
524 *Global Ecol Biogeogr* 23: 541-549. doi: [10.1111/geb.12151](https://doi.org/10.1111/geb.12151)

525 GAVIRIA, J., ENGELBRECHT, B.M.J. 2015. Effects of drought, pest pressure and light availability  
526 on seedling establishment and growth: Their role for distribution of tree species across a  
527 tropical rainfall gradient. PloS ONE 10: e0143955. doi:  
528 [10.1371/journal.pone.0143955](https://doi.org/10.1371/journal.pone.0143955)

529 GIVNISH, T.J. 1999. On the causes of gradients in tropical tree diversity. J Ecol 87: 193-210. doi:  
530 [10.1046/j.1365-2745.1999.00333.x](https://doi.org/10.1046/j.1365-2745.1999.00333.x)

531 HAMBÄCK, P.A., INOUYE, B.D., ANDERSSON, P., UNDERWOOD, N. 2014. Effects of plant  
532 neighborhoods on plant-herbivore interactions: resource dilution and associational  
533 effects. Ecology 95: 1370-1383. doi: [10.1890/13-0793.1](https://doi.org/10.1890/13-0793.1)

534 HOWE, A., LÖVEI, G.L., NACHMAN, G. 2009. Dummy caterpillars as a simple method to assess  
535 predation rates on invertebrates in a tropical agroecosystem. Entomol Exp Appl 131: 325-  
536 329. doi: [10.1111/j.1570-7458.2009.00860.x](https://doi.org/10.1111/j.1570-7458.2009.00860.x)

537 JACTEL, H., BROCKERHOFF, E.G. 2007. Tree diversity reduces herbivory by forest insects. Ecol  
538 Lett 10: 835-848. doi: [10.1111/j.1461-0248.2007.01073.x](https://doi.org/10.1111/j.1461-0248.2007.01073.x)

539 JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. Am Nat 104:  
540 501-528.

541 JEFFS, C., KENNEDY, P., GRIFFITH, P., GRIPENBERG, S., MARKESTEIJN, L., LEWIS, O.T. In revision.  
542 Seed predation by insects across a tropical forest precipitation gradient. Ecol Entomol.

543 KIM, S. 2015. ppcor: An R Package for a Fast Calculation to Semipartial Correlation  
544 Coefficients. Communications for Statistical Applications and Methods 22: 665-674.

545 LEIGH, E.G., DAVIDAR, P., DICK, C.W., PUYRAVAUD, J.P., TERBORGH, J., TER STEEGE, H.,  
546 WRIGHT, S.J. 2004. Why do some tropical forests have so many species of trees? Biotropica  
547 36: 447-473. doi: [10.1111/j.1744-7429.2004.tb00342.x](https://doi.org/10.1111/j.1744-7429.2004.tb00342.x)

548 LORANGER, J., MEYER, S.T., SHIPLEY, B., KATTGE, J., LORANGER, H., ROSCHER, C., WIRTH, C.,  
549 WEISSER, W.W. 2013. Predicting invertebrate herbivory from plant traits: Polycultures  
550 show strong nonadditive effects. *Ecol* 94: 1499-1509. doi: [10.1890/12-0328.1](https://doi.org/10.1890/12-0328.1)

551 MARQUIS, R.J. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* 226: 537-539.  
552 doi: [10.1126/science.226.4674.537](https://doi.org/10.1126/science.226.4674.537)

553 MAZÍA, C.N., KITZBERGER, T., CHANETON, E.J. 2004. Interannual changes in folivory and bird  
554 insectivory along a natural productivity gradient in northern Patagonian forests.  
555 *Ecography* 27: 29-40. doi: [10.1111/j.0906-7590.2004.03641.x](https://doi.org/10.1111/j.0906-7590.2004.03641.x)

556 MOLLEMAN, F., REMMEL, T., SAM, K. 2016. Phenology of predation on insects in a tropical  
557 forest: temporal variation in attack rate on dummy caterpillars. *Biotropica* 48: 229-236. doi:  
558 [10.1111/btp.12268](https://doi.org/10.1111/btp.12268)

559 NORGHAUER, J.M., MALCOLM, J.R., ZIMMERMAN, B.L. 2006. Juvenile mortality and attacks by a  
560 specialist herbivore increase with conspecific adult basal area of Amazonian *Swietenia*  
561 *macrophylla* (Meliaceae). *J Trop Ecol* 22: 451-460. doi: [10.1111/j.1752-](https://doi.org/10.1111/j.1752-4598.2008.00035.x)  
562 [4598.2008.00035.x](https://doi.org/10.1111/j.1752-4598.2008.00035.x)

563 NOVOTNY, V. 2009. Beta diversity of plant-insect food webs in tropical forests: a conceptual  
564 review. *Insect Conserv Divers* 2: 5-9. doi: [10.1111/j.1752-4598.2008.00035.x](https://doi.org/10.1111/j.1752-4598.2008.00035.x)

565 OKSANEN, L., FRETWELL, S.D., ARRUDA, J., NIEMELÄ, P. 1981. Exploitation ecosystems in  
566 gradients of primary productivity. *Am Nat* 118: 240-261.

567 OTWAY, S.J., HECTOR, A., LAWTON, J.H. 2005. Resource dilution effects on specialist insect  
568 herbivores in a grassland biodiversity experiment. *J Anim Ecol* 74: 234-240. doi:  
569 [10.1111/j.1365-2656.2005.00913.x](https://doi.org/10.1111/j.1365-2656.2005.00913.x)

570 PAINE, C.E.T., NORDEN, N., CHAVE, J., FORGET, P.M., FORTUNEL, C., DEXTER, K.G., BARALOTO,

571 C. 2012. Phylogenetic density dependence and environmental filtering predict seedling  
572 mortality in a tropical forest. *Ecol Lett* 15: 34-41. doi: [10.1111/j.1461-0248.2011.01705.x](https://doi.org/10.1111/j.1461-0248.2011.01705.x)

573 PETERS, H.A. 2003. Neighbour-regulated mortality: the influence of positive and negative  
574 density dependence. *Ecol Lett* 6: 757-765. doi: [10.1046/j.1461-0248.2003.00492.x](https://doi.org/10.1046/j.1461-0248.2003.00492.x)

575 PLATH, M., DORN, S., RIEDEL, J., BARRIOS, H., MODY, K. 2012. Associational resistance and  
576 associational susceptibility: specialist herbivores show contrasting responses to tree stand  
577 diversification. *Oecologia* 169: 477-487. doi: [10.1007/s00442-011-2215-6](https://doi.org/10.1007/s00442-011-2215-6)

578 PURCELL, J., AVILÉS, L. 2008. Gradients of precipitation and ant abundance may contribute to the  
579 altitudinal range limit of subsocial spiders: insights from a transplant experiment. *Proc R*  
580 *Soc B* 275: 2617-2625. doi: [10.1098/rspb.2008.0582](https://doi.org/10.1098/rspb.2008.0582)

581 PYKE, C.R., CONDIT, R., AGUILAR, S., LAO, S. 2001. Floristic composition across a climatic  
582 gradient in a neotropical lowland forest. *J Veg Sci* 12: 553-566. doi: [10.2307/3237007](https://doi.org/10.2307/3237007)

583 R CORE TEAM. 2015. R: A language and environment for statistical computing. R Foundation  
584 for Statistical Computing. Vienna, Austria.

585 RASBAND, W. 2006. ImageJ 1.36b. National Institutes of Health, Bethesda, MD.

586 RICHARDS, L.A., COLEY, P.D. 2007. Seasonal and habitat differences affect the impact of food  
587 and predation on herbivores: a comparison between gaps and understory of a tropical  
588 forest. *Oikos* 116: 31-40. doi: [10.1111/j.2006.0030-1299.15043.x](https://doi.org/10.1111/j.2006.0030-1299.15043.x)

589 RODRÍGUEZ-CASTAÑEDA, G. 2013. The world and its shades of green: a meta-analysis on trophic  
590 cascades across temperature and precipitation gradients. *Glob Ecol Biogeogr* 22: 118-  
591 130. doi: [10.1111/j.1466-8238.2012.00795.x](https://doi.org/10.1111/j.1466-8238.2012.00795.x)

592 ROOT, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats:  
593 The fauna of collards (*Brassica Oleracea*). *Ecol Monogr* 43: 95-124. doi:

594 [10.2307/1942161](https://doi.org/10.2307/1942161)

595 ROSLIN, T., HARDWICK, B., NOVOTNY, V., ET AL. 2017. Higher predation risk for insect prey  
596 at low latitudes and elevations. *Science* 356: 742-744. doi:[10.1126/science.aaj1631](https://doi.org/10.1126/science.aaj1631)

597 RUSSELL, E.P. 1989. Enemies Hypothesis: A Review of the Effect of Vegetational Diversity on  
598 Predatory Insects and Parasitoids. *Env Entomol* 18: 590-599.

599 SAM, K., KOANE, B., NOVOTNY, V. 2015 Herbivore damage increases avian and ant predation of  
600 caterpillars on trees along a complete elevational forest gradient in Papua New Guinea.  
601 *Ecography* 38: 293-300. doi: [10.1111/ecog.00979](https://doi.org/10.1111/ecog.00979)

602 SANTIAGO, L.S., KITAJIMA, K., WRIGHT, S.J., MULKEY, S.S. 2004 Coordinated changes in  
603 photosynthesis, water relations and leaf nutritional traits of canopy trees along a  
604 precipitation gradient in lowland tropical forest. *Oecologia* 139: 495-502. doi:  
605 [10.1007/s00442-004-1542-2](https://doi.org/10.1007/s00442-004-1542-2)

606 STIREMAN III, J.O., DYER, L.A., JANZEN, D.H., ET AL. 2005. Climatic unpredictability and  
607 parasitism of caterpillars: implications of global warming. *PNAS* 102: 17384-17387. doi:  
608 [10.1073/pnas.0508839102](https://doi.org/10.1073/pnas.0508839102)

609 SULLIVAN, J.J. 2003. Density-dependent shoot-borer herbivory increases the age of first  
610 reproduction and mortality of neotropical tree saplings. *Oecologia* 136: 96-106. doi:  
611 [10.1007/s00442-003-1233-4](https://doi.org/10.1007/s00442-003-1233-4)

612 TAHVANAINEN, J.O., ROOT, R.B. 1972. The influence of vegetational diversity on the population  
613 ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae).  
614 *Oecologia* 10: 321-346. doi: [10.1007/BF00345736](https://doi.org/10.1007/BF00345736)

615 TVARDIKOVA, K., NOVOTNY, V. 2012. Predation on exposed and leaf-rolling artificial caterpillars  
616 in tropical forests of Papua New Guinea. *J Trop Ecol* 28: 331-341. doi:

617 [10.1017/S0266467412000235](https://doi.org/10.1017/S0266467412000235)

618 WELDEN, C.W., HEWETT, S.W., HUBBELL, S.P., FOSTER, R.B. 1991. Sapling survival, growth,  
619 and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* 72: 35-50. doi:  
620 [10.2307/1938900](https://doi.org/10.2307/1938900)

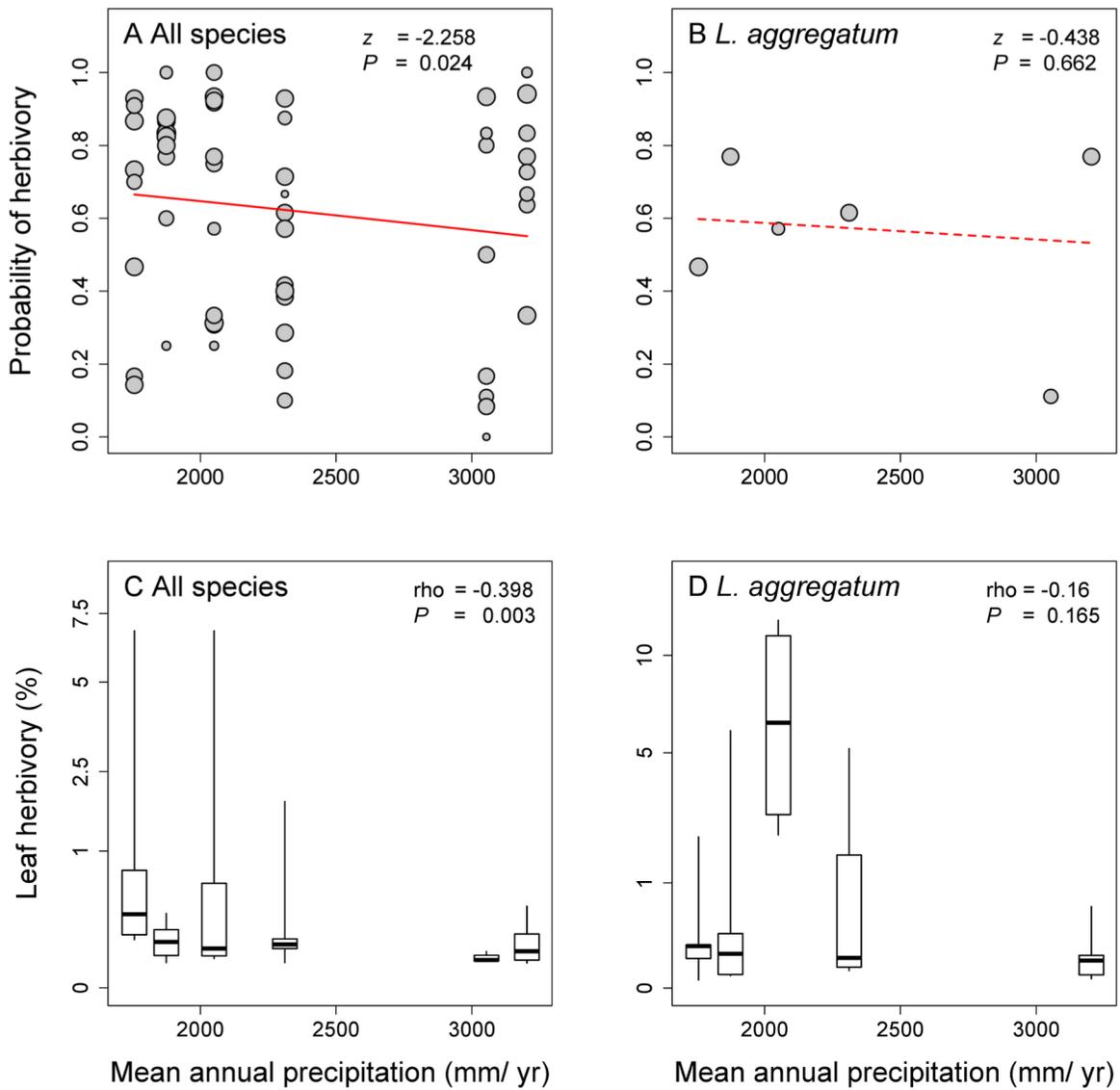
621 WIRTH, R., LEAL, I.R. 2001. Does rainfall affect temporal variability of ant protection in  
622 *Passiflora coccinea*? *Ecoscience* 8: 450-453.

623 ZHU, Y., COMITA, L.S., HUBBELL, S.P., MA, K. 2015. Conspecific and phylogenetic density-  
624 dependent survival differs across life stages in a tropical forest. *J Ecol* 103: 957-966. doi:  
625 [.1111/1365-2745.12414](https://doi.org/10.1111/1365-2745.12414)

626 TABLE 1 Study sites (1-ha), their coordinates, mean annual rainfall, and number of woody  
 627 species with stems  $\geq 1$  cm dbh (Condit 1998b and this study) and small saplings ( $\geq 20$  cm tall, <  
 628 1 cm dbh).

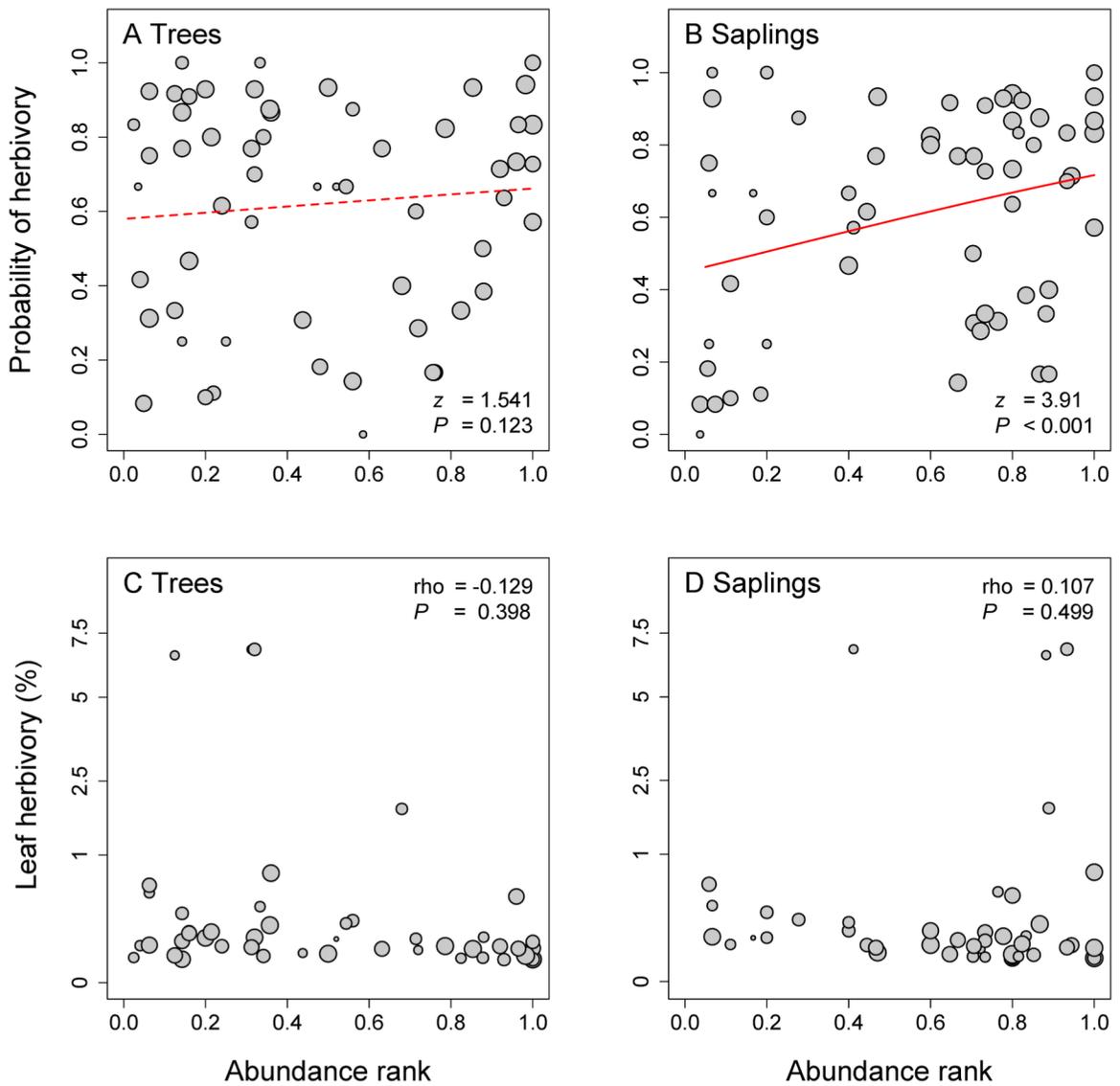
<b>Forest site</b>	<b>Location</b>	<b>Rainfall [mm/ yr]</b>	<b>Species No. (<math>\geq 1</math> cm dbh)</b>	<b>Species No. (<math>&lt; 1</math> cm dbh)</b>
Panama Pacifico	8°56'36.60"N 79°36'5.52"W	1756	74	46
Metropolitano	8°59'40.52"N 79°32'34.80"W	1874	47	33
Charco	9°5'2.58"N 79°39'48.24"W	2050	82	53
Pipeline Road	9°9'23.40"N 79°44'39.12"W	2311	130	79
Santa Rita	9°20'8.08"N 79°46'50.67"W	3053	201	108
San Lorenzo	9°16'51.13"N 79°58'28.92"W	3203	161	65

629 FIGURE 1 Relationship of (A, B) mean probability and (C, D) species median percentage of  
 630 insect herbivory with rainfall. Data are shown for (A, C) the full set of 42 tree species and for (B,  
 631 D) only *Lacistema aggregatum*. Point sizes reflect the (A, C) number of individuals measured  
 632 per plant species and the (B, D) the number of individuals per site. (A, B) Lines give results of  
 633 logistic regressions (continuous and dashed for significant and non-significant results,  
 634 respectively). (C, D) Results of Spearman rank sum tests are shown.



635

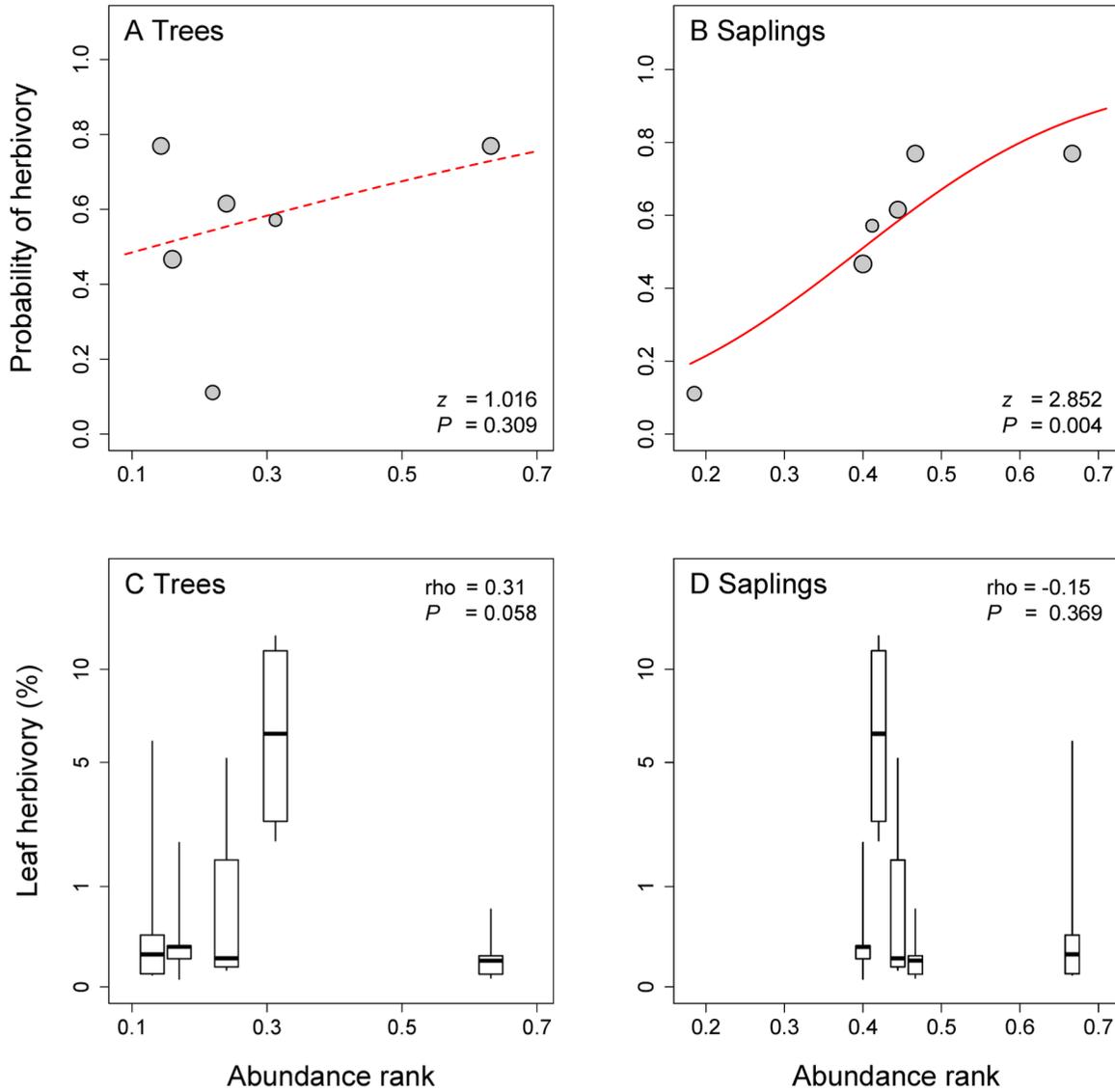
636 FIGURE 2 Relationship of (A, B) species' mean probabilities of herbivory and (C, D) median  
 637 amount of herbivory with (A, C) species tree and (B, D) sapling abundance ranks. Higher ranks  
 638 indicate higher individual numbers. Point sizes reflect the number of individuals measured per  
 639 plant species. Results from (A, B) logistic regressions and (C, D) Spearman rank sum tests are  
 640 given.



641

642

643 FIGURE 3 Probability of (A, B) leaf herbivory and (C, D) amount of herbivory for saplings of  
 644 *Lacistema aggregatum* in relation to (A, C) tree and (B, D) sapling abundance rank. (A, B) Point  
 645 sizes reflect the number of individuals measured per site. (A, B) Lines give results of logistic  
 646 regressions. (C, D) Results of Spearman rank sum tests are presented.

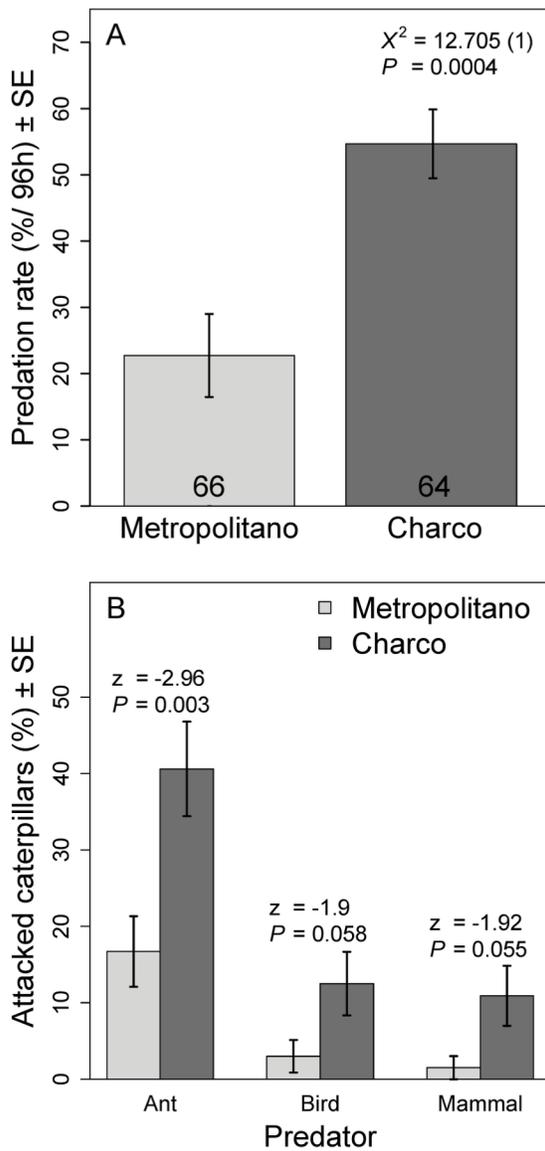


647

648

649

650 FIGURE 4 Predation pressure on artificial caterpillars in a drier (Metropolitano; 1874 mm/ yr)  
 651 and a wetter (Charco; 2050 mm/ yr) tropical forest. Shown is (A) the proportion of caterpillars  
 652 attacked after 96 hours of exposure and the result of an equal proportions test, and (B) the  
 653 proportion of caterpillars showing attack marks of three main predator groups and the results of  
 654 generalized linear models.



655