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LRH: Weissflog et al.

RRH: Herbivory and Predation across Rainfall Gradient

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

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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 (≥ 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 (≥ 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, ≤ 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 ≤ 100 cm

203 tall, ≥ 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 (± 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

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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:**

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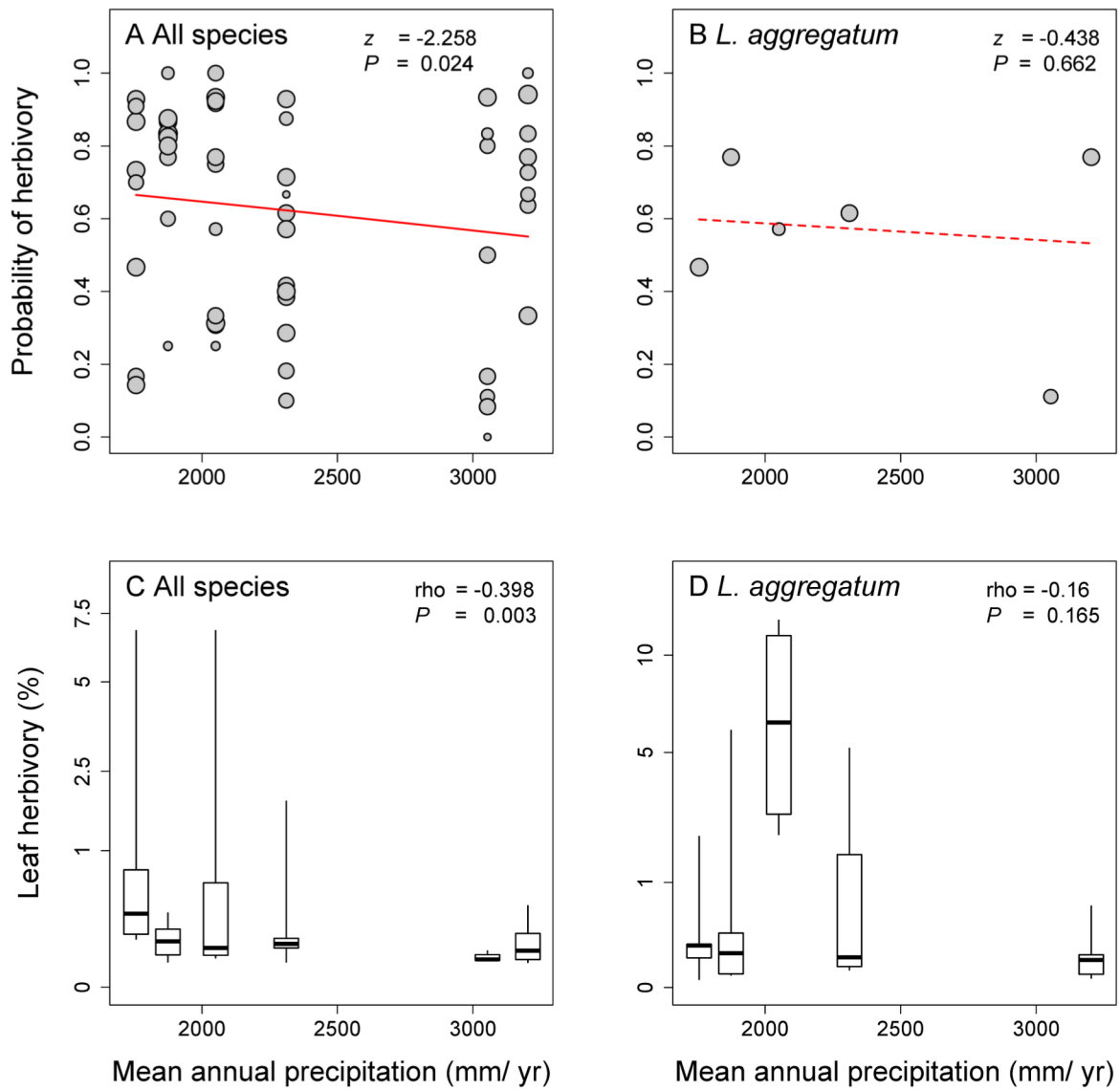
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626 TABLE 1 Study sites (1-ha), their coordinates, mean annual rainfall, and number of woody
 627 species with stems ≥ 1 cm dbh (Condit 1998b and this study) and small saplings (≥ 20 cm tall, <
 628 1 cm dbh).

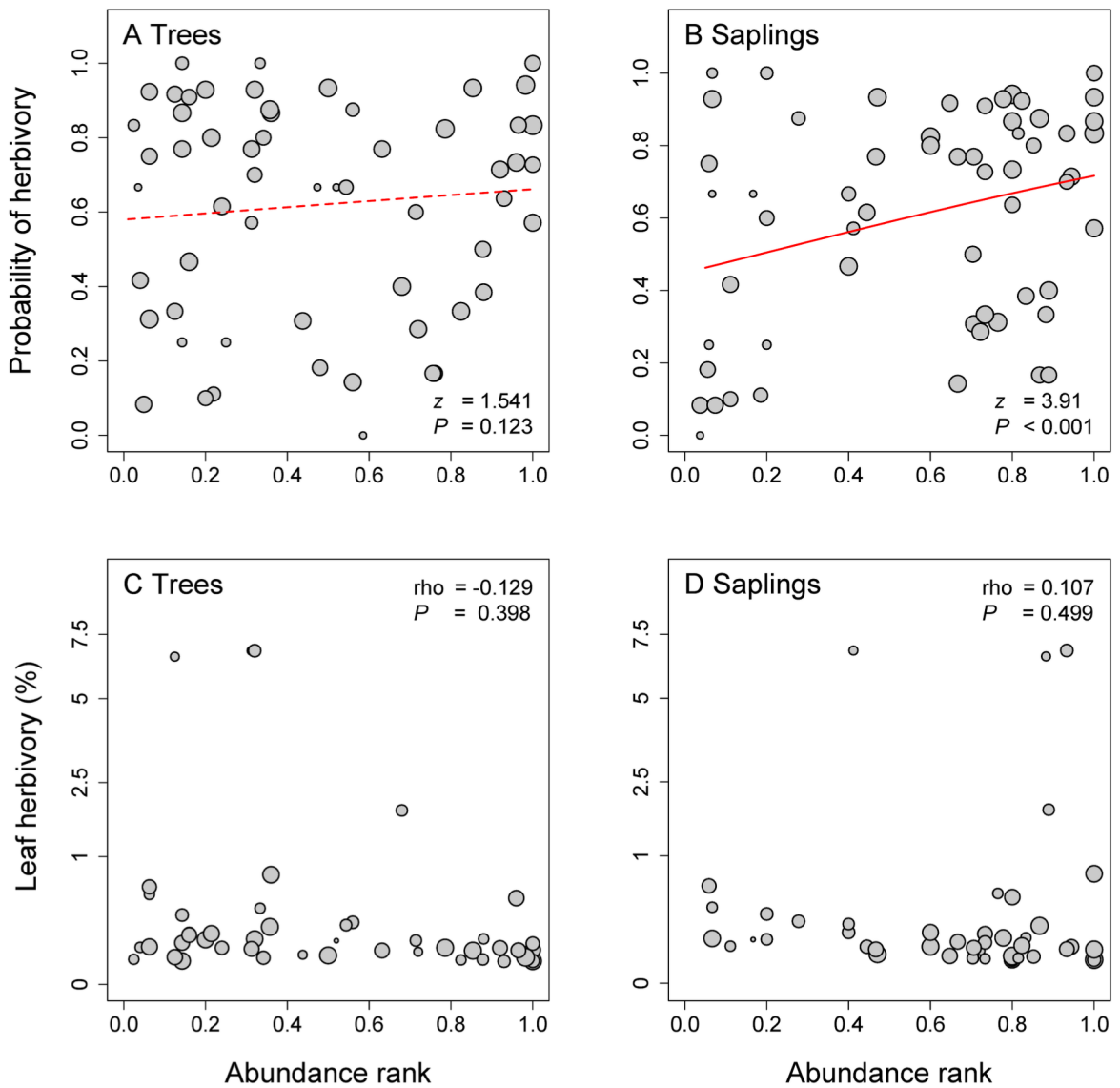
Forest site	Location	Rainfall [mm/ yr]	Species No. (≥ 1 cm dbh)	Species No. (< 1 cm dbh)
Panama Pacifico	8°56'36.60"N 79°36'5.52"W	1756	74	46
Metropolitano	8°59'40.52"N 79°32'34.80"W	1874	47	33
Charco	9°5'2.58"N 79°39'48.24"W	2050	82	53
Pipeline Road	9°9'23.40"N 79°44'39.12"W	2311	130	79
Santa Rita	9°20'8.08"N 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.



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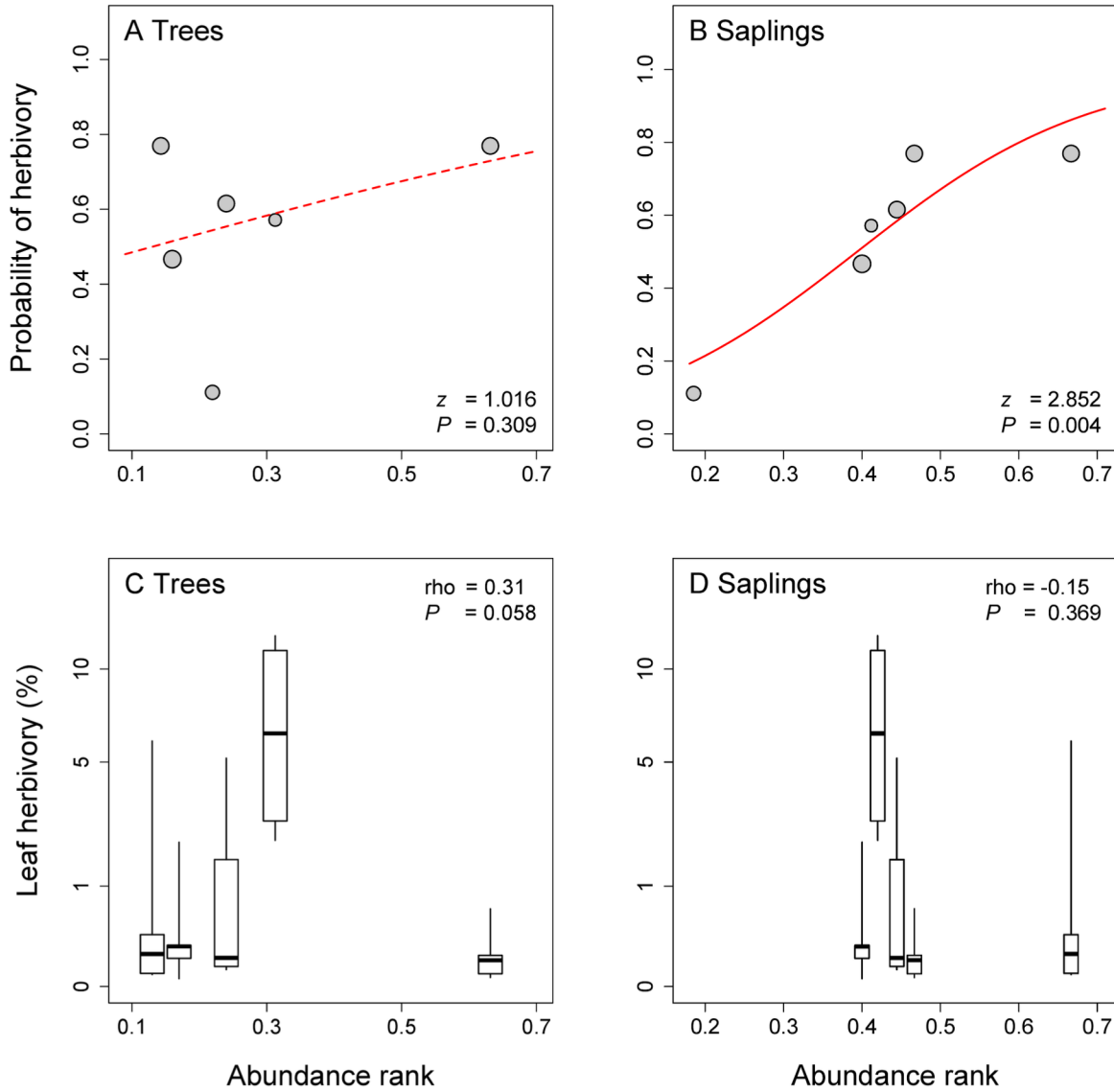
636 FIGURE 2 Relationship of (A, B) species' mean probabilities of herbivory and (C, D) median
637 amount of herbivory with (A, C) species tree and (B, D) sapling abundance ranks. Higher ranks
638 indicate higher individual numbers. Point sizes reflect the number of individuals measured per
639 plant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



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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.

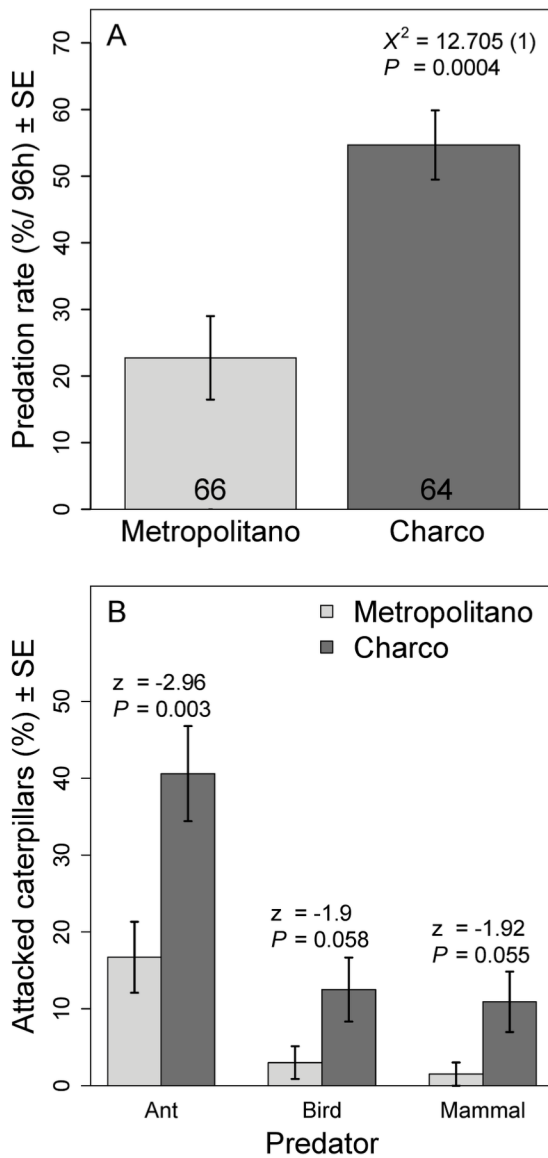


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650 FIGURE 4 Predation pressure on artificial caterpillars in a drier (Metropolitano; 1874 mm/ yr)
 651 and a wetter (Charco; 2050 mm/ yr) tropical forest. Shown is (A) the proportion of caterpillars
 652 attacked after 96 hours of exposure and the 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.



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