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1 **Desiccation resistance traits predict freshwater invertebrate survival and community**
2 **response to drought scenarios in a Neotropical ecosystem**

3

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22

23

24 **Abstract**

25 The intensification of dry seasons is a major threat to freshwater biodiversity in Neotropical
26 regions. Little is known about resistance to drying stress and the underpinning traits in
27 Neotropical freshwater species, so we don't know whether desiccation resistance allows to
28 anticipate shifts in biological diversity under future climate scenarios. Here, we used the
29 aquatic invertebrates that live in the rainwater-filled leaves of tank bromeliads, to examine the
30 extent to which desiccation resistance of species measured in the laboratory predicts
31 community response to drought intensification in nature. We measured desiccation resistance
32 in 17 invertebrate species (>90% of the biomass usually found in bromeliads of French
33 Guiana) by recording the median lethal time (LT50) of experimental populations exposed to
34 controlled conditions of residual moisture. In the field, we placed rainshelters above tank
35 bromeliads to emulate drought scenarios ranging from the ambient norm to IPCC scenarios
36 and extreme events, and we recorded the response of functional community structure. LT50
37 ranged from 4.18 to 19.06 days, and was related to cuticle content and dry body mass. Among
38 other functional indicators that represent strategies to optimize resource use under stressful
39 conditions (e.g., habitat use, trophic specialization), LT50 was the best predictor of
40 community structure responses along a gradient of emulated drought intensities. Therefore,
41 species' LT50s measured under laboratory conditions can be used to forecast aquatic
42 community response to drying stress in nature. Anticipating how species will cope with
43 drought has never been more important for environmental managers to support climate
44 change adaptation. We show that desiccation resistance in freshwater invertebrates is a key
45 indicator of potential population size and local-global range shifts, and this could be
46 especially true in the Neotropics where species have narrow physiological tolerances for
47 climatic variation.

48 **Keywords:** climate change; functional traits; LT50; macroinvertebrates; rainforests

49 **1. Introduction**

50 Drought is currently a major threat to biodiversity and ecosystem functioning (IPCC,
51 2013; Srivastava et al. 2020a), notably in tropical regions where a decrease in water
52 availability is expected to exacerbate extinctions (Hugueny et al., 2011; Oberdorff et al.,
53 2015). Understanding and anticipating how species will cope with droughts has never been
54 more important as the urgency to better predict future ecosystem functioning grows. The
55 autecology of species and the resulting trait-based framework could provide relevant
56 functional indicators for scientists to predict individual- to ecosystem-level responses to
57 climate change, and for environmental managers to implement climate change adaptation
58 plans (Dias et al., 2013; Piano et al., 2019; Wieczynski et al., 2019; Schleuning et al., 2020).
59 The rationale is that the physiological, biological, behavioural, and ecological attributes of
60 species directly describe their interactions with the biotic and abiotic environment (Wilman et
61 al., 2014). In particular, species responses to drought events depend both on physiological
62 tolerance and resistance to desiccation (Pallarés et al., 2016), and on behavioural traits such as
63 avoidance or migration to refuge microhabitats that trigger rapid responses to unsuitable
64 conditions (Dézerald et al., 2015; Strachan et al., 2015). Assuming however that physiological
65 limitations are the most fundamental constraints on species distributions across spatial scales
66 (Kearney and Porter, 2009; Start et al., 2018), traits that confer physiological tolerance and/or
67 resistance to desiccation stress could be among the best indicators of biodiversity responses to
68 drought across ecosystems and regions of the tropics (Chown, 2012).

69 Invertebrates contribute disproportionately to the biodiversity of tropical regions,
70 where they play significant roles in multi-trophic processes and ecosystem functions (Ewers
71 et al., 2015). The desiccation tolerance of invertebrates (ability to withstand body water loss)
72 depends on the body water content, which influences water loss dynamics (Thorat and Nath,
73 2018). Desiccation resistance (ability to reduce water loss) is rather related to body size and

74 integumental permeability (Dias et al., 2013; Pallarés et al., 2017). Compared to their
75 temperate counterparts, the invertebrates found in tropical rainforests are expected to have
76 low tolerance-resistance to desiccation because they thrive in relatively stable conditions of
77 habitat humidity or hydrology (Gibbs et al., 2001; Hoffman et al., 2003). Yet, traits
78 underpinning sensitivity to drought among coexisting species and the consequences at
79 community level remain poorly documented, notably in freshwaters where responses to
80 drying stress play a primary role in the distribution of species at multiple spatial scales (Datry
81 et al., 2014; Pallarés al., 2016). Theory about local adaptation suggests that tolerance and
82 resistance traits could allow species to withstand modest to average drought intensities at the
83 active stage (Lake, 2011). Nevertheless, once drought intensifies, reconfigurations of
84 communities could occur if co-existing species were to respond asynchronously to desiccation
85 stress. These assumptions remain however untested, first because we lack established
86 relationships between species' desiccation tolerance-resistance traits and survival to drought
87 in tropical rainforests (see review in Thorat and Nath, 2018), and second because we don't
88 know which trait combinations are selected (or counter-selected) along a gradient of
89 increasing drought intensity in these ecosystems.

90 Assembling data on trait variation among coexisting species in rivers, lakes or
91 wetlands is however challenging, because of their very high taxonomic diversity. Natural
92 microcosms that host smaller numbers of co-evolved species in contained habitats form
93 relevant alternatives to test ecological hypotheses (Kitching, 2000; Srivastava et al., 2004).
94 Here, we focused on the aquatic invertebrates inhabiting tank bromeliads, a discrete
95 ecosystem that is commonly found across a wide array of Neotropical environments.
96 Bromeliads are flowering plants represented by 3403 species native to the Neotropics (Ulloa
97 et al., 2017). The leaves of tank-forming bromeliads are arranged in rosettes that trap water,
98 forming "freshwater islands" in a terrestrial matrix. Tank bromeliads collect rainwater and

99 detritus, providing a habitat for aquatic organisms ranging from bacteria to
100 macroinvertebrates. Detailed descriptions of the bromeliad macroinvertebrate fauna and
101 functional traits can be found in Frank & Lounibos (2009) and Céréghino et al. (2018).

102 To the best of our knowledge, there is nothing in the published literature about time to
103 death of freshwater invertebrate species submitted to standardized drying stress in tropical
104 ecosystems, so we don't know whether upscaling species' lethal times at community level
105 allows to anticipate shifts in community structure under future climate scenarios. Growth
106 rates measured under controlled hydrology have been used as a proxy to sensitivity to drought
107 of Neotropical aquatic insects (Amundrud and Srivastava, 2015). Although this approach
108 allows to rank species by sensitivity, it does not tell us how long species can withstand
109 absence of water, what traits predict time to death, and what drought intensity coexisting
110 invertebrates can survive within the range of current to predicted climate scenarios. This study
111 was designed to address these issues. Our experiments took place in French Guiana, the
112 epicentre of bromeliad radiation and a hotspot of biodiversity for bromeliad invertebrates.
113 First, we established species-specific sensitivity to drought as the median lethal time (LT50)
114 of experimental populations under controlled conditions of residual moisture in the
115 laboratory. We examined which morphological and anatomical attributes forming desiccation
116 tolerance and resistance traits (e.g., water content, cuticle content, body length, etc.) predict
117 LT50. Second, in order to test whether species-specific LT50s measured in the laboratory
118 predict community response to drought in nature, we used rainshelters placed above tank
119 bromeliads to emulate drought scenarios ranging from ambient conditions to IPCC scenarios
120 and extreme events in a field experiment, and we recorded the response of functional
121 community composition to these treatments. We upscaled LT50 (this study) as well as
122 ecological traits that describe the life history strategies of species (after Céréghino et al.,
123 2018) at community level, to explore co-variation between drought intensity and traits

124 constrained by the abundance of invertebrate species. We therefore asked: what traits indicate
125 sensitivity to drought in Neotropical aquatic invertebrates, and specifically, does desiccation
126 resistance of species measured under standardized laboratory conditions predict aquatic
127 community response to drought in nature?

128

129 **2. Methods**

130

131 *2.1. Study area*

132 This study was carried out in French Guiana from October 2018 to April 2019, near
133 the Petit-Saut Dam, Sinnamary (5°03'043"N, 53°02'046"W; elevation <80 m a.s.l.; Fig. 1).
134 French Guiana is an overseas region of France located on the north-eastern coast of South
135 America. About 96% of its surface area (83.534 km²) is covered by equatorial forest. The
136 climate is tropical moist with 3000 mm of annual precipitation, little seasonal variation in air
137 temperature (monthly average = 20.5-33.5°C), and a relative humidity between 70% and
138 100%. There is a major reduction in rainfall between September and November, and a shorter
139 and more irregular dry period in March.

140

141 *2.2. Lethal times and underpinning traits*

142 We sampled the two dominant bromeliad species in the study area, namely *Lutheria*
143 *splendens* and *Aechmea aquilega*. We used 10-mL micropipettes, with the end trimmed to
144 widen the aperture, to suck out the water and aquatic invertebrates from the leaf axils
145 (Dézerald et al., 2018). The bromeliad content was collected in plastic bottles and
146 immediately brought to the laboratory, where aquatic invertebrates were sorted alive and
147 identified to species or morphospecies (hereafter “species”). With the exception of a
148 crustacean and an annelid, these invertebrates were all aquatic insect larvae (the emerging

149 adult usually being terrestrial). The bromeliad invertebrate fauna in our study area comprised
150 33 species (see lists in Céréghino et al., 2011; Dézerald et al., 2015; Leroy et al., 2017).
151 About half of these species are rare (both in terms of occurrence and number of individuals),
152 so we were able to obtain individuals from 17 species in sufficient numbers to carry out our
153 observations (Table 1). These species however represented the dominant invertebrate orders
154 and families in Neotropical bromeliads in general (see Fig. 2 in Céréghino et al., 2018), and
155 >90% of the invertebrate biomass found in bromeliads of French Guiana (Leroy et al., 2017;
156 Dézerald et al., 2018). Prior to the experiment, invertebrates were acclimatized for 48h in
157 50mL Falcon® tubes filled with bromeliad water. Predators were fed *ad libitum* with prey
158 (mosquito larvae), detritivores were provided with leaf litter and fine particulate organic
159 matter collected in bromeliads. Invertebrate sorting and all observations were carried out in a
160 temperature-controlled room at 25°C under a natural circadian rhythm (day:night = 12:12h).

161 Our study of median lethal times (LT50) and desiccation tolerance-resistance traits
162 was based on the largest individuals of each species. We acknowledge that not all life-stages
163 of a species might be equally sensitive to a given disturbance (van der Lee et al., 2020), and
164 therefore, the trait and LT50 values reported in this work should be seen as potentials rather
165 than absolute values. Such individuals corresponded to the last instar of holometabolous
166 insects (e.g., instar IV in most Diptera), and to the largest individuals in a cohort in
167 heterometabolous insects (Odonata) and other invertebrates (Ostracoda, Annelida). Detailed
168 studies of invertebrate larval stages and population dynamics in bromeliads at our study site
169 can be found in Dézerald et al. (2017; 2018). For each species, individuals were isolated in
170 glass tubes (i.e., 1 individual per tube; tube diameter = 13.36 mm, height = 43.7 mm, volume
171 = 6.5 mL) covered with a mosquito net and containing a 1x3 cm folded piece of Whatman
172 paper n°1 dampened with 1 mL of filtered bromeliad water (to simulate residual moisture in a
173 leaf crevice). We usually used ca. 30 individuals per species for the trials, but only 10-12

174 suitable individuals were available for five infrequent species (see Table 1 for numbers). Each
175 tube was then inspected every day using magnifying glasses, to record the status of
176 individuals (dead vs. alive). Death was confirmed by the absence of movement when refilling
177 the tube with water. Daily observations for any given species continued until all individuals
178 died. In order to test for a potential “tube effect” on mortality (control), similar observations
179 were simultaneously conducted on the same number of individuals per species isolated in
180 tubes filled to their maximum capacity with filtered bromeliad water. A constant water
181 volume was maintained in the control tubes during the experiment. For each species, we
182 stopped the observations when mortality reached 100% in the treatment tubes, resulting in
183 right-censored data in the controls.

184 Desiccation tolerance and resistance traits for each species consisted in an average
185 value obtained from measurements of 30 last-instar individuals (Table 1). Body length (BL,
186 the longest length from mouth to anus, mm) was measured from pictures of the individuals
187 using Image J software. We used a microbalance (MX5; Mettler Toledo, Viroflay, France) to
188 quantify fresh mass (FM, mg), and dry mass (DM, mg) after oven-drying individuals at 60°C
189 for 48h. Water content (WC, %) was calculated as $((FM-DM)/FM) * 100$. To obtain the
190 cuticle dry mass (CM, mg), we adapted the protocol described in Sasso Porto et al. (2016).
191 Individuals were placed in a 10M potassium hydroxide – sodium hydroxide solution
192 (50%:50%) heated at 95°C in a water bath to dissolve the soft tissues (see also Harrison et al.,
193 2012). Incubation times ranged from 15 min to 1hr depending on the degree of chitinization.
194 Individuals were then transferred into 3-5% peroxide hydrogen (H₂O₂) at room temperature
195 for 20 minutes, and finally immersed in 70% boiling ethanol for 10 min. Cuticles were oven-
196 dried (60°C, 24hrs) and weighted. Cuticle content (CC, %) was calculated as $(CM/DM) *$
197 100. Though annelids have a very thin cuticle coating their external epithelium, the material

198 obtained following chemical treatments of *A. superterrenus* individuals was below detection
199 limits of the microbalance. We therefore arbitrarily set CC to 0 for *A. superterrenus*.

200

201 2.3. Community response to drought scenarios

202 The field experiment took place in a lowland rainforest plot nearby the Petit-Saut Dam,
203 where we extensively studied the bromeliad fauna and have a thorough grasp of the local
204 species pool (e.g., Dézerald et al., 2015; 2017; 2018). Based on vegetative traits (number of
205 leaves, plant canopy diameter, water holding capacity), we selected 120 *Lutheria splendens*
206 bromeliads of similar size. We used rainshelters placed over individual bromeliads
207 (transparent plastic tarpaulin as in Trzcinski et al., 2016) to emulate dry periods representing:
208 (i) the current norm (26 days, the average maximum number of consecutive days without
209 rainfall over the past 20 years for the study months in the area), (ii) IPCC prediction in the
210 area (current norm +40% = 37 consecutive dry days), (iii) an extreme event (the maximum
211 number of consecutive dry days observed over the past 20 years = 67 days), and (iv) an
212 extreme event +40% = 94 dry days. Each treatment had 30 replicates (bromeliads).
213 Treatments started from (iv) to (i) in rank order, so all bromeliads reached the end of their dry
214 period simultaneously. The environmental variables recorded were: drought treatment (the
215 number of consecutive days without rainfall), dry bromeliad days (the number of days a
216 bromeliad was completely dried out under a drought treatment), and water depth at the end of
217 the experiment (the average of two measurements in two well developed leaf axils, mm). The
218 water holding capacity of each bromeliad (V_{max} , maximum water volume in mL) was
219 calculated from an allometric relationship developed by us in anticipation of various
220 experiments that make use the bromeliad *L. splendens*. This relationship is based on actual
221 measurements of maximum water volume (overflow of a known water volume using a
222 graduate cylinder), number of leaves (NL) and plant canopy diameter (D) of 123 small to

223 large bromeliads: $\text{LnVmax} = 1.46\text{LnD} + 1.993\text{LnNL} - 6.331$ (see Dézerald et al., 2018 for
224 size and volume ranges). In order to standardize the invertebrate sampling at the end of the
225 experiment, we rewetted two well-developed leaf axils per bromeliad with 10mL of rainwater
226 each (*as per* Dézerald et al., 2015). The water was immediately sucked in and out three times
227 with micropipettes to re-homogenize the content of the tanks, which was then extracted and
228 collected in plastic bottles. The invertebrates were sorted, identified and counted in the
229 laboratory.

230

231 *2.4.Data analysis*

232 Kaplan-Meier survival curves (Kaplan and Meier, 1958) were used to estimate the
233 probability of survival of each species through time. Based on these curves, median lethal
234 time (LT50, days) was calculated with the EcoTox package in R. Survival curves in the
235 treatment vs. control tubes were compared using G-rho family tests of Harrington and
236 Fleming (1982) implemented in the *Survival* package in R. Covariation among traits was
237 examined using pairwise Pearson correlations. We then used generalized linear models
238 (GLMs) to test the effect of desiccation tolerance-resistance traits on LT50. The models were
239 fitted with Gamma error distribution and a log link function to deal with skewed distributions
240 in the data. Model selection started from a model including all the traits listed in Table 1, and
241 backwards removal of less significant variable until all variables contributed with a $p < 0.05$ to
242 the fitting of the model.

243 RLQ analysis was used to analyse the relationships between environmental variables
244 and resistance to desiccation as well as key ecological strategies of invertebrate species
245 (hereafter “functional traits”). The RLQ analysis is a double inertia analysis of the
246 environment and functional trait tables (R and Q, respectively) constrained by the abundance
247 of invertebrate species (L table) (detailed in Dray et al., 2014). The original data is available

248 in the online Appendix A, Tables S1-S3. The R table included drought-related variables
249 (drought treatment, dry bromeliad days, water depth at end of experiment) and Vmax. Vmax
250 was included in the model to account for a potential effect of habitat size on functional
251 community structure (Petermann et al., 2015). The functional trait table Q included LT50, and
252 four other synthetic traits that represent ecological strategies to optimize resource use in
253 bromeliad-dwelling invertebrates. We used LT50 as the synthetic desiccation resistance trait,
254 not measures of anatomical traits such as body mass or cuticle content, first because LT50
255 accounts for the combined role of multiple anatomical traits (see results), and second to
256 prevent the issue of multicollinearity and variance inflation in subsequent ordinations. The
257 other data in our Q table were obtained from Céréghino et al. (2018), who proposed a
258 database of four synthetic traits for Neotropical bromeliad invertebrates, after an ordination of
259 64 traits states of all known taxa (852 species or morphospecies): trophic position (with
260 increasing scores from predators to detritivores), habitat use (from pelagic to benthic),
261 morphological defence (body armoured to the absence of defence), and life cycle complexity
262 (from simple to complex). The L table was $\log(x+1)$ -transformed and underwent
263 correspondence Analysis (CA). The R and Q tables underwent separate Principal Component
264 Analyses (PCA) with the bromeliad scores from the CA as row weights and CA species
265 scores as column weights, respectively. The results of these three separate ordinations were
266 used as inputs in the RLQ analysis, a three-table ordination method which maximises
267 covariation between environmental variables and species traits. We assessed the overall
268 significance of the RLQ using two Monte Carlo permutations tests: (i) permutations of the
269 table rows of R (bromeliads) to test the null hypothesis that species are distributed
270 irrespective of the environmental variables, and (ii) permutations of the table rows of Q
271 (species) to test the null hypothesis that species are distributed irrespective of functional traits
272 that describe survival to desiccation and ecological strategies. From these two tests, we took

273 the highest P-value to establish overall significance. Fourth-corner tests were used to test
274 significant associations between functional traits and R axes, and between environmental
275 variables and Q axes in RLQs. Significant associations were evaluated using Pearson r
276 correlations, and P-values were corrected for false discovery rate to account for possible bias
277 due to multiple comparisons. These analyses were conducted with the ade4 package in R.

278

279 **3. Results**

280

281 *3.1. Lethal times and underpinning traits*

282 Survival curves were significantly and consistently different between the treatments
283 and controls (Gehan-Wilcoxon tests, $p < 0.05$). A potential “tube effect” on our LT50 estimates
284 was null or negligible, because none of the control populations reached a LT50 within the
285 timeframe of the observations, and mortality in the controls ranged from 0% to less than 20%
286 of the individuals at the end of the trials. In the drought treatments, LT50 varied from 4.18 to
287 19.06 days depending on the species (Fig. 2; Table 1). The least sensitive species were
288 *Elpidium bromeliarum* (Ostracoda, LT50 = 19 days), *Toxorhynchites haemorrhoidalis*
289 (Diptera, LT50 = 9.6 days), and *Scirtes* sp. (Coleoptera, LT50 = 8 days). Conversely,
290 *Telmatoscopus* sp., Chironomini sp1 and *Corethrella* sp. (all Diptera, LT50 = ca. 4 days)
291 showed the lowest survival to drought.

292 There were significant positive correlations between fresh and dry mass (Pearson’s $r =$
293 0.95, $P < 0.001$), fresh mass and cuticle mass ($r = 0.83$, $P = 0.021$), and dry mass and cuticle
294 mass ($r = 0.78$, $P = 0.024$). Cuticle content correlated negatively with body length ($r = -0.54$,
295 $P = 0.004$). All other pairwise relationships were not significant ($P > 0.05$). Generalized linear
296 models showed that interspecific variation in LT50 among all study invertebrates were related
297 to two desiccation resistance traits, namely dry mass and cuticle content ($P < 0.05$ and $P <$

298 0.001, respectively, Table 2). When only insect species were considered, only dry mass was
299 retained in the final model, so there was a significant linear relationship between dry mass and
300 LT50 ($P < 0.05$).

301

302 *3.2. Community response to drought scenarios*

303 Though there was some variation among bromeliads, the number of days a bromeliad
304 dried out in our field experiment increased consistently with the number of consecutive days
305 without rainfall (Fig. 3). On average, bromeliads subjected to treatments emulating the current
306 norm (26 consecutive days without rainfall) and to the norm +40% (37 days) were completely
307 dried out for 2.36 ± 3.55 and 8.30 ± 7.03 days (mean \pm SD), respectively. Emulating extreme
308 events of 67 and 94 days without rainfall resulted in 33.06 ± 12.33 and 59.63 ± 15.50 dry
309 bromeliad days respectively, durations that are above the range of invertebrate LT50s
310 measured in the laboratory (Fig. 3).

311 Overall, there was a significant relationship between invertebrate functional traits and
312 environmental variables (permutation tests (i) and (ii) as described in method, simulated P -
313 values = 0.001 and 0.014). Axes 1 and 2 of the RLQ accounted for 98% and 0.82% of the
314 total variance in trait-environment associations, respectively. Given the very low contribution
315 of axis 2, we focussed on environmental and biological gradients along axis 1. Specifically,
316 RLQ axis 1 accounted for 84.5% of the variance of the table Q and 94% of the variance of the
317 environment table R. We thus interpreted correlations between functional traits and the
318 drought-hydrology gradient represented by the first RLQ environmental axis, and correlations
319 between environmental variables and combinations of functional traits represented by the first
320 RLQ trait axis (Table 3).

321 Vector lengths for the environmental variables along axis 1 (Fig. 4) and correlations
322 with the trait axes (Table 3) revealed a gradient of decreasing drought intensity, from the left

323 end (longer absence of rainfall, bromeliads completely dried out for a number of days), to the
324 right end of the axis (shorter drought duration, bromeliads still held water at the end of the
325 experiment). Invertebrate functional community structure along this gradient of drought
326 intensity was best predicted by LT50 (Pearson $r = -0.25$, $P = 0.005$) and species' habitat ($r = -$
327 0.38 , $P = 0.005$), and to a lesser extent by species' trophic position ($r = 0.28$, $P = 0.045$) (Table
328 3). The prevalence of drought-resistant species and/or species that crawl on the bottom of the
329 bromeliad tanks increased with drought intensification. Conversely, the prevalence of pelagic
330 detritivores and small predators with higher sensitivity to desiccation increased at weaker
331 drought intensities. Species' scores along RLQ axis 1 in terms of weighted average and
332 distribution amplitude further portrayed hydrological niche breadths within the simulated
333 gradient of drought intensity (Fig. 4). Overall, twelve species were found in the bromeliads at
334 the end of the experiment. Pelagic Culicidae (*Culex* and *Wyeomyia* species) and their
335 predators (*Corethrella* sp., *M. maculatum*) were dominant in wetter bromeliads, whereas
336 benthic detritivores (*Chironomini*, *Scirtes* sp., *Trentepohlia* sp1., *E. bromeliarum*) dominated
337 the invertebrate community in drier bromeliads.

338

339 **4. Discussion**

340 We found that time to death of bromeliad invertebrates subject to drying stress is
341 determined by desiccation-resistance traits, namely body mass and cuticle content, rather than
342 desiccation-tolerance traits such as body water content. The LT50 of most species varied from
343 4 to 9 days in the laboratory, and reached 19 days in the ostracod *Elpidium bromeliarum*,
344 suggesting that the conspicuous plant-held waters of Neotropical forests host drought-
345 resistant invertebrates. Considering future climate scenarios, extreme drought events, rather
346 than shifts in mean intensity, could potentially wipe out entire invertebrate populations
347 because under such circumstance mortality could exceed the hydrological buffering capacities

348 of the bromeliad habitat. The functional structure of communities showed clear shifts in the
349 prevalence of ecological traits related to habitat use and trophic habits along a gradient of
350 emulated drought intensities, however, species-specific LT50 remained the best predictor of
351 structural responses to drought intensification. The LT50 values reported here must be seen as
352 potentials that did well at assigning resistance capacities to species, but not as absolute values
353 that directly translate to natural conditions. Future work could probably improve our
354 protocols, first by examining whether LT50s are habitat-dependent, and second by examining
355 what would be the most relevant laboratory conditions to produce LT50s that could be
356 compared across freshwater ecosystems and/or biomes. Still, an important implication of our
357 study is that species' LT50s measured under standardized conditions can be used to forecast
358 aquatic community response to drying stress in nature.

359

360 *4.1. Desiccation-resistance traits*

361 Invertebrate survival to drying stress was significantly correlated to cuticle content and
362 dry body mass. Interestingly, these two predictors were not correlated. The absence of a
363 significant effect of body size (here “body length”) on survival may seem *a priori* surprising,
364 given the frequently reported, positive relationship between body size and survival to
365 desiccation (Harrison et al. 2012). When applicable, the rationale for this relationship is that
366 larger organisms have lower surface area to volume ratio than the smaller ones, and are thus
367 less prone to water loss (Bujan et al., 2016). We however note that a body size to resistance
368 relationship was usually found when investigators studied interspecific variation in resistance
369 to desiccation within a given taxonomic group (e.g., a family or sub-family, a genus), where
370 species show rather similar morphologies (Addo-Bediako et al., 2001, but see Hood and
371 Tschinkel, 1990). In this case, it is more likely to observe covariation among traits like body
372 size and water content. Conversely, our study species spanned a broad range of invertebrate

373 clades and morphologies, combining cylindrical to flat sections and ovoid to elongate shapes.
374 Thus, there was little covariation among traits. An implicit conclusion is that LT50 of late-
375 instar larvae of a small species cannot be extrapolated to the early instars of larger species
376 within a clade.

377 LT50 increased with dry body mass. Hood and Tschinkel (1990) and Bujan et al. (2016)
378 found a similar positive relationship between body mass and time to death under desiccation
379 stress in terrestrial insects (ants). Although the assumption cannot be verified directly from
380 our data, larger body mass is supposed to reduce water loss because it allows larger lipid
381 content (Pallarés et al., 2017). Water is mostly lost through the integument in invertebrates
382 (Dias et al., 2013), and higher cuticle thickness was found to reduce water loss in
383 Chironomidae larvae (Nakahara et al., 2008). Our results shed interesting new light on the
384 relationships between anatomical features and survival to desiccation stress across a number
385 of aquatic invertebrate orders and families. Within the range of measured cuticle contents
386 (CC), the annelid *A. superterrenus* (CC below detection limits) and the ostracod *E.*
387 *bromeliarum* (CC= 86%) represented extremes, whereas insects showed less variation (CC= 6
388 – 26%). It is therefore certain that the highly significant relationship between CC and LT50
389 was mostly driven by extreme values found in non-insect species. However, the later species
390 are amongst the numerically dominant invertebrates within the detritus-based food webs of
391 bromeliad ecosystems of French Guiana (Dézerald et al., 2017), where they play major
392 functional roles as bottom-up facilitators (Brouard et al., 2012; Trzcinski et al., 2016).

393 Assuming that a system-level understanding of ecological responses to drought is needed to
394 forecast and mitigate the consequences of global change on biodiversity (Fu, 2015; Srivastava
395 et al., 2020a), we kept these species in our models. Last, we quantified the role of the cuticle
396 as a resistance trait using its mass relative to that of the body, but the biochemical nature of
397 the cuticle (e.g., chitin, cuticular hydrocarbons) also determines its permeability (Farnesi et

398 al., 2015; Ferveur et al., 2018). Hence, biochemical traits would undoubtedly deserve to form
399 part of those sets of functional attributes that usually support trait-based ecology of
400 community responses to drought, e.g., adult lifespan and dispersal mode, presence of
401 desiccation-resistance forms such as cysts or cocoons, body armouring limiting water loss,
402 spiracle respiration, etc. (Datry et al., 2014; Aspin et al., 2019; Crabot et al., 2019).

403

404 *4.2. Invertebrate survival in the face of drought scenarios*

405 The distribution of LT50 values among our study species did not show marked
406 indication of phylogenetic signal and/or trophic constraints on survival to desiccation that
407 could be expected, respectively, from the conservatism of traits in freshwater and terrestrial
408 invertebrates (Poff et al., 2006; Dias et al., 2013; Céréghino et al., 2018) and food web
409 disassembly patterns under drying stress (Ledger et al., 2013). Indeed, representatives of the
410 various invertebrate families and/or orders distributed along the LT50 gradient, and predators
411 (*T. haemorrhoidalis*, *Corethrella* sp., *Bezzia* sp2, *Erythrodiplax* sp., *M. maculatum*) were not
412 more sensitive to drought than the detritivore species (see also Amundrud and Srivastava
413 2015). Recent research evidence that large predatory invertebrates such as damselfly larvae
414 instead minimize desiccation risk by selecting large bromeliads that are less likely to dry
415 before larvae complete their development (Srivastava et al., 2020b).

416 Not surprisingly, live invertebrates were present in the bromeliads at the end of each drought
417 treatment, because in addition to physiological resistance to desiccation, both biological and
418 physical buffering counteracted the detrimental effects of drought. In terms of biology, some
419 species such as *Contacyphon* sp. (Coleoptera), *Microstigma maculatum* (Odonata) or
420 *Trentepohlia* sp. (Diptera) are capable of short-range movements from leaf to leaf to find
421 water, whereas others such *Aulophorus superterrenus* (Oligochaeta), Chironomini (Diptera)
422 or *Elpidium bromeliarum* (Ostracoda) dive at the very bottom of the tanks, or find moist

423 microrefuges into the axil cracks (Dézerald et al., 2015). In terms of physical buffering,
424 precipitation and evaporation are distinct components of the hydrology of freshwater
425 ecosystems in general (Kebede et al., 2006), and this is also true of tank bromeliads. The
426 water volume held by a bromeliad is divided by the multiple leaf axils that form the rosette, a
427 structural complexity which reduces evaporation rates and confers hydrological inertia to
428 changes in water inputs. In the forest understory, it took 30 ± 12 days (mean \pm SD) to
429 completely dry out the reservoirs of a large *Lutheria splendens* bromeliad, something that has
430 two important implications. First, in addition to a temporal pattern of drying, the variance in
431 bromeliad hydrological responses highlights a spatial pattern of drying. Both local
432 environmental heterogeneity (canopy cover) and habitat complexity ensure that there are
433 always a few bromeliads that maintain water during an average to moderately prolonged
434 drought, thus preserving a metacommunity (as well as source patches to support resilience),
435 even though the overall effect is to reduce the number of water-filled bromeliads. Second,
436 extreme drought events should have the harshest effects on the aquatic invertebrates of
437 Neotropical forests, both through the hydrological dynamics of the habitat, and spatial drying
438 patterns (Crabot et al., 2019). By comparison, the detrimental effects of shifts in the mean
439 ambient conditions could be buffered to some extent by environmental-habitat features, and
440 by the behavioural-ecological traits of species (Bogan et al., 2015).

441

442 *4.3. Community- to ecosystem-level responses to drought*

443 Although trait-based ecology revisited community ecology's paradigm about
444 environmental drivers of species' distributions and abundance (McGill et al., 2006), it has
445 proven challenging to determine what traits best predict organisms' performance within the
446 multidimensional niche space defined by a set of environmental conditions (Chase and
447 Leibold, 2003). Traits accounting for desiccation resistance drove invertebrate species

448 distributions among experimental bromeliads that represented gradients of drought intensity
449 and water availability. Though we attempted to standardize bromeliads by structural
450 complexity and water holding capacity, variation in plant traits, and probably microhabitat
451 variation in canopy cover, induced some variability in the number of dry bromeliad days
452 resulting from a drought treatment. Still, our use of rainout shelters in the field generated a
453 gradient of drought and bromeliad hydrology that clearly selected (or counterselected)
454 invertebrates according to their traits. Overall, we therefore believe that this methodological
455 issue had a negligible impact on the conclusions drawn from our community-level
456 experiment. As drought intensified, there was a shift from a dominance of desiccation-
457 sensitive to more desiccation-resistant species within communities. In the context of global
458 change biology, LT50 of species measured under standard laboratory conditions could
459 therefore form a relevant predictor of drought-related changes in community structure and
460 functions in nature (Dias et al., 2013; Bujan et al., 2016). Predators and detritivores were
461 equally sensitive to drought (see above paragraph 4.2.), so it is likely that trophic biomass
462 pyramids were unaffected. The overall shift towards desiccation-resistant species was rather
463 consistent with a shift from pelagic species that swim in the water column to species that
464 crawl or burrow in the wet detritus that accumulates at the bottom of the bromeliad tanks
465 (Dézerald et al., 2015). A functional consequence is that ecosystems likely shifted from a
466 benthic-pelagic food web to a strictly benthic food web. Because the dominant pelagic species
467 were filter-feeders of fine particulate organic matter (FPOM) and algae and benthic species
468 are mostly detritivores, drought could foster a shift from a “green-brown” (FPOM- and algal-
469 based) to a “brown” (detritus-based) food web. Owing to their capacity to reach refuge
470 microhabitats where they can maintain their water balance, benthic species are theoretically
471 less exposed to hydrological stochasticity. This type of drought-induced shift in habitat-
472 related traits has frequently been observed in freshwater communities (Bonada et al., 2007;

473 Diaz et al., 2008; Dézerald et al., 2015), leading to the idea that habitat use and/or preference
474 is a good proxy for desiccation resistance (Robson et al., 2011). However, LT50, the time
475 before 50% of a population reaches a critical water balance, provides a more mechanistic
476 understanding of the link between species performance and drought, much like critical
477 thermal maximum (CT_{max} , the temperature at which animals lose ability to control muscle
478 contraction) relates species performance to temperature (Lutterschmidt and Hutchison, 1997).

479

480 **5. Conclusion**

481 As future climate scenarios predict declines in precipitation in many regions of the
482 world, anticipating how species will cope with drought is of utmost importance for
483 environmental managers to support climate change adaptation. Our study supports the idea
484 that physiology can bridge the gap between ecology and climate change (Kearney and Porter,
485 2009), under the basic assumption that organisms cannot survive in environments that do not
486 allow them to maintain basic regulatory functions as well as homeostasis (Barnes et al., 2009;
487 Sokolova et al., 2012). In a context of declining water availability, traits underlying
488 physiological resistance to desiccation in freshwater invertebrates are certainly key
489 determinants and relevant indicators of potential population size, and local-global range
490 shifts. Whether species persistence and community stability are best (or equally) predicted by
491 measures of survival (LT50), morphology (e.g., body mass), fluxes (e.g., water loss rates) or
492 molecules (e.g., cuticular hydrocarbons) remains to be elucidated. Still, there is growing
493 evidence that integrating physiological knowledge into global change biology will improve
494 our ability to produce robust predictions of structural and functional shifts over ranges of
495 climatic parameter space (Verberk et al., 2016), and this could be especially true in the
496 Neotropics, where species have narrower physiological tolerances for climatic variation than
497 their temperate counterparts (Tewksbury et al., 2008).

498

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506

507 **Appendix A. Supplementary data**

508 Supplementary data to this article can be found online at XXXX

509

510

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Table 1. Values for the desiccation tolerance and resistance traits (mean± sd), and survival to desiccation (estimate ± 95% confidence interval). FM=fresh mass, DM= dry mass, WC = water content, CM= cuticle mass, BL = body length. LT50 is the median lethal time in the treatment populations. “n” is the number of individuals used to measure LT50 in the treatments, and the same number of individuals was used in the controls (see text).

Species	Traits						n	Survival
	FM (mg)	DM (mg)	WC (%)	CM (mg)	CC (%)	BL (cm)		LT50 (days)
Diptera								
Culicidae								
<i>Anopheles nevai</i>	0.239 ± 0.131	0.095 ± 0.098	60.314	0.025 ± 0.020	26.128	0.351 ± 0.054	12	4.987 ± 0.001
<i>Culex</i> sp1	0.348 ± 0.200	0.101 ± 0.031	70.979	0.007 ± 0.002	7.131	0.443 ± 0.047	34	4.855 ± 0.116
<i>Microculex pleuristriatus</i>	0.320 ± 0.121	0.188 ± 0.042	41.250	0.015 ± 0.006	7.979	0.335 ± 0.037	12	7.941 ± 0.217
<i>Microculex stonei</i>	0.201 ± 0.142	0.069 ± 0.022	65.518	0.006 ± 0.003	8.214	0.892 ± 0.285	32	4.688 ± 0.145
<i>Toxorhynchites haemorrhoidalis</i>	9.848 ± 6.742	2.024 ± 1.301	79.451	0.117 ± 0.182	5.757	0.751 ± 0.182	10	9.608 ± 0.260
<i>Wyeomyia aphobema</i>	0.371 ± 0.316	0.176 ± 0.060	52.481	0.015 ± 0.008	8.357	0.545 ± 0.088	31	4.921 ± 0.110
Chironomidae								
Chironomini sp.	0.112 ± 0.06	0.083 ± 0.018	26.231	0.003 ± 0.003	3.299	0.523 ± 0.076	32	4.255 ± 0.204
Corethrellidae								
<i>Corethrella</i> sp.	0.214 ± 0.107	0.041 ± 0.01	80.820	0.008 ± 0.004	19.961	0.303 ± 0.019	32	4.377 ± 0.116
Psychodidae								
<i>Telmatoctopus</i> sp1	1.449 ± 0.815	0.3 ± 0.216	79.322	0.025 ± 0.014	8.438	0.518 ± 0.111	38	4.182 ± 0.098
Tipulidae								
<i>Trentepohlia</i> sp1	7.968 ± 5.296	1.037 ± 0.757	86.982	0.072 ± 0.067	6.969	1.206 ± 0.247	31	5.792 ± 0.163
Ceratopogonidae								
<i>Bezzia</i> sp2	0.234 ± 0.156	0.101 ± 0.017	56.920	0.01 ± 0.006	9.785	0.462 ± 0.285	32	4.817 ± 0.102
Coleoptera								
Scirtidae								
<i>Contacyphon</i> sp.	0.935 ± 0.683	0.599 ± 0.42	35.873	0.048 ± 0.026	7.972	0.544 ± 0.081	30	4.751 ± 0.095

<i>Scirtes</i> sp.	1.419 ± 0.579	0.340 ± 0.084	76.043	0.047 ± 0.040	13.82	0.457 ± 0.072	12	8.099 ± 0.272
Odonata								
Libellulidae								
<i>Erythrodiplax</i> sp.	7.09 ± 12.646	1.014 ± 1.913	85.705	0.177 ± 0.386	17.434	0.456 ± 0.202	10	6.904 ± 0.264
Pseudostigmatidae								
<i>Microstigma maculatum</i>	6.908 ± 5.757	1.082 ± 0.889	84.332	0.194 ± 0.594	17.923	0.764 ± 0.216	24	5.273 ± 0.202
Annelida								
Oligochaeta. Naididae								
<i>Aulophorus superterrenus</i>	0.062 ± 0.031	0.055 ± 0.047	11.253	0	0	1.357 ± 0.749	30	4.415 ± 0.096
Crustacea								
Ostracoda. Limnocytheridae								
<i>Elpidium bromeliarium</i>	0.16 ± 0.040	0.058 ± 0.011	63.753	0.05 ± 0.026	86.075	0.085 ± 0.006	75	19.063 ± 0.242

Table 2. Results of the GLM evaluating the effects of desiccation tolerance and resistance traits on median lethal time (LT50) (minimum model after backward selection of variables). *P<0.05; ***P< 0.001.

	Estimate	Standard Error	t-value	P-value
Intercept	1.421713	0.095921	14.822	5.96e-10***
Dry mass	0.283235	0.113951	2.486	0.026186*
Cuticle content	0.016273	0.003231	5.037	0.000182***

Table 3. Correlation coefficients for the relationships between environmental variables and traits with RLQ axis 1. Only variables and traits showing correlations at $P < 0.05$ are listed. P-values were adjusted for false discovery rate: * $P < 0.05$, ** $P < 0.01$.

	Pearson's r	Adjusted P-value
<i>Environmental variables</i>		
Drought treatment	-0.3074	0.004**
Dry bromeliad days	-0.2538	0.004**
Depth at end of experiment	0.2773	0.029*
<i>Traits</i>		
LT50	-0.2588	0.005**
Trophic position	0.2890	0.046*
Habitat	-0.3894	0.005**

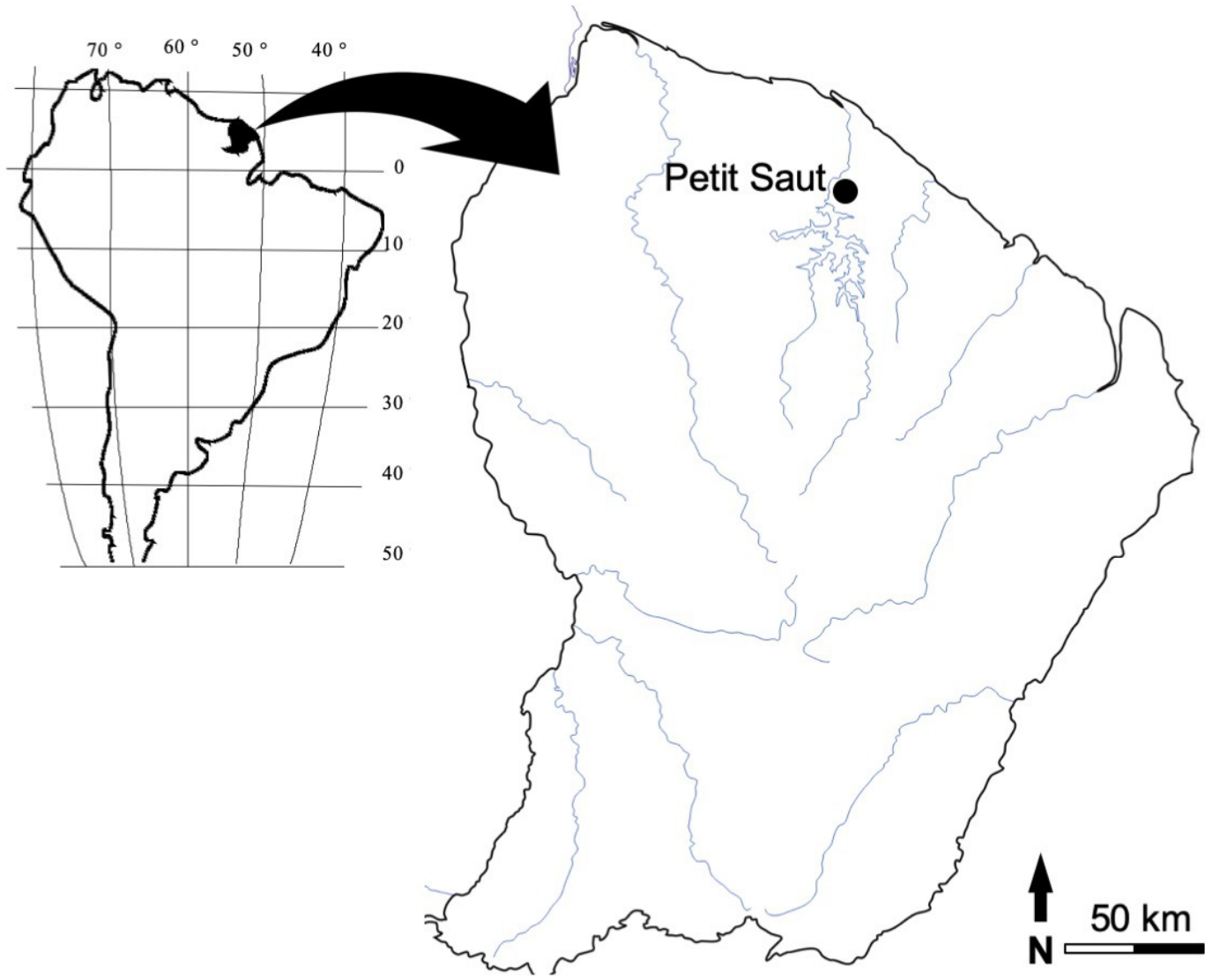
Figure legends

Fig. 1. Location of French Guiana in South-America (left), and of our study site near the Petit-Saut Dam (right).

Fig. 2. Selected example of survival curves: A) *Aulophorus superterrenus* (Annelida, Naididae), B) *Microculex stonei* (Diptera, Culicidae), C) *Contacyphon* sp. (Coleoptera, Scirtidae), D) *Microstigma maculatum* (Odonata, Pseudostigmatidae). Dark = treatment, grey = control, “+” = right censored data in the control. Horizontal lines represent survival durations. Vertical distances between the horizontal lines represent changes in cumulative probability of surviving.

Fig. 3. Boxplots of the number of dry bromeliad days by drought treatment (n= 30 bromeliads per treatment). Boxes delineate the 25th and 75th quartiles, thick lines represent the medians, whiskers extend to maxima and minima. All pairwise Mann–Whitney tests indicate significant differences among treatments ($P < 0.01$). The *Corethrella* sp. to *E. bromeliarum* range (bottom-right) shows the distribution of LT50s (see Table 1).

Fig. 4. Left: Ordination of the environmental variables and functional traits along the first two RLQ axes. Numbers on the axes are the variance explained by RLQ axes 1 and 2. Vectors represent environmental variables (solid lines) and functional traits (dotted lines). Directions show the gradients, arrow length represents the strengths of the variables and traits on the ordination space. Blue = significant negative correlation with axis 1, red = significant positive correlation with axis 1 (fourth-corner tests, $p < 0.05$). Right: weighted average and variance of invertebrate species on the first RLQ axis.



Legend + Control + Treatment

