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

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Abstract

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

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

1. Introduction

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

Invertebrates contribute disproportionately to the biodiversity of tropical regions, where they play significant roles in multi-trophic processes and ecosystem functions (Ewers et al., 2015). The desiccation tolerance of invertebrates (ability to withstand body water loss) depends on the body water content, which influences water loss dynamics (Thorat and Nath, 2018). Desiccation resistance (ability to reduce water loss) is rather related to body size and integumental permeability (Dias et al., 2013; Pallarés et al., 2017). Compared to their temperate counterparts, the invertebrates found in tropical rainforests are expected to have low tolerance-resistance to desiccation because they thrive in relatively stable conditions of habitat humidity or hydrology (Gibbs et al., 2001; Hoffman et al., 2003). Yet, traits underpinning sensitivity to drought among coexisting species and the consequences at community level remain poorly documented, notably in freshwaters where responses to drying stress play a primary role in the distribution of species at multiple spatial scales (Datry et al., 2014; Pallarés al., 2016). Theory about local adaptation suggests that tolerance and resistance traits could allow species to withstand modest to average drought intensities at the active stage (Lake, 2011). Nevertheless, once drought intensifies, reconfigurations of communities could occur if co-existing species were to respond asynchronously to desiccation stress. These assumptions remain however untested, first because we lack established relationships between species' desiccation tolerance-resistance traits and survival to drought in tropical rainforests (see review in Thorat and Nath, 2018), and second because we don't know which trait combinations are selected (or counter-selected) along a gradient of increasing drought intensity in these ecosystems.

Assembling data on trait variation among coexisting species in rivers, lakes or wetlands is however challenging, because of their very high taxonomic diversity. Natural microcosms that host smaller numbers of co-evolved species in contained habitats form relevant alternatives to test ecological hypotheses (Kitching, 2000; Srivastava et al., 2004). Here, we focused on the aquatic invertebrates inhabiting tank bromeliads, a discrete ecosystem that is commonly found across a wide array of Neotropical environments. Bromeliads are flowering plants represented by 3403 species native to the Neotropics (Ulloa et al., 2017). The leaves of tank-forming bromeliads are arranged in rosettes that trap water, forming "freshwater islands" in a terrestrial matrix. Tank bromeliads collect rainwater and detritus, providing a habitat for aquatic organisms ranging from bacteria to macroinvertebrates. Detailed descriptions of the bromeliad macroinvertebrate fauna and functional traits can be found in Frank & Lounibos (2009) and Céréghino et al. (2018).

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

2. Methods

2.1.Study area

This study was carried out in French Guiana from October 2018 to April 2019, near the Petit-Saut Dam, Sinnamary (5°03043″N, 53°02046″W; elevation <80 m a.s.l.; Fig. 1). French Guiana is an overseas region of France located on the north-eastern coast of South America. About 96% of its surface area (83.534 km^2) is covered by equatorial forest. The climate is tropical moist with 3000 mm of annual precipitation, little seasonal variation in air temperature (monthly average = 20.5-33.5°C), and a relative humidity between 70% and 100%. There is a major reduction in rainfall between September and November, and a shorter and more irregular dry period in March.

2.2.Lethal times and underpinning traits

We sampled the two dominant bromeliad species in the study area, namely *Lutheria splendens* and *Aechmea aquilega*. We used 10-mL micropipettes, with the end trimmed to widen the aperture, to suck out the water and aquatic invertebrates from the leaf axils (Dézerald et al., 2018). The bromeliad content was collected in plastic bottles and immediately brought to the laboratory, where aquatic invertebrates were sorted alive and identified to species or morphospecies (hereafter “species”). With the exception of a crustacean and an annelid, these invertebrates were all aquatic insect larvae (the emerging adult usually being terrestrial). The bromeliad invertebrate fauna in our study area comprised 33 species (see lists in Céréghino et al., 2011; Dézerald et al., 2015; Leroy et al., 2017). About half of these species are rare (both in terms of occurrence and number of individuals), so we were able to obtain individuals from 17 species in sufficient numbers to carry out our observations (Table 1). These species however represented the dominant invertebrate orders and families in Neotropical bromeliads in general (see Fig. 2 in Céréghino et al., 2018), and >90% of the invertebrate biomass found in bromeliads of French Guiana (Leroy et al., 2017; Dézerald et al., 2018). Prior to the experiment, invertebrates were acclimatized for 48h in 50mL Falcon® tubes filled with bromeliad water. Predators were fed *ad libitum* with prey (mosquito larvae), detritivores were provided with leaf litter and fine particulate organic matter collected in bromeliads. Invertebrate sorting and all observations were carried out in a temperature-controlled room at 25°C under a natural circadian rhythm (day:night = 12:12h).

Our study of median lethal times (LT50) and desiccation tolerance-resistance traits was based on the largest individuals of each species. We acknowledge that not all life-stages of a species might be equally sensitive to a given disturbance (van der Lee et al., 2020), and therefore, the trait and LT50 values reported in this work should be seen as potentials rather than absolute values. Such individuals corresponded to the last instar of holometabolous insects (e.g., instar IV in most Diptera), and to the largest individuals in a cohort in heterometabolous insects (Odonata) and other invertebrates (Ostracoda, Annelida). Detailed studies of invertebrate larval stages and population dynamics in bromeliads at our study site can be found in Dézerald et al. (2017; 2018). For each species, individuals were isolated in glass tubes (i.e., 1 individual per tube; tube diameter = 13.36 mm, height = 43.7 mm, volume = 6.5 mL) covered with a mosquito net and containing a 1x3 cm folded piece of Whatman paper n°1 dampened with 1 mL of filtered bromeliad water (to simulate residual moisture in a leaf crevice). We usually used ca. 30 individuals per species for the trials, but only 10-12 suitable individuals were available for five infrequent species (see Table 1 for numbers). Each tube was then inspected every day using magnifying glasses, to record the status of individuals (dead vs. alive). Death was confirmed by the absence of movement when refilling the tube with water. Daily observations for any given species continued until all individuals died. In order to test for a potential “tube effect” on mortality (control), similar observations were simultaneously conducted on the same number of individuals per species isolated in tubes filled to their maximum capacity with filtered bromeliad water. A constant water volume was maintained in the control tubes during the experiment. For each species, we stopped the observations when mortality reached 100% in the treatment tubes, resulting in right-censored data in the controls.

Desiccation tolerance and resistance traits for each species consisted in an average value obtained from measurements of 30 last-instar individuals (Table 1). Body length (BL, the longest length from mouth to anus, mm) was measured from pictures of the individuals using Image J software. We used a microbalance (MX5; Mettler Toledo, Viroflay, France) to quantify fresh mass (FM, mg), and dry mass (DM, mg) after oven-drying individuals at 60°C for 48h. Water content (WC, %) was calculated as ((FM-DM)/FM) *100. To obtain the cuticle dry mass (CM, mg), we adapted the protocol described in Sasso Porto et al. (2016). Individuals were placed in a 10M potassium hydroxide – sodium hydroxide solution (50%:50%) heated at 95°C in a water bath to dissolve the soft tissues (see also Harrison et al., 2012). Incubation times ranged from 15 min to 1hr depending on the degree of chitinization. Individuals were then transferred into 3-5% peroxide hydrogen (H_2O_2) at room temperature for 20 minutes, and finally immerged in 70% boiling ethanol for 10 min. Cuticles were oven-dried (60°C, 24hrs) and weighted. Cuticle content (CC, %) was calculated as (CM/DM) * 100. Though annelids have a very thin cuticle coating their external epithelium, the material obtained following chemical treatments of *A. superterrenus* individuals was below detection limits of the microbalance. We therefore arbitrarily set CC to 0 for *A. superterrenus*.

2.3.Community response to drought scenarios

The field experiment took place in a lowland rainforest plot nearby the Petit-Saut Dam, where we extensively studied the bromeliad fauna and have a thorough grasp of the local species pool (e.g., Dézerald et al., 2015; 2017; 2018). Based on vegetative traits (number of leaves, plant canopy diameter, water holding capacity), we selected 120 *Lutheria splendens* bromeliads of similar size. We used rainshelters placed over individual bromeliads (transparent plastic tarpaulin as in Trzcinski et al., 2016) to emulate dry periods representing: (i) the current norm (26 days, the average maximum number of consecutive days without rainfall over the past 20 years for the study months in the area), (ii) IPCC prediction in the area (current norm +40% = 37 consecutive dry days), (iii) an extreme event (the maximum number of consecutive dry days observed over the past 20 years = 67 days), and (iv) an extreme event +40% = 94 dry days. Each treatment had 30 replicates (bromeliads). Treatments started from (iv) to (i) in rank order, so all bromeliads reached the end of their dry period simultaneously. The environmental variables recorded were: drought treatment (the number of consecutive days without rainfall), dry bromeliad days (the number of days a bromeliad was completely dried out under a drought treatment), and water depth at the end of the experiment (the average of two measurements in two well developed leaf axils, mm). The water holding capacity of each bromeliad (Vmax, maximum water volume in mL) was calculated from an allometric relationship developed by us in anticipation of various experiments that make use the bromeliad *L. splendens*. This relationship is based on actual measurements of maximum water volume (overflow of a known water volume using a graduate cylinder), number of leaves (NL) and plant canopy diameter (D) of 123 small to large bromeliads: $\mathrm{Ln}V\mathrm{max} = 1.46\mathrm{Ln}D + 1.993\mathrm{Ln}NL - 6.331$ (see Dézerald et al., 2018 for size and volume ranges). In order to standardize the invertebrate sampling at the end of the experiment, we rewetted two well-developed leaf axils per bromeliad with 10mL of rainwater each (*as per* Dézerald et al., 2015). The water was immediately sucked in and out three times with micropipettes to re-homogenize the content of the tanks, which was then extracted and collected in plastic bottles. The invertebrates were sorted, identified and counted in the laboratory.

2.4. Data analysis

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

RLQ analysis was used to analyse the relationships between environmental variables and resistance to desiccation as well as key ecological strategies of invertebrate species (hereafter "functional traits"). The RLQ analysis is a double inertia analysis of the environment and functional trait tables (R and Q, respectively) constrained by the abundance of invertebrate species (L table) (detailed in Dray et al., 2014). The original data is available in the online Appendix A, Tables S1-S3. The R table included drought-related variables (drought treatment, dry bromeliad days, water depth at end of experiment) and Vmax. Vmax was included in the model to account for a potential effect of habitat size on functional community structure (Petermann et al., 2015). The functional trait table Q included LT50, and four other synthetic traits that represent ecological strategies to optimize resource use in bromeliad-dwelling invertebrates. We used LT50 as the synthetic desiccation resistance trait, not measures of anatomical traits such as body mass or cuticle content, first because LT50 accounts for the combined role of multiple anatomical traits (see results), and second to prevent the issue of multicollinearity and variance inflation in subsequent ordinations. The other data in our Q table were obtained from Céréghino et al. (2018), who proposed a database of four synthetic traits for Neotropical bromeliad invertebrates, after an ordination of 64 traits states of all known taxa (852 species or morphospecies): trophic position (with increasing scores from predators to detritivores), habitat use (from pelagic to benthic), morphological defence (body armoured to the absence of defence), and life cycle complexity (from simple to complex). The L table was log(x+1)-transformed and underwent correspondence Analysis (CA). The R and Q tables underwent separate Principal Component Analyses (PCA) with the bromeliad scores from the CA as row weights and CA species scores as column weights, respectively. The results of these three separate ordinations were used as inputs in the RLQ analysis, a three-table ordination method which maximises covariation between environmental variables and species traits. We assessed the overall significance of the RLQ using two Monte Carlo permutations tests: (i) permutations of the table rows of R (bromeliads) to test the null hypothesis that species are distributed irrespective of the environmental variables, and (ii) permutations of the table rows of Q (species) to test the null hypothesis that species are distributed irrespective of functional traits that describe survival to desiccation and ecological strategies. From these two tests, we took the highest P-value to establish overall significance. Fourth-corner tests were used to test significant associations between functional traits and R axes, and between environmental variables and Q axes in RLQs. Significant associations were evaluated using Pearson r correlations, and P-values were corrected for false discovery rate to account for possible bias due to multiple comparisons. These analyses were conducted with the ade4 package in R.

3. Results

3.1.Lethal times and underpinning traits

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

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

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

3.2. *Community response to drought scenarios*

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

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

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

4. Discussion

We found that time to death of bromeliad invertebrates subject to drying stress is determined by desiccation-resistance traits, namely body mass and cuticle content, rather than desiccation-tolerance traits such as body water content. The LT50 of most species varied from 4 to 9 days in the laboratory, and reached 19 days in the ostracod *Elpidium bromeliarum*, suggesting that the conspicuous plant-held waters of Neotropical forests host drought-resistant invertebrates. Considering future climate scenarios, extreme drought events, rather than shifts in mean intensity, could potentially wipe out entire invertebrate populations because under such circumstance mortality could exceed the hydrological buffering capacities of the bromeliad habitat. The functional structure of communities showed clear shifts in the prevalence of ecological traits related to habitat use and trophic habits along a gradient of emulated drought intensities, however, species-specific LT50 remained the best predictor of structural responses to drought intensification. The LT50 values reported here must be seen as potentials that did well at assigning resistance capacities to species, but not as absolute values that directly translate to natural conditions. Future work could probably improve our protocols, first by examining whether LT50s are habitat-dependent, and second by examining what would be the most relevant laboratory conditions to produce LT50s that could be compared across freshwater ecosystems and/or biomes. Still, an important implication of our study is that species' LT50s measured under standardized conditions can be used to forecast aquatic community response to drying stress in nature.

4.1.Desiccation-resistance traits

Invertebrate survival to drying stress was significantly correlated to cuticle content and dry body mass. Interestingly, these two predictors were not correlated. The absence of a significant effect of body size (here "body length") on survival may seem *a priori* surprising, given the frequently reported, positive relationship between body size and survival to desiccation (Harrison et al. 2012). When applicable, the rationale for this relationship is that larger organisms have lower surface area to volume ratio than the smaller ones, and are thus less prone to water loss (Bujan et al., 2016). We however note that a body size to resistance relationship was usually found when investigators studied interspecific variation in resistance to desiccation within a given taxonomic group (e.g., a family or sub-family, a genus), where species show rather similar morphologies (Addo-Bediako et al., 2001, but see Hood and Tschinkel, 1990). In this case, it is more likely to observe covariation among traits like body size and water content. Conversely, our study species spanned a broad range of invertebrate clades and morphologies, combining cylindrical to flat sections and ovoid to elongate shapes. Thus, there was little covariation among traits. An implicit conclusion is that LT50 of late-instar larvae of a small species cannot be extrapolated to the early instars of larger species within a clade.

LT50 increased with dry body mass. Hood and Tschinkel (1990) and Bujan et al. (2016) found a similar positive relationship between body mass and time to death under desiccation stress in terrestrial insects (ants). Although the assumption cannot be verified directly from our data, larger body mass is supposed to reduce water loss because it allows larger lipid content (Pallarés et al., 2017). Water is mostly lost through the integument in invertebrates (Dias et al., 2013), and higher cuticle thickness was found to reduce water loss in Chironomidae larvae (Nakahara et al., 2008). Our results shed interesting new light on the relationships between anatomical features and survival to desiccation stress across a number of aquatic invertebrate orders and families. Within the range of measured cuticle contents (CC), the annelid *A. superterrenus* (CC below detection limits) and the ostracod *E. bromeliarum* (CC= 86%) represented extremes, whereas insects showed less variation (CC= 6 – 26%). It is therefore certain that the highly significant relationship between CC and LT50 was mostly driven by extreme values found in non-insect species. However, the later species are amongst the numerically dominant invertebrates within the detritus-based food webs of bromeliad ecosystems of French Guiana (Dézerald et al., 2017), where they play major functional roles as bottom-up facilitators (Brouard et al., 2012; Trzcinski et al., 2016). Assuming that a system-level understanding of ecological responses to drought is needed to forecast and mitigate the consequences of global change on biodiversity (Fu, 2015; Srivastava et al., 2020a), we kept these species in our models. Last, we quantified the role of the cuticle as a resistance trait using its mass relative to that of the body, but the biochemical nature of the cuticle (e.g., chitin, cuticular hydrocarbons) also determines its permeability (Farnesi et al., 2015; Ferveur et al., 2018). Hence, biochemical traits would undoubtedly deserve to form part of those sets of functional attributes that usually support trait-based ecology of community responses to drought, e.g., adult lifespan and dispersal mode, presence of desiccation-resistance forms such as cysts or cocoons, body armouring limiting water loss, spiracle respiration, etc. (Datry et al., 2014; Aspin et al., 2019; Crabot et al., 2019).

4.2.Invertebrate survival in the face of drought scenarios

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

Not surprisingly, live invertebrates were present in the bromeliads at the end of each drought treatment, because in addition to physiological resistance to desiccation, both biological and physical buffering counteracted the detrimental effects of drought. In terms of biology, some species such as *Contacyphon* sp. (Coleoptera), *Microstigma maculatum* (Odonata) or *Trentepohlia* sp. (Diptera) are capable of short-range movements from leaf to leaf to find water, whereas others such *Aulophorus superterrenus* (Oligochaeta), Chironomini (Diptera) or *Elpidium bromeliarum* (Ostracoda) dive at the very bottom of the tanks, or find moist microrefuges into the axil cracks (Dézerald et al., 2015). In terms of physical buffering, precipitation and evaporation are distinct components of the hydrology of freshwater ecosystems in general (Kebede et al., 2006), and this is also true of tank bromeliads. The water volume held by a bromeliad is divided by the multiple leaf axils that form the rosette, a structural complexity which reduces evaporation rates and confers hydrological inertia to changes in water inputs. In the forest understory, it took 30±12 days (mean±SD) to completely dry out the reservoirs of a large *Lutheria splendens* bromeliad, something that has two important implications. First, in addition to a temporal pattern of drying, the variance in bromeliad hydrological responses highlights a spatial pattern of drying. Both local environmental heterogeneity (canopy cover) and habitat complexity ensure that there are always a few bromeliads that maintain water during an average to moderately prolonged drought, thus preserving a metacommunity (as well as source patches to support resilience), even though the overall effect is to reduce the number of water-filled bromeliads. Second, extreme drought events should have the harshest effects on the aquatic invertebrates of Neotropical forests, both through the hydrological dynamics of the habitat, and spatial drying patterns (Crabot et al., 2019). By comparison, the detrimental effects of shifts in the mean ambient conditions could be buffered to some extent by environmental-habitat features, and by the behavioural-ecological traits of species (Bogan et al., 2015).

4.3.Community- to ecosystem-level responses to drought

Although trait-based ecology revisited community ecology's paradigm about environmental drivers of species' distributions and abundance (McGill et al., 2006), it has proven challenging to determine what traits best predict organisms' performance within the multidimensional niche space defined by a set of environmental conditions (Chase and Leibold, 2003). Traits accounting for desiccation resistance drove invertebrate species distributions among experimental bromeliads that represented gradients of drought intensity and water availability. Though we attempted to standardize bromeliads by structural complexity and water holding capacity, variation in plant traits, and probably microhabitat variation in canopy cover, induced some variability in the number of dry bromeliad days resulting from a drought treatment. Still, our use of rainout shelters in the field generated a gradient of drought and bromeliad hydrology that clearly selected (or counterselected) invertebrates according to their traits. Overall, we therefore believe that this methodological issue had a negligible impact on the conclusions drawn from our community-level experiment. As drought intensified, there was a shift from a dominance of desiccation-sensitive to more desiccation-resistant species within communities. In the context of global change biology, LT50 of species measured under standard laboratory conditions could therefore form a relevant predictor of drought-related changes in community structure and functions in nature (Dias et al., 2013; Bujan et al., 2016). Predators and detritivores were equally sensitive to drought (see above paragraph 4.2.), so it is likely that trophic biomass pyramids were unaffected. The overall shift towards desiccation-resistant species was rather consistent with a shift from pelagic species that swim in the water column to species that crawl or burrow in the wet detritus that accumulates at the bottom of the bromeliad tanks (Dézerald et al., 2015). A functional consequence is that ecosystems likely shifted from a benthic-pelagic food web to a strictly benthic food web. Because the dominant pelagic species were filter-feeders of fine particulate organic matter (FPOM) and algae and benthic species are mostly detritivores, drought could foster a shift from a “green-brown” (FPOM- and algal-based) to a “brown” (detritus-based) food web. Owing to their capacity to reach refuge microhabitats where they can maintain their water balance, benthic species are theoretically less exposed to hydrological stochasticity. This type of drought-induced shift in habitat-related traits has frequently been observed in freshwater communities (Bonada et al., 2007;

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

5. Conclusion

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at XXXX

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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).

	Traits							Survival
Species	FM (mg)	DM (mg)	WC (%)	CM (mg)	CC (%)	BL (cm)	n	LT50 (days)
Diptera								
Culicidae								
Anopheles nevai	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
Culex 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
Microculex pleuristriatus	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
Microculex stonei	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
Toxorhynchites haemorrhoidalis	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
Wyeomyia aphobema	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								
Corethrella 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								
Telmatoscopus 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								
Trentepohlia 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								
Bezzia 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								
Contacyphon 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

Scirtes 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								
Erythrodiplax 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								
Microstigma maculatum	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								
Aulophorus superterrenus	0.062 ± 0.031	0.055 ± 0.047	11.253	0	0	1.357 ± 0.749	30	4.415 ± 0.096
Crustacea								
Ostracoda. Limnocytheridae								
Elpidium bromeliarium	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
Environmental variables		
Drought treatment	-0.3074	0.004**
Dry bromeliad days	-0.2538	0.004**
Depth at end of experiment	0.2773	0.029*
Traits		
LT50	-0.2588	0.005**
Trophic position	0.2890	0.046*
Habitat	-0.3894	0.005**

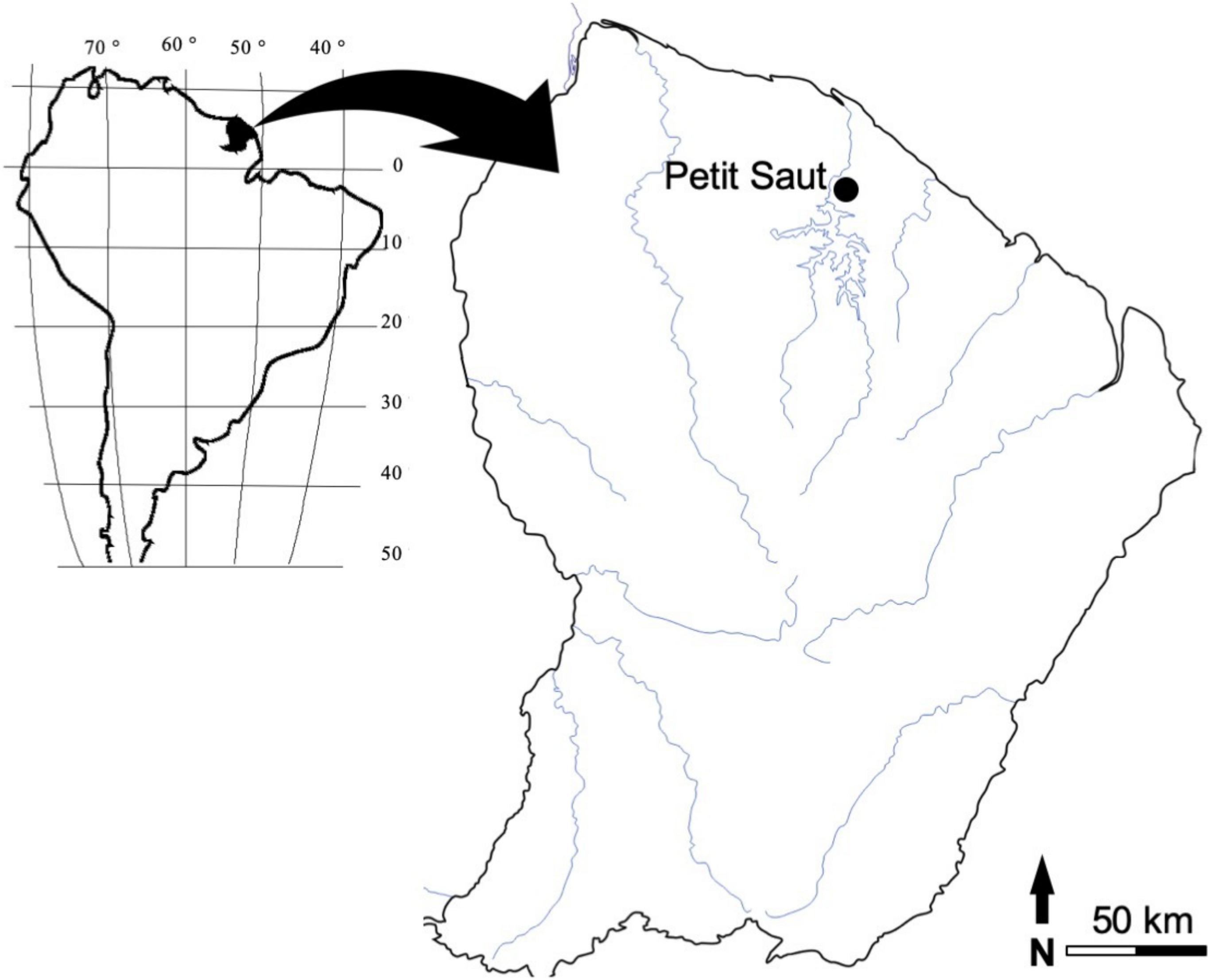
Figure legends

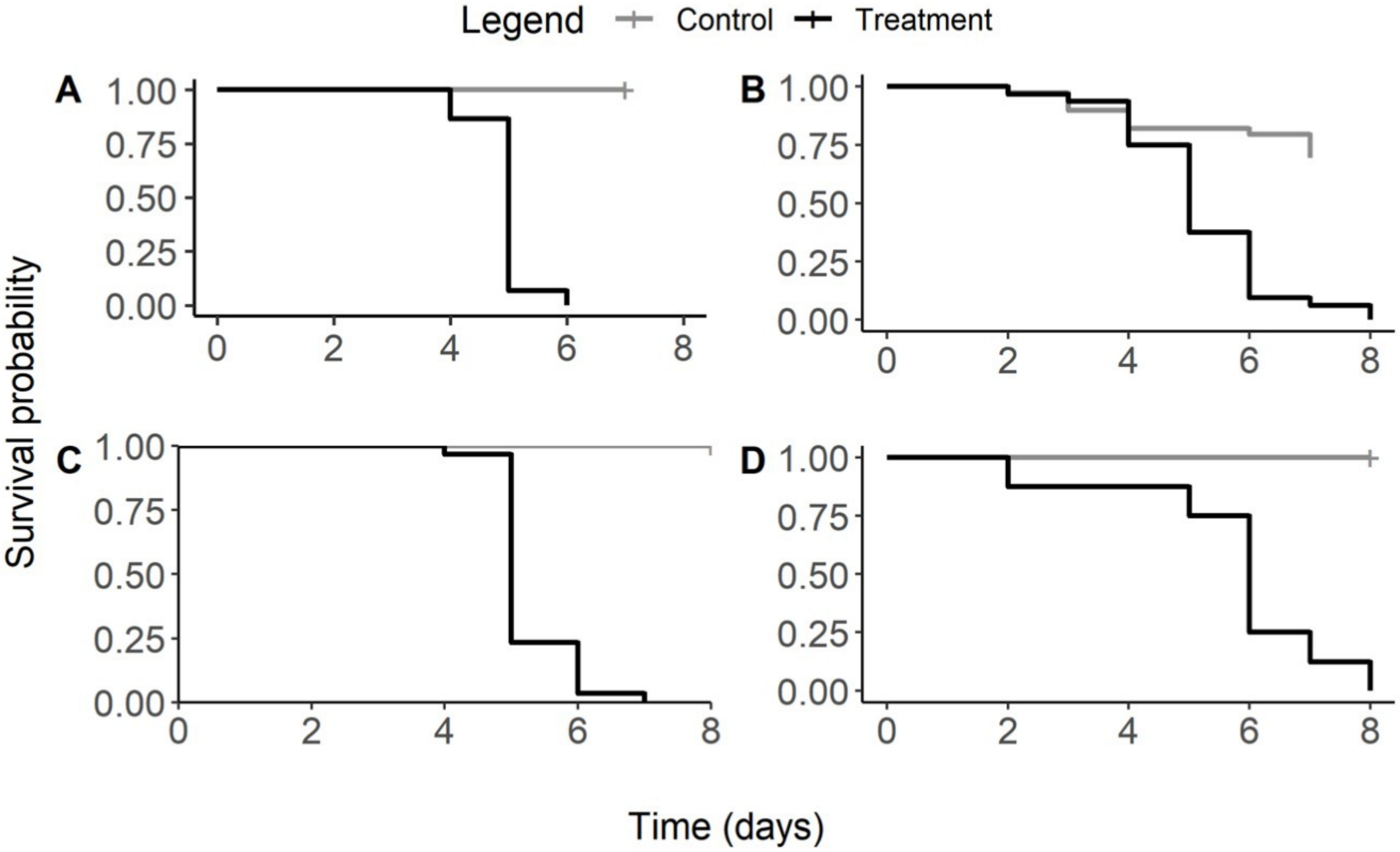
Fig. 1. Location of French Guiana in South-America (left), and of our study site near the Petit-Saut Dam (right).

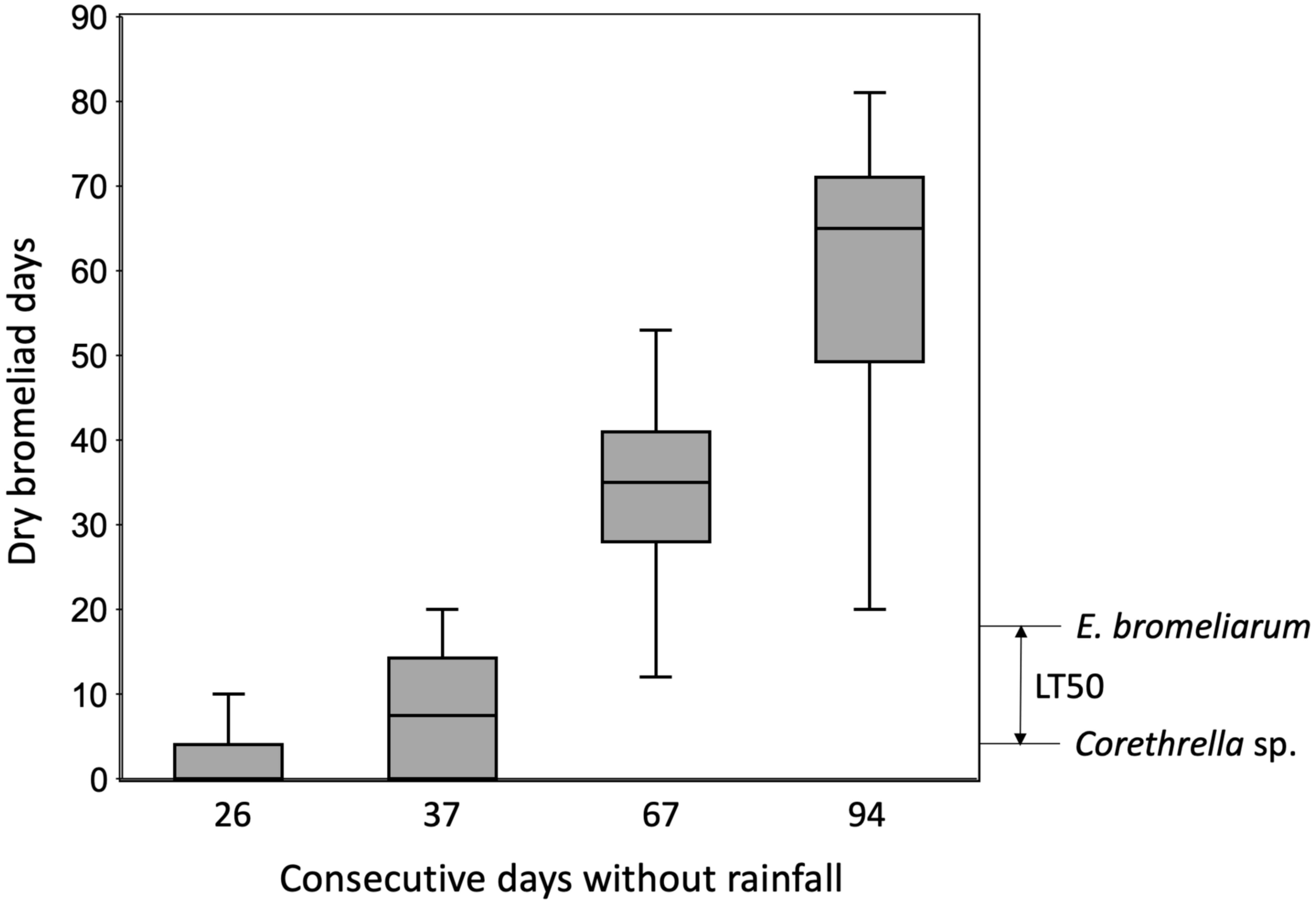
Fig. 2. Selected example of survival curves: A) *Aulophorus superterrenus* (Annelida, Naididae), B) *Microculex stonei* (Diptera, Culicidae), C) *Contacyphon* sp. (Coleoptera, Scirtidae), D) *Microstigma maculatum* (Odonata, Pseudostigmatidae). Dark = treatment, grey = control, "+" = right censored data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

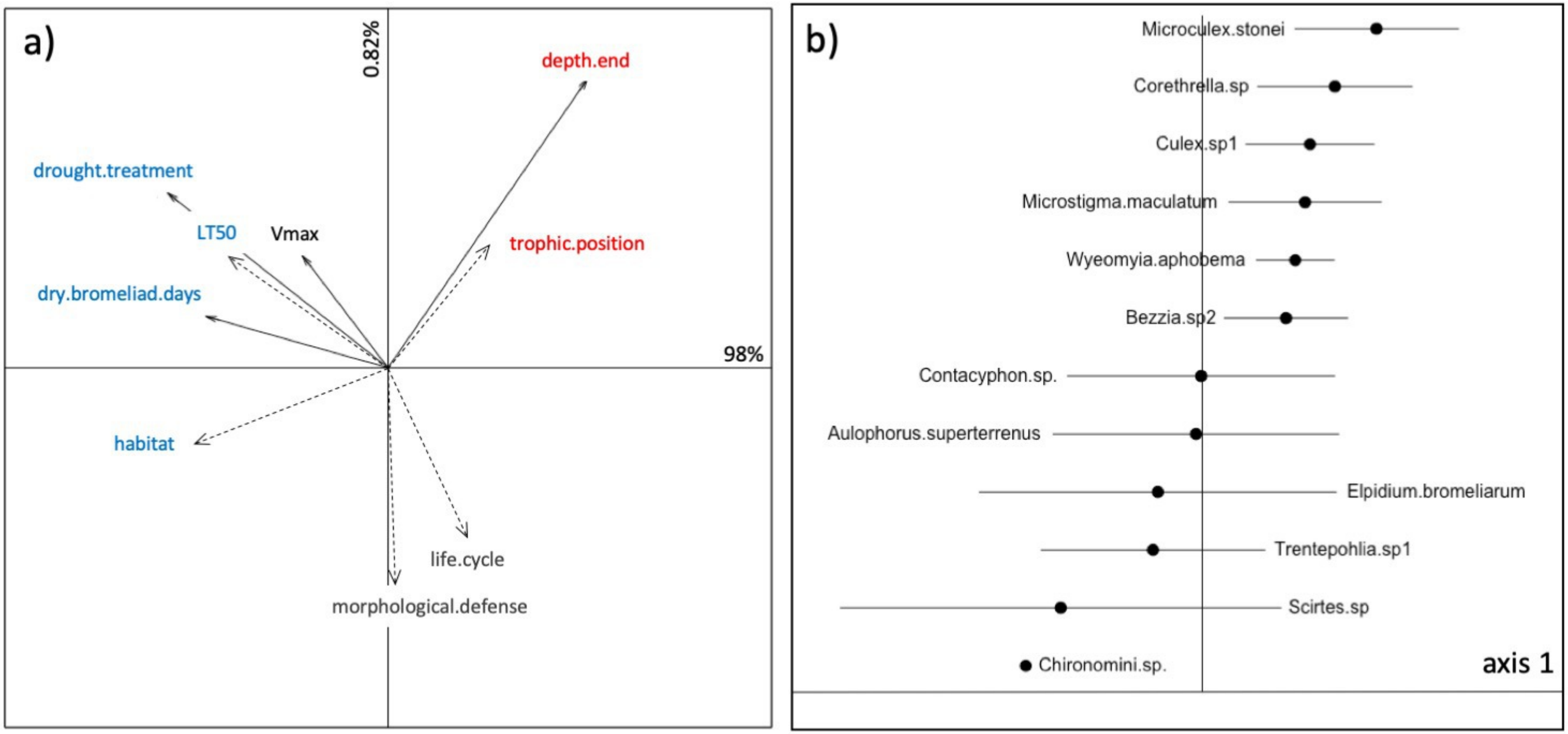
Fig. 3. Boxplots of the number of dry bromeliad days by drought treatment (n= 30 bromeliads per treatment). Boxes delineate the 25th and 75th quartiles, thick lines represent the medians, whiskers extend to maxima and minima. All pairwise Mann–Whitney tests indicate significant differences among treatments ($P < 0.01$). 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.


70 °
60 °
50 °
40 °
0
10
20
30
40
50
Petit Saut
N
50 km


Legend
Control
Treatment
A
B
C
D
Survival probability
1.00
0.75
0.50
0.25
0.00
0
2
4
6
8
Time (days)


90
80
70
60
50
40
30
20
10
0
Dry bromeliad days
26
37
67
94
Consecutive days without rainfall
E. bromeliarum
LT50
Corethrella sp.


a)
0.82%
depth.end
drought.treatment
LT50
Vmax
trophic.position
dry.bromeliad.days
98%
habitat
life.cycle
morphological.defense
b)
Microculex.stonei
Corethrella.sp
Culex.sp1
Microstigma.maculatum
Wyeomyia.aphobema
Bezzia.sp2
Contacyphon.sp.
Aulophorus.superterrenus
Elpidium.bromeliarum
Trentepohlia.sp1
Scirtes.sp
Chironomini.sp.
axis 1