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PRIMARY RESEARCH PAPER

Influence of isolation on the resilience of tank bromeliad ecosystems to drought in a Neotropical rainforest

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Abstract Little is known of how Neotropical freshwater ecosystems will respond to future climate scenarios. In Neotropical rainforests, a substantial fraction of the freshwater available to the aquatic fauna is found within phytotelmata, plant-held waters that form aquatic islands in a terrestrial matrix. We hypothesized that phytotelmata in close proximity have higher resilience capacity to severe drought than the isolated ones, under the assumption that immigration from nearby sources promotes faster recovery. We used rainshelters to emulate an extreme drought (67 days without rainfall) in tank-forming bromeliads arranged in patches of 1, 3 or 6 plants in a primary forest of French Guiana. Habitat size was a stronger determinant of invertebrate species richness and biomass per bromeliad than patch size. Larger bromeliad patches attenuated the adverse effect of drought on the biomass of predators, probably because short-range migration within dense patches allowed individuals to find moist refuges. However, the recovery of aquatic communities and ecosystem functions was mostly supported by in situ resistance, and a rescue effect of immigration was weak. Whilst environmental management plans tend to focus on dense networks of connected water bodies, our study shows that efforts should not omit the isolated ones.

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Introduction

Climate change impacts the distribution of species (Pecl et al., 2017), thereby affecting the structure of multitrophic communities (Harvey et al., 2015), and ecosystem functions (Glassman et al., 2018). Among predicted changes, the increase in the frequency and intensity of droughts in several regions of the World within the next decades (IPCC, 2021) questions the long-term integrity of many ecosystems. In South America, the northern and eastern coasts and Central Amazonia should experience 10 to 50% declines in precipitation (IPCC, 2021). Such forecasts are concerning, as natural environments in the Neotropics are already threatened by extensive habitat destruction (Flores et al., 2024). Freshwater ecosystems are notably vulnerable to drought and habitat modifications, for declining water availability and isolation of remnant water bodies are major threats to aquatic life and ecosystem functions (Oberdorff et al., 2015). We know that drought affects freshwater ecosystems in Neotropical environments, both directly through physiological consequences on the survival and activity of organisms (Rodríguez-Pérez et al., 2018; Céréghino et al., 2020) and indirectly, through food-web-mediated effects on species abundance (Pires et al., 2016; Trzcinski et al., 2016). For instance, drought can either increase predation on litter-processing invertebrates by concentrating species in smaller volumes during water shrinkage (Srivastava, 2006) or release detritivores from predation by disassembling food webs from the top (Ruiz et al., 2022), resulting in negative or positive effects on decomposition rates, respectively (Trzcinski et al., 2016). Isolation could therefore compound the adverse effects of drought on multitrophic communities and ecosystem functions, if colonization rates among spatially discrete habitats are insufficient to compensate drought-induced mortality after the disturbance has passed (Mestre et al., 2018).

In Neotropical rainforests, a substantial fraction of the freshwater available to the aquatic fauna is found within phytotelmata ("plant-held waters," e.g. tree holes, bamboo stems, *Heliconia* bracts, fallen fruit husks, etc.). In particular, tank bromeliads (Bromeliaceae) are conspicuous component of the Neotropical flora, for they occur from the soil to the canopy (as epiphytes), can reach a density of up to 175,000 individuals per hectare and altogether impound up to 50,000 L of water per hectare (Richardson, 1999). The interlocking leaf axils of tank-forming bromeliads collect rainwater (up to a few litres) and leaf litter from the surrounding forest, hence providing a habitat for aquatic organisms (Lounibos & Frank, 2009). Not only tank bromeliads are important to freshwater biodiversity and aquatic–terrestrial energy fluxes in rainforests (de Omena et al., 2017; Céréghino et al., 2018; Dézerald et al., 2018; Pereira et al., 2022) but these phytotelmata also allow ecologists to manipulate a natural aquatic ecosystem that is small and contained (complete census of the aquatic organisms), widely distributed in nature (across environmental gradients) and highly replicated (statistical power). Because bromeliad hydrology is sensitive to short-term weather fluctuations, these small water bodies are relevant to investigate ecological effects of drought in experimental research (Srivastava et al., 2020). Moreover, because the roots of tank bromeliads primarily have an anchoring role (nutrients are obtained from the water tank though leaf trichomes), individual plants can be easily moved, e.g. to test the effects of habitat patch size (e.g. bromeliad isolation or aggregation) on ecosystem responses to water inputs.

Discrete aquatic ecosystems such as phytotelmata, ponds or pools can be seen as freshwater islands in a terrestrial matrix (Jocque & Field, 2014). The theory of island biogeography (MacArthur & Wilson, 2001) predicts that isolated and small islands have lower abundance of organisms and species richness than clumped and larger islands (Steiner & Asgari, 2022). Therefore, once we account for the well-known habitat size effect (Oertli et al., 2002; Petermann et al., 2015), clumped islands (e.g. bromeliads arranged in patches) could theoretically show higher ecosystem resilience to drought than the isolated ones. This could occur because inter-island movements in spatially aggregated systems facilitate access to refuge microhabitats during the drought spell, and/or because higher colonization rates within larger, species-rich metacommunities provide a spatial insurance effect on ecosystem stability (Yachi & Loreau, 1999; Limberger et al., 2019). These assumptions remain to be tested, because the dependence of

ecosystem resilience on in situ resistance (ability to pass a drought event at an active or dormant stage) *vs*. immigration is modulated by species' functional traits (Thompson & Gonzalez, 2016; Limberger et al., 2019; Bonhomme et al., 2021). For instance, Mediterranean wetlands that are subject to harsh seasonal drought are highly resilient because their species exhibit desiccation resistance traits that allow resident populations and communities to cope with frequent hydrological resetting (Ruhí et al., 2012). By comparison, most freshwater species could be considered as "naïve" in the face of extreme hydrological events, and the ecological mechanisms underlying ecosystem resilience after a severe drought are poorly understood (Bonal et al., 2016). We see three reasons for this gap. First, "resilience" includes two components: resistance and recovery (Hodgson et al., 2015). Yet, most studies focused on resistance, the immediate response of communities and ecosystems to drought (Hodgson et al., 2015), ignoring the recovery phase, i.e. the return of the system to an equilibrium state after the drought has passed (Ingrisch & Bahn, 2018). Second, testing the effects of stressors at the whole-ecosystem level in manipulative experiments is a challenging issue. Third, most ecosystem types lack the natural replication needed to support statistically robust models.

In this study, we manipulated drought and the number of bromeliads (bromeliad patch size) whilst controlling for the effect of leaf litter species, the detrital resource that supports the aquatic food web. We used rainshelters to emulate an extreme drought event in bromeliads arranged in patches of various size, and we then examined the effects of drought, patch size and their interaction, on community structure and ecosystem functioning during the course of the post-drought, rewetting phase. We used litter decomposition, an effective metrics of the functional integrity of ecosystems (Benfield et al., 2017) as a proxy of ecosystem functioning. The decomposition of plant litter is a key ecosystem process in nutrient and carbon cycling, because the biological conversion of dead plant biomass to fine particulate, dissolved organic matter and mineral nutrients fuels microbial and plant productivity, and returns CO_2 to the atmosphere (Gessner et al., 1999, 2010; Gholz et al., 2000). Specifically, we asked whether clumped bromeliad ecosystems show higher resistance and faster recovery after an extreme drought, compared to the isolated ones. This could occur either because larger patches host higher species richness and/or densities (Watling et al., 2020), because aggregated bromeliads are more attractive to background colonization (Staddon et al., 2010) or because isolation exacerbates the adverse effects of drought by limiting inter-island dispersion of organisms. Alternatively, ecosystem recovery could be mostly driven by food-web-mediated effects such as trophic control of decomposers (Trzcinski et al., 2016) or asynchronous recovery among feeding guilds (Ruiz et al., 2022). This could occur if resilience is mostly supported by in situ resistance (Fournier et al., 2023) and colonization rates are similar for isolated and aggregated bromeliads.

Material and methods

Study area

Our experiment was conducted in French Guiana from July to November 2021 in the understory of a primary lowland rainforest, near the Petit-Saut Dam (5° 03′ 43″ N, 53° 02′ 46″ W; elevation < 80 m). The climate is tropical humid, with 3000 mm annual precipitation, low seasonal variation in temperature (monthly average: 20.5–33.5 °C) and humidity (70–100%). The dry season extends from September to November, and there is another shorter and irregular dry season in March. The remaining months correspond to the rainy season. Based on daily rainfall records over the past 20 years at the Paracou weather station (8 km away from our field site), the average number of consecutive days without rainfall in a dry season in the area is 26 ± 5.3 days (annual mean ± SD).

Experimental set up

We designed an experiment manipulating drought and bromeliad patch size (1, 3 or 6 bromeliads), with drought applied to patches and ecological responses analysed at the bromeliad level. *Lutheria splendens* (Brongn.) Barfuss & W. Till, 2016 is the only tank bromeliad species in our study area, with a mean density (± SD) of 3558 ± 538 plants per ha (Dézerald et al., 2018). Six months prior to the experiment, we selected 144 *L. splendens* with similar vegetative traits, to minimize the effects of plant size and

complexity on communities. The mean plant diameter (Diam ± SD) was 68.01 ± 9.88 cm, and the number of leaves forming wells (NL ± SD) was 12 ± 2 leaves. The pre-drought conditions for all bromeliads were typical of a rainy season, where plants are filled at 51.8 ± 0.06% of their capacity (see survey in Dézerald et al., 2017). These bromeliads were carefully collected avoiding water spill and arranged as 8 patches of 6 bromeliads, 16 patches of 3 bromeliads and 48 "patches" of 1 bromeliad, thus keeping a similar number of bromeliads (the sample unit) per drought treatment. This design and the sampling scheme are summarized in Table 1. The leaves were overlapping in patches of 3 and 6 bromeliads, to allow for potential movements among tanks by aquatic invertebrates crawling on the aerial parts (Amundrud & Srivastava, 2015; Dézerald et al., 2015). The spatial coordinates of each bromeliad were recorded with a Garmin® field GPS.

After six months of acclimatization, the experiment started with a "dry phase" of 67 consecutive days without rainfall, emulating the most extreme event recorded in the area over the past 20 years (Bonhomme et al., 2021). To emulate drought, we placed rainshelters made of transparent tarpaulin 1 m above 45 patches of 1 to 6 bromeliads (Table 1). These shelters prevent natural rainfall inputs and do not interfere with macroinvertebrate colonization nor increase air temperatures (Marino et al., 2017). During the dry phase, we noted the number of days where all the tanks of the bromeliad remained dry ("dry bromeliad days") before reaching the rewetting phase. Dry bromeliad days in the treatment bromeliads averaged 32 ± 10 days. The remaining patches served as baseline controls (Table 1). Because invertebrate communities show marked temporal changes in the abundance of species in relation to population dynamics at our study site (Dézerald et al., 2017), we evaluated changes in community and ecosystem function in treatments against baseline bromeliads over time, rather than against pre-disturbance bromeliads (Ingrisch & Bahn, 2018).

At the end of the dry phase (T0), we removed the rainshelters and we refilled the plants with filtered rainwater (mesh size of the filter: 150-µm) to their capacity. This initiated the "rewetting phase" (60 days), when plants were subject to natural rainfall. Source patches for colonization consisted of resident bromeliads in the field site. Leaf litter strips were placed in bromeliad tanks at T0, to follow up detrital decomposition as well as the biomass of attached bacteria and fungi during the rewetting phase. Dead leaves of *Goupia glabra* Aubl., 1775 (Goupiaceae) are commonly found in bromeliad tanks (Rodríguez-Pérez et al., 2018) and are among the fastest species to decompose in French Guiana (Coq et al. 2010; Carrias et al., 2020). Freshly fallen leaves were collected using nets placed under a single *G. glabra* tree, to

Table 1 Summary of the experimental and sampling designs

Phase (length)	Treatment	Patch size	No. of patches	No. of plant sampled at each sampling time
Acclimatization (6 months)	–	1	48	–
	–	3	16	–
	–	6	8	–
Dry phase (67 days)	Drought	1	30	–
	Drought	3	10	–
	Drought	6	5	–
	Control	1	18	–
	Control	3	6	–
	Control	6	3	–
Rewetting phase (60 days)	Drought	1	30	10
	Drought	3	10	10
	Drought	6	5	10
	Control	1	18	6
	Control	3	6	6
	Control	6	3	6

Patch size = number of bromeliads in the patch (1, 3 or 6). At each sampling time, invertebrates were returned alive to their original bromeliad after identification to preserve the metacommunity

avoid variation in leaf traits. All leaves were hydrated in filtered rainwater for 24 h and then cut into rectangle strips, avoiding the central vein. Leaf strips were oven-dried at 60 °C for 48 h and weighted to the nearest 0.1 mg. Leaf packs placed in the bromeliads at T0 consisted in one 2×3 cm strip and two 2×4 cm strips of leaf litter, and each bromeliad received two leaf packs in two separate axils. The initial dry weight of a 2×3 cm strip was 0.128 ± 0.019 g (mean ± SD); these pieces were used to estimate decomposition along the rewetting phase. The 2×4 cm strips were used to assess the biomass of bacteria (µg dry weight per gram dry weight litter) and the ergosterol content (µg per mg dry weight leaf litter, a proxy of fungal biomass) within the leaf litter matrix (see below).

Data collection

We followed changes in invertebrate communities (taxonomic composition, species biomass, biomass of functional feeding groups), bacterial and fungal biomass at the surface of the leaf litter, as well as litter decomposition rate after the dry phase by sampling treatment and control bromeliads at 7, 15 and 60 days after T0. At each date, we sampled 48 bromeliads from the different patch sizes, rotating plants across dates so each bromeliad was only sampled once and a constant number of bromeliads was sampled within the treatment and control sets (Table 1). The content of each bromeliad, including live organisms, was returned to the plant after each observation (see below) to prevent defaunation and preserve the metacommunity during the course of the experiment.

In the field, we first collected the leaf litter strips and kept them in a cooler. The biomass of attached bacteria was quantified from counts after sonication of the first set of 2×4 cm leaf strips using a FACSCalibur flow cytometer (Becton Dickinson). The attached biomass (µg dry weight per gram dry weight of litter) was then calculated from bacteria biovolume-to-mass relationships, considering that 10 $\mu m^3 = 0.4$ pg dry weight (Norland et al., 1987). The other set of 2×4 cm leaf strips was used to measure ergosterol content, obtained by lipid extraction and HPLC analysis according to Gessner & Schmitt (1996). In the laboratory, the 2×3 cm leaf strips were oven-dried (60 °C, 48 h) and weighted. Leaf mass loss through time was used to estimate the decomposition rate k (d^{-1}) at the three sampling dates, based on the log-transformed exponential model (Olson, 1963):

$$k = \frac{-\ln\left(\frac{mt}{m0}\right)}{t}$$

where *m0* is the initial leaf mass, *mt* is the mass after decomposition and *t* relates to the time in day (7, 15 or 60 days).

After sampling the leaf litter in the field, the content of bromeliads (water, particulate organic matter, invertebrates) was entirely pipetted out using micropipettes of appropriate dimensions (Céréghino et al., 2011). Though we standardized bromeliad size (i.e. the size of the container), microenvironmental variations (e.g. overhanging tree canopy, throughfall) could mediate the aquatic habitat size available to communities. We therefore recorded the water volume at the time of sampling (WV, mL) to account for actual habitat size. Macroinvertebrates were identified at the species or morphospecies level (hereafter "species"), separated by larval instars (holometabolous insects) or size class, and counted alive in white trays using magnifying glasses. Size–mass relationships developed by us (Dézerald et al., 2017, 2018) and abundance data were then used to calculate species' biomass (mg dry weight per bromeliad). Invertebrates were also partitioned into functional feeding groups (FFGs) sensu Merritt & Cummins (1978), as categorized by Brouard et al. (2012) for bromeliad invertebrates (Supplementary Table S1). These FFGs were: filter feeders (sift fine particulates and living micro-organisms from the column of water); gathering collectors (gather fine particulates of organic matter from the accumulated debris); shredders (chew the leaf litter and other coarse particulate organic matter); scrapers (scrape off the surface of the leaf litter and coarse organic matter to feed on biofilm layers); and predators (feed on other animals).

Data analysis

Invertebrate community structure

We first removed from the dataset one plant in which we found no invertebrates (from a patch of 6 bromeliads subjected to drought) as well as 8 invertebrate species occurring in less than two bromeliads out of 144, that were considered as stochastic occurrences.

The final dataset was composed of 14 species × 143 bromeliads. Prior to further analysis, we evaluated spatial autocorrelation of invertebrate communities among bromeliads, using partial Mantel test in the *vegan* R package (Supplementary Material S2). Mantel tests showed no evidence for spatial autocorrelation of species assemblages among bromeliads (Supplementary Material S2). A non-spatial approach was thus suitable in subsequent models.

Variation in community structure (species and their biomass) among drought and patch size treatments was analysed with multivariate general linear models developed in the *mvabund* R package (Wang et al., 2012). We preferred this method over distance-based analysis because it avoids potentially misleading results due to misspecification of mean–variation relationship (Warton et al., 2012). We built a full generalized linear model with the main and interactive effects of drought (2 levels: drought and control), patch size (3 levels: 1, 3 and 6 bromeliads) and time after T0 (3 levels: 7, 15 and 60 days). We added the number of bromeliad leaves and water volume (habitat complexity and size) as well as dry bromeliad days as covariates. The model was fitted to a negative binomial distribution to account for overdispersion. From this full model, we identified the best fitting multivariate model based on the Akaike information criterion (AIC). Model assumptions were checked graphically. We tested for the importance of each explanatory variable with likelihood ratio tests, comparing the best model previously identified with other identical models minus one of the explanatory variables. Then, we tested multivariate hypotheses about the main and interactive effects of treatments with the function *"anova.manyglm,"* running 6 000 pit-trap resampling iterations for each model to estimate p-values. To highlight which species explained the community response to treatment, this function fits separate generalized linear models for each species (Supplementary Table S3).

Invertebrate species richness and FFGs

We used linear models to determine the main and interactive effects of drought, bromeliad patch size and time after T0 on species richness and on the biomass of the various FFGs. Dry bromeliad days, number of bromeliad leaves and water volume were added as covariates. Biomass values were log-transformed to meet the assumption of normality. For each model, we started with a full model containing all treatment variables and covariates. We used stepwise regression to select the best model based on the AIC, and we only assessed the significance of the predicted variables of the retained model.

Ecosystem functioning

Changes in multivariate causal relationships among components of the bromeliad ecosystem during the rewetting phase were studied with structural equation modelling (SEM; Grace et al., 2012, 2014). We constructed a model of hypothesized relationships within a path diagram for each sampling time (7, 15 and 60 days). Relationships involved drought, bromeliad patch size, the biomass of invertebrate detritivores and predators, the biomass of fungi and bacteria at the surface of the leaf litter, and decomposition rates. "Detritivores" consisted in the sum of leaf shredder and scraper biomass. These two groups have a mechanical action on the leaf litter and are usually considered as good predictors of decomposition rates (Srivastava, 2006). We used the "psem" function from the "piecewiseSEM" R package (Lefcheck, 2016) to create SEMs where each part represents a linear model between the explanatory variables and the explained variable. Each SEM was built with five linear models that were selected based on AICc and graphically verification of assumptions. SEMs allowed us to include correlated errors for variables with a relationship that was neither causal nor unidirectional. We included correlated errors involving bacteria and fungi to account for their indirect interactions through the decomposition process. Following the same method as previous analysis, model selection for invertebrate biomass was based on multiple linear models including the number of leaves, water volume and dry bromeliad days as covariables (Supplementary Table S4). Patch size was categorical (1, 3 or 6 bromeliads), so we compared the effect of each level by running post hoc estimated marginal means adjusted by Tukey tests, using the *emmeans* R package. (Supplementary Table S5). Because we were primarily interested in relationships between treatments, biological communities and decomposition, the potential effects of covariates were not included in figures showing the final path diagrams,

but can be found (if any) in supplementary material (Table S4). All analyses were conducted in R version 4.1.1 (R Core Team 2021).

Results

Invertebrate species richness

We collected a total of 13,600 individuals and identified 22 invertebrate species from all bromeliads (see Table S1 for affiliations to taxonomic and functional groups). Insects represented 73% of the species, among which 81% were Diptera. Bromeliad patch size had no effect on the species richness found in individual bromeliads. The number of dry bromeliad days had a negative effect on species richness per bromeliad (Table 2, estimate = −0.029 ± 0.015, $P < 0.05$) on the contrary of water volume that correlated positively (Table 2, estimate = 0.017 ± 0.002, $P < 0.001$). The pure effect of drought on species richness was not significant. However, in interaction at 60 days after rewetting, species richness was significantly higher than in earlier sampling time (Table 2, estimate = 1.364 ± 0.581, $P < 0.02$).

Table 2 Linear models testing the influence of drought, bromeliad patch size, time after rewetting and habitat covariables on macroinvertebrate species richness

	Estimate	Std error	T value	P value
(Intercept)	3.525	0.353	9.982	$<2.22*10^{-16}$***
Drought	−0.613	0.638	−0.96	0.339
T15	0.215	0.454	0.473	0.637
T60	3.815	0.462	8.251	$1.249*10^{-13}$***
Dry bromeliad days	−0.029	0.0145	−2.003	0.0472*
WV	0.017	0.002	7.755	$1.92*10^{-12}$***
Drought: T15	0.443	0.575	0.771	0.442
Drought: T60	1.364	0.581	2.349	0.02*

Estimates ± standard errors correspond to the best fitting models according to AIC scores. Adjusted $R^2 = 0.767$, F statistics = 67.741, $P < 2.22*10^{-16}$. Variables not shown were not retained in the final model. WV = water volume at the time of sampling (ml), T15 and T60 = 15 and 60 days after rewetting, N. brom 3 and N. brom 6 = patches of 3 and 6 bromeliads. *$P < 0.05$, ***$P < 0.001$

Invertebrate community structure

Overall, variation in community structure was explained by the interaction between drought and time after T0, and by the number of dry bromeliad days (Table 3). In other words, changes in community structure over time were greater in bromeliads that suffered drought compared to the control ones, and the extent of changes in the treatment plants was modulated by the number of dry bromeliad days but not by bromeliad patch size.

Not all species were equally affected by drought (Table S3). Drought mostly provoked a decline in the biomass of *Anopheles neivai* Howard, Dyar & Knab, 1913 and *Culex stonei* Lane & Whitman, 1943 (filter-feeding Culicidae), *Toxorhynchites* sp. (Culicidae, top predator), *Microstigma maculatum* Hagen, 1860 (Odonate, top predator) and Cecidomyiidae (diptera, bromeliad leaf piercer). Biomasses, however, increased at 15 and 60 days after rewetting, as shown by the positive interaction of drought and time for these species. Conversely, drought had a positive impact on the biomass of *Culex* sp1 (filter-feeding Culicidae) at day 7, but their biomass declined at day 15 and day 60. Regardless of drought, bromeliad patch size had the strongest, negative effects on the biomass of the top predators *Microstigma maculatum* and *Toxorhynchites* sp., and the filter feeder *Culex stonei*, mostly at the intermediate patch size (3 bromeliads) (Table S3). Other species were weakly or not affected by drought and patch size.

Table 3 Analysis of deviance of the best fitting multivariate generalized linear model, according to "AICsum" scores and assumption assessment (graphically checked), explaining invertebrate community structure in the bromeliads

	Residual degrees of freedom	Deviance	P value
(Intercept)	142	–	–
Drought	141	47.8220993	0.0038**
Number of bromeliads	139	34.3585196	0.2712
Time from T0	137	519.793364	0.0001***
Dry bromeliad days	136	43.3885061	0.0011**
Water volume	135	152.248321	0.0001***
Drought: Time from T0	133	109.11115	0.0001**

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Functional feeding groups

The biomass of all FFGs was negatively affected by drought, either as a factor (significantly lower biomass in treatment bromeliads compared to baseline bromeliads) or more specifically expressed as number of dry bromeliad days (Fig. 1, Table 4). Marginally and highly significant interactions between drought and bromeliad patch size were observed in predators ($P<0.1$) and collectors ($P<0.01$), respectively. Whilst the pure effect of drought was to reduce the biomass of predators and collectors, negative deviations from the baseline were the lowest in patches of 3 ($P<0.01$) and 6 bromeliads ($P<0.05$), respectively. Finally, we note that biomass correlated positively with water volume in all FFGs (P values <0.05 to 0.001). We did not find significant interaction between drought and habitat patch size predictors.

Ecosystem resilience

Our SEM models allowed us to examine direct and indirect effects of drought and patch size on the relationships among components of the bromeliad ecosystem through time (Fig. 2, Table S4). One week after rewetting (day 7, Fig. 2a), predator and

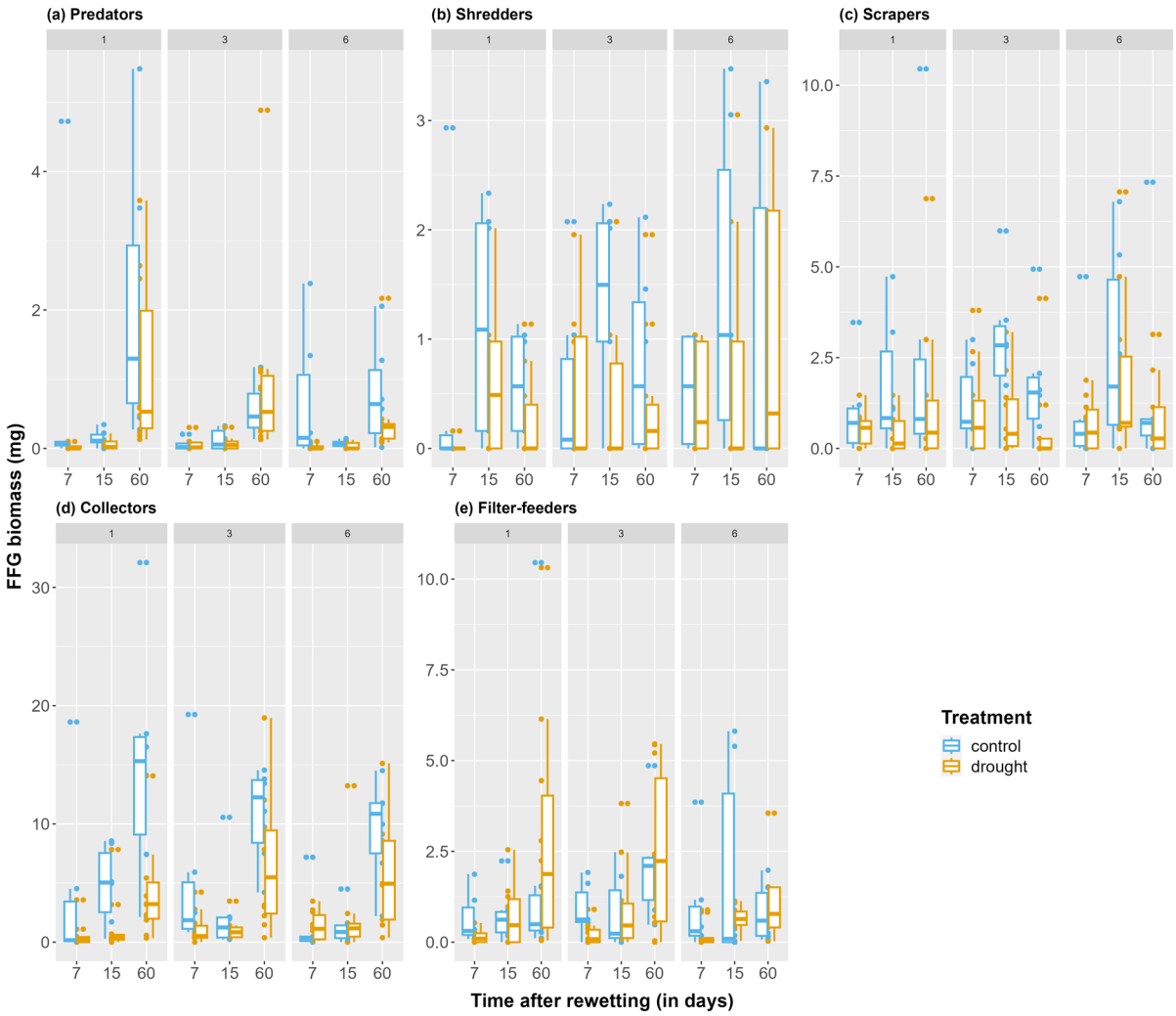

Fig. 1 Changes in functional feeding group (FFG) biomass (mg dry weight per bromeliad) in patches of 1, 3 and 6 bromeliads, in both control and treatment sets

Table 4 Influence of drought, bromeliad patch size, time after rewetting and their interaction on the biomass of invertebrate FFGs

	Predators	Shredders	Scrapers	Collectors	Filter feeders
R^2 adjusted	0.512	0.062	0.118	0.47	0.464
F statistic	13.426	4.1	10.525	16.717	21.464
(Intercept)	0.677 ± 0.187***	0.382 ± 0.081***	0.626 ± 0.106***	0.903 ± 0.197***	0.127 ± 0.108
Drought	− 0.061 ± 0.148	− 0.196 ± 0.077*	–	− 0.859 ± 0.202***	− 0.407 ± 0.125**
T15	− 0.202 ± 0.092*	− 0.222 ± 0.092	–	0.104 ± 0.138	− 0.007 ± 0.139
T60	0.248 ± 0.094**	0.116 ± 0.092	–	1.15 ± 0.140***	0.037 ± 0.142
Brom 3	− 0.275 ± 0.092**	–	–	− 0.033 ± 0.226	–
Brom 6	− 0.149 ± 0.092	–	–	− 0.491 ± 0.226*	–
Dry bromeliad days	− 0.009 ± 0.003**	–	− 0.01 ± 0.003***	–	–
NL	− 0.04 ± 0.015*	–	–	–	–
WV	0.003 ± 0.001***	–	0.002 ± 0.001*	0.004 ± 0.001***	0.006 ± 0.0006***
Drought: Brom 3	0.221 ± 0.116$	–	–	0.27 ± 0.286	–
Drought: Brom 6	0.048 ± 0.116	–	–	0.842 ± 0.286**	–
Drought: T15	0.196 ± 0.116$	–	–	–	0.305 ± 0.176$
Drought: T60	0.206 ± 0.117$	–	–	–	0.673 ± 0.178***

Dry bromeliad days, number of bromeliad leaves (NL) and water volume (WV) were included in the models as covariables (see text). T15 and T60 = 15 and 60 days after rewetting, Brom 3 and Brom 6 = patches of 3 and 6 bromeliads. Estimates and their standard deviation are for the best fitting linear models based on AIC scores. Variables not shown (–) were not retained in the best fitting model. $$P < 0.1$$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

detritivore biomass (here shredders + scrapers) were significantly reduced in treatment bromeliads compared to the control ones, denoting drought-induced mortality ($P < 0.05$ and $P < 0.001$, respectively). Detritivore and bacterial biomass were negatively related to predator and detritivore biomass, respectively ($P < 0.01$ and $P < 0.05$), suggesting a top-down control of populations. Decomposition rates were positively affected by invertebrate detritivore biomass (detritivore–decomposition SEM path = 0.001, $P < 0.05$). Bromeliad patch size had no significant influence on any of the biotic compartments of the system at this stage. Two weeks after the drought (day 15, Fig. 2b), there was no significant effect of drought on detritivore biomass, that is, no difference between treatment and control bromeliads, suggesting recovery of the shredder and scraper FFGs. Predators were still suffering the adverse effects of drought (drought–predators SEM path = − 0.058, $P < 0.01$); however, the negative deviation from baseline bromeliads was lower within patches of 6 plants compared to isolated bromeliads ($P < 0.05$, Fig. 1, Supplementary Tables S4, S5). Correlated errors indicated a positive relationship between fungal and bacterial biomass at the surface of the leaf litter ($P < 0.01$). Last, decomposition did not relate to any of the biotic compartments. Two months after rewetting (day 60, Fig. 2c), predator biomass was enhanced in treatment bromeliads (drought–predators SEM path = 0.915, $P < 0.01$), and there was no significant causal relationship between predator and detritivore biomass. Detritivores significantly reduced bacterial biomass (detritivore–bacteria SEM path = − 0.327, $P < 0.05$). Decomposition rates increased with fungal biomass (fungi–decomposition SEM path = 0.004, $P < 0.01$). At this time, correlated errors indicated a negative relationship between fungal and bacterial biomass at the surface of the leaf litter ($P < 0.05$). Among the habitat covariables, water volume had a significant positive effect on detritivore biomass at day 7 and on predator biomass at all sampling times (Table S4, $P < 0.01$), and a significant negative effect on bacterial biomass ($P < 0.05$) and fungal biomass ($P < 0.001$) at day 15 and day 60, respectively. Among covariables, dry bromeliad days had a marginally negative impact on detritivore biomass ($P = 0.05$) and a significant negative effect on predator biomass ($P < 0.001$) after 60 days. Finally, the number of bromeliad leaves (habitat complexity) negatively affected predator biomass at day 7 ($P < 0.01$) but correlated positively with fungal biomass at day 60 ($P < 0.01$).

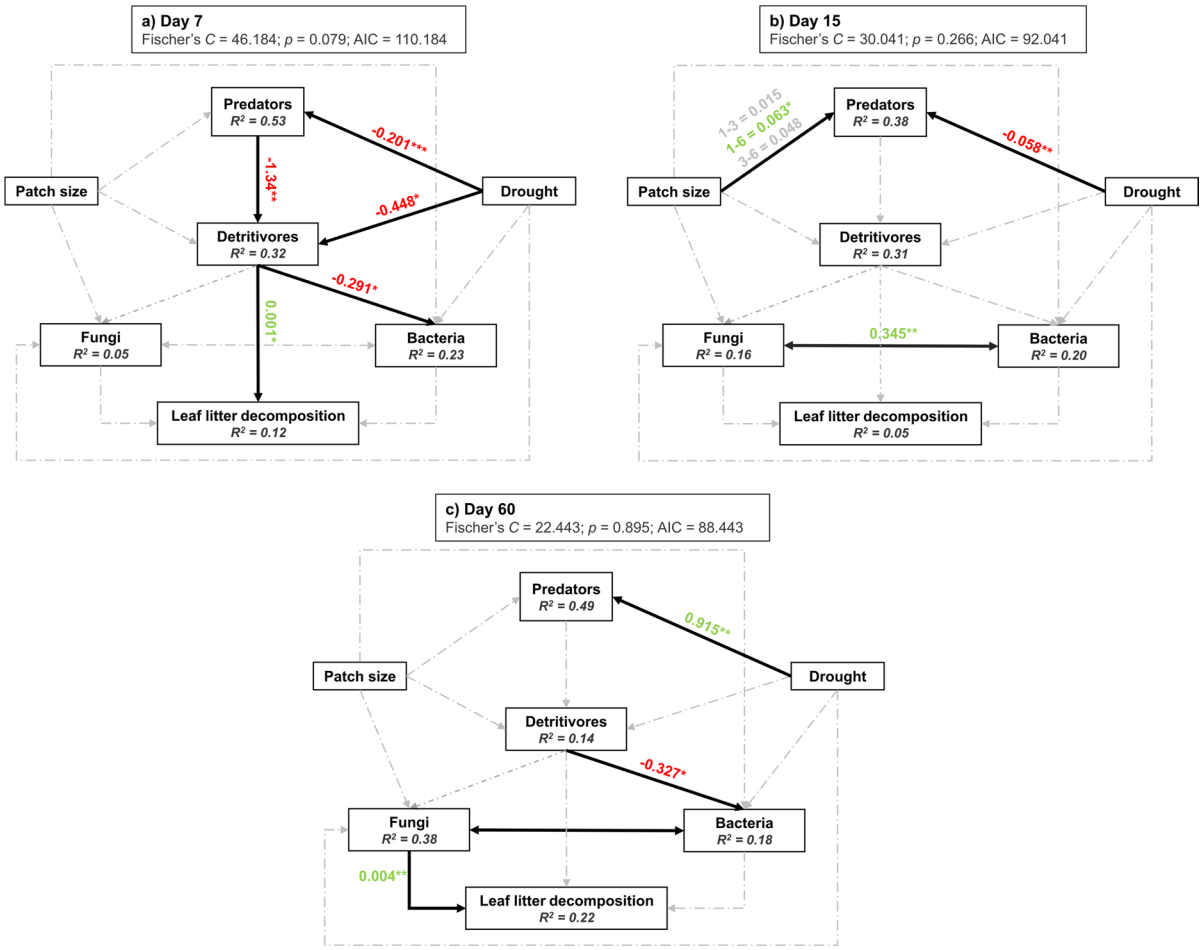

Fig. 2 Structural equation modelling (SEM) of the relationships between drought, bromeliad patch size, biotic compartments (predators, detritivores, bacteria, fungi) and decomposition rate for each sampling time. Linear relationships are represented by simple arrows, and double arrows represent correlated errors. Solid lines indicate a significant effect. Standardized coefficients for each significant path indicate its weight. Coefficients for patch size–predator path at day 15 represent the estimates of contrast post hoc tests. Green and red numbers indicate positive and negative relationships, respectively (*$P<0.05$; **$P<0.01$; ***$P<0.001$). Figure was created using PowerPoint Office 2019 and edited with Inkscape

Discussion

Understanding whether and how isolation of water bodies in rainforests affects their biodiversity and resilience to drought is important to our knowledge of the ecology of Neotropical freshwater environments under environmental constraints. It also helps anticipate management efforts in the perspective of climate change adaptation (Boucek & Rehage, 2014). We found that habitat size (water volume) was a stronger determinant of invertebrate species richness and biomass per bromeliad than patch size, though the biomass of certain species (notably the large-bodied predators) declined at intermediate patch size. When ecosystems were subject to a severe drought, larger bromeliad patches attenuated the adverse effect on the biomass of predators, probably because short-range migration in dense patches allowed individuals to find moist refuges (see discussion below). Still, the recovery of aquatic communities and ecosystem functions within tank bromeliads was mostly supported by in situ resistance, whilst overall, the rescue effect of immigration was weak. The resilience of multitrophic aquatic communities and ecosystem functions thus relied on survival and on the persistence of suitable habitats. Whilst environmental management plans

tend to focus on dense networks of connected water bodies (Hill et al., 2021), our study shows that efforts should not omit the small, isolated ones.

Contrary to our expectation, bromeliad invertebrate communities in close proximity did not recover faster after an extreme drought than the isolated ones. There was no significant interaction between bromeliad patch size and time after rewetting in any of our models, that is, temporal changes in species and FFG biomass after a drought were not conditioned by island aggregation vs. isolation. We conclude that inter-island colonization rates among clumped bromeliads were negligible compared to background colonization from the surrounding forest, and that colonization rates were similar for all bromeliads. Because our manipulations were carried out at the level of bromeliad patches, it is likely that the regional species pool contributed to colonization through oviposition from undisturbed patches. The female adults of bromeliad insects in particular can travel distances ranging from a few hundred metres to 25 km to lay their eggs (Guzman & Srivastava, 2020). This background colonization, which is challenging to control in a field experiment, could be seen as undesired noise in our results. However, assuming that (i) recovery mostly relied on survival (see paragraph below) and (ii) colonization depends on the amount of source patches but not necessarily proximity (Watling et al., 2020), we conclude that the resilience capacity of the bromeliad ecosystem should decline with increasing spatial extent of drought events, *e.g.* from local to regional (López-Hoffman et al., 2013). Finally, though we standardized bromeliad (container) size, rainfall and variation in the immediate environment of each bromeliad (e.g. overhanging tree canopy, throughfall) created spatial variation in the actual habitat size (water volume) during the post-drought phase. As predicted by theory, larger aquatic habitats at any given time hosted more species and individuals than the smaller ones (see also Petermann et al., 2015). Altogether, these results mean that the resilience of the bromeliad ecosystem to drought will be more sensitive to habitat-dependent variation in the abundance of organisms among individual spatial units, rather than to spatial aggregation of habitats.

In line with our alternative hypothesis, in situ resistance was an important driver of invertebrate recovery to drought (see also Bonhomme et al., 2021; Fournier et al., 2023). Resistance was mostly apparent during the first days after rewetting (7 days), where species suffered mortality (lower abundances than in the control bromeliads), but overall were still occurring in the treatment bromeliads. Survival to drought depends on desiccation resistance traits (Céréghino et al., 2020) and on whether individuals can find moist refuges that buffer adverse conditions (Scheffers et al., 2014a, b; Strachan et al., 2015). Hence, not all species were equally affected. Interestingly, the negative deviation from baseline predator and collector biomass was less important in the larger groups of bromeliads than in isolated bromeliads. Therefore, though the community-weighted signal of patch size was not significant (Table 3), some species could take advantage of large patches to maintain larger populations (supplementary Table S3). Many aquatic larvae of bromeliad insects, notably Odonates and Tipulidae, are able to crawl on the aerial parts of leaves to find water or food in more suitable leaf axils (Lounibos & Frank, 2009; Dézerald et al., 2015). Other invertebrate species are transported between adjacent bromeliads by means of phoresy (e.g. the annelid *Aulophorus superterrenus* Michaelsen, 1912, *Elpidium bromeliarum* Müller, 1880, see Lopez et al., 2005). Assuming that habitat complexity plays an important climate buffering role in all ecosystem types (Scheffers et al., 2014a, b), our observations suggest that bromeliad aggregation can dampen the adverse effects of drought in some invertebrate species, by facilitating access to refuge microhabitats. This could be particularly true of species such as Odonates that use spatial avoidance as a prevailing strategy to cope with water shrinkage (Dézerald et al., 2015). Two weeks after rewetting (day 15), we observed the combined effects of resistance and re-colonization. Re-colonization was suggested by a sharp increase in the abundance of species with very short generation times such as Culicidae (< 15 days, e.g. *Anopheles neivai*, *Culex stonei*; Dézerald et al., 2017). At the end of our experiment (day 60), species returned to, or even exceeded, their baseline abundance. A return to a "normal" state of communities after 15 to 60 days might a priori suggest either a weak impact of extreme drought or high resilience of aquatic invertebrates in the bromeliad ecosystem. Nevertheless, resilience should not be interpreted in absolute time units (e.g. days), but in biologically relevant units such as generation times of the study populations (Srivastava et al., 2004). We know that the time from

hatching to adult stage of bromeliad invertebrates at our study site ranges from 10 to 54 days in most species (i.e. less than 60 days), and from 70 to 99 days in two species (*Cyphon* sp., *Elpidium bromeliarum*; Dézerald et al., 2017). This means that up to 6 successive generations were required to return to a reference state of populations.

Theory predicts that food webs subject to environmental disturbance disassemble from the upper trophic levels (Holt, 1996; Ledger et al., 2011), resulting in a disruption of species interactions and ecosystem functions (Mestre et al., 2018). Our results were partially consistent with these predictions, as predators were more sensitive to drought and bromeliad patch size than their detritivorous prey, and the recovery of predator biomass lagged behind that of detritivores. Yet, despite the negative effects of drought on predator and detritivore biomass, significant SEM pathways at incipient rewetting (day 7) depicted a typical top-down control of trophic levels and litter decomposition. However, ecological determinism of food web components and decomposition, including abiotic factors and trophic interactions, declined over time as both survivors and colonizers rebuilt communities. It is therefore likely that homogeneous colonization rates in our study area (see above) reduced the statistical variance within most functional groups (including macro- and micro-organisms) after 7 days, so models detected few causal relationships at days 15 and 60. Among these relationships, the SEM suggested a shift from a detritivore-based to a microbial-based decomposition at day 60. Although we did not directly test for the pure effect of micro-organisms on decomposition (e.g. by excluding invertebrates with fine mesh enclosures), this result is consistent with previous findings of a dominant role of fungal biomass and activity upon litter decomposition in the geographic area (Leroy et al., 2017; Rodríguez-Pérez et al., 2018). Finally, we note that the lasting effect of drought on predator biomass included a positive effect at day 60, i.e. predator biomass in the treatment plants exceeded those found in control plants. Interestingly, filter feeders, the most frequent prey of all invertebrate predators in bromeliads (Dézerald et al., 2013; Trzcinski et al., 2016), reached much higher biomass values in the treatment than in the control bromeliads from day 15 to day 60 (Table 4). It is thus likely that the predator biomass increased with a time lag in response to increasing prey availability. This result also suggests a shift from environmental determinism to bottom-up control of predator biomass after a drought that could potentially be modulated by the harshness of the disturbance and the biomass of prey.

A mechanistic understanding of aquatic ecosystem resistance and recovery to drought is relevant to fundamental and applied ecology in geographic areas such as the Neotropics, where little is known of how ecosystems will respond to rainfall reductions under future climate scenarios (Crausbay et al., 2020). Theory often suggests that small water bodies or wetlands in close proximity could benefit from a rescue effect of immigration from the nearby ecosystems, something that should promote the restoration of biodiversity and ecological functions after a drought event (Jeffries, 1994; Chanut et al., 2023). Yet, our study of small but widespread phytotelmata supports the idea that the effects of in situ resistance and trophic interactions on the post-drought trajectory of aquatic ecosystems exceed those of immigration and habitat isolation in Neotropical rainforests. For fundamental research, functional traits that allow species to move within microhabitats and exploit favourable microclimates should therefore be relevant to further development of predictive models (Scheffers, et al., 2014a, b; Céréghino et al., 2020). For applied research, our results add to the growing evidence that mitigation-oriented plans should promote environments that foster the provision of microclimatic buffering in rainforests (Braem et al., 2023), without omitting the small, isolated habitats.

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Data availability The dataset and code can be found in supplementary material.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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References

Amundrud, S. L. & D. S. Srivastava, 2015. Drought sensitivity predicts habitat size sensitivity in an aquatic ecosystem. Ecology 96(7): 1957–1965. https://doi.org/10.1890/14-1828.1.

Benfield, E. F., K. M. Fritz & S. D. Tiegs, 2017. Leaf-Litter Breakdown. In Methods in Stream Ecology. Elsevier: 71–82. https://doi.org/10.1016/B978-0-12-813047-6.00005-X.

Bonal, D., B. Burban, C. Stahl, F. Wagner & B. Hérault, 2016. The response of tropical rainforests to drought—lessons from recent research and future prospects. Annals of Forest Science 73(1): 27–44. https://doi.org/10.1007/s13595-015-0522-5.

Bonhomme, C., R. Céréghino, J. Carrias, A. Compin, B. Corbara, V. E. J. Jassey, J. Leflaive, V. F. Farjalla, N. A. C. Marino, T. Rota, D. S. Srivastava & C. Leroy, 2021. In situ resistance, not immigration, supports invertebrate community resilience to drought intensification in a Neotropical ecosystem. Journal of Animal Ecology 90(9): 2015–2026. https://doi.org/10.1111/1365-2656.13392.

Boucek, R. E. & J. S. Rehage, 2014. Climate extremes drive changes in functional community structure. Global Change Biology 20(6): 1821–1831. https://doi.org/10.1111/gcb.12574.

Braem, S., M. Crucifix, C. Nieberding & H. Van Dyck, 2023. Microclimatic buffering in forest, agricultural, and urban landscapes through the lens of a grass-feeding insect. Ecosphere 14(7): e4611. https://doi.org/10.1002/ecs2.4611.

Brouard, O., R. Céréghino, B. Corbara, C. Leroy, L. Pelozuelo, A. Dejean & J.-F. Carrias, 2012. Understorey environments influence functional diversity in tank-bromeliad ecosystems: Functional diversity in bromeliad ecosystems. Freshwater Biology 57(4): 815–823. https://doi.org/10.1111/j.1365-2427.2012.02749.x.

Carrias, J. F., M. Gerphagnon, H. Rodríguez-Pérez, G. Borrel, C. Loiseau, B. Corbara, R. Céréghino, I. Mary & C. Leroy, 2020. Resource availability drives bacterial succession during leaf-litter decomposition in a bromeliad ecosystem. FEMS Microbiology Ecology, 96(4): fiaa045. https://doi.org/10.1093/femsec/fiaa045

Céréghino, R., C. Leroy, J.-F. Carrias, L. Pelozuelo, C. Ségura, C. Bosc, A. Dejean & B. Corbara, 2011. Ant-plant mutualisms promote functional diversity in phytotelm communities: mutualism promotes functional diversity. Functional Ecology 25(5): 954–963. https://doi.org/10.1111/j.1365-2435.2011.01863.x.

Céréghino, R., V. D. Pillar, D. S. Srivastava, P. M. Omena, A. A. M. MacDonald, I. M. Barberis, B. Corbara, L. M. Guzman, C. Leroy, F. Ospina Bautista, G. Q. Romero, M. K. Trzcinski, P. Kratina, V. J. Debastiani, A. Z. Gonçalves, N. A. C. Marino, V. F. Farjalla, B. A. Richardson, M. J. Richardson, D. Dézerald, B. Gilbert, J. Petermann, S. Talaga, G. C. O. Piccoli, M. Jocqué & G. Montero, 2018. Constraints on the functional trait space of aquatic invertebrates in bromeliads. Functional Ecology 32(10): 2435–2447. https://doi.org/10.1111/1365-2435.13141.

Céréghino, R., L. Françoise, C. Bonhomme, J.-F. Carrias, A. Compin, B. Corbara, V. Jassey, J. Leflaive, T. Rota, V. Farjalla & C. Leroy, 2020. Desiccation resistance traits predict freshwater invertebrate survival and community response to drought scenarios in a Neotropical ecosystem. Ecological Indicators 119: 106839. https://doi.org/10.1016/j.ecolind.2020.106839.

Chanut, P. C. M., F. J. Burdon, T. Datry & C. T. Robinson, 2023. Convergence in floodplain pond communities indicates different pathways to community assembly. Aquatic Sciences 85(2): 59. https://doi.org/10.1007/s00027-023-00957-9.

Coq, S., J.-M. Souquet, E. Meudec, V. Cheynier & S. Hättenschwiler, 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology 91(7): 2080–2091. https://doi.org/10.1890/09-1076.1.

Crausbay, S. D., J. Betancourt, J. Bradford, J. Cartwright, W. C. Dennison, J. Dunham, C. A. F. Enquist, A. G. Frazier, K. R. Hall, J. S. Littell, C. H. Luce, R. Palmer, A. R. Ramirez, I. Rangwala, L. Thompson, B. M. Walsh & S. Carter, 2020. Unfamiliar territory: emerging themes for ecological drought research and management. One Earth 3(3): 337–353. https://doi.org/10.1016/j.oneear.2020.08.019.

de Omena, P. M., D. S. Srivastava & G. Q. Romero, 2017. Does the strength of cross-ecosystem trophic cascades vary with ecosystem size? A test using a natural microcosm. Freshwater Biology 62(4): 724–736. https://doi.org/10.1111/fwb.12897.

Dézerald, O., C. Leroy, B. Corbara, J.-F. Carrias, L. Pélozuelo, A. Dejean & R. Céréghino, 2013. Food-web structure in relation to environmental gradients and predator-prey ratios in tank-bromeliad ecosystems. PLoS ONE 8(8): e71735. https://doi.org/10.1371/journal.pone.0071735.

Dézerald, O., R. Céréghino, B. Corbara, A. Dejean & C. Leroy, 2015. Functional trait responses of aquatic macroinvertebrates to simulated drought in a Neotropical bromeliad ecosystem. Freshwater Biology 60(9): 1917–1929. https://doi.org/10.1111/fwb.12621.

Dézerald, O., C. Leroy, B. Corbara, A. Dejean, S. Talaga & R. Céréghino, 2017. Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads.

Freshwater Biology 62(2): 229–242. https://doi.org/10.1111/fwb.12862.

Dézerald, O., C. Leroy, B. Corbara, A. Dejean, S. Talaga & R. Céréghino, 2018. Tank bromeliads sustain high secondary production in neotropical forests. Aquatic Sciences 80(2): 14. https://doi.org/10.1007/s00027-018-0566-3.

Flores, B. M., E. Montoya, B. Sakschewski, N. Nascimento, A. Staal, R. A. Betts, C. Levis, D. M. Lapola, A. Esquível-Muelbert, C. Jakovac, C. A. Nobre, R. S. Oliveira, L. S. Borma, D. Nian, N. Boers, S. B. Hecht, H. ter Steege, J. Arieira, I. L. Lucas, E. Berenguer, J. A. Marengo, L. V. Gatti, C. R. C. Mattos & M. Hirota, 2024. Critical transitions in the Amazon forest system. Nature 626(7999): 555. https://doi.org/10.1038/s41586-023-06970-0.

Fournier, R. J., G. De Mendoza, R. Sarremejane & A. Ruhi, 2023. Isolation controls reestablishment mechanisms and post-drying community structure in an intermittent stream. Ecology 104(2): e3911. https://doi.org/10.1002/ecy.3911.

Gessner, M. O. & A. L. Schmitt, 1996. Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. Applied and Environmental Microbiology 62(2): 415–419. https://doi.org/10.1128/aem.62.2.415-419.1996.

Gessner, M. O., E. Chauvet & M. Dobson, 1999. A perspective on leaf litter breakdown in streams. Oikos 85(2): 377–384. https://doi.org/10.2307/3546505.

Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall & S. Hättenschwiler, 2010. Diversity meets decomposition. Trends in Ecology & Evolution 25(6): 372–380. https://doi.org/10.1016/j.tree.2010.01.010.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon & W. J. Parton, 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6(7): 751–765. https://doi.org/10.1046/j.1365-2486.2000.00349.x.

Glassman, S. I., C. Weihe, J. Li, M. B. N. Albright, C. I. Looby, A. C. Martiny, K. K. Treseder, S. D. Allison & J. B. H. Martiny, 2018. Decomposition responses to climate depend on microbial community composition. Proceedings of the National Academy of Sciences 115(47): 11994–11999. https://doi.org/10.1073/pnas.1811269115.

Grace, J. B., D. R. Schoolmaster, G. R. Guntenspergen, A. M. Little, B. R. Mitchell, K. M. Miller & E. W. Schweiger, 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3(8): 73. https://doi.org/10.1890/ES12-00048.1.

Grace, J. B., P. B. Adler, W. Stanley Harpole, E. T. Borer & E. W. Seabloom, 2014. Causal networks clarify productivity–richness interrelations, bivariate plots do not. Functional Ecology 28(4): 787–798. https://doi.org/10.1111/1365-2435.12269.

Guzman, L. M. & D. S. Srivastava, 2020. Genomic variation among populations provides insight into the causes of metacommunity survival. Ecology 101(12): e03182. https://doi.org/10.1002/ecy.3182.

Harvey, J. A. & M. Malcicka, 2015. Climate change, range shifts and multitrophic interactions. In Lo, Y.-H., J. A. Blanco & S. Roy (eds), Biodiversity in Ecosystems - Linking Structure and Function. InTech. https://doi.org/10.5772/59269.

Hill, M. J., H. M. Greaves, C. D. Sayer, C. Hassall, M. Milin, V. S. Milner, L. Marazzi, R. Hall, L. R. Harper, I. Thornhill, R. Walton, J. Biggs, N. Ewald, A. Law, N. Willby, J. C. White, R. A. Briers, K. L. Mathers, M. J. Jeffries & P. J. Wood, 2021. Pond ecology and conservation: research priorities and knowledge gaps. Ecosphere 12(12): e03853. https://doi.org/10.1002/ecs2.3853.

Hodgson, D., J. L. McDonald & D. J. Hosken, 2015. What do you mean, 'resilient'? Trends in Ecology & Evolution 30(9): 503–506. https://doi.org/10.1016/j.tree.2015.06.010.

Holt, R. D., 1996. Food webs in space: An island biogeographic perspective. In Polis, G. A. & K. O. Winemiller (eds), Food Webs: Integration of Patterns & Dynamics Springer: 313–323. https://doi.org/10.1007/978-1-4615-7007-3_30.

Ingrisch, J. & M. Bahn, 2018. Towards a comparable quantification of resilience. Trends in Ecology & Evolution 33(4): 251–259. https://doi.org/10.1016/j.tree.2018.01.013.

IPCC, 2021. Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou, Eds.; 1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157896.

Jeffries, M., 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology 32(3): 603–612. https://doi.org/10.1111/j.1365-2427.1994.tb01151.x.

Jocque, M. & R. Field, 2014. Aquatic invertebrate communities in tank bromeliads: how well do classic ecological patterns apply? Hydrobiologia 730(1): 153–166. https://doi.org/10.1007/s10750-014-1831-7.

Ledger, M. E., F. K. Edwards, L. E. Brown, A. M. Milner & G. Woodward, 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms: drought impacts on streams. Global Change Biology 17(7): 2288–2297. https://doi.org/10.1111/j.1365-2486.2011.02420.x.

Lefcheck, J. S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7(5): 573–579. https://doi.org/10.1111/2041-210X.12512.

Leroy, C., B. Corbara, O. Dézerald, M. K. Trzcinski, J.-F. Carrias, A. Dejean & R. Céréghino, 2017. What drives detrital decomposition in neotropical tank bromeliads? Hydrobiologia 802(1): 85–95. https://doi.org/10.1007/s10750-017-3242-z.

Limberger, R., A. Pitt, M. W. Hahn & S. A. Wickham, 2019. Spatial insurance in multi-trophic metacommunities. Ecology Letters 22(11): 1828–1837. https://doi.org/10.1111/ele.13365.

Lopez, L. C. S., B. Filizola, I. Deiss & R. I. Rios, 2005. Phoretic behaviour of bromeliad annelids (Dero) and ostracods (Elpidium) using frogs and lizards as dispersal

vectors. Hydrobiologia 549(1): 15–22. https://doi.org/10.1007/s10750-005-1701-4.

López-Hoffman, L., D. D. Breshears, C. D. Allen & M. L. Miller, 2013. Key landscape ecology metrics for assessing climate change adaptation options: rate of change and patchiness of impacts. Ecosphere 4(8): 1–18. https://doi.org/10.1890/ES13-00118.1.

Lounibos, L. P. & J. H. Frank, 2009. Insects and allies associated with bromeliads: a review. Terrestrial Arthropod Reviews 1(2): 125–153. https://doi.org/10.1163/187498308X414742.

MacArthur, R. H. & W. O. Wilson, 2001. The Theory of Island Biogeography, Princeton University Press, Princeton:

Marino, N. A. C., D. S. Srivastava, A. A. M. MacDonald, J. S. Leal, A. B. A. Campos & V. F. Farjalla, 2017. Rainfall and hydrological stability alter the impact of top predators on food web structure and function. Global Change Biology 23(2): 673–685. https://doi.org/10.1111/gcb.13399.

Merritt, R. W. & K. W. Cummins (Eds.), 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Pub. Co.

Mestre, L., N. Jansson & T. Ranius, 2018. Saproxylic biodiversity and decomposition rate decrease with small-scale isolation of tree hollows. Biological Conservation 227: 226–232. https://doi.org/10.1016/j.biocon.2018.09.023.

Norland, S., M. Heldal & O. Tumyr, 1987. On the relation between dry matter and volume of bacteria. Microbial Ecology 13(2): 95–101. https://doi.org/10.1007/BF02011246.

Oberdorff, T., C. Jézéquel, M. Campero, F. Carvajal-Vallejos, J. F. Cornu, M. S. Dias, F. Duponchelle, J. A. Maldonado-Ocampo, H. Ortega, J. F. Renno & P. A. Tedesco, 2015. Opinion paper: how vulnerable are Amazonian freshwater fishes to ongoing climate change? Journal of Applied Ichthyology 31(S4): 4–9. https://doi.org/10.1111/jai.12971.

Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin & J.-B. Lachavanne, 2002. Does size matter? The relationship between pond area and biodiversity. Biological Conservation 104(1): 59–70. https://doi.org/10.1016/S0006-3207(01)00154-9.

Olson, J. S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44(2): 322–331. https://doi.org/10.2307/1932179.

Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengård, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-Scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, M.-N. Tuanmu, A. Vergés, C. Villanueva, T. Wernberg, E. Waspstra & S. E. Williams, 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355(6332): eaai9214. https://doi.org/10.1126/science.aai9214.

Pereira, T. A., S. A. Vieira, R. S. Oliveira, P. A. P. Antiqueira, G. H. Migliorini & G. Q. Romero, 2022. Local drivers of heterogeneity in a tropical forest: epiphytic tank bromeliads affect the availability of soil resources and conditions and indirectly affect the structure of seedling communities. Oecologia 199(1): 205–215. https://doi.org/10.1007/s00442-022-05179-8.

Petermann, J. S., V. F. Farjalla, M. Jocque, P. Kratina, A. A. M. MacDonald, N. A. C. Marino, P. M. De Omena, G. C. O. Piccoli, B. A. Richardson, M. J. Richardson, G. Q. Romero, M. Videla & D. S. Srivastava, 2015. Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. Ecology 96(2): 428–439. https://doi.org/10.1890/14-0304.1.

Pires, A. P. F., N. A. C. Marino, D. S. Srivastava & V. F. Farjalla, 2016. Predicted rainfall changes disrupt trophic interactions in a tropical aquatic ecosystem. Ecology 97(10): 2750–2759. https://doi.org/10.1002/ecy.1501.

R Core Team, 2021. R: A language and environment for statistical computing. Version 4.1.1. Vienna: R Foundation for Statistical Computing. Available at https://www.r-project.org.

Richardson, B. A., 1999. The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest1. Biotropica 31(2): 321–336. https://doi.org/10.1111/j.1744-7429.1999.tb00144.x.

Rodríguez-Pérez, H., G. Borrel, C. Leroy, J.-F. Carrias, B. Corbara, D. S. Srivastava & R. Céréghino, 2018. Simulated drought regimes reveal community resilience and hydrological thresholds for altered decomposition. Oecologia 187(1): 267–279. https://doi.org/10.1007/s00442-018-4123-5.

Ruhí, A., J. Herrmann, S. Gascón, J. Sala & D. Boix, 2012. How do early successional patterns in man-made wetlands differ between cold temperate and Mediterranean regions? Limnologica 42(4): 328–339. https://doi.org/10.1016/j.limno.2012.07.005.

Ruiz, T., J.-F. Carrias, C. Bonhomme, V. F. Farjalla, V. E. J. Jassey, J. Leflaive, A. Compin, C. Leroy, B. Corbara, D. S. Srivastava & R. Céréghino, 2022. Asynchronous recovery of predators and prey conditions resilience to drought in a neotropical ecosystem. Scientific Reports 12(1): 8392. https://doi.org/10.1038/s41598-022-12537-2.

Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams & T. A. Evans, 2014a. Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20(2): 495–503. https://doi.org/10.1111/gcb.12439.

Scheffers, B. R., T. A. Evans, S. E. Williams & D. P. Edwards, 2014b. Microhabitats in the tropics buffer temperature in a globally coherent manner. Biology Letters 10(12): 20140819. https://doi.org/10.1098/rsbl.2014.0819.

Srivastava, D. S., 2006. Habitat structure, trophic structure and ecosystem function: Interactive effects in a bromeliad–insect community. Oecologia 149(3): 493–504. https://doi.org/10.1007/s00442-006-0467-3.

Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider & M. K. Trzcinski, 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology & Evolution 19(7): 379–384. https://doi.org/10.1016/j.tree.2004.04.010.

Srivastava, D. S., R. Céréghino, M. K. Trzcinski, A. A. M. MacDonald, N. A. C. Marino, D. A. Mercado, C. Leroy, B. Corbara, G. Q. Romero, V. F. Farjalla, I. M. Barberis, O. Dézerald, E. Hammill, T. B. Atwood, G. C. O. Piccoli,

F. Ospina-Bautista, J. Carrias, J. S. Leal, G. Montero, P. A. P. Antiqueira, R. Freire, E. Realpe, S. L. Amundrud, P. M. deOmena & A. B. A. Campos, 2020. Ecological response to altered rainfall differs across the Neotropics. Ecology 101(4): e02984. https://doi.org/10.1002/ecy.2984.

Staddon, P., Z. Lindo, P. D. Crittenden, F. Gilbert & A. Gonzalez, 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. Ecology Letters 13(5): 543–552. https://doi.org/10.1111/j.1461-0248.2010.01450.x.

Steiner, C. F. & M. Asgari, 2022. Habitat isolation reduces intra- and interspecific biodiversity and stability. Royal Society Open Science 9(2): 211309. https://doi.org/10.1098/rsos.211309.

Strachan, S. R., E. T. Chester & B. J. Robson, 2015. Freshwater invertebrate life history strategies for surviving desiccation. Springer Science Reviews 3(1): 57–75. https://doi.org/10.1007/s40362-015-0031-9.

Thompson, P. L. & A. Gonzalez, 2016. Ecosystem multifunctionality in metacommunities. Ecology 97(10): 2867–2879. https://doi.org/10.1002/ecy.1502.

Trzcinski, M. K., D. S. Srivastava, B. Corbara, O. Dézerald, C. Leroy, J.-F. Carrias, A. Dejean & R. Céréghino, 2016. The effects of food web structure on ecosystem function exceeds those of precipitation. Journal of Animal Ecology 85(5): 1147–1160. https://doi.org/10.1111/1365-2656.12538.

Wang, Y., U. Naumann, S. T. Wright & D. I. Warton, 2012. mvabund - an R package for model-based analysis of multivariate abundance data: The mvabund R package. Methods in Ecology and Evolution 3(3): 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x.

Warton, D. I., S. T. Wright & Y. Wang, 2012. Distance-based multivariate analyses confound location and dispersion effects: mean-variance confounding in multivariate analysis. Methods in Ecology and Evolution 3(1): 89–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x.

Watling, J. I., V. Arroyo-Rodríguez, M. Pfeifer, L. Baeten, C. Banks-Leite, L. M. Cisneros, R. Fang, A. C. Hamel-Leigue, T. Lachat, I. R. Leal, L. Lens, H. P. Possingham, D. C. Raheem, D. B. Ribeiro, E. M. Slade, J. N. Urbina-Cardona, E. M. Wood & L. Fahrig, 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23(4): 674–681. https://doi.org/10.1111/ele.13471.

Yachi, S. & M. Loreau, 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences 96(4): 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

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