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RESEARCH ARTICLE

Functional redundancy dampens precipitation change impacts on species-rich invertebrate communities across the Neotropics

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Abstract

1. Animal community responses to extreme climate events can be predicted from the functional traits represented within communities. However, it is unclear whether geographic variation in the response of functional community structure to climate change is primarily driven by physiological matching to local conditions (local adaptation hypothesis) or by differences between species pools in functional redundancy (insurance hypothesis).
2. We conducted a coordinated experiment to understand how aquatic invertebrate traits mediate the responses of multitrophic communities to changes in the quantity and evenness of rainfall in 180 natural freshwater microcosms (tank bromeliads) distributed across six sites from 18°N in the Caribbean to 29°S in South America. At each site, we manipulated the mean and dispersion of the daily amount of rainfall that entered tank bromeliads over a 2-month period.

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Manipulations covered a response surface representing 50% to 200% of the dispersion of daily rainfall crossed with 10% to 300% of the mean amounts of rainfall.

3. The response of functional community structure to precipitation regimes differed across sites. These geographic differences were not consistent with the local adaptation hypothesis, as responses did not correlate with the current amplitude in precipitation. Geographic differences in community responses were consistent with the insurance hypothesis: sites with the lowest functional redundancy in their species pools had the strongest response to a gradient in hydrological variability induced by uneven precipitation. In such sites, an increase in the hydrologic variability induced a shift from communities with both pelagic and benthic traits using both green and brown energy channels to strictly benthic, brown energy communities.
4. Our results predict uneven impacts of precipitation change on community structure and energy channels within communities across Neotropical regions. This geographic variation is due more to differences in the size and redundancy of species pools than to local adaptation. Strategies for climate change adaptation should thus seek to identify and preserve functionally unique species and their habitats.

KEYWORDS

freshwater, functional traits, hydrology, insurance hypothesis, precipitation, species richness

1 | INTRODUCTION

Anthropogenic climate change is predicted to increase the frequency and intensity of extreme climatic events (IPCC, 2021). Ecosystems will be affected through temperature-related changes in physiological rates (Sheldon et al., 2011) and through disruption of the precipitation patterns (Aspin et al., 2019). In many tropical regions, the frequency of prolonged dry seasons related to more severe El Niño Southern Oscillation (ENSO) events has increased since 1976 (Collins, 2005). Future climate scenarios, however, vary in the direction and magnitude of precipitation changes depending on geographic location. For example, Southern Central America and Northern South America are predicted to experience a 10% to 40% decrease in annual precipitation by 2050, together with an increased frequency of ecological and agricultural droughts (IPCC, 2021). Conversely, the western equatorial and south-eastern coasts are predicted to become 10%–30% wetter and could experience more frequent heavy precipitation events (IPCC, 2021). These changes will notably have large effects on the water quality and hydrology of freshwater ecosystems (Woodward et al., 2010). In addition to consequences on the goods and services that ecosystems provide to humans, changes in the temporal dynamics of water could affect the distribution of aquatic species from local habitat shifts to changes in geographic ranges (Oberdorff et al., 2015). Most of our current understanding of freshwater community responses to precipitation

change in Neotropical environments has come from experimental studies at a single site (Gutiérrez-Fonseca et al., 2020). However, differences in local environments and biogeographic turnover in species composition and traits often result in context dependency that limits our ability to make generalizations (Srivastava et al., 2020a). Understanding the interaction between biogeographic contexts and climate change is therefore crucial to producing a multiregional theoretical framework of how climate will affect ecosystems and to support climate change adaptation.

Trait-based ecology provides a relevant framework to predict community- to ecosystem-level responses to climate change across habitat types and biogeographic regions (Wieczynski et al., 2019), because traits directly describe how species interact with their biotic and abiotic environment (Violle et al., 2014). For instance, temperate freshwater communities that are periodically subject to droughts and/or floods (e.g. in Mediterranean rivers) are resilient to extreme climatic events, because species possess tolerance and resistance traits that ensure their persistence in the system. Little is known however of the response of the biota to altered precipitation in tropical systems, especially those without historical seasonal exposure to extreme events (Gutiérrez-Fonseca et al., 2020). Assuming that environmental conditions provide a template for ecological strategies (Southwood, 1977), the elimination or depletion of coexisting populations could be predicted by combinations of traits that trigger similar responses to disturbance. For instance, environmental

filtering should theoretically increase the prevalence of animal traits that confer resistance to desiccation stress under severe drought (e.g. small body size, short generation times, drought-resistant eggs or cysts; Detry et al., 2014), with subsequent effects on biotic interactions (Gravel et al., 2016) and on the main trophic pathways represented in communities (Romero et al., 2020). Although functional traits have the potential to link environmental drivers and community structure to ecosystem functioning (McGill et al., 2006), only a handful of studies have considered the response of functional community structure to climate parameter space (Ledger et al., 2011), and next to none have further addressed the issue of consistency in responses across biogeographic regions (Guzman et al., 2021).

Manipulating rainfall at the ecosystem level is impractical in terrestrial or aquatic macrocosms, where it has also proven challenging to collect functional diversity data on entire communities that are too diverse and/or spatially diffuse to allow adequate sampling. The discrete communities found within natural freshwater microcosms (e.g. tank bromeliads, tree holes, rock pools) allow ecologists to take advantage of systems that are small and contained (allowing exhaustive sampling of the organisms), widely distributed (allowing to test the generality of results over broad geographic gradients) and easy to manipulate (Srivastava et al., 2004). Bromeliads are flowering plants represented by 3,672 species distributed from Florida to central Argentina (Butcher & Gouda, cont. updated). This range includes important biogeographic features such as the epicentre of bromeliad radiation (the Guyana Shield), the isolation effects of Caribbean islands and the effects of the Great American Interchange on Central America. In Neotropical forests, the rosettes of tank-forming bromeliads (c. 1,500 species) form 'freshwater islands' connected by adult dispersal in a terrestrial matrix, altogether impounding up to 50,000 L of water per hectare (McCracken & Forstner, 2006). Tank bromeliads collect rainwater and provide a habitat for aquatic organisms ranging from prokaryotes to invertebrates, and occasionally amphibians. On a local scale, allochthonous detrital inputs such as leaf litter and autochthonous algal production (favoured by light incidence) provide food sources to the aquatic community (Farjalla et al., 2016). In addition to food sources, the water volume held by the plants is a key environmental determinant of the taxonomic composition and functional community structure of bromeliad invertebrates (Srivastava, Ware, et al., 2020). Because bromeliad hydrology is sensitive to weather fluctuations (i.e. tracks rainfall patterns), these ecosystems are relevant to investigate the ecological effects of altered precipitation patterns in experimental research (Trzcinski et al., 2016).

Here, we conducted a geographically coordinated experiment at six sites representing biotic and environmental gradients that range from 18°N in the Caribbean to 29°S in South America (Puerto Rico, Costa Rica, Colombia, French Guiana, Brazil and Argentina). At each site, we manipulated both the mean and dispersion of the daily amount of rainfall that entered tank bromeliads over a 2-month period. Our factorial manipulations of these two aspects of rainfall covered a response surface representing 50% to 200% of the dispersion of daily rainfall crossed with 10% to 300% of the mean amounts

of rainfall. Within this precipitation parameter space, we expected changes in community trait composition when populations with particular combinations of traits are depleted either directly by drying or flushing, or indirectly by changes in hydrological dynamics within bromeliad ecosystems.

We ask what drives functional community responses to the emulated climate parameter space across geographic regions. Two alternative theories have been proposed to answer this question. Under a local adaptation hypothesis (Runquist et al., 2020), we expected a greater impact of precipitation change at locations with narrower amplitude in current precipitation, because organisms should have narrower hydrological niches at locations with less hydrologic variation. We predict that at these low-amplitude locations a variety of traits will correlate with experimental changes in precipitation and associated hydrology, either because these traits directly control the response of the organisms (response traits) or because effect traits (that determine the effect of species on ecosystem processes) covary with response traits (Blanquart et al., 2013). Alternatively, under an insurance hypothesis (Yachi & Loreau, 1999), we expect a weaker impact of precipitation change on community trait structure at locations with larger species pools, because functional redundancy will increase the probability that trait combinations are preserved by surviving species. By contrast, at locations with low functional redundancy, our experimental changes in precipitation will be correlated with significant changes in functional community structure because only a few combinations of functional response and effects traits are realized in the species pool. Both of the above hypotheses explain geographic variation in the strength of community responses to precipitation and hydrologic change. Under either hypothesis, sites with strong responses are expected to show congruent patterns in terms of the traits that are selected (or counter selected), because traits reflect solutions to environmental constraints shared by many species.

2 | MATERIALS AND METHODS

2.1 | Study sites and bromeliads

From October 2012 to December 2013, we replicated a 2-month experiment of altered rainfall entering tank bromeliads at six sites distributed in six neotropical countries. Research permits were obtained from the US Department of Agriculture and Forest Service in Puerto Rico (permit number: CNF-2126), from the Ministerio del Ambiente y Energía in Costa Rica (permit number: ACG-PI-031-2012), from the Instituto Chico Mendes de Conservação da Biodiversidade in Brazil (permit number: SISBIO/ICMBio 47232-1) and from the Ministry of Production of the Province of Santa Fe in Argentina (permanent *Specific Collaboration Agreement* with the Facultad de Ciencias Agrarias, National University of Rosario). No permit was required in the study areas of Colombia and French Guiana at the time of the experiment. This study did not require ethical approval.

TABLE 1 Main characteristics of the experimental sites and bromeliads

	Puerto Rico	Costa Rica	Colombia	French Guiana	Brazil	Argentina
Site characteristics						
Location	El Verde, Rio Grande	Pitilla, Guanacaste	Rio Blanco, Manizales	Petit Saut, Sinnamary	Macaé, Rio de Janeiro	Las Gamas, Santa Fe
Northing	18°20'N	10°59'N	4°46'N	5°03'N	22°23'S	29°28'S
Easting	60°50'W	85°26'W	74°10'W	53°02'W	41°45'W	60°28'W
Elevation (m a.s.l.)	350	600	2100	80	10	58
Monthly precipitation (mm) ^a	38–398	5–429	51–427	37–530	20–282	4–264
Rainfall amplitude (mm)	360	424	376	493	262	260
Air temperature (°C) ^a	21–30	25.8–29.4	10–14	20.5–35.5	21.7–26.9	10.8–24.5
Bromeliads						
Species	<i>Guzmania berteroniana</i>	<i>Guzmania</i> spp.	<i>Guzmania</i> spp.	<i>Lutheria splendens</i>	<i>Neoregelia cruenta</i>	<i>Aechmea distichantha</i>
Number of leaves	24 ± 5	26 ± 5	23 ± 6	14 ± 2	17 ± 2	31 ± 2
Plant diameter (cm)	79 ± 12	96 ± 14	95 ± 20	71 ± 11	40 ± 4	61 ± 8

^amin–max monthly averages.

Sites and bromeliad characteristics are given in Table 1. These sites naturally vary in the amount and distribution of rainfall. Minimum and maximum monthly averages for ambient precipitation and air temperature were obtained from an open access compilation of high-resolution (30 arcsec, ~1 km) climate data (CHELSA, Karger et al., 2017). Ambient rainfall amplitude was calculated as the difference between maximum and minimum monthly precipitation. Because bromeliad species differed across sites, they were matched in terms of growth form (i.e. crateriform rosettes sensu Mori et al., 1997). At each site, we selected 30 plants belonging to the most common tank bromeliad species in the area. We used measurements of vegetative traits (number of leaves, plant diameter in cm) and maximum water volume in ml (the difference between a known volume of water used to fill the empty bromeliad and the remaining volume when the bromeliad overflowed) to select plants that were similar in size and complexity within a site. Each individual bromeliad was placed under a clear plastic tarpaulin to deflect natural rainfall, and the minimum distance between two bromeliads was 3 m. Earlier studies of bromeliad micro-organisms and macroinvertebrates found no spatial autocorrelation of community structure in this system (Céréghino et al., 2019; Petermann, Kratina, et al., 2015), even when bromeliad leaves overlap within patches of plants (Céréghino et al., 2020). We were thus confident that a non-spatial approach was suitable in subsequent analyses. We simulated rainfall patterns by watering bromeliad tanks manually every day for 60 days, according to their assigned precipitation treatment (see below).

2.2 | Precipitation treatments

The precipitation treatments used in this study were determined from ambient rainfall data obtained at each site for the experimental period, following the method described in Srivastava et al. (2020a). These data were fit to a negative binomial distribution described by two parameters: the mean (μ) and the variance or dispersion parameter (k). The estimated values were rescaled to $\mu = 1$ and $k = 1$, so manipulations of precipitation are proportional to current site conditions. Treatments were thus factors relative to the unit values of μ and k , where μ represented the mean amount of rainfall and k represented the dispersion of daily rainfall amounts (i.e. evenness in number of days between 1 mm bins of rainfall per day). At each site, each bromeliad represented a precipitation treatment out of 30 treatments which were combinations of 10 levels of μ ($\mu = 0.1, 0.2, 0.4, 0.6, 0.8, 1, 1.5, 2, 2.5, 3$) and three levels of k ($k = 0.5, 1, 2$). At each site, the range of experimentally imposed μ and k included and exceeded IPCC scenarios, with extreme values representing frequent downpours to severe droughts. For instance, the most extreme drought treatment ' $\mu 0.1k 0.5$ ' means that the mean rainfall of this treatment is 1/10 of the normal rainfall, and that the rainfall is half as dispersed among days as normal at this specific site. Empirical field measurements were used to convert ambient rainfall (in mm) into the actual volume of water an average plant would collect at each site. Specifically, the mean catchment area of our bromeliads

was estimated by image analysis, and a combined correction factor accounting for canopy interception and bromeliad deflection was calculated following Srivastava et al. (2020a). Multiplying the rainfall amount by the mean catchment area by the combined correction factor gives the water volume a plant should receive at the climatic norm of $\mu 1k1$.

2.3 | Experimental set-up

Prior to the experiment, we equalized the abundances of the major invertebrate taxa and detritus amounts between bromeliads at each site. All bromeliads were turned upside down and their wells were flushed using a pressure sprayer with filtered non-chlorinated water (e.g. rain, spring or stream water). The invertebrates and the detritus were captured in a bucket. Invertebrates were sorted, identified to family in trays and kept alive in separate containers (with detritus and insect larvae as food for detritivores and predators respectively). We then divided the total amount of detritus and the total invertebrate numbers in each family by 30, so that all bromeliads started the experiment in the same conditions.

During the experiment, rainwater was added daily over 60 days to each bromeliad with a small watering can according to its treatment schedule, dividing the volume among leaves. To measure changes in hydrology over time, we measured water depth (cm) in two leaves of each bromeliad every day or every other day, before watering. At the end of the experiment, bromeliads were placed in separate buckets and returned to the laboratory where they were dissected leaf by leaf, washing all detritus and invertebrates off the dissected leaves into a bucket. All aquatic invertebrates were sorted, identified to species or morphospecies (hereafter 'species') and enumerated.

2.4 | Environmental and biological data

Ten environmental variables were measured for each individual bromeliad. These variables can be grouped into three categories: (a) habitat size and complexity (bromeliad catchment area, number of leaves, final water volume), (b) precipitation treatment (relative μ and k) and (c) hydrological variables associated with each bromeliad (proportion of dried-out days, proportion of overflow days, mean water depth, coefficient of variation of water depth, wetness). The proportions of overflow and dried-out days were the % number of days a bromeliad reached its maximum water volume and a volume <1 ml respectively. Daily water depth records were used to calculate, at the plant level, mean depth and the coefficient of variation (CV) of depth over the experimental period. Wetness was calculated as the mean:maximum depth ratio and is a measure of habitat availability based on the proportion an average tank is filled on an average day. These data were used to build a table of bromeliad \times environmental variables (hereafter R table) for each site.

The invertebrate species data (composition and abundance) recorded in each bromeliad at the end of the experiment allowed us to

build a bromeliad \times invertebrate species abundance table (hereafter L table). The 12 functional traits for each taxon were obtained from a database of traits for all 852 known bromeliad invertebrates across the Neotropics (Céréghino, Pillar, et al., 2018; Céréghino, Srivastava, et al., 2018): maximum body size (BS), aquatic developmental stage (AS), reproduction mode (RE), dispersal mode (DM), resistance forms (RF), respiration mode (RM), locomotion (LO), food (FD), feeding group (FG), morphological defence (MD), body form (BF) and cohort production interval (CP, the number of days from hatching to emergence or adult stage). Each of these was a nominal trait with a certain number of states or modalities. Modalities used for the different traits and their definitions, as well as their interpretations in a context of precipitation change are given in Table S1. Information on the functional traits was structured using a fuzzy-coding technique (Chevenet et al., 1994): scores ranged from '0', indicating 'no affinity' to '3', indicating 'high affinity' for a given trait modality. This procedure allowed us to build a species \times modalities table (hereafter Q table).

Species pool's richness was the total number of species found at the site level. Functional redundancy (FR) refers to the repetition of trait combinations by different species and is calculated as the difference between the Simpson index of species diversity and Rao's quadratic entropy (RaoQ) based on their functional dissimilarity (De Bello et al., 2007). Functional redundancy was calculated at the site (i.e. species pool) level from the sum of abundances of species in 30 bromeliads and the corresponding Q table. The FR metric was calculated using the package SYNCSA in R software.

2.5 | Statistical analyses

Site-specific RLQ analyses were used to explore covariation between environmental variables and traits. The RLQ analysis is a double inertia analysis of environment (R) and trait modalities tables (Q) with a link expressed by a contingency table of species abundance data (L) (Dray et al., 2014). Prior to each RLQ analysis, the L table was $\log(x + 1)$ -transformed to downweight abundant species 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. The results of these three separate ordinations were used as inputs in the RLQ analysis, a three-table ordination method which maximizes covariation between environmental variables and species traits. Bromeliad and species scores in the RLQ were evaluated against the score obtained from the separate analyses of the R, L and Q tables. The total inertia of each RLQ analysis (the sum of eigenvalues) was used as a multivariate statistic to measure the correlation between the trait modalities table and the table of environmental variables (Dray & Legendre, 2008). Linear and exponential models were then used to test any relationship between total inertia of RLQs and (a) natural rainfall amplitude across sites (thus testing the local adaptation hypothesis), (b) number of species in the local pools and (c) functional redundancy at species pool level (with

b and c testing the insurance hypothesis). To further ascertain that any relationship or lack of relationship between total inertia of RLQs and the range of natural rainfall at sites experienced by invertebrates was not contingent on the specific precipitation variable selected (here the amplitude of rainfall), we also tested relationships between inertia and all precipitation-related variables available from the bioclimatic database CHELSA (Karger et al., 2017).

We assessed the overall significance of each RLQ analysis using two Monte Carlo permutation tests. The first of these tests, referred to as Model 2 by Thioulouse et al. (2018), consists of 999 Monte Carlo permutations of the table rows of R (bromeliads), to test the null hypothesis that species are distributed irrespective of the study environmental variables (precipitation treatments, bromeliad size and hydrology). Model 4 (sensu Thioulouse et al., 2018) consists in 999 permutations of the table rows of Q (species), thus testing the null hypothesis that species are distributed irrespective of the measured functional traits. From these two tests, we took the highest *p*-value to establish overall significance. We used a combination of RLQ and fourth-corner analyses to test significant associations between traits and R axes, and between environmental variables and Q axes in RLQs. Significant associations were evaluated using Pearson's *r* correlations, and *p*-values were corrected for false discovery rate to account for possible bias due to multiple comparisons. RLQ analyses and the associated tests were conducted with the ADE4 package in R software.

3 | RESULTS

3.1 | What drives functional community responses to precipitation treatments?

Our six sites varied substantially in the total amount of variance explained by trait–environment associations, varying from 42% to 88% for axis 1 of the site-specific RLQs, and from 6% to 37% in axis 2

(Table 2). There was no significant relationship between the strength of the trait–environment associations (technically the total inertia of RLQs) and natural rainfall amplitude (Figure 1a, $p > 0.05$). More generally, the strength of trait–environment associations did not correlate with any of the precipitation-related variables available from the bioclimatic database (data not shown).

By contrast, the strength of trait–environment associations increased with the number of species in the local pools (Figure 1b, negative exponential adjusted $R^2 = 0.84$, $p = 0.006$) as well as functional redundancy (Figure 1c, negative exponential adjusted $R^2 = 0.62$, $p = 0.039$). Specifically, environmental variables had the strongest effect on community trait structure at sites whose species pools had the fewest species and the lowest functional redundancy (Puerto Rico, Argentina, French Guiana, Figure 2). The relationship between community trait structure and environmental variables was significant in Puerto Rico (model 2 simulated $p = 0.004$; model 4 simulated $p = 0.029$) and Argentina (model 2 $p = 0.001$; model 4 $p = 0.028$), and marginally significant in French Guiana (model 2 $p = 0.047$; model 4 $p = 0.088$). By contrast, the community trait and environmental variable tables were not significantly correlated at sites with the largest numbers of species and unique species in their local pool (Colombia, Costa Rica, Brazil; highest simulated $p = 0.421$ – 0.671 , Figure S1).

3.2 | Responses of species and functional community structure to hydrologic gradients

At the three sites where RLQs were significant, communities were influenced by a consistent and dominant hydrologic gradient. Uneven precipitation and lower amounts of incoming rainwater provoked frequent drying and higher hydrological variability in the recipient bromeliads, resulting in a gradient of water permanence. At these sites, the first RLQ axis can therefore be interpreted as a gradient in hydrologic disruption by drought (Figure 2; Table S2).

	PR	CR	CO	FG	BR	AR
Total inertia	2.58	0.865	1.514	0.956	0.462	4.613
Projected inertia						
Axis 1	80.75	42.12	65.93	78.32	66.35	87.62
Axes 1 + 2	89.33	79.33	80.78	87.77	82.44	93.66
Co-inertia R						
Axis 1	97.60	37.07	89.12	99.25	82.75	95.35
Axes 1 + 2	84.89	74.29	93.60	90.68	84.24	93.01
Co-inertia Q						
Axis 1	80.33	46.40	24.82	55.03	30.15	73.35
Axes 1 + 2	77.16	47.23	40.35	59.60	60.60	81.68
Correlation ratio L						
Axis 1	53.98	40.55	49.52	39.94	43.23	55.29
Axis 2	43.07	35.32	26.96	30.85	27.28	35.85

TABLE 2 Summary of the RLQ analyses

Abbreviations: AR, Argentina; BR, Brazil; CO, Colombia; CR, Costa Rica; FG, French Guiana; PR, Puerto Rico.

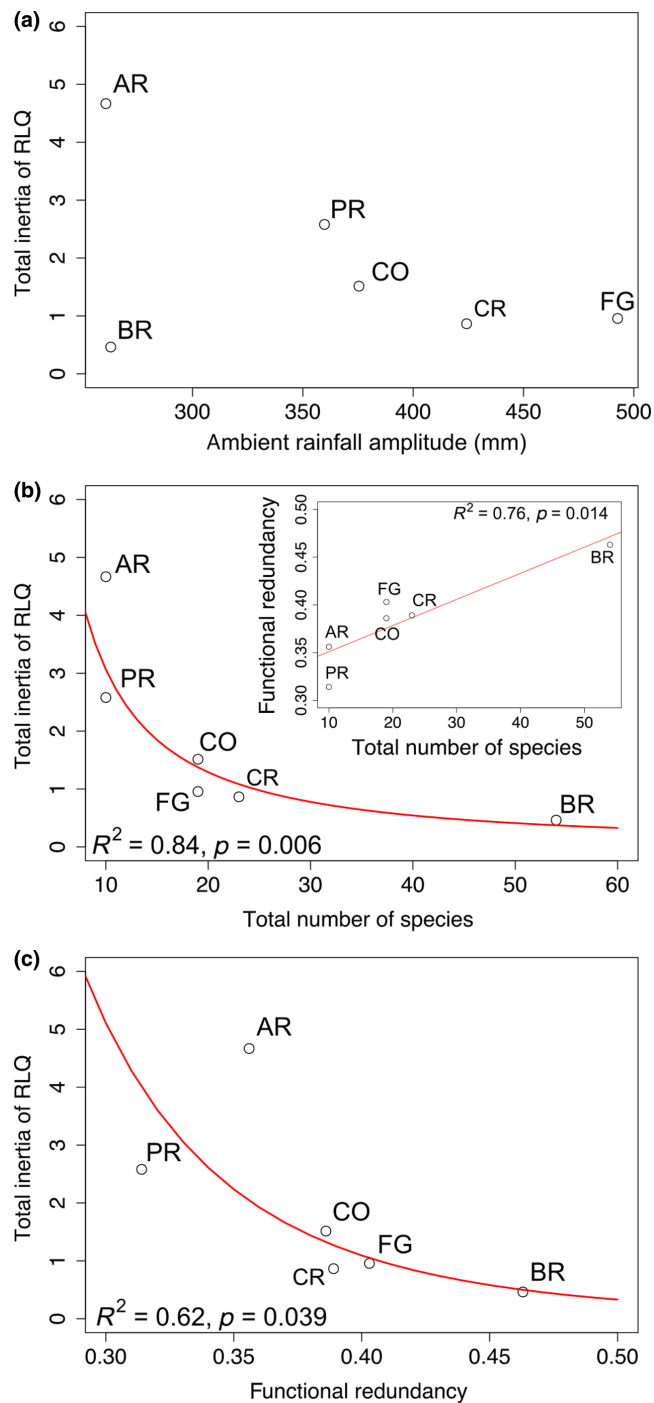


FIGURE 1 Relationship between ambient rainfall amplitude, total number of species, functional redundancy and strength of trait–environment correlations (total inertia of RLQs) across sites (see text). The inset shows the relationship between species pool's species richness and functional redundancy. AR, Argentina; BR, Brazil; CO, Colombia; CR, Costa Rica; FG, French Guiana; PR, Puerto Rico (see Table 1 for locations)

Axis 1 contrasted permanent aquatic habitats on the left end (wetness, overflow days, mean depth), and frequently desiccated bromeliads with higher variability in water depth on the right end (higher values for dried-out days and cv depth) (Figure 2). Axis

2 mostly portrayed a gradient of precipitation-related variables (higher k – lower μ vs. lower k – higher μ) in combination with variables representing bromeliad structure (catchment area, leaf number).

In the three sites with lowest functional redundancy, RLQ axis 1 accounted for 80.33% (Puerto Rico), 55.03% (French Guiana) and 73.35% (Argentina) of the variance of the trait modalities' table Q (Table 2). After corrections of p -values for false discovery rate in fourth-corner tests, we found no significant bivariate correlations between particular traits and environmental variables at any of the three sites, which means that groups of interacting environmental variables (i.e. not variables in isolation) influenced trait combinations (i.e. not traits in isolation). We therefore considered correlations between trait modalities and the multivariate hydrological gradient represented by the first RLQ environmental axis, and correlations between environmental variables and combinations of traits represented by the first RLQ trait axis (Figure 2; Table S2). We focus here on the first RLQ environmental axis as it accounted for more than 95% of the variability of the environmental table R. In Puerto Rico and Argentina, large-bodied shredders that feed on dead plants (BS4, FG2, FD3) and that crawl on the bottom of the bromeliad tanks or burrow in the detritus (LO4, LO5) are positively associated with the first RLQ environmental axis. These benthic organisms also have intermediate larval development times, from 2 weeks to 2 months (CP2). Conversely, filter feeders that feed on algae or occasionally on dead invertebrates (FG4, FD4, FD6) and that swim under the surface or in the water column (LO2, LO3) are negatively associated with the first RLQ environmental axis. These pelagic organisms also have fast development times <2 weeks (CP1) and an aquatic pupal stage (AS3). Only a few trait modalities were marginally and negatively associated with the first environmental axis in French Guiana; the corresponding organisms were deposit feeders that burrow in the accumulated detritus and have long hairs as morphological defence (FD1, LO5, MD3). Taken together, these results indicate a shift along the first RLQ environmental axis from communities that have both benthic and pelagic organisms that use green and brown sources of energy, to communities that are primarily benthic and based on brown energy. At all three sites, cv depth and dried-out days were positively correlated with the first RLQ trait axis, whereas water volume, mean depth and wetness correlated negatively with the first RLQ trait axis (Table S2). In French Guiana, overflow days also showed a negative, marginally significant correlation with trait axis 1.

Trait–environment correlations were mediated by the response of species to the hydrological gradient. We therefore used species' scores along RLQ axis 1 (weighted average and distribution amplitude) to visualize the hydrological niche breadth of species at a site. These site and species scores were robust, for example correlating 40%–55% with those obtained by separate correspondence analyses (CAs). Most species had broad niche breadths and showed overlapping niches. Still, axis 1 of the site-specific RLQs contrasted species at the extremes (Figure 2). In Puerto Rico, the presence of *Trentepohlia dominicana* (Tipulidae, a large-bodied leaf shredder with

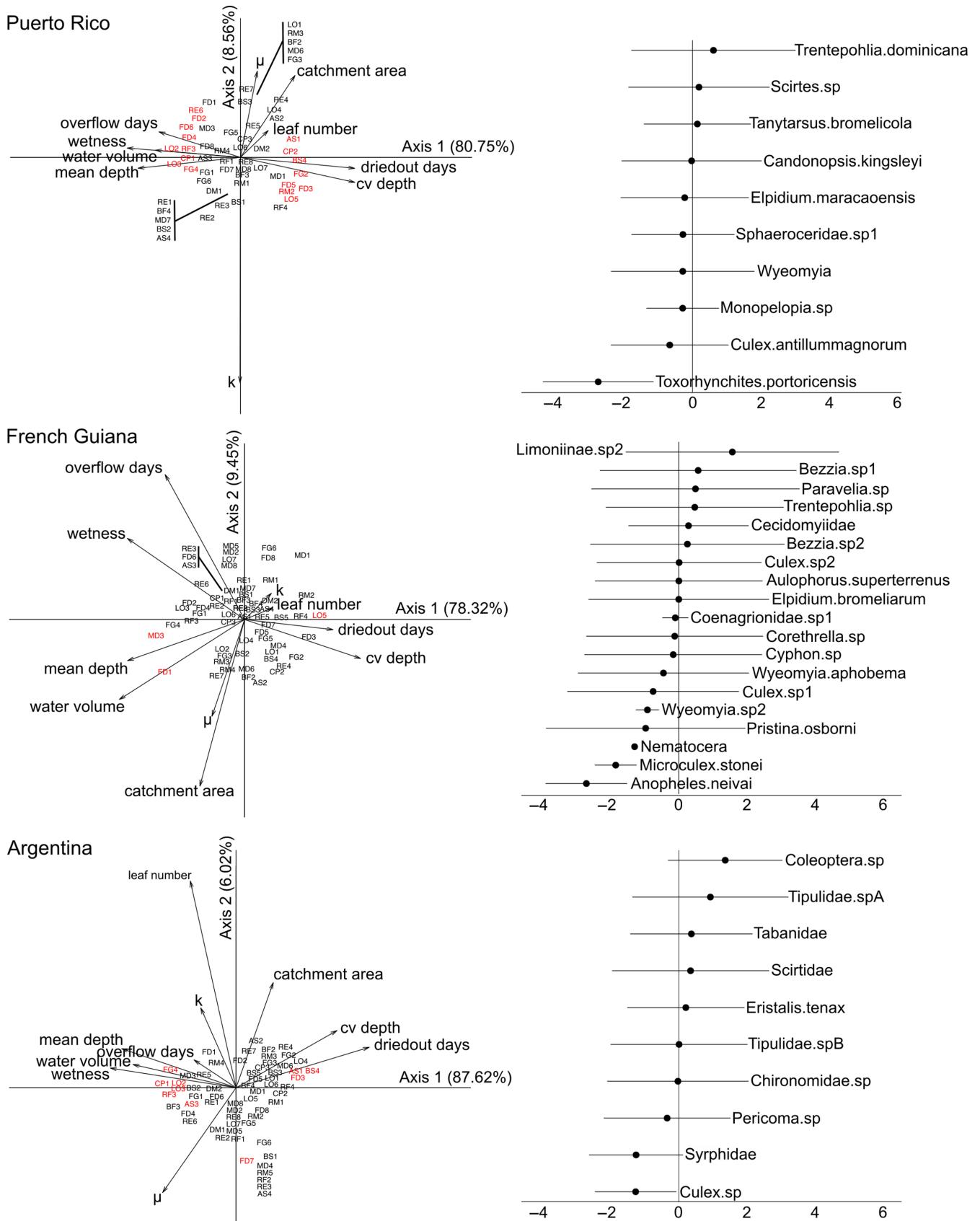


FIGURE 2 Left panels: ordination of environmental variables and functional traits along the first two RLQ axes for Puerto Rico, French Guiana and Argentina. Percentages are the variance explained by RLQ axes 1 and 2. See Table 2 for summary statistics. Trait abbreviations are as in Table S1. Trait modalities in red are significantly correlated with RLQ axis 1, see Table S2 for correlation coefficients and p-values. Environmental variables are represented as vectors: directions show the gradients, arrow length represents the strengths of the variables on the ordination space. Right panels: niche position (weighted average) and niche breadth (variance) of invertebrate species along the gradient of bromeliad hydrology represented by the first RLQ axis for Puerto Rico, French Guiana and Argentina

a benthic microhabitat) is associated with bromeliads that dried out more frequently. At the opposite end of axis 1, *Toxorhynchites portoricensis* (a large engulfing predator), *Culex antillummagnorum* (a filter feeder) and two other Culicidae with a pelagic microhabitat were typical of more permanent (and even overflowing) bromeliad waters. Similar patterns occurred in French Guiana and Argentina: leaf shredders *Trentepohlia* sp. of French Guiana and an unknown Tipulidae of Argentina were associated with drier bromeliads, whereas filter feeders *Culex stonei* and *Anopheles neivai* Culicidae of French Guiana and *Culex* sp. of Argentina were associated with more permanent bromeliads.

In the three sites with high functional redundancy and low total inertia of the RLQs (Costa Rica, Colombia, Brazil), there were no correlations between traits and RLQ axis 1 despite species turnover along this axis (Figure S1). Species also showed largely overlapping hydrologic niches, although again benthic and pelagic species (including Tipulidae and Culicidae respectively) tended to occur at opposing ends of the hydrologic gradient represented along RLQ axis 1.

4 | DISCUSSION

Geographically distributed experiments advance the field of global change biology when they allow the exploration of ecological responses to large climate parameter spaces (Reum et al., 2020), and the testing of generalities in functional relationships across broad spatial scales (Borer et al., 2014). Our study meets both criteria in that we manipulated precipitation entering bromeliad ecosystems over broad climate parameter space, emulating extreme droughts to frequent downpours relative to the current local baselines, and tested geographic generality at six sites distributed across 47° of latitude from the Caribbean to Argentina. Within the bromeliad ecosystem, frequent drying and higher hydrological variability induced by uneven precipitation had the harshest effects on community traits. Importantly, these effects were strongest at naturally depauperate sites with low functional redundancy in their species pools. By contrast, natural precipitation patterns at sites did not explain geographic differences in the strength of the community trait structure responses to the manipulations. These results support the insurance hypothesis rather than the local adaptation hypothesis. Although the effects of rainfall on community traits varied geographically, this spatial variance was still predicted by the size of the species pool. In sites where community traits were affected by rainfall change (frequent drying and/or higher hydrological variability), the responses of functional structure were generally consistent among sites: on a gradient from permanent to hydrologically variable aquatic systems, there was a shift from communities with benthic-pelagic organisms that use green and brown sources of energy to benthic communities that are based on brown energy.

Because the capture and conversion of energy and nutrients within communities occurs through autotrophy, predation and decomposition, any shift in the prevalence of certain traits, notably

those traits related to food acquisition and trophic position, could have important consequences for the trophic economy of the system (Ledger et al., 2011). Traits that responded to our manipulations can be assigned to the categories of 'response traits' (e.g. body size, morphological defence, aquatic stage) or 'effect traits' (e.g. diet, functional groups) (Mensens et al., 2017). While the former will allow us to predict changes in species abundance (e.g. *Anopheles* mosquitoes, potential vectors of malaria, will be more abundant when rainfall is more frequent), the latter are expected to drive resource use and the diversity of energy pathways (Ledger et al., 2011). The sensitivity of ecosystems to climate change could depend on how energy flows through their food webs (Rooney & MacCann, 2012). Higher hydrological variability due to less frequent rainfall consistently selected against trait combinations associated with a pelagic lifestyle while favouring benthic detritivores. This finding implies changes in the relative importance of energy channels at the less species-rich sites when rainfall was uneven (drought conditions). Like many freshwater food webs, the bromeliad food web is supported by allochthonous (detrital inputs) and autochthonous resources (algal production) (Farjalla et al., 2016). Together with bacteria and fungi, invertebrate shredders (here benthic Tipulidae) breakdown incoming coarse particulate organic matter to fine particulate organic matter, making it available to filter-feeding and gathering-collector invertebrates (here pelagic Culicidae) in a 'brown', benthic to pelagic energy channel. Pelagic species also generally feed on planktonic algae, and as such are involved in a 'green', pelagic channel characterized by higher biomass turnover rate than the brown channel (Dézerald et al., 2017). Interestingly, food webs missing one channel or the other would be less stable than food webs with both channels (Rooney & MacCann, 2012), while predators that couple the two channels contribute to stabilize the system (Ledger et al., 2011; McCann & Rooney, 2009). We note that (a) uneven rainfall and frequent droughts were detrimental to those species involved in the pelagic channel, and (b) top predators, notably odonates which have large impacts on nutrient and carbon dynamics in bromeliad ecosystems (Petermann, Farjalla, et al., 2015), are missing in Puerto Rico and Argentina. Our results therefore allow us to speculate that the species-rich communities of Costa Rica, Colombia and Brazil will support more stable ecosystem functioning in the face of climate change than the comparatively depauperate systems of the Caribbean and Northern Argentina, for functional redundancy will ensure that food webs preserve both green and brown energy channels (Trzcinski et al., 2016).

We found that relationships between community trait structure and hydrology were significant at the species-poor sites, where the loss of few species under extreme scenarios was more likely to eliminate unique trait combinations. Moreover, community trait structure was increasingly insensitive to changes in hydrology as species richness and functional redundancy increased. These results suggest that an insurance effect of species richness on the stability of functional community composition operated through a portfolio effect (Yachi & Loreau, 1999), that is, variance in trait composition in climate parameter space was dampened by the co-occurrence of

multiple species that possess similar traits. Finally, we note that depauperate communities that were sensitive to precipitation change were in the Caribbean island of Puerto Rico (isolation effect), and at the southern range limit of bromeliads and their biota in Argentina. Therefore, our results highlight an insurance effect of species richness and functional redundancy on the stability of functional community structure and suggest that the effect of biogeography on the species pool will be an important component of community responses to climate change.

We observed congruent patterns in terms of traits that were selected or counter selected by drought conditions across the species-poor locations. We also found that associations between community trait structure and the hydrology gradient were non-random at these sites. These results indicate that environmental filtering, rather than stochastic processes, determined local community assembly and food web structure under drying stress (Chase & Leibold, 2003). Specifically, drought intensification filtered species by trophic and habitat occupancy traits—two ecological dimensions that are strongly coupled in freshwater invertebrates (Merritt & Cummins, 1996). As bromeliads dried out more frequently, we recorded a shift from pelagic filter feeders to benthic shredders in the habitat \times trophic trait dimensions. Interestingly, we note that benthic shredders (Tipulidae larvae) were much larger in size and had much longer larval life spans than the pelagic filterers (Culicidae). This contrasts with the frequent observation that drought in freshwaters increases the prevalence of small and short-lived species that take advantage of refuge microhabitats and high turnover rates to limit exposure to environmental stochasticity (Ledger & Hildrew, 2001). We suggest that spatial avoidance was a prevailing strategy to ensure in situ resistance to drought. Unlike Culicidae larvae that cannot escape the water column, bromeliad Tipulidae can crawl on the aerial parts of bromeliads to move to more suitable leaf axils, burrow in the wet detritus when the water column declines (Dézerald et al., 2015) and even start to consume invertebrates instead of detritus (Amundrud et al., 2019). Not only does spatial avoidance represent an immediate response to short-term hydrological fluctuations, but this strategy allows species to channel more energy into the formation of body mass over longer time periods. Life cycle-based strategies, notably those r-strategies that are typical of Culicidae (Céréghino, Pillar, et al., 2018), could possibly be more relevant to recolonization by ovipositing adults once the disturbance has passed (Dézerald et al., 2015). Finally, we did not observe significant changes in the prevalence of predators under drought conditions, though larger body size and longer generation times often make them vulnerable to desiccation and habitat contraction (Romero et al., 2020; Srivastava, Ware, et al., 2020). In summary, predators at our study sites in Puerto Rico, French Guiana and Argentina were opportunist 'mesopredators' (e.g. *Corethrella* and *Bezzia* Diptera), that compare to our filter feeders in terms of body size and population turnover (Dézerald et al., 2015) and that were unaffected by drought throughout our study sites, probably because they are less

sensitive to environmental change than the larger top predators (Prugh et al., 2009).

Apart from their implications for community structure and food web functioning, our results did not support the hypothesis of local adaptation of invertebrates to water availability. Perhaps more importantly, they showed that the sensitivity to climate change of tropical invertebrates cannot be naively extended from temperature to precipitation. Tropical animals, notably ectotherms, have narrower thermal niches than higher latitude species and are living close to their physiological limits in terms of temperature (Tewksbury et al., 2008). They are therefore theoretically unable to tolerate even the smallest temperature change predicted by future climate scenarios. In contrast, most invertebrate species in our study had broad hydrological niche breaths at all sites, and there was no evidence for local adaptation to natural amplitudes in precipitation. These results are in line with experimental data in Dézerald et al. (2015, 2017), who found that invertebrate species were able to persist in the bromeliad tanks until the water volume dropped by 90% in French Guiana, though bromeliads were naturally filled to c. 50% of their capacity throughout the year in the area. We conclude that, while shifts in mean temperatures will have important ecological effects on Neotropical ectotherms (Sheldon et al., 2011), extreme precipitation change (or extreme events) will be required to provoke significant changes in species-rich Neotropical invertebrate communities. If these climate-induced changes occur, then ecosystems with the smallest species pool will be the most vulnerable to regime shift.

From the perspective of community trait composition, our results support the idea that the future of Neotropical ecosystems cannot be solely predicted from projected climate scenarios when both local environments and biological diversity mediate the impacts of global changes (Pires et al., 2018; Pokhrel et al., 2014). Freshwater communities in general are strongly constrained by the quality and the flux of water within their host system (Lake, 2011). Climate-dependent hydrology is mediated by habitat size and complexity in tank bromeliads (e.g. number of leaves dividing the overall water volume), and by understory environments that determine ambient humidity, throughfall and evaporation. This situation compares to that of other small freshwater ecosystems such as ponds, wetlands or rivers, where geological and morphological attributes (e.g. surface:volume ratio, porosity) and landscape features (e.g. drainage basin area, riparian vegetation) mediate the hydrological signals of climate change (Chezik et al., 2017; Pokhrel et al., 2014). The ecological impacts of precipitation change might therefore be heterogeneous across geographic locations in relation to the spatial extent of extreme events (local vs. regional), and to the magnitude of hydrological responses (House et al., 2016).

A potential limitation of our study is that manipulations were carried out at the bromeliad level, so part of the regional species pool was not affected and effects of precipitation change on the broader forest ecosystem were not included. It is likely that the metacommunity as a whole, including the aquatic and terrestrial stages, would suffer mortality if the whole forest was subjected to severe

droughts or heavy precipitations. Moreover, immigration from unmanipulated source patches (e.g. ovipositing adult insects, phoretic annelids) could result in a rescue effect possibly preventing extinctions, thus influencing observed community responses. Although we cannot exclude this possibility, recent experiments showed that the resilience of bromeliad invertebrate communities to drought intensification mostly relies on the in situ resistance traits of the aquatic stages, while immigration makes a minor contribution to community dynamics (Bonhomme et al., 2021). We therefore suggest that our methodologies remain relevant to bring out causal relationships between biological communities and climate-related variables across geographic regions.

Understanding the mechanisms that drive biotic responses to various climate scenarios is of utmost importance to anticipate future ecosystem functioning. Recent studies highlighted that variability in the response of community structure to extreme climate events is partly to mostly driven by the functional traits represented within communities (Boucek & Rehage, 2014), notably those response traits that confer resistance to abiotic stress (Griffin-Nolan et al., 2018). Based on our experiments, we can predict uneven impacts of precipitation change on community structure across Neotropical regions, and we attribute much of this variation to species richness and functional redundancy within the species pools. Our study thus takes a step towards integration of the emergent field of functional biogeography to global change biology (Violle et al., 2014). Moreover, if ecosystem stability declines together with functional redundancy (McCann & Rooney, 2009), our study further suggests that ill-considered land use and habitat degradation that extirpate species from local pools could weaken ecosystems in the face of extreme climate events. Incremental strategies for climate change adaptation should therefore seek to identify and preserve those functionally unique species and their habitats, while promoting the integrity of environmental conditions that buffer climate change signals.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.A.M.M., B.C., C.L., D.A.M., D.S.S., J.F.C., G.C.O.P., G.Q.R., I.M.B., N.A.C.M., R.C. and V.F.F. conceived the ideas and designed the methodology; D.A.M., D.S.S., E.H., E.R., F.O.B., G.M., G.Q.R., I.M.B., R.C. and V.F.F. organized site-level experiments; R.C. analysed the data with inputs from M.K.T. and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The environment and species data are available from Zenodo at <https://doi.org/10.5281/zenodo.1124951> (Srivastava et al., 2020b). The trait data are available from the Knowledge Network for Biocomplexity at <https://knb.ecoinformatics.org/#view/doi:10.5063/F1VD6WMF> (Céréghino, Srivastava, et al., 2018).

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