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# The effects of food web structure on ecosystem function exceeds those of precipitation

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## Summary

1. Ecosystems are being stressed by climate change, but few studies have tested food web responses to changes in precipitation patterns and the consequences to ecosystem function. Fewer still have considered whether results from one geographic region can be applied to other regions, given the degree of community change over large biogeographic gradients.

2. We assembled, in one field site, three types of macroinvertebrate communities within water-filled bromeliads. Two represented food webs containing both a fast filter feeder–microbial and slow detritivore energy channels found in Costa Rica and Puerto Rico, and one represented the structurally simpler food webs in French Guiana, which only contained the fast filter feeder–microbial channel. We manipulated the amount and distribution of rain entering bromeliads and examined how food web structure mediated ecosystem responses to changes in the quantity and temporal distribution of precipitation.

3. Food web structure affected the survival of functional groups in general and ecosystem functions such as decomposition and the production of fine particulate organic matter. Ecosystem processes were more affected by decreased precipitation than were the abundance of micro-organisms and metazoans. In our experiments, the sensitivity of the ecosystem to precipitation change was primarily revealed in the food web dominated by the single filter feeder–microbial channel because other top-down and bottom-up processes were weak or absent.

4. Our results show stronger effects of food web structure than precipitation change *per se* on the functioning of bromeliad ecosystems. Consequently, we predict that ecosystem function in bromeliads throughout the Americas will be more sensitive to changes in the distribution of species, rather than to the direct effects caused by changes in precipitation.

**Key-words:** bromeliad, climate change, community interactions, drought, ecosystem function, French Guiana, invertebrates, micro-organisms, phytotelmata, precipitation

## Introduction

Anthropogenic climate change has already started to affect the distribution of species (Sheldon, Yang & Tewksbury 2011; Breed, Stichter & Crone 2012; Virkkala &

Lehikoinen 2014). However, the observed effects of climate change on single species cannot be easily extrapolated to the responses of a complex network of species interactions within ecosystems (Murdoch, Briggs & Nisbet 2003; McCann 2010; Traill *et al.* 2010). Climate change will modify basal physiological rates of organisms (Brown *et al.* 2004; Humphries & McCann 2014) as well as the behavioural interactions between species (Hawlena &

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Schmitz 2010; Harley 2011; Houston & McNamara 2014). Interacting species may respond asynchronously to climate change, leading to the collapse or reconfiguration of the current food web (Winder & Schindler 2004; Le Roux & McGeoch 2008; Ledger *et al.* 2013), with unknown consequences to ecosystem function. Thus, a great challenge for community ecology is to provide a strong multi-trophic theory of how climate-dependent changes in species distributions will impact the flow of energy and nutrients within ecosystems (Lovejoy & Hannah 2005; Loreau 2010; Montoya & Raffaelli 2010).

Much of our knowledge about species effects on ecosystems is disconnected from climate change and comes from experiments in single locations where species occurrence is manipulated (Tilman, Reich & Knops 2006; Srivastava & Bell 2009; Borer, Seabloom & Tilman 2012). Field experiments have shown that species composition can be exceptionally important in determining ecosystem functions (Hooper *et al.* 2005, 2012), suggesting that the responses to climate change in one location may not translate to other locations when species traits, richness and/or numerical dominance differ among biogeographic regions. There is therefore a need for a multi-faceted approach which links the results of local experiments with observations and experiments across biogeographic regions (Smith, Knapp & Collins 2009; Kueffer, Pysek & Richardson 2013).

Climate change scenarios vary widely among biogeographic regions. Changes in the cloud base in Central America may cause up to a 40% decrease in local precipitation (Karmalkar, Bradley & Diaz 2008). In South America, the northern and eastern coasts, as well as central Amazonia, are predicted to become drier (seasonal estimates range from -10 to -50%), whereas the western equatorial and south-eastern coasts are predicted to become wetter by 2100 (seasonal estimates +10 to +50%; IPCC 2013). Here, we investigate the effects of altered precipitation because it has a potentially profound impact on ecosystems, particularly Neotropical ecosystems (Fu *et al.* 2013; Hilker *et al.* 2014). Neotropical ecosystems are expected to lose more species as a result of climate change than their temperate counterparts, because they contain a disproportionate number of the world's species, and because tropical organisms, notably ectotherms, are much closer to their physiological limits (in terms of temperature and perhaps drought) than their temperate counterparts (Janzen 1967; Tewksbury, Huey & Deutsch 2008; Sheldon, Yang & Tewksbury 2011). The disproportionate sensitivity of tropical organisms to climate change could be extended from temperature to other factors, such as precipitation, because the theory is based on greater local adaptation in the tropics (Janzen 1967; García-Robledo *et al.* 2016).

Many ecosystems throughout the Neotropics will experience changes in precipitation due to climate change. Altered patterns of precipitation are likely to have direct effects on the behaviour and physiology of aquatic biota,

and indirect effects through species interactions and the food web. The response of the biota, from physiological to population and community levels, will inevitably alter the functioning of the entire ecosystem. Therefore, there is an urgent need to predict how ecosystems will respond as they experience increasingly strong and variable patterns of precipitation. The sensitivity of an ecosystem to a climatic stressor may depend on food web structure and how energy flows through the food web (Rooney *et al.* 2006; McCann & Rooney 2009). In particular, food webs with both slow and fast production to biomass (P : B) compartments are likely to be more stable than food webs missing one compartment or the other. Within freshwater systems, the slow P : B compartment is typically along a detrital/fungal/detritivore pathway and a fast compartment is typically algal/pelagic. Higher biodiversity is typically found along the slow pathway and higher energy transfer and secondary production along the fast pathway (Moore *et al.* 2004; Rooney & McCann 2012). The food web is stabilized when a top predator links these two compartments and creates asynchrony in production (Rooney *et al.* 2006; McCann & Rooney 2009). Thus, food webs lacking top predators or otherwise having synchronous dynamics in production are predicted to be less stable (Rooney & McCann 2012), a prediction currently supported in agricultural systems (de Vries *et al.* 2012). We ask: Does the functional structure of food webs mediate both the sensitivity and vulnerability of an ecosystem to changes in precipitation?

Our study fits within a larger research programme which aims to understand (i) how bromeliad ecosystems in different biogeographic regions will respond to climate change and (ii) whether the variance between regions is driven by biogeographic changes in species composition. Here, we focus on how the functional structure of food webs, assembled to resemble those found in different biogeographic regions, mediates the ecosystem response to drought. These representative communities of biogeographically separated food webs may give us some information, or at least hypotheses, about how distant native communities may respond to climate change (LeCraw 2014).

Our experiment took place in a biologically diverse region containing most of the functional feeding groups recorded in bromeliads (French Guiana). This diversity is partly due to its biogeographic location, and part due to the wide diversity of habitat types bromeliads are found in. At our field site in French Guiana, we assembled food webs resembling – in terms of functional groups and trophic links – those found in bromeliads in three geographic regions: Costa Rica, Puerto Rico and French Guiana. These geographic regions cover the range of species diversity in the Americas: French Guiana (latitude 5° N), the centre of bromeliad radiation and a large pool of aquatic macroinvertebrate species associated with bromeliads, Costa Rica (10° N) which has a moderate species pool, and Puerto Rico (18° N), a Caribbean site

with a depauperate species pool (Supporting information; Brouard *et al.* 2012). It is interesting to note, however, that although French Guiana has the highest regional diversity of both bromeliads and bromeliad macrofauna, our data for one bromeliad species (*Aechmea aquilega*) at one site showed a simpler food web structure than found in either Costa Rica or Puerto Rico. After community assembly, we experimentally manipulated the amount and frequency of water entering bromeliad ecosystems from baseline precipitation levels and measured responses, including (i) invertebrate (survival and emergence), (ii) ecosystem (decomposition, the production of fine particulate organic matter, final CO<sub>2</sub> concentration), (iii) water chemistry and (iv) micro-organisms (viruses, bacteria, protists). We predicted that the presence or abundance of functional groups (i.e. food web structure) will mediate the effects of precipitation on ecosystem function. Ecosystems which contain more functionally diverse food webs (e.g. Costa Rica-like) will be less sensitive (more resistant) to drought and maintain ecosystem function over a wider range of drought stress. Conversely, ecosystems which contain less functionally diverse food webs and are missing the detritivore food chain (e.g. French Guiana) will be more sensitive to drought.

## Materials and methods

If certain organisms are more or less functionally equivalent, then it is possible to assemble examples of food webs that functionally resemble those found in different biogeographic regions (LeCraw 2014). Using the invertebrates available to us in French Guiana, we manipulated which functional feeding groups were present and the densities within each functional group. By assembling these food webs at a single study site, we control for environmental differences and focus on the effect of drought and food web structure on ecosystem function. This experimental design allows us to separate the ecosystem response into the effect of food web structure and changes in precipitation (drought effect) from other historical and environmental effects. We predicted that food web structure will mediate ecosystem responses to drought treatments, as entire functional feeding groups were missing from some communities, or when present in all communities, numerical dominance differed among communities.

We use the aquatic invertebrates living in bromeliads (Bromeliaceae) as our model system. Bromeliads are flowering plants represented by some 3140 species of which ~1000 have the capacity to hold water within their leaf axils (Givnish *et al.* 2011). In Neotropical forests, a substantial fraction of the freshwater available is impounded within the rosettes of these 'tank' bromeliads, forming freshwater islands in a terrestrial matrix (Richardson 1999). The rosettes of tank bromeliads form wells that collect rainwater and leaf litter, and provide a habitat for aquatic organisms ranging from prokaryotes to invertebrates (Carrias, Cussac & Corbara 2001; Brouard *et al.* 2012). The detritus constitutes a source of nutrients for the aquatic food web, as well as for the plant itself. Tank bromeliads obtain nutrients from their aquatic microcosm via water-absorbing leaf trichomes (Benzing *et al.* 1976). Incoming leaf litter is reduced by invertebrate scrapers and shredders, which create fine particles of organic matter and faeces

(known as FPOM) that collects in the plant pools. FPOM is further processed in the gut of invertebrate collectors and filter feeders, and is utilized by bacteria and other micro-organisms (Ngai & Srivastava 2006). This miniature ecosystem has been studied throughout its range and is viewed by ecologists as a model system for testing ecological theory (much in the same way that *Drosophila* fruit flies are used by geneticists; Srivastava *et al.* 2004). Unlike many food webs, which are too complex or spatially diffuse to allow manipulations in nature, the bromeliad food web can be exhaustively sampled and reassembled from even the smallest micro-organisms to the largest metazoans, giving us important insight into how species interactions lead to changes in ecosystem functioning.

Our experiment was located in the Amazonian ecoregion in French Guiana, in a secondary forest near the Petit Saut hydroelectric dam (latitude: 5°03'43" N; longitude: 53°02'46" W; elevation a.s.l.: 80 m). We chose the bromeliad *Aechmea aquilega* as the host plant and study ecosystem, because of its large size which could easily contain flow-through enclosures (hosting invertebrate assemblages, described below) in the leaf wells. Approximately 80 plants were collected in the surrounding region in September 2013, were emptied of their contents, thoroughly rinsed under high water pressure and placed at the study site to collect rain water and acclimate. In late October 2013, a subset of 28 plants of similar size and shape were selected for the experiment. The experiment started on 3 November 2013 and ended on 13 January 2014 for a total of 68 days (including set-up and take down). The duration of the experiment was chosen because all taxa (except odonates) could complete one or more generations. Thus, the response to the amount and frequency of precipitation is accumulated over several generations increasing the probability of detecting an effect of drought and food web structure on ecosystem function.

## FOOD WEB STRUCTURE

Data from previous field surveys of bromeliad invertebrate communities in Costa Rica (CR), Puerto Rico (PR) and French Guiana (FG) were summarized for each country, to calculate a representative experimental food web for each. Hereafter we refer to these experimental food webs as 'CR-like', 'PR-like' and FG food webs. To determine the composition of each experimental food web, we fitted linear regression models (Gaussian distribution, no transformation) of functional feeding group abundance as a function of bromeliad size to survey data (actual water volume measured at the time of sampling and the number of leaves; Fig. S1). Summary statistics (mean, range, etc.) of invertebrate abundance by family (or taxonomic group) and functional group, as well as statistics for models of functional group abundance for each study area, are in Tables S1–S3.

Functional group abundance was affected by bromeliad size for our Costa Rica and Puerto Rico data, but not for French Guiana (Table S3, Fig. S1). The abundance of functional groups for a similar size plant (1 L actual volume, 26 leaves) in Costa Rica and Puerto Rico was predicted from the abundance-bromeliad size models. This required extrapolating to a larger plant than is typical for Puerto Rico (beyond the data range, Table S2, but still found in the field). Since there was no correlation between the average abundance of functional groups and actual water volume in French Guiana, we used the mean abundances. The plant-level abundances of functional groups were



standardized to the abundance per leaf assuming equal distribution among leaves (Fig. 1, Table S4). The food webs we assembled differed in the composition and relative abundance of their functional feeding groups. When a functional group was absent from an experimental food web, this does not necessarily mean it was absent in the corresponding country, but rather that it was much less frequently found and likely to be missing from any given bromeliad (e.g. shredders and scrapers are scarce in French Guiana bromeliads in general; Brouard *et al.* 2012).

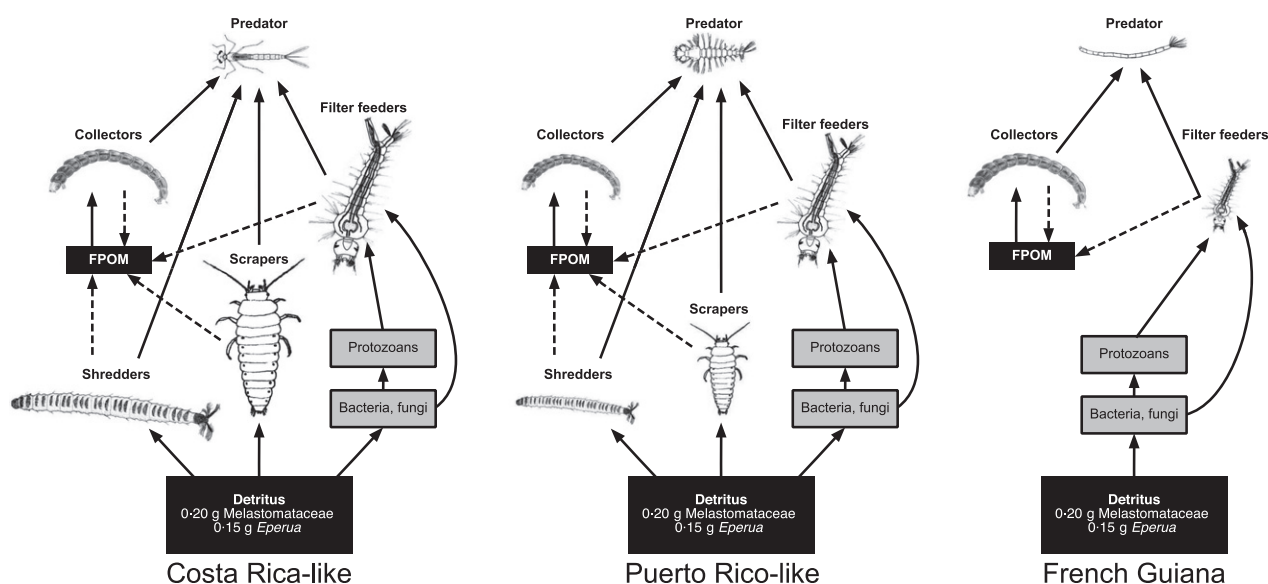
#### DROUGHT TREATMENTS

Rainfall patterns were determined using data collected at Petit Saut (~8 km away from the study site; 5°03' N, 53°02' W; elevation a.s.l.: 80 m) for October–December, for the years 2006 through 2010. These data were fitted to a negative binomial distribution. This distribution is described by two parameters,  $\mu$  and  $k$ , which measure the mean, and variance or dispersion parameter, respectively. The estimated values were rescaled to  $\mu = 1$  and  $k = 1$ . Treatments were factors relative to the unit values of  $\mu$  and  $k$ . It was necessary to make the model results discrete to the unit of one field day. Thus, precipitation treatments differed in two ways: the mean amount of rainfall per day and the frequency of rainfall events. The code used to calculate the precipitation treatments used in this study was developed by A.A.M. MacDonald & D. Srivastava as part of a larger multiregion study (The Bromeliad Working Group, MacDonald & Srivastava (2015), data and R code found at 10.5281/zenodo.18548). Bromeliads were assigned to one of four treatments which were combinations of two levels of  $\mu$  and two levels of  $k$  ( $\mu = 1.0, 0.2, k = 1.0, 0.5$ ). When  $\mu = 1.0$  and  $k = 1.0$ , plants received a mean amount of water (487 mL) at a typical frequency. At our most extreme drought treatment ( $\mu = 0.2$  and  $k = 0.5$ ), plants received 80% less water than the norm (97 mL) and at half the frequency (on the negative binomial scale).

Several steps were necessary to convert rainfall in mm into the actual volume of water an average plant would collect. The mean catchment area of our study bromeliads was estimated by image analysis, and a combined correction factor which accounts for canopy interception and bromeliad deflection was calculated (Supplementary Material). 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 ( $\mu = 1.0, k = 1.0$ ).

#### DROUGHT FOOD WEB ORIGIN EXPERIMENT

The per-leaf abundances were used to assemble experimental food webs in leaf wells of similar sized plants in Costa Rica, Puerto Rico and French Guiana (Fig. 1, Table S4). The week before the experiment started, invertebrates were collected from bromeliads of several species and were sorted into taxonomic groups. On the first day of the experiment (3 November 2013), experimental food webs were assembled in flow-through enclosures following the invertebrate abundances in Table S4 (same as Fig. 1) along with 0.1965 g (0.003 SE) dry weight of an unidentified species of Melastomataceae and 0.1453 g (0.002 SE) dry weight of *Eperua falcata* senescent leaves to provide the community with food and nutrients. We intentionally chose these two leaf species because they are common and represent different leaf traits found at our study site. *Eperua falcata* has a thick cuticle, and ligneous and glabrous leaves, Melastomataceae have thin and soft leaves (detailed information about differences in leaf chemistry can be found in Coq *et al.* 2010). Flow-through enclosures were constructed from 50-mL Falcon® tubes, with four holes (~5 mm diameter) at the bottom, covered with 80  $\mu$ m Nitex® mesh to allow for water flow, but prevent invertebrate movement. The tube tops were fitted with emergence traps, similar to those used by Starzomski, Suen & Srivastava (2010). Three tubes, one each for the CR-like, PR-like and FG food webs, were put into



**Fig. 1.** Food webs in experimental Costa Rica-like (CR), Puerto Rico-like (PR) and French Guiana (FG) bromeliad invertebrate communities. The size of each functional group represents their relative abundance. The taxonomy and abundance used are in Table S4. Solid arrows represent the main energy pathways. Dashed arrows indicate the generation of fine particulate organic matter (FPOM), which occurs through the process of feeding (chewing/shredding or passing through the gut). Detritus weights are dry weight.

separate leaf wells of the same bromeliad at a randomized position within the plant (high, middle and low). So, there were four precipitation treatments with three tubes per plant replicated seven times, for a total of 28 plants and 84 tubes. Each bromeliad was placed under a clear plastic tarpaulin to deflect natural rainfall and was separated by ~3 m. Every day, for 65 days, water depth was measured and plants were watered according to their assigned treatment values of  $\mu$  and  $k$ .

#### DATA COLLECTION

During the experiment, insects that emerged were collected and replaced as soon as possible. Given the difficulty in finding some species, the average time to replacement was 3.05 (0.190 SE) days. Part-way through the experiment (13–15 December, days 38–40), mosquito larvae (Culicidae) and oligochaete annelids (Naididae) were added to tubes in the same abundances as at the start of the experiment to simulate natural colonization and to ensure enough prey for predators. At the end of the experiment, we quantified invertebrate abundance, leaf decomposition and fine particulate organic matter (FPOM) within the tubes. CO<sub>2</sub> concentration, fluorescence (chlorophyll a), turbidity, conductivity, water temperature and water samples for microbiological analysis were collected in the leaf well next to the tube. Samples for CO<sub>2</sub> were collected early in the morning using a 5-mL glass syringe, were put into 3-mL sealed evacuated vials and transferred immediately to the laboratory at Petit Saut for analysis (by gas chromatography; SRI, Torrance, CA, USA) within 6 h of collecting the sample. The experimental tubes and their contents were removed and transferred to the laboratory. Invertebrates were counted immediately and preserved in alcohol. Leaves were dried at 55–60 °C for 72 h and weighed to estimate weight loss. To measure the amount of fine particulate organic matter (FPOM), the contents of each tube were rinsed through 150- $\mu$ m Nitex® mesh. The water and material which passed through the mesh were subsampled and collected on a 2.5-cm Whatman® GF/C filter, dried and weighed.

The content of the leaf well was stirred, prior to collecting water samples for microbiological analysis. A 3 mL sample was taken to estimate fluorescence (chlorophyll a) and turbidity in the field using a fluorometer (Aquafluor, Turner Designs). A 4 mL sample was collected for virus and bacteria counts, and preserved with a formaldehyde–borax solution (4% final concentration of formaldehyde). A 2 mL sample was fixed with Lugol iodine for protist enumeration. The microbiological samples were kept cool until they could be returned to a microbiology laboratory and processed to estimate the number of micro-organisms per mL: viruses, bacteria and protists (algae, ciliates and non-ciliate protozoans). Viruses and bacteria were counted by flux cytometry (virus and bacteria were separated by size), and protists were counted in settled chambers using a Leica® inverted microscope. Heterotrophic flagellates and naked and testate amoebae were pooled as non-ciliate protozoans. Detailed microbial protocols are available in Brouard *et al.* (2012) and Carrias *et al.* (2012).

#### STATISTICAL ANALYSIS

Several summary statistics of changes in the invertebrate community were calculated. The proportion of individuals which emerged ('proportion emerged') was calculated as the number of emerged adults divided by the total number of insects (excluding

non-insects, as these are entirely aquatic). The proportion of individuals that survived ('proportion survived') was calculated as the sum of emerged adults and surviving individuals at the end of the experiment divided by the total number of invertebrates at the start and those added to the community to replace emergences, and those added midway to simulate oviposition. Functional group survival was calculated in the same fashion but separately for each functional group. Response variables can be roughly divided into conceptual groups: (i) invertebrate community responses: emergence and survival; (ii) ecosystem response: decomposition, FPOM, CO<sub>2</sub> concentration; (iii) water chemistry: turbidity, conductivity, water temperature, fluorescence (chl-a); and (iv) micro-organisms: virus, bacteria, algae, ciliate and non-ciliate protozoan densities (mL<sup>-1</sup>) for a total of 20 response variables. The basic correlation structure among the response variables was examined. Separate mixed-effects models were run for each response variable using *lme* in the *nlme* package in R (Pinheiro *et al.* 2014; R Development Core Team, 2014). All models estimated the among-plant and among-tube (within-plant) variation as random effects and tested for the fixed effects of drought treatments and food web structure (*fw\_struct*). We also tested for the effect of several covariates and derived variables. We tested for a systematic effect of the tube position (*tube\_pos*) within a plant with a class variable (high, middle, low). Three measures of water level dynamics were calculated from the daily water level measurements; mean water level (*dbar*), variability in water level (*dvar*) and days below a critical level (*cdays*), defined as the number of days the water level fell below the lowest hole in the tube (remaining water volume ~1 mL). These derived variables were entered into the statistical model after the main effects. Two- and three-way interactions were tested for  $\mu$ ,  $k$  and food web structure (*fw\_struct*), but not covariates. All variables were retained in the model, and residual patterns were plotted to evaluate model fit (Zuur *et al.* 2009). Ciliate and non-ciliate protozoan densities required log transformation. Further models tested potential mechanisms leading to the patterns observed in the base models. For example, the effect of shredder survival on leaf pack weight loss was tested. In these models, two-way interactions with the treatments were tested and non-significant variables were removed. All analyses were carried out in R statistical software version 3.1.2.

#### Results

Food webs of aquatic macroinvertebrates inhabiting bromeliads differed substantially among countries (Fig. 1; Tables S1–S4; see also Kitching 2000). While there are many processes that can lead to such differences, at the broadest scale, this can be interpreted as a biogeographic effect on food web structure and functional diversity. Typically, a bromeliad that has a maximum volume of 1 L and 26 leaves in Costa Rica has large odonate predators, which is rare in French Guiana and absent in Puerto Rican bromeliads. Bromeliads of this size in Costa Rica have more invertebrates per leaf than Puerto Rico and French Guiana. CR-like food webs have the highest abundance of shredders and scrapers, whereas PR-like food webs typically have a third as many, and they are rare or absent in French Guiana (Tables S4). These patterns formed the basis for the food webs we assembled in our

experimental tubes. Our experiment independently tested for the effect of food web structure (fw\_struct) and drought on ecosystem function.

Food web structure consistently affected ecosystem function and the survival of functional groups. Survival of detritivores was lowest (effect sizes: CR scraper survival: 0.47 less; collector survival 4.17 less than PR) and the survival of predators was highest (2.11 higher than PR) in CR-like food webs. These food webs also had the lowest insect emergence rates (0.11 less than PR), indicating that the strongest top-down effects were by odonates (Fig. 2; Table 1). CR-like food webs also had the highest virus ( $4.08 \times 10^7 \text{ mL}^{-1}$  more than PR), bacteria ( $1.99 \times 10^7 \text{ mL}^{-1}$  more than PR), algal ( $11.07 \times 10^3 \text{ mL}^{-1}$  more than PR) and ciliate ( $8.02 \text{ mL}^{-1}$  more than PR) densities, but only intermediate non-ciliate protozoan densities (Fig. 3; Table 2). Weight loss of Melastomataceae leaf packs was highest in PR-like food webs (mean: 0.0414 g), intermediate in CR-like food webs (mean: 0.0387 g) and lowest in FG food webs (mean: 0.0323 g). FPOM production (fine particles produced by the feeding activity of invertebrates) was also highest in CR-like food webs (effect size: 0.40 mg/25 mL greater than PR; Fig. 4; Table 3). These effects of food web structure did not, however, affect water chemistry [turbidity, conductivity, water temperature and fluorescence (chl-a); results not shown].

The survival of functional groups was correlated even after accounting for hydrological and plant-specific variables, suggesting species interactions among functional feeding groups. The survival of filter feeders and scrapers decreased with predator survival, indicating an effect of predation. Filter feeder survival increased with collector survival ( $P = 0.05$ ) and tended to increase with scraper survival ( $P = 0.09$ ) in what might be considered a bottom-up processing chain. The survival of scrapers, shredders and filter feeders was all positively correlated, but only that of scrapers and shredders was significant (Table 4).

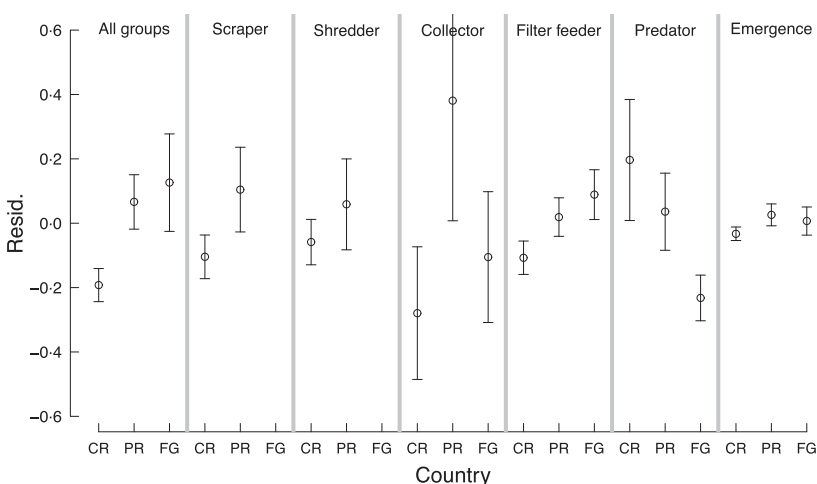
Our precipitation treatments had, at most, modest effects on water levels or other derived measures of the hydrology within a plant (Figs S2 and S3). We know that our treatments were effective, in that the tarpaulins kept the plants dry and the only water the plants received was

from our additions, and substantial in that the three rainfall change treatments represented large deviations from ambient conditions. However, even our most extreme treatments did not produce plants that dried out. By and large, functional group survival and insect emergence were not directly affected by the precipitation manipulations ( $\mu$  and  $k$ ) nor by an interaction between precipitation and food web structure. The exception was filter feeder survival, which increased (coefficient = 0.39,  $P = 0.03$ ) with the main effect of  $k$  (as the precipitation frequency approached the norm, Table 1), and an interaction between  $\mu$  and food web structure (fw\_struct) where the amount of precipitation had the strongest positive effect on filter feeder survival in CR-like food webs (Table 1). Summary measures of water level dynamics [mean water level (dbar), variability in water level (dvar) and days below a critical level (cdays)] did not explain patterns in food web structure or ecosystem function any better than our  $\mu$ - and  $k$ -based manipulations of precipitation. Despite this buffering of the precipitation treatments on bromeliad water levels, we still saw some biological responses to our precipitation treatments.

Overall, there were few significant interaction effects of precipitation treatments and food web structure (fw\_struct) on ecosystem function. Mass loss of the Melastomataceae leaf packs was the lowest in PR-like food webs with normal amounts of precipitation after accounting for tube position, hydrology and the interaction between  $\mu$  and  $k$  (marginally significant; Fig. 5a; Table 3). FPOM production was highest in FG food webs at the most severe drought treatments (three-way interaction; Fig. 5b; Table 3). In terms of food web response, non-ciliate protozoan density was higher in CR-like food webs and lower in FG food webs when water was added less frequently ( $k = 0.5$ ; Table 3).

## Discussion

We found that food web structure has stronger effects on ecosystem function than changes in precipitation and that the functional structure of the food web mediates the



**Fig. 2.** Functional group survival and insect emergence (partial residuals) in experimental Costa Rica-like (CR), Puerto Rico-like (PR) and French Guiana (FG) bromeliad invertebrate communities. The corresponding model results are in Table 1. Error bars are  $\pm 2$  SE.

Table 1. Linear mixed-effects model results for the effect of rainfall manipulations on functional group survival and insect emergence

| Fixed                  | Survival – All groups |       |         |         |           |         | Collector survival |       |           | Shredder survival |       |       | Scrapper survival |         |           | Filterer survival |           |         | Predator survival |       |           | Emergence |           |       |           |         |
|------------------------|-----------------------|-------|---------|---------|-----------|---------|--------------------|-------|-----------|-------------------|-------|-------|-------------------|---------|-----------|-------------------|-----------|---------|-------------------|-------|-----------|-----------|-----------|-------|-----------|---------|
|                        | numDF                 | denDF | F-value | P-value | F-value   | P-value | numDF              | denDF | F-value   | P-value           | numDF | denDF | F-value           | P-value | numDF     | denDF             | F-value   | P-value | numDF             | denDF | F-value   | P-value   | numDF     | denDF | F-value   | P-value |
|                        |                       |       |         |         |           |         |                    |       |           |                   |       |       |                   |         |           |                   |           |         |                   |       |           |           |           |       |           |         |
| Intercept              | 1                     | 43    | 159.93  | <0.0001 | 80.25     | <0.0001 | 1                  | 24    | 47.05     | <0.0001           | 1     | 43    | 151.81            | <0.0001 | 1         | 43                | 43.89     | <0.0001 | 1                 | 43    | 43.89     | <0.0001   | 1         | 43    | 211.80    | <0.0001 |
| $\mu$                  | 1                     | 24    | 0.18    | 0.67    | 1.66      | 0.21    | 1                  | 24    | 0.15      | 0.70              | 1     | 24    | 0.14              | 0.71    | 1         | 24                | 0.02      | 0.88    | 1                 | 24    | 0.02      | 0.88      | 1         | 24    | 0.37      | 0.55    |
| $k$                    | 1                     | 24    | 0.01    | 0.92    | 0.69      | 0.41    | 1                  | 24    | 1.74      | 0.20              | 1     | 24    | 5.55              | 0.03    | 1         | 24                | 1.76      | 0.20    | 1                 | 24    | 1.76      | 0.20      | 1         | 24    | 3.27      | 0.08    |
| fw_struct              | 2                     | 43    | 11.02   | 0.0001  | 6.00      | 0.01    | 1                  | 19    | 1.97      | 0.18              | 2     | 43    | 12.99             | <0.0001 | 2         | 43                | 9.56      | 0.0004  | 2                 | 43    | 9.56      | 0.0004    | 2         | 43    | 3.97      | 0.03    |
| tube_pos               | 2                     | 43    | 0.04    | 0.90    | 0.49      | 0.61    | 2                  | 19    | 0.94      | 0.41              | 2     | 43    | 1.06              | 0.35    | 2         | 43                | 0.27      | 0.61    | 2                 | 43    | 0.27      | 0.61      | 2         | 43    | 1.33      | 0.27    |
| dbar                   | 1                     | 43    | 0.04    | 0.84    | 2.53      | 0.12    | 1                  | 19    | 0.49      | 0.49              | 1     | 43    | 2.13              | 0.15    | 1         | 44                | 1.44      | 0.24    | 1                 | 43    | 1.44      | 0.24      | 1         | 43    | 3.29      | 0.08    |
| dvar                   | 1                     | 43    | 1.31    | 0.26    | 0.75      | 0.39    | 1                  | 19    | 2.01      | 0.17              | 1     | 43    | 0.01              | 0.93    | 1         | 43                | 0.98      | 0.33    | 1                 | 43    | 0.98      | 0.33      | 1         | 43    | 0.73      | 0.40    |
| edays                  | 1                     | 43    | 0.50    | 0.48    | 0.12      | 0.73    | 1                  | 19    | 0.31      | 0.59              | 1     | 43    | 0.86              | 0.36    | 1         | 43                | 0.04      | 0.85    | 1                 | 43    | 0.04      | 0.85      | 1         | 43    | 1.15      | 0.29    |
| $\mu : k$              | 1                     | 24    | 0.78    | 0.39    | 0.01      | 0.93    | 1                  | 24    | 0.11      | 0.74              | 1     | 24    | 0.52              | 0.48    | 1         | 24                | 0.01      | 0.91    | 1                 | 24    | 0.01      | 0.91      | 1         | 24    | 0.05      | 0.83    |
| $\mu : fw\_struct$     | 2                     | 43    | 1.13    | 0.33    | 0.14      | 0.87    | 1                  | 19    | 0.28      | 0.60              | 2     | 43    | 9.03              | 0.0005  | 2         | 43                | 1.81      | 0.18    | 2                 | 43    | 1.81      | 0.18      | 2         | 43    | 0.28      | 0.87    |
| $k : fw\_struct$       | 2                     | 43    | 1.01    | 0.37    | 0.95      | 0.40    | 1                  | 19    | 0.02      | 0.89              | 2     | 43    | 0.15              | 0.86    | 2         | 43                | 0.58      | 0.56    | 2                 | 43    | 0.58      | 0.56      | 2         | 43    | 0.76      | 0.76    |
| $\mu : k : fw\_struct$ | 2                     | 43    | 1.45    | 0.25    | 1.87      | 0.17    | 1                  | 19    | 0.05      | 0.82              | 2     | 43    | 0.99              | 0.38    | 2         | 43                | 0.31      | 0.74    | 2                 | 43    | 0.31      | 0.74      | 2         | 43    | 0.56      | 0.57    |
| Random                 |                       |       | SD      | P       | SD        | P       |                    |       | SD        | P                 | SD    | P     | SD                | P       | SD        | P                 | SD        | P       | SD                | P     | SD        | P         | SD        | P     | SD        | P       |
| Plant                  |                       |       | 0.090   | 0.21    | 4.29E-005 | 0.00    |                    |       | 1.21E-005 | 0.00              | 0.025 | 0.07  | 0.135             | 0.32    | 4.29E-005 | 0.00              | 5.59E-006 | 0.00    | 5.59E-006         | 0.00  | 5.59E-006 | 0.00      | 5.59E-006 | 0.00  | 5.59E-006 | 0.00    |
| Tube (plant)           |                       |       | 0.256   | 0.59    | 7.38E-001 | 0.99    |                    |       | 3.13E-001 | 1.00              | 0.280 | 0.81  | 0.212             | 0.49    | 7.38E-001 | 0.99              | 1.16E-001 | 0.99    | 1.16E-001         | 0.99  | 1.16E-001 | 0.99      | 1.16E-001 | 0.99  | 1.16E-001 | 0.99    |
| Residual               |                       |       | 0.084   | 0.20    | 3.70E-003 | 0.00    |                    |       | 1.08E-003 | 0.00              | 0.043 | 0.12  | 0.081             | 0.19    | 3.70E-003 | 0.00              | 5.09E-004 | 0.00    | 5.09E-004         | 0.00  | 5.09E-004 | 0.00      | 5.09E-004 | 0.00  | 5.09E-004 | 0.00    |

Significant effects ( $P < 0.05$ ) are in bold face.  $P$  is the proportion of variation explained by random effects.

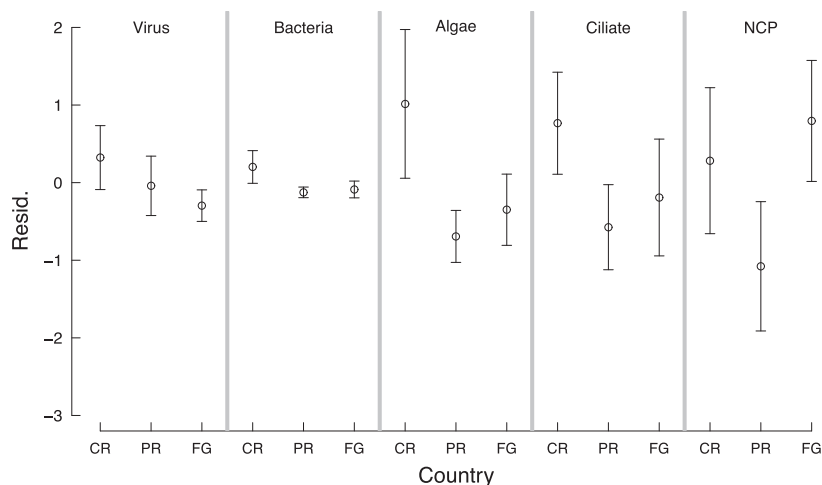
effects of drought on ecosystem function. Our results support theory that predicts that food webs containing both fast and slow food channels will be more stable and thus more resistant to climate change (Rooney *et al.* 2006; McCann & Rooney 2009). Specifically, we found that our food webs which contained both detritivore and filter feeder–microbial channels (our Costa Rica- and Puerto Rica-like food webs) were more resistant to changes in precipitation than the single detritivore channel food web (our French Guiana food web). The distribution and abundance of organisms are already changing due to climate change (Sheldon, Yang & Tewksbury 2011; VanDerWal *et al.* 2013), and changes in species distribution will inevitably create new food webs which we predict will have a larger effect on ecosystem function than any direct changes caused by changes in precipitation. In particular, we predict that factors which limit the colonization or abundance of top predators or bottom-up facilitators (shredders and scrapers) will have larger and more immediate effects on ecosystem function than changes in precipitation.

#### EFFECTS OF DROUGHT

Our manipulations created both the climatic norm and extreme drought conditions for the bromeliad ecosystem in our study area, over a 2-month study period that covered the generation time of most bromeliad invertebrates. Models of future climate change in South America predict up to 50% reductions in precipitation in eastern Amazonia by 2100 (IPCC 2013). Our manipulations were even stronger with up to an 80% reduction in precipitation ( $\mu = 0.2$ ) at half the frequency (negative binomial scale;  $k = 0.5$ ). In addition, the experiment was conducted in November and December, which is at the end of the dry season, so our precipitation manipulations were at a time when they should have had their strongest effect. Yet we found that the bromeliad ecosystem was largely resistant to drought at our experimental field site in French Guiana, and there are both hydrological and biological explanations for this resistance.

In terms of the hydrology, many lentic freshwater systems show some hydrological inertia to changes in precipitation. For example, lakes with high outflow can show little sensitivity of lake level to annual variation in rainfall (Kebede *et al.* 2006). Because tank bromeliads in general have evolved to collect, hold and retain water, the entire ecosystem is relatively resistant to the effects of drought. Bromeliads divide impounded water with multiple leaves which reduces evaporation rates, are able to overflow excess water and effectively retain water between days creating carry-over effects from past rain events. Thus, bromeliad architecture creates greater temporal autocorrelation in water depths than in the inputs of precipitation, as well as buffering the extremes of rainfall (Figs S2 and S3). These results further suggest that, while climate





**Fig. 3.** Microbial community counts (partial residuals) in experimental Costa Rica-like (CR), Puerto Rico-like (PR) and French Guiana (FG) bromeliad invertebrate communities. NCP = log non-ciliate protozoan density. The corresponding model results are in Table 2. Error bars are  $\pm 2$  SE.

change (including precipitation) affects broad regions, ecological components will likely show a range of system-specific response (Plattner 2009).

In addition to the hydrological buffering of drought, there is also biological buffering. Organisms may simply respond to water stress by leaving the area. In terms of overflow, macroinvertebrates can be washed out, although several components of the bromeliad fauna take advantage of claws and flattened bodies to maintain their position and/or to squeeze into the bottom of tanks (Picado 1913), much in the same way that stream invertebrates prevent drift. In terms of drought, Dézerald *et al.* (2015) found a high degree of resistance to drought in bromeliad communities (*Vriesea splendens*; same study site), such that functional diversity was maintained for 6 or 7 weeks in the absence of rainfall before they collapsed. Interestingly, they also found a high degree of resilience as the community quickly rebounded through a combination of colonization and revival of resistance stages. The bromeliads in Dézerald *et al.* (2015) were placed under tarpaulins and they did not water them until they dried up completely, whereas we manipulated precipitation patterns (amount and frequency). In a recent study, many Costa Rican bromeliad insects were found to require 2 or more weeks of complete desiccation before dying (Amundrud & Srivastava 2015), a situation which never occurred in our experiment. These different approaches set up a contrast in the definition of drought as being either system specific (little or no water) or meteorological (less precipitation). In other freshwater systems, invertebrates have proven to be adept at withstanding drought (Sim *et al.* 2013) through resistance traits such as desiccant-resistant eggs and aestivation, rapid recolonization (Jeffries 1994) or through behavioural adaptations such as use of microrefuges (Strachan, Chester & Robson 2014). In summary, although we created very different precipitation patterns which resulted in plants receiving much less water than their norm, the combination of the ability of the plant to buffer changes in precipitation and the ability of organisms to behaviourally and/or physiologically tolerate these

changes resulted in the resistance of the bromeliad fauna to drought.

#### FOOD WEB CONTEXT DEPENDENCE

Food web structure strongly impacted the survival of invertebrates and ecosystem functions. CR-like food webs had both the lowest detritivore survival (including filter feeders) and the highest predator survival, suggesting substantial predation on detritivores (Fig. 2), as recently confirmed by comparative analyses of predator/detritivore ratios across the Neotropics (Petermann *et al.* 2015). Drought increases predation by concentrating insects in a smaller water volume (Srivastava 2006). We hypothesize that predation on filter feeders and other detritivores was likely stronger in the CR-like food webs because of the unique presence of odonates in these food webs, as opposed to very small, piercing ceratopogonids in French Guiana, and mid-sized engulfing corethrellids in Puerto Rico. Odonate larvae are generalist predators with the largest individual biomass and gape size within bromeliad food webs and have large impacts on detritivore biomass, decomposition and nitrogen cycling where they occur (Ngai & Srivastava 2006; Starzomski, Suen & Srivastava 2010; Petermann *et al.* 2015). Gut content analyses of the three predators used in our experiments (Dézerald *et al.* 2013) further confirmed that ceratopogonids and corethrellids used in this experiment are specialized predators primarily feeding on small-bodied chironomids and culicids, respectively. Our results highlight that the strength of any drought-mediated top-down effects upon communities will depend on the biological traits of the apex predators and, therefore, on the geographic distribution of these species.

Ecosystem and microbial processes were also strongly affected by community composition. CR-like and PR-like food webs had higher leaf pack decomposition, presumably because shredders and scrapers were present in these food webs but absent in the FG food webs (Fig. 4; Richardson 1999; Srivastava & Bell 2009). Scrapers and

**Table 2.** Linear mixed-effects model results for the effect of drought on micro-organism density ( $\text{mL}^{-1}$ )

| Fixed                  | Virus density/ $10^7$ |       |         | Bacteria density/ $10^7$ |         |         | Algae density/ $10^3$ |         |       | Log (Ciliate density + 1) |         |         | Log (non-ciliate protozoan density + 1) |       |         |         |
|------------------------|-----------------------|-------|---------|--------------------------|---------|---------|-----------------------|---------|-------|---------------------------|---------|---------|---|-------|---------|---------|
|                        | numDF                 | denDF | F-value | P-value                  | F-value | P-value | F-value               | P-value | numDF | denDF                     | F-value | P-value | numDF                                   | denDF | F-value | P-value |
| Intercept              | 1                     | 41    | 73.69   | <0.0001                  | 91.30   | <0.0001 | 28.42                 | <0.0001 | 1     | 43                        | 346.75  | <0.0001 | 1                                       | 43    | 182.61  | <0.0001 |
| $\mu$                  | 1                     | 24    | 1.63    | 0.21                     | 0.10    | 0.76    | 0.38                  | 0.54    | 1     | 24                        | 1.97    | 0.17    | 1                                       | 24    | 0.06    | 0.80    |
| $k$                    | 1                     | 24    | 0.61    | 0.44                     | 2.51    | 0.13    | 1.77                  | 0.20    | 1     | 24                        | 0.68    | 0.42    | 1                                       | 24    | 5.46    | 0.03    |
| fw_struct              | 2                     | 41    | 4.53    | 0.02                     | 5.92    | 0.01    | 7.85                  | 0.001   | 2     | 43                        | 4.70    | 0.01    | 2                                       | 43    | 6.64    | 0.003   |
| tube_pos               | 2                     | 41    | 0.14    | 0.87                     | 0.43    | 0.66    | 0.37                  | 0.69    | 2     | 43                        | 1.87    | 0.17    | 2                                       | 43    | 1.40    | 0.26    |
| dubar                  | 1                     | 41    | 0.18    | 0.67                     | 0.41    | 0.53    | 0.82                  | 0.37    | 1     | 43                        | 0.31    | 0.58    | 1                                       | 43    | 0.21    | 0.65    |
| dvar                   | 1                     | 41    | 0.07    | 0.79                     | 0.31    | 0.58    | 1.19                  | 0.28    | 1     | 43                        | 0.04    | 0.84    | 1                                       | 43    | 0.07    | 0.79    |
| edays                  | 1                     | 41    | 0.00    | 1.00                     | 0.02    | 0.89    | 0.34                  | 0.56    | 1     | 43                        | 0.22    | 0.64    | 1                                       | 43    | 0.08    | 0.78    |
| $\mu : k$              | 1                     | 24    | 0.29    | 0.60                     | 0.00    | 0.98    | 0.02                  | 0.89    | 1     | 24                        | 0.58    | 0.46    | 1                                       | 24    | 3.03    | 0.09    |
| $\mu : fw\_struct$     | 2                     | 41    | 0.39    | 0.68                     | 0.15    | 0.86    | 1.27                  | 0.29    | 2     | 43                        | 0.46    | 0.64    | 2                                       | 43    | 0.98    | 0.38    |
| $k : fw\_struct$       | 2                     | 41    | 0.77    | 0.47                     | 0.33    | 0.72    | 1.69                  | 0.20    | 2     | 43                        | 1.30    | 0.28    | 2                                       | 43    | 3.32    | 0.05    |
| $\mu : k : fw\_struct$ | 2                     | 41    | 2.34    | 0.11                     | 0.71    | 0.50    | 0.32                  | 0.73    | 2     | 43                        | 0.91    | 0.41    | 2                                       | 43    | 0.23    | 0.80    |
| Random                 |                       |       | SD      | P                        | SD      | P       | SD                    | P       |       |                           | SD      | P       |   |       | SD      | P       |
| Plant                  |                       |       | 0.546   | 0.35                     | 0.132   | 0.21    | 0.411                 | 0.16    |       |                           | 0.600   | 0.22    |   |       | 0.600   | 0.22    |
| Tube (plant)           |                       |       | 0.716   | 0.46                     | 0.364   | 0.59    | 1.630                 | 0.65    |       |                           | 1.600   | 0.58    |   |       | 1.600   | 0.58    |
| Residual               |                       |       | 0.286   | 0.18                     | 0.120   | 0.19    | 0.473                 | 0.19    |       |                           | 0.535   | 0.20    |   |       | 0.535   | 0.20    |

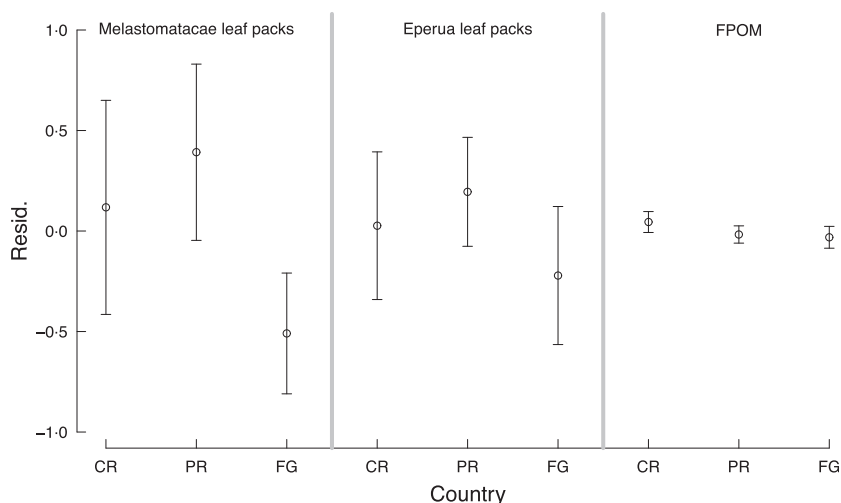
Significant effects ( $P < 0.05$ ) are in bold face.  $P$  is the proportion of variation explained by random effects.

shredders break down leaf material into smaller particles, which has a positive effect on invertebrates feeding 'downstream' in the processing chain (Heard 1994; Starzomski, Suen & Srivastava 2010). In our study, the survival of filter feeders increased with the survival of scrapers in our Costa Rica-like food webs ( $r = 0.28$ ,  $P = 0.04$ ), although not in our Puerto Rica-like food webs. Similarly, the highest production of FPOM was in CR-like food webs (Fig. 4), which had the highest density of shredders and scrapers and the presence of an odonate predator. We suspect that these bottom-up and top-down effects in our CR-like food webs created an enriched environment that led to increased microbial densities (Fig. 3).

#### FOOD WEB STRUCTURE AND DROUGHT

Overall, drought did not have direct lethal effects on bromeliad invertebrates (see also Amundrud & Srivastava 2015), but rather had sublethal effects which affected invertebrate per capita functions, such as feeding activities and predation. Future studies of the effects of climate change will need to measure not only survival rates, but changes in food web interactions as well. Drought increased filter feeder survival in French Guiana (FG) food webs, but reduced filter feeder survival in Costa Rican (CR-like) and Puerto Rican (PR-like) food webs (Fig. 6a, Table 1). Non-ciliate protozoan densities responded in the opposite way to drought in each country, suggesting that their densities were under top-down control from filter feeders (Fig. 6b, Table 2). Strong top-down effects of filter feeders on protozoans (and on the microbial communities in general) have been shown in other studies of bromeliad fauna (Brouard *et al.* 2011; Hammill *et al.* 2014) and other phytotelmata (Kneitel & Miller 2002; Trzcinski, Walde & Taylor 2005, 2008). In our study, we found that filter feeder survival (and abundance) decreased virus counts ( $r = -0.34$ ,  $P = 0.002$ ), bacterial densities ( $r = -0.40$ ,  $P = 0.002$ ), algal densities ( $r = -0.25$ ,  $P = 0.02$ ), log ciliate densities ( $r = -0.60$ ,  $P < 0.001$ ) and water turbidity ( $r = -0.24$ ,  $P = 0.03$ ). Even though CR-like food webs had the most filter feeders at the start of the experiment, predation or the risk of predation strongly reduced the effect of filter feeders on the microbial communities. So if we follow the cascading effects of predators, we see that when filter feeders were under much stronger top-down control by the odonate in CR-like food webs, the density of micro-organisms was higher (Fig. 3). This trophic cascade creates a biogeographic context dependence in ecosystem function wherever the distribution or abundance of odonates is limited (absent in small bromeliads in Costa Rica, Srivastava, Melnychuk & Ngai 2005; rare in French Guiana, Brouard *et al.* 2012; absent in Puerto Rico, Richardson 1999).

Finally, the most extreme drought treatment (decreased  $\mu$  and  $k$ ) had a strong positive effect on FPOM production in FG food webs, but not in CR-like or PR-like food webs (hence the three-way interaction; Fig. 5; Table 3).



**Fig. 4.** Ecosystem response (residual leaf pack weight loss and FPOM production) in experimental Costa Rica-like (CR), Puerto Rico-like (PR) and French Guiana (FG) bromeliad invertebrate communities. The corresponding model results are in Table 3. Error bars are  $\pm 2$  SE.

**Table 3.** Linear mixed-effects model results for the effect of drought on ecosystem function

| Fixed                  | Melastomataceae leaf pack weight loss (g) |       |          |                    | Eperua leaf pack weight loss (g) |                    | FPOM (mg per 25 mL) |           |         |                    |
|------------------------|---|-------|----------|--------------------|----------------------------------|--------------------|---------------------|-----------|---------|--------------------|
|                        | numDF                                     | denDF | F-value  | P-value            | F-value                          | P-value            | numDF               | denDF     | F-value | P-value            |
| Intercept              | 1   | 43    | 878.00   | <b>&lt; 0.0001</b> | 118.39                           | <b>&lt; 0.0001</b> | 1                   | 41        | 112.24  | <b>&lt; 0.0001</b> |
| $\mu$                  | 1   | 24    | 0.07     | 0.79               | 1.52                             | 0.23               | 1                   | 24        | 1.13    | 0.30               |
| $k$                    | 1   | 24    | 0.27     | 0.61               | 0.23                             | 0.63               | 1                   | 24        | 0.32    | 0.58               |
| fw_struct              | 2   | 43    | 5.02     | <b>0.01</b>        | 2.40                             | 0.10               | 2                   | 41        | 6.20    | <b>0.004</b>       |
| tube_pos               | 2   | 43    | 3.92     | <b>0.03</b>        | 2.12                             | 0.13               | 2                   | 41        | 0.06    | 0.94               |
| dbar                   | 1   | 43    | 0.70     | 0.41               | 1.22                             | 0.27               | 1                   | 41        | 0.23    | 0.64               |
| dvar                   | 1   | 43    | 1.08     | 0.30               | 4.00                             | <b>0.05</b>        | 1                   | 41        | 0.00    | 0.96               |
| cdays                  | 1   | 43    | 2.31     | 0.14               | 2.84                             | 0.10               | 1                   | 41        | 3.20    | 0.08               |
| $\mu : k$              | 1   | 24    | 0.00     | 0.99               | 0.10                             | 0.75               | 1                   | 24        | 0.40    | 0.53               |
| $\mu : fw\_struct$     | 2   | 43    | 2.81     | 0.07               | 0.13                             | 0.88               | 2                   | 41        | 0.93    | 0.40               |
| $k : fw\_struct$       | 2   | 43    | 0.18     | 0.84               | 0.35                             | 0.71               | 2                   | 41        | 0.82    | 0.45               |
| $\mu : k : fw\_struct$ | 2   | 43    | 2.47     | 0.10               | 1.28                             | 0.29               | 2                   | 41        | 3.67    | <b>0.03</b>        |
| <b>Random</b>          | <b>SD</b>                                 |       | <b>P</b> |                    | <b>SD</b>                        | <b>P</b>           |                     | <b>SD</b> |         | <b>P</b>           |
| plant                  | 4.83E-007                                 |       | 0.00     |                    | 5.24E-003                        | 0.36               |                     | 1.03E-004 |         | 0.48               |
| tube (plant)           | 1.09E-002                                 |       | 1.00     |                    | 6.64E-003                        | 0.46               |                     | 7.63E-005 |         | 0.36               |
| residual               | 5.02E-005                                 |       | 0.00     |                    | 2.68E-003                        | 0.18               |                     | 3.53E-005 |         | 0.16               |

Significant effects ( $P < 0.05$ ) are in bold face.  $P$  is the proportion of variation explained by random effects.

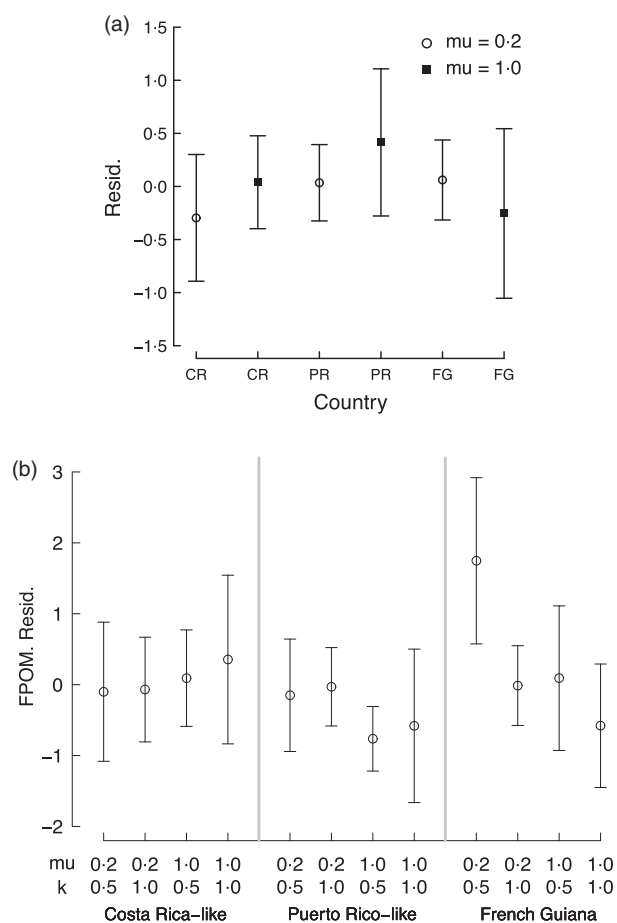
Although the mechanism here is less clear, FPOM production in FG food webs could be primarily originating from mosquito faeces and thus also be a result of high filter feeder survival in this community. Species that typically produce high amounts of FPOM, such as shredders, scrapers and odonates, are scarce in the bromeliad food webs of French Guiana (Brouard *et al.* 2012) and absent in our experimental FG food webs. These results indicate that bromeliad ecosystems without strong top-down and bottom-up effects that are primarily driven by the fast bacteria/protozoan/filter feeder food chain, as they are in French Guiana, will be more sensitive to drought. In summary, FG food webs may have shown stronger responses to drought because their food webs were missing important functional feeding groups or taxa, namely shredders, scrapers and large-bodied predators (odonates). These results support theoretical predictions that food webs

missing a slow detritivore food chain will be less stable (Rooney *et al.* 2006; McCann & Rooney 2009).

Our results suggest that a key part of the biogeographic contingency in this system is the presence of odonates in the species pool (also shown by Petermann *et al.* 2015) and the dominance of the filter feeder–microbial channel. However, there are two caveats that should be added. First, our approach only isolates the effects of biogeographic differences in functional group composition. Geographically separated sites will also differ in their environmental characteristics. To partition biogeographic contingency into functional composition vs. local environment, the next step is to also conduct geographically replicated (same experiment in different locations, where differences are the result of both functional composition and local environment; Menge *et al.* 1999) and transplant experiments (same community structure in different

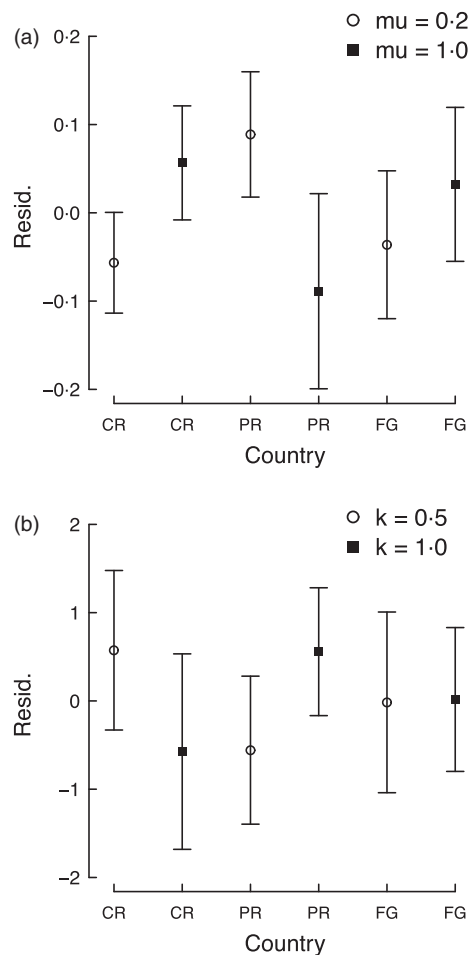
**Table 4.** Person correlation matrix of invertebrate functional group survival after accounting for drought treatment ( $\mu$  and  $k$ ) and random effects (plant and tube within plant): (a) coefficients and (b)  $P$ -values

|               | Collector | Shredder | Scraper | Filter feeder |
|---------------|-----------|----------|---------|---------------|
| a)            |           |          |         |               |
| Shredder      | -0.078    |          |         |               |
| Scraper       | 0.032     | 0.298    |         |               |
| Filter feeder | 0.258     | 0.165    | 0.230   |               |
| Predator      | -0.197    | -0.199   | -0.299  | -0.403        |
| b)            |           |          |         |               |
| Shredder      | 0.570     |          |         |               |
| Scraper       | 0.810     | 0.030    |         |               |
| Filter feeder | 0.050     | 0.220    | 0.090   |               |
| Predator      | 0.150     | 0.140    | 0.030   | 0.002         |



**Fig. 5.** Response of ecosystem processes to (a) the interaction between  $\mu$  and food web structure ( $fw\_struct$  for each country) on Melastomataceae leaf pack weight loss (partial residuals) in grams ( $F_{2,43} = 2.83$ ,  $P = 0.07$ ) and (b) the interaction of  $\mu$ ,  $k$  and  $fw\_struct$  on FPOM (partial residuals;  $F_{2,41} = 3.67$ ,  $P = 0.03$ ). The corresponding model results are in Table 3. Error bars are  $\pm 2$  SE.

locations, isolates the effects of site environment; LeCraw 2014). Secondly, our community analogue approach is explicitly based on the assumption that species with



**Fig. 6.** (a) Filter feeder survival (partial residuals) and (b) log non-ciliate protozoan density (partial residuals;  $mL^{-1}$ ) in experimental Costa Rica-like (CR), Puerto Rico-like (PR) and French Guiana (FG) bromeliad invertebrate communities. The corresponding model is not presented. Error bars are  $\pm 2$  SE.

similar functional traits in different parts of the world can 'stand in' for each other (functional equivalency). Thus, we suggest that our results tell us about how these functional groups generally affect bromeliad ecosystem function, while making predictions about how other unstudied bromeliad ecosystems will respond to changes in climate and food web structure. This approach will undoubtedly be difficult for ecologists studying different ecosystems, but we encourage further exploration and development of this approach as it seeks to synthesize the generality and contingency of ecosystem responses to climate change.

## CONCLUSION

Climate change is expected to alter both the distribution and abundance of species through range contraction and expansion (Rosset & Oertli 2011; Sheldon, Yang & Tewksbury 2011), and through changes in precipitation patterns (Dejean *et al.* 2011; VanDerWal *et al.* 2013). Our results show stronger effects of food web structure than



precipitation change *per se* on the functioning of bromeliad ecosystems. Consequently, ecosystem function in bromeliads throughout the Americas will be more sensitive to changes in the distribution of species, rather than to the direct effects of precipitation. Furthermore, existing biogeographic differences in the representation of functional groups in food webs can mask or reveal compartments or channels that are particularly sensitive to climate change. In our experiments, the sensitivity of the ecosystem to precipitation change was primarily revealed in the food web dominated by the fast microbial–protozoan–filter feeder channel because other top-down and bottom-up processes were weak or absent. Thus, both current and future patterns in species distribution will be essential for understanding the effects of climate change on the functioning of ecosystems.

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## Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.b658g> (Trzcinski et al. 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

### Appendix S1. Supplementary Material.

**Table S1.** Mean community structure found in field surveys of bromeliads in Costa Rica (*Vriesea* spp. and *Guzmania* spp.), Puerto Rico (*Guzmania* spp.) and French Guiana (*Aechmea aquilega*) by invertebrate family or taxonomic group.

**Table S2.** Mean community structure found in field surveys of bromeliads in Costa Rica, Puerto Rico and French Guiana by functional group.

**Table S3.** Multiple linear regression model fit and parameter estimates for the abundance of a functional group as a function of bromeliad water volume at time of sampling and the number of

leaves for plants sampled in Costa Rica, Puerto Rico and French Guiana.

**Table S4.** Estimated per leaf abundance of an average invertebrate community found in bromeliads (1 L of water, 26 leaves) in Costa Rica (CR-like), Puerto Rico (PR-like) and French Guiana (FG) communities.

**Fig. S1.** Invertebrate functional feeding group abundance vs. actual water volume (per bromeliad) at time of sampling for Costa Rica, Puerto Rico and French Guiana field surveys.

**Fig. S2.** Precipitation manipulations (solid line in L) for four treatments, and changes in water level (box plots) in three leaves within a plant belonging to one of the four treatments: (a)  $\mu = 0.2$ ,  $k = 0.5$ , (b)  $\mu = 0.2$ ,  $k = 1$ , (c)  $\mu = 1$ ,  $k = 0.5$ , (d)  $\mu = 1$ ,  $k = 1$ .

**Fig. S3.** Summary measure of water level dynamics in three leaves within a plant belonging to one of the four treatments: (a) mean days below a critical water depth, (b) mean water depth (cm), (c) the coefficient in variation (CV) in water depth, and (d) the temporal autocorrelation function (lag = 1).