

# When the rainforest dries: Drought effects on a montane tropical stream ecosystem in Puerto Rico

Pablo E. Gutiérrez-FONSECA<sup>1,7</sup>, Alonso Ramírez<sup>2,8</sup>, Catherine M. Pringle<sup>3,9</sup>, Pedro J. Torres<sup>3,10</sup>, William H. McDowell<sup>4,11</sup>, Alan Covich<sup>3,12</sup>, Todd Crowl<sup>5,13</sup>, and Omar Pérez-Reyes<sup>6,14</sup>

<sup>1</sup>Department of Environmental Sciences, University of Puerto Rico-Río Piedras, Juan Ponce de León Avenue, San Juan 00925-2537 Puerto Rico

<sup>2</sup>Department of Applied Ecology, North Carolina State University, 100 Eugene Brooks Avenue, Raleigh, North Carolina 27695-7617 USA

<sup>3</sup>Odum School of Ecology, University of Georgia, 140 East Green Street, Athens, Georgia 30602 USA

<sup>4</sup>Department of Natural Resources and the Environment, University of New Hampshire, Garrison Avenue, Durham, New Hampshire 03824 USA

<sup>5</sup>Department of Biological Sciences, Florida International University, 11200 Southwest 8<sup>th</sup> Street, Miami, Florida 33199 USA

<sup>6</sup>Department of Biology, University of Puerto Rico-Río Piedras, Juan Ponce de León Avenue, San Juan 00931-3360 Puerto Rico

**Abstract:** Global climate change predictions include decreased precipitation and more frequent droughts in many world regions. In the aseasonal wet tropics, predicting potential impacts is particularly challenging because droughts are rare and therefore poorly understood. In 2015, the Caribbean islands experienced the most severe drought within the past 5 decades. Here, we use this extreme event as an opportunity to assess how tropical stream ecosystems draining the Luquillo Experimental Forest (LEF) in Puerto Rico respond to severe drought. During 2015, precipitation was 45% lower than the long-term (1975–2016) average for the LEF, resulting in a 54% reduction in stream discharge. After 5 mo of declining discharge (April–August 2015), one branch of our focal study stream system became a series of isolated pools and a few riffle-type runs, while the other branch had greatly reduced flow between its pools. Concentrated biotic activity within pools resulted in elevated and highly-variable nutrient ( $5.1\text{--}12.1\text{ }\mu\text{g PO}_4^{3-}\text{-P/L}$ ;  $12.9\text{--}57.2\text{ }\mu\text{g NH}_4^+\text{-N/L}$ ;  $80.0\text{--}160.0\text{ }\mu\text{g NO}_3^-\text{-N/L}$ ) and specific conductance (95–114  $\mu\text{S/cm}$ ) levels among pools. However, the algal standing crop was 14 $\times$  lower than the previous 15-y average despite increases in nutrient levels, reflecting intense grazing pressure of insect and shrimp consumers, potentially due to decreased pool volume. Higher nutrient levels in stream pools did increase biofilm productivity, and at the peak of the drought daily fluctuations in dissolved oxygen ranged from  $\sim 1.0$  to  $6.5\text{ mg/L}$ . Significantly-higher riparian inputs of organic matter (7.6 $\times$  the long-term average) occurred during a 15-d period in May. The drought caused a general increase in macroinvertebrate density, with collector-gatherers and some grazer taxa increasing significantly at the peak of the drought, but taxonomic richness did not change. Omnivorous shrimp abundance increased slightly in response to decreased stream flow in one branch of our focal stream. Our study highlights the marked effects of severe droughts on neotropical streams in the wet tropics, with large effects on basal resources and consequent changes in trophic dynamics. Ultimately, our findings underline the need for a whole-ecosystem perspective to understand how streams respond to increased frequencies of extreme events associated with climate change.

**Key words:** aseasonality, disturbances, low flow, neotropical streams, precipitation

E-mail addresses: <sup>7</sup>Present Address: Department of Biology and Center for Research in Marine Science and Limnology, University of Costa Rica, 7<sup>th</sup> Avenue, San José 11501-2060 Costa Rica, pablo.gutierrezfonseca@gmail.com; <sup>8</sup>alonso.ramirez@ncsu.edu; <sup>9</sup>cpringle@uga.edu; <sup>10</sup>pjtorres@uga.edu; <sup>11</sup>bill.mcowell@unh.edu; <sup>12</sup>alanc@uga.edu; <sup>13</sup>tcrowl@fiu.edu; <sup>14</sup>macrobrachium@gmail.com

DOI: 10.1086/708808. Received 15 January 2019; Accepted 9 July 2019; Published online 31 March 2020.

Freshwater Science. 2020. 39(2):197–212. © 2020 by The Society for Freshwater Science. All rights reserved. This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0), which permits non-commercial reuse of the work with attribution. For commercial use, contact journalpermissions@press.uchicago.edu.

Global climate change is expected to have large effects on tropical freshwater ecosystems (Woodward et al. 2010, IPCC 2014). General circulation models vary widely, but there is a consensus that annual rainfall patterns will change significantly for most of the tropics, leading to higher magnitude and frequency of extreme rainfall and drought events (O'Gorman and Schneider 2009, Pendergrass and Hartmann 2014) that will subsequently alter stream flow patterns. The effects of floods are relatively well understood in the wet tropics, where they follow extreme rainfall events and have localized effects that last from days to weeks (e.g., Dudgeon 1993, Rayner et al. 2008). In contrast, the effects of droughts are less understood because droughts are less frequent and it is difficult to identify drought conditions until long after they begin (Lake 2003, 2011, Boulton and Lake 2008, Pearson 2014). The ecological effects of droughts can develop over extended time periods that last for months or years (Wilhite 2000). Moreover, many tropical species that are not fully adapted to the stress imposed by prolonged dry periods can be locally extirpated, decline in density, or suffer physiological damage (e.g., Ramírez et al. 2018).

The deleterious effects of drought on freshwater ecosystems have been summarized by Lake (2000). In this conceptual framework, drought disturbances are described as ramps, or disturbances that gradually increase in strength and extent, that trigger a decline in groundwater levels and, thereby, the disruption of longitudinal hydrologic connectivity. This loss of connectivity transforms streams into a series of isolated pools, where temperatures increase and water chemistry is altered. Nutrient transport is reduced, stimulating algal blooms in isolated pools. Biotic interactions (e.g., competition and predation) may become more intense as habitat space is reduced. This conceptual framework has been strongly supported by numerous empirical studies (e.g., Covich et al. 2003, Lynch and Magoulick 2016) and provides clear evidence of ecosystem breakdown as streams dry up. However, most studies have been focused on a single component of the ecosystem rather than addressing complex ecosystem dynamics and community-wide responses to drought.

During 2015, the Caribbean islands suffered the most severe and widespread drought that has occurred in the last 50 y (Herrera and Ault 2017, Mote et al. 2017). The Caribbean experienced a rainfall deficit from late 2013 to early 2016, and during 2015 more than 50% of the islands experienced severe drought conditions (Herrera and Ault 2017). In Puerto Rico, 45% of the territory experienced moderate to severe drought, and 25% experienced extreme drought, which is the 2<sup>nd</sup> most intense category according to the US Drought Monitor (DRNA 2016). The only similar event in recent history was a drought that occurred in 1994, which was the 3<sup>rd</sup> most severe drought of the last century (Larsen 2000).

In this study, we evaluate stream ecosystems responses to the severe and potentially-devastating drought in Puerto Rico. Droughts are uncommon in tropical wet areas, so this

drought provided a unique opportunity to assess the effects of prolonged drying on freshwater ecosystems in an aseasonal tropical montane rainforest. We use data from the Luquillo Long-Term Ecological Research (LUQ-LTER) program, where biological and physicochemical parameters have been collected for >3 decades. We used 2 approaches to characterize drought effects on the ecosystem. First, we compared parameters (mostly physicochemical) during drought with long-term averages. Second, we used the data collected throughout 2015 (mostly biological) to evaluate ecosystem responses during and after the drought. We expected the drought to cause declines in stream discharge that would strongly influence stream physicochemistry. We also predicted that the hydrological disturbance would cause significant changes in ecosystem structure and function. We use our findings to adjust and expand the conceptual model developed by Lake (2000) to include not only the effects of drought on multiple components of aquatic ecosystems but on the terrestrial components (i.e., riparian vegetation) as well. Our conceptual framework is presented as a generalized tool that identifies linkages, interactions, and potential effects among ecosystem components during a drying event. This whole-ecosystem perspective allows us to elucidate the hierarchical effects and progressive impacts of drought on stream ecosystems (Fig. 1). Our study provides a window into the future that freshwater ecosystems in many tropical areas may experience because of climate change.

## METHODS

### Study design overview

Our study was conducted in Quebrada Prieta, which is composed of 2 converging tributaries (hereafter: Prieta A and B). All samples were collected during the 2015 drought, and in some cases we were able to compare our parameters with available long-term data collected by the LUQ-LTER. We measured shrimp abundance in 2 pools along a 500-m reach in Prieta A, in the same sites where the LUQ-LTER has been sampling shrimp since 1998. In Prieta B, we established a 100-m reach where we studied 6 pools and 4 riffles that were the only available habitat during the drought. In those habitats, we measured leaf litter, benthic organic matter, epilithon, macroinvertebrates, specific conductance, and nutrients. In both tributaries, we selected pools of similar sizes for our observations. In addition, we studied a single pool downstream of the confluence of the 2 tributaries (hereafter: confluence pool) where we measured shrimp abundance, discharge, and physicochemical variables (i.e., specific conductance, temperature, dissolved oxygen, and nutrients; Fig. 2).

As a long-term study site of the LUQ-LTER, stream monitoring in Quebrada Prieta is coordinated to minimize disturbances. Prieta A is exclusively dedicated to decapod monitoring and Prieta B to multiple other components, including algae, benthic macroinvertebrates, and organic

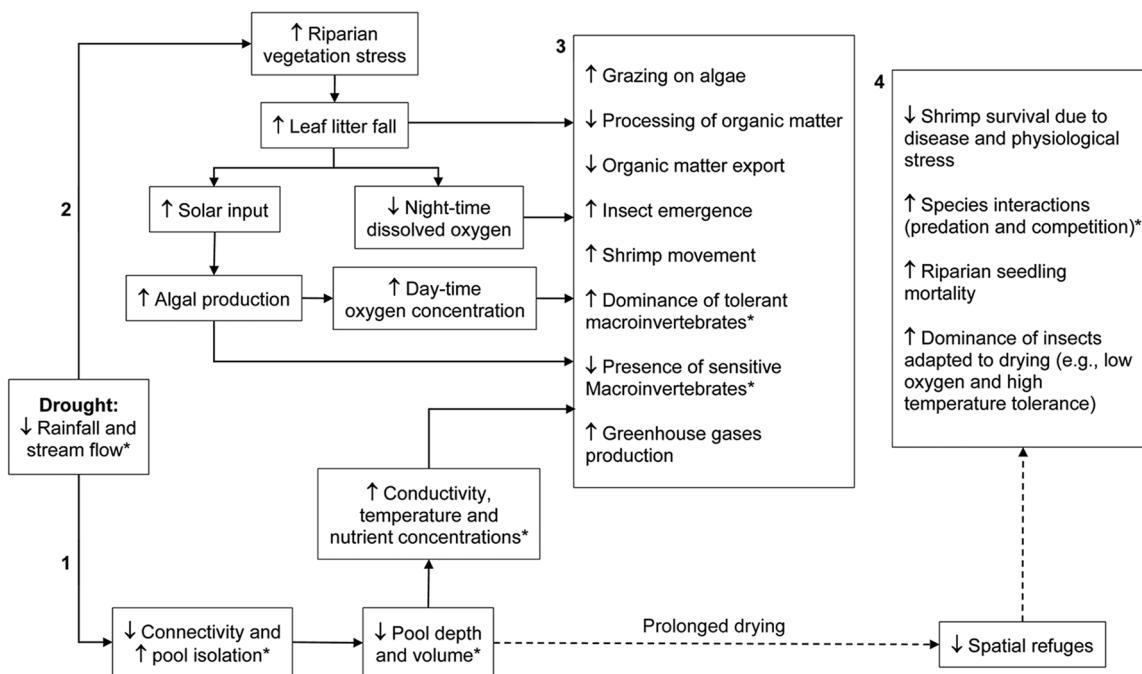


Figure 1. Conceptual framework of the progressive effects of drought on stream ecosystems in aseasonal tropical montane rainforests. In our model, drought affects aquatic and terrestrial components of the ecosystem, clearly demonstrating the complexity of interactions between them. During drying, precipitation deficit reduces stream flow and stream ecosystems (1) start losing connectivity, which results in isolated pools of differing physicochemical conditions. Simultaneously, riparian vegetation (2) enters physiological stress, which causes leaf loss. Reduced canopy cover allows the passage of sunlight, stimulating algal production. Decomposition of organic matter and primary production causes drastic daily changes in oxygen concentrations. Responses of stream biota and ecosystem processes (3) to these new conditions are highly variable. More extreme responses (4) can be expected when droughts are prolonged, as occurred in 1994, or more frequent (dashed line). Up arrows ( $\uparrow$ ) indicate an increase, while down arrows ( $\downarrow$ ) indicate a decrease in the measured variable. \* represent the original model predictions in Lake (2000).

matter. We conducted additional sampling in Prieta B during the 2015 drought. However, we did not quantify shrimp populations in Prieta B due to the small size of its isolated pools, which did not allow for standard trapping techniques. Visual surveys indicated that shrimp were conspicuously absent from Prieta B during peak drought.

### Study system

We studied the Luquillo Experimental Forest (LEF), which is part of El Yunque National Forest, in northeastern Puerto Rico ( $18^{\circ}19'N$ ,  $65^{\circ}45'W$ ). The LEF includes 4 life zone categories based on the Holdridge system: subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rainforest (Ewel and Whitmore 1973). Annual precipitation is  $\sim 3500$  mm at 350 m a.s.l. and ranges from 1416 to 5023 mm/y (1975–1994; García-Martinó et al. 1996). The climate in the LEF is aseasonal because all months receive  $>100$  mm of rain (Zimmerman and Covich 2007, Zimmerman et al. 2007), although there is slightly less rainfall from January to April. The coefficient of variation of total monthly precipitation, which can indicate regional hydrologic disturbance and inter-annual var-

ability (Oliver 1980), is typically 47.5% (1975–2016). The precipitation concentration index (indicator of rainfall concentration) in this area is 10.3, which means the distribution of precipitation throughout the year is uniform to moderate (Michiels et al. 1992). Precipitation variability in the region is primarily driven by the North Atlantic Oscillation (Jury et al. 2007, Mote et al. 2017) and El Niño–Southern Oscillation (Herrera and Ault 2017). Mean monthly temperatures range from 20.6 to 25.8°C, and the annual mean is 23.0°C (González et al. 2014). The landscape in the LEF is steep and rocky, and soils have developed from volcanic-lastic sediments.

The drainage network in the LEF is comprised of 1<sup>st</sup>- and 2<sup>nd</sup>-order streams that have steep slopes and closed evergreen riparian canopies. Stream channels are dominated by bedrock, boulders, and cobbles, while pools are dominated by gravel and sand. Riparian vegetation is dominated by *Dacryodes excelsa* (tabonuco) and *Prestoea montana* (Sierra palm). Discharge is highly variable and increases rapidly during local storm events (Covich and McDowell 1996).

Aquatic fauna in Quebrada Prieta is dominated by 10 species of decapod crustaceans (shrimp) that are widely distributed in Puerto Rico and the Caribbean (Pérez-Reyes et al.

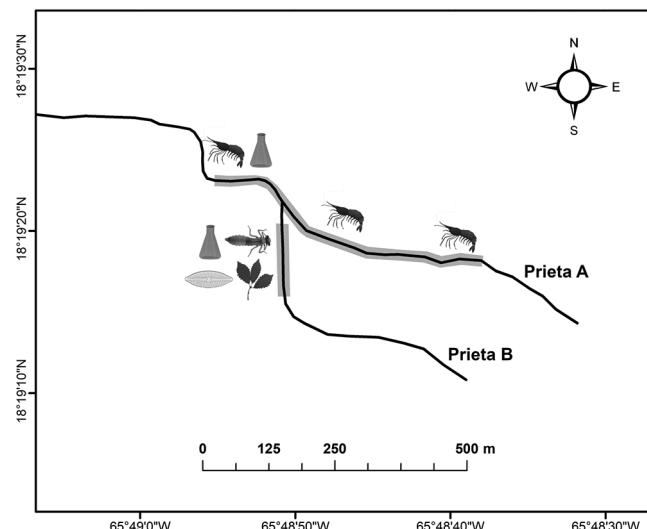


Figure 2. Section of the El Verde Research Area in the Luquillo Experimental Forest where this study was conducted. The gray areas represent the 500-m and 100-m study reach in Prieta A and Prieta B, respectively. Figures within the map indicate the variables measured in each study site. Shrimp figures indicate the location of the confluence pool and the 2 pools in Prieta A where the shrimp were collected. Erlenmeyer flask figures indicate the sites where the physicochemical variables were measured. Figures depicting an Odonata nymph (macroinvertebrates), leaves (litter input and benthic organic matter), and a diatom (epilithon) indicate the location of the pools and riffles in Prieta B where these samples were collected. The symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/symbols>).

2013, Wehrtmann et al. 2016). The family Atyidae includes 4 species (*Atya lanipes*, *A. innocuous*, *A. scabra*, and *Micratya poeyi*), Palaemonidae includes 5 species (*Macrobrachium acanthurus*, *M. carcinus*, *M. faustinum*, *M. crenulatum*, and *M. heterochirus*), and Xiphocarididae includes 1 species (*Xiphocaris elongata*). *Xiphocaris elongata* and *A. lanipes* dominate shrimp assemblages (>90% of individuals). An endemic crab species of the family Pseudothelphusidae (*Epilobocera sinuatifrons*) is also present but less common in these streams. Aquatic insects are abundant and dominated by mayflies, mostly in the family Leptophlebiidae (Ephemeroptera), and midge larvae (Diptera:Chironomidae). Case-building caddisflies (Trichoptera:Calamoceratidae) are also present but not continuously (Rincón and Covich 2014). The algivorous green stream goby (*Sicydium plumieri*, Gobiidae), is the only fish species that occurs in the LEF headwater streams.

#### Precipitation and hydrology

We characterized the 2015 drought period with long-term precipitation data based on 42 y (1975–2016) of meteorological data collected at El Verde Field Station, one of the

main field stations within the LEF. We used a pressure transducer sensor to continuously record stream water level in the confluence pool and used the water level measurements to calculate discharge during 2015. Water level was automatically recorded every 15 min, supplemented with weekly manual stage readings, and converted to discharge ( $\text{m}^3/\text{s}$ ) with a stage height–discharge relationship developed for Quebrada Prieta. We calculated mean daily discharge with 7-d moving averages to smooth variations in data (Smakhtin 2001). Missing values (30% of the data set) were imputed with a decision tree approach with the *missForest* function of the *missForest* package (Stekhoven 2013) in R (all analyses done in R version 3.4.3; R Project for Statistical Computing, Vienna, Austria). The *missForest* method uses random forest models to impute missing values based on the non-missing variables of the data set (Stekhoven 2013). We evaluated the performance of *missForest* with the normalized root mean square error, where values close to 0 indicate high accuracy and values near 1 suggest low accuracy (Stekhoven 2013). The normalized root mean square error of our imputed data was <0.001.

#### Stream physicochemistry

We measured stream water physicochemical characteristics and discharge weekly during 2015 at the confluence pool. We also measured specific conductance at individual pools ( $n = 6$ ) in Prieta B on 6 dates (14 August; 6, 11, and 25 September; 6 October; 6 November 2015). Drying during peak drought conditions isolated these pools from one another, making them ideal to quantify the magnitude of physicochemical changes due to drought.

The confluence pool was the monitoring point for specific conductance, dissolved oxygen, and temperature. We measured stream specific conductance in situ with a handheld meter (model PCSTestr 35 multi-parameter; Oakton® Instruments, Vernon Hills, Illinois). We recorded dissolved oxygen concentration and stream temperature in the confluence pool every 15 min during 2015 with a dissolved oxygen data logger (Hobo® model U26-001; Onset®, Bourne, Massachusetts). We used the logger data to calculate the average as well as the range of the daily oxygen concentration on each Tuesday in 2015. Additionally, we evaluated long-term changes in stream temperature by comparing average daily temperatures (based on the logger data) taken each Tuesday with the weekly long-term temperature measurements taken in situ with a handheld thermometer every Tuesday morning between 2000 and 2014.

We filtered water for nutrient analyses through glass-fiber filters (GF/F; Whatman, Maidstone, UK) in situ and stored the filters at  $-5^{\circ}\text{C}$  until analysis. Samples for  $\text{NH}_4^+$  (method: phenol hypochlorite) and  $\text{PO}_4^{3-}$  (measured as soluble reactive P; method: molybdate blue) were analyzed with automated colorimetry (Westco Scientific Instruments, Brookfield, Connecticut). We measured  $\text{NO}_3^-$  with an

ICS-3000 Ion Chromatography System (Dionex<sup>TM</sup>, Sunnyvale, California).

### Litter fall

We measured vertical inputs of leaf litter that fell directly into the stream channel in Prieta B with 6 litter baskets ( $0.29 \text{ m}^2/\text{ea}$ ) suspended ~1 m above the channel. We collected leaf litter every 2 wk during 2015. Samples were oven dried at  $65^\circ\text{C}$  for 24 h, weighed, and reported as  $\text{g m}^{-2} \text{ d}^{-1}$ .

### Benthic organic matter

Benthic organic matter was measured in 4 riffles and 4 pools along the 100-m reach in Prieta B on 5 dates in 2015 (9 February, 8 June, 23 July, 13 September, and 7 November). We collected organic matter along with macroinvertebrate samples (see details below) and separated it into coarse (CPOM, particles  $>1 \text{ mm}$  including leaf detritus, twigs, and miscellaneous organic matter) and fine (FPOM,  $<250 \mu\text{m}$ ) particulate organic matter. We sampled FPOM in pools by collecting a known volume subsample of the material that passed through the 250- $\mu\text{m}$ -mesh stainless steel sieve when we processed the corer samples used for macroinvertebrates. In riffles, fine particles are lost because of flow, so we sampled FPOM from a corer sample taken next to each Surber sample and processed it as described above. In the laboratory, we homogenized the FPOM samples from each corer, filtered them through a glass fiber filter (0.7- $\mu\text{m}$  mesh, GF/C; Whatman), and placed each filter into an aluminum envelope. We then dried the filters for 24 h at  $65^\circ\text{C}$  and weighed them individually before ashing them for 1 h at  $500^\circ\text{C}$  and reweighing them to obtain ash-free dry mass (AFDM). We quantified CPOM from both the corer and Surber samples. CPOM from the corer samples was quantified directly from the material retained in the sieves, whereas CPOM from the Surber samples was taken from the material retained in the net. Sorted CPOM (organic matter minus macroinvertebrates) from each corer and Surber was placed into aluminum envelopes and dried at  $65^\circ\text{C}$  to a constant mass, weighed, ashed for 1 h at  $500^\circ\text{C}$ , and reweighed. Values of FPOM and CPOM are reported as  $\text{g AFDM/m}^2$ .

### Epilithon

We sampled benthic periphyton quantitatively in individual pools ( $n = 6$ ) in Prieta B on 3 dates (14 August, 25 September, and 6 November 2015). On each date, we collected 6 periphyton samples from randomly-chosen locations within each pool with a modified Loeb sampler (Loeb 1981). The Loeb sampler was a cylinder ( $5.07\text{-cm}^2$  area) with a brush-fitted plunger that removed epilithon from rock substrata. We combined the 6 samples from each pool on each date into a composite sample. Subsequently, we took quantitative subsamples from each composite sample to estimate

the standing stocks of algal biomass (as chlorophyll-*a* [Chl *a*]), fine benthic inorganic matter (FBIM), and fine benthic organic matter (FBOM). We filtered subsamples for FBIM and FBOM through pre-ashed, pre-weighed glass fiber filters (0.7- $\mu\text{m}$  mesh, GF/C; Whatman) in the laboratory. We dried the filters for 24 h at  $60^\circ\text{C}$ , weighed them, ashed them in a muffle furnace for 1 h at  $500^\circ\text{C}$ , and reweighed them to obtain  $\text{g AFDM/m}^2$ . We analyzed Chl *a* subsamples fluorometrically following standard methods (APHA 1998). We compared the epilithon measurements that we collected during the 2015 drought (Chl *a*, FBIM, and FBOM) with our long-term data set, which included samples taken 2  $\times$  /y from 6 pools along Quebrada Prieta between 2002 and 2016.

### Macroinvertebrates

We sampled benthic macroinvertebrates (other than shrimp) on the same 5 dates that we measured benthic organic matter in 2015. We collected macroinvertebrates from pools (dominant substrate: silt, sand, and pebbles) and riffles (dominant substrate: gravel, pebbles, and cobbles) along a 100-m reach in Prieta B. We sampled 4 randomly selected pools with a corer sampler ( $0.0314 \text{ m}^2$ ) and 4 randomly selected riffles with a Surber sampler ( $0.093 \text{ m}^2$ , 250- $\mu\text{m}$  mesh size). We took corer samples to a depth of 10 cm or until the corer reached the bedrock. We placed the collected material into a graduated bucket, recorded the volume, and stirred the material vigorously before pouring it through a 250- $\mu\text{m}$  sieve. We put the material retained in the sieve into individual plastic bags.

We took Surber samples by placing the sampler over the substrata and allowing water to flow through the mesh net. We manually disturbed the substrate within the frame of the sampler and scrubbed rocks in the flowing water through the entrance of the collecting net. All material collected in the net was transferred into plastic bags. We preserved all macroinvertebrate samples with 37% formaldehyde (to obtain a final solution of ~5%) at our study sites before transporting them to the laboratory, where we separated organisms from sediment and organic matter (i.e., CPOM).

We identified macroinvertebrates to the lowest possible taxonomic level (usually genus) and counted them. We identified Chironomidae to subfamily or tribe, whereas the sub-classes Oligochaeta, Hirudinea, Acari, Copepoda, and the Phylum Nematoda and Platyhelminthes were not identified further. We calculated biomass by measuring the length of each individual to the nearest 0.5 mm and applying the length-mass regression developed by Benke et al. (1999). Macroinvertebrate density and biomass were expressed as  $\text{ind/m}^2$  and  $\text{mg AFDM/m}^2$ , respectively. All taxa were assigned to a functional feeding group based on Merritt et al. (2008) and Ramírez and Gutiérrez-Fonseca (2014) as follows: predators, collector-gatherers, filterers, grazer-scrappers, and shredders.

### Shrimp

We sampled shrimp abundance weekly in 2 pools along Prieta A and in the confluence pool. For convenience, we hereafter refer to these pools according to their location along the study reach: high, middle, and low (confluence pool). We placed baited traps (galvanized minnow traps: 43-cm long, 19-cm diameter, 0.5-cm mesh) in the pools for 24 h. Upon collection, we counted and identified all individuals to species level, and then released them in the same pool. We adjusted the number of traps in each pool to equal 0.5 traps/m<sup>2</sup> of pool surface area, following Covich et al. (2006). We report shrimp abundance/pool as catch/unit effort (CPUE).

### Statistical analyses

Changes in stream water variables over time were tested against discharge or sampling date. We related stream physicochemistry at the confluence pool (i.e., specific conductance, average and range of daily oxygen concentration, and nutrients) to discharge with Spearman's rank correlation. We calculated these correlations and their statistical significance with the *cor.test* function within the *stats* package. We compared the specific conductance of individual pools among sampling events with a 1-way repeated measures analysis of variance (rmANOVA) with the *lme* function in the *nlme* package (Pinheiro et al. 2018). We used the *glht* function in the *multcomp* package (Hothorn et al. 2008) to conduct pairwise comparisons with Tukey's honestly significant difference test.

Stream temperature during 2015 was compared with the long-term weekly average (2000–2014) to identify a possible temperature rise because of the drought. We used a paired *t*-test to detect differences between the average daily temperature during 2015 and our long-term dataset. We did the paired *t*-test with the *t.test* function in the *stats* package.

We tested the response of benthic epilithon to drought over time and in relation to long-term averages for the study stream. Trends in epilithon in individual pools were assessed with a 1-way rmANOVA, as for specific conductance. We were unable to normalize the FBOM data with a transformation (based on homogeneity of variance and inspection of residuals), so we did a nonparametric analysis of variance (Kruskal–Wallis rank sum) test to assess differences between sampling events with the *kruskal.test* function in the *stats* package.

Temporal changes in shrimp abundance were assessed to determine whether the shrimp populations increased or decreased over time at each of the 3 study pools. We tested whether there was a linear trend in shrimp data with a Mann–Kendall non-parametric trend analysis (M–K). The M–K test has the advantage of being unaffected by the distribution of the data, which makes it useful for series with outliers, missing values, and non-linear trends. When we detected a linear trend in a time series, we calculated the true slope of the trend with the non-parametric Sen's slope esti-

imator (Sen 1968). Sen's slope is the median slope of all pairwise differences between 2 time steps and represents change/unit time. We used the non-parametric Pettitt change point test (Pettitt 1979) to detect the occurrence of abrupt changes in the shrimp weekly data, and then to calculate whether this change was statistically significant. A change point occurs when a point is higher, on average, than points that occur to one side but lower, on average, than all points that occur to its other side. The Pettitt test uses a version of the Mann–Whitney statistic to verify whether 2 samples are from the same population. Thus, the null hypothesis of the Pettitt test is the absence of a change point (Pettitt 1979). We did the M–K test, Sen's slope estimator, and Pettitt test with the *mk.test*, *sens.slope*, and *pettitt.test* functions, respectively, which are all in R's *trend* package (Pohlert 2018).

### Long-term data

All long-term data on precipitation, discharge, specific conductance, temperature, nutrients, leaf-litter fall, and epilithon that were used as baselines for comparative purposes in figures and analyses in our study were provided by the LUQ-LTER. Long-term data for these variables was available for different ranges of years and is specified in the figure captions. Raw data sets are freely available at <http://luq.lternet.edu/>.

## RESULTS

### Precipitation and hydrology

Total rainfall in 2015 was 2035.6 mm, which is 44.6% less (1639.9 mm) than the average annual total precipitation (3675.8 mm; Fig. 3A). Rainfall was also below the long-term average during all months except February (Fig. 3B) in 2015. On 27 August 2015 (day of the year 239), rainfall from tropical storm Erika partially ended the drought. However, the rainfall deficit continued after the storm, throughout September until late October.

Low precipitation during the 2015 drought was reflected by low stream discharge (Fig. 3C) that caused Prieta A and B to become a series of isolated pools by August 2015. Precipitation decreased progressively from March until late August then peaked when tropical storm Erika struck in late August (day of the year 239). Discharge also decreased from March to August but increased during the heavy rains from tropical storm Erika. After this increase, we observed another period of low discharge until October. In October, discharge increased and nearly reached the annual average (0.0154 m<sup>3</sup>/s). Minimum daily discharge was recorded in March (0.0084 m<sup>3</sup>/s).

### Stream physicochemistry

Specific conductance in the confluence pool and Prieta B changed throughout the year. Specific conductance in the confluence pool was 3× higher during peak drought

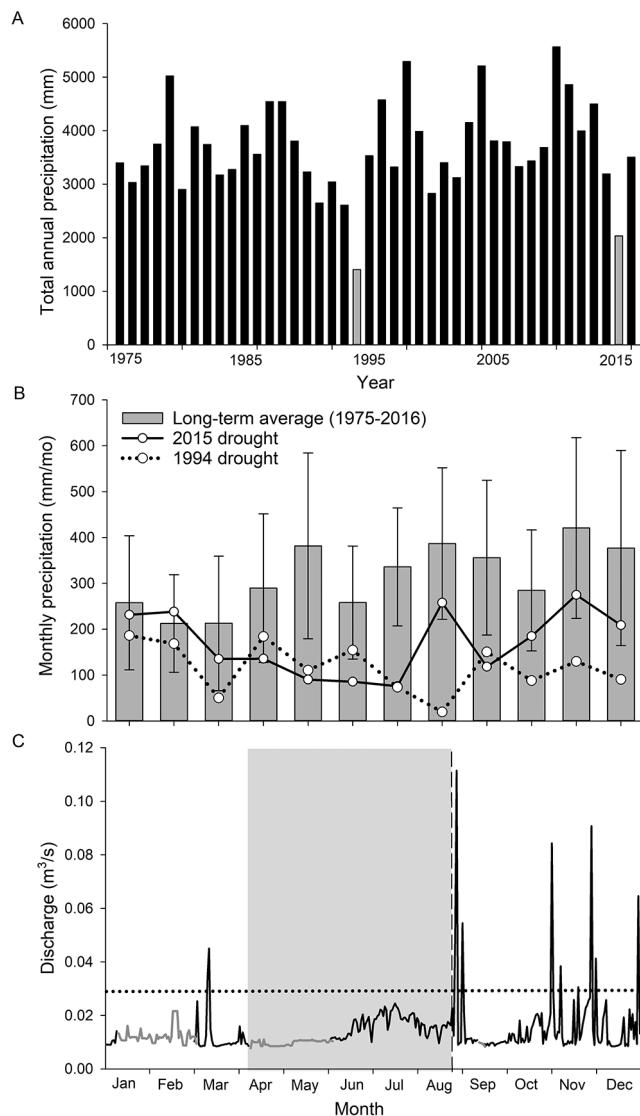


Figure 3. A.—Total annual precipitation measured at the El Verde Field Station (EVFS) between 1975 and 2016. The gray bars represent the droughts of 1994 and 2015. B.—Monthly precipitation measured during the 2015 drought (solid line) and the 1994 drought (dotted line) against the backdrop (bars) of long-term (1975–2016) mean ( $\pm$ SD) monthly precipitation measured at EVFS. C.—Hydrograph of Prieta stream at the confluence pool; the black line is the 7-d running average ( $m^3/s$ ) during 2015. The gray solid line represents 2015 discharge values that we reconstructed with precipitation data. The shaded gray area indicates the drought period before tropical storm Erika and the dashed vertical line indicates the date that tropical storm Erika struck Puerto Rico. The dotted horizontal line represents the long-term annual average discharge (2006–2015).

(26 May 2015) than during peak flow conditions (range: 50–162  $\mu$ S/cm). Further, there was a significant negative relationship between specific conductance and discharge in the confluence pool ( $r_s = -0.66, p < 0.0001$ ; Fig. 4A). Specific conductance within individual pools in Prieta B varied

significantly among sampling periods (rmANOVA:  $F_{5,30} = 236.61, p = 0.0001$ ; Table S1). During the peak of the drought, specific conductance in individual pools in Prieta B was 1.4 $\times$  higher (107  $\mu$ S/cm) than the long-term average (77  $\mu$ S/cm) in the confluence pool. Specific conductance declined sharply after tropical storm Erika (day of the year 239) but increased again when drought conditions resumed. Finally, rain events during late October caused another reduction in mean specific conductance, which was recorded in the November sampling (Fig. 5).

Dissolved oxygen concentration was moderately affected by drought. The average daily dissolved oxygen concentration was positively correlated with discharge ( $r_s = 0.50, p < 0.001$ ;

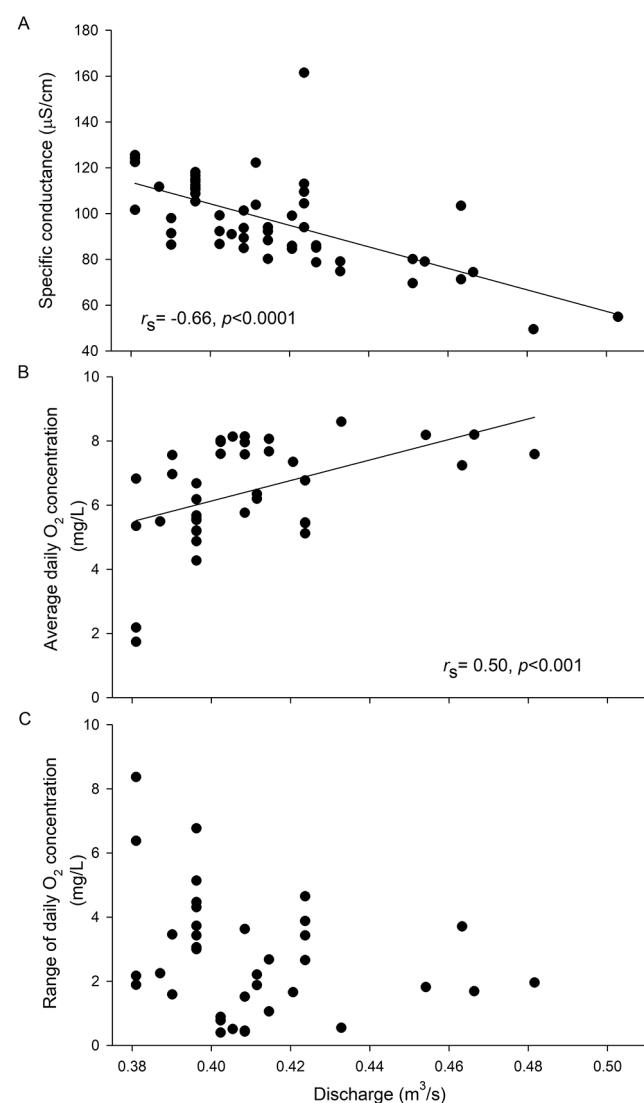


Figure 4. Correlation analysis of discharge with specific conductance (A), average (B), and range (C) of daily dissolved oxygen concentration at the confluence pool. Each dot represents a weekly reading made on a Tuesday during 2015. When these correlations were significant, we report the values in the panel and show the relationship between the variables with solid lines.

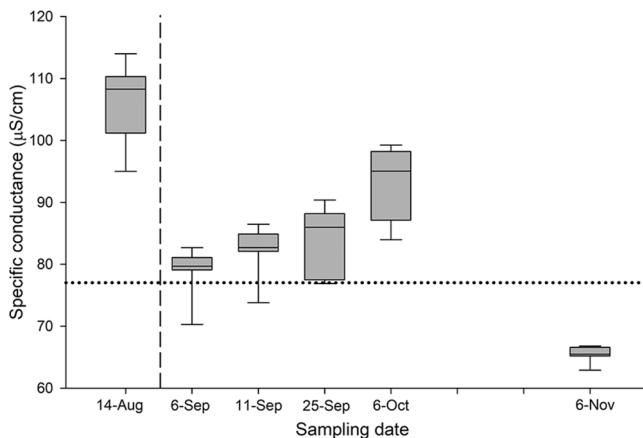


Figure 5. Mean ( $\pm$ SD) specific conductance in pools ( $n = 6$ ) along Prieta B during 2015. Dashed vertical line indicates the date that tropical storm Erika struck Puerto Rico. The dotted horizontal line shows the long-term (2000–2014) average specific conductance in the confluence pool.

Fig. 4B). However, no meaningful relationship was found between the range of daily oxygen and discharge ( $r_s = -0.30$ ,  $p = 0.06$ ; Fig. 4C). During the most severe part of the drought, daily changes in dissolved oxygen showed that stream water became saturated with dissolved oxygen during the day but was nearly anoxic at night (Fig. 6A, B).

In contrast, the weekly temperature changes that occurred during 2015 were probably not influenced by the drought. Stream temperature ranged from 20.5°C in March to 23.6°C in October, which represents a maximum change of 3.1°C during 2015. The average temperature during 2015 was 22.1°C and the weekly long-term average was 21.9 °C. Annual temperature variability reflected a slight seasonal pattern that follows the same trend as the long-term average (2000–2014, paired  $t$ -test:  $p > 0.05$ ; Fig. 6C).

Dissolved nutrient concentrations varied throughout the year and were not clearly related to drought conditions. At the confluence pool,  $\text{PO}_4^{3-}$  was weakly correlated with discharge ( $r_s = -0.28$ ,  $p = 0.04$ ). No significant ( $p > 0.05$ ) relationships were found between  $\text{NH}_4^+$  or  $\text{NO}_3^-$  and discharge. However,  $\text{PO}_4^{3-}$  (rmANOVA:  $F_{3,18} = 11.34$ ,  $p < 0.0001$ ; Fig. 7A),  $\text{NH}_4^+$  (rmANOVA:  $F_{3,18} = 24.63$ ,  $p < 0.0001$ ; Fig. 7B), and  $\text{NO}_3^-$  (rmANOVA:  $F_{3,18} = 16.65$ ,  $p < 0.0001$ ; Fig. 7C) each changed significantly throughout the year within the smaller pools along Prieta B. Differences in the concentration of nutrients between sampling events were associated with the isolation and reconnection of the pools during and after the drought (Pairwise multiple comparison: Tables S2–4).

### Litter fall

A major peak in litter fall entering Prieta B occurred during May, shortly after the beginning of severe drought

conditions (Fig. 8). Mean litter fall during 2015 was  $1.28 \text{ g m}^{-2} \text{ d}^{-1}$  and the May peak was  $7.56 \text{ g m}^{-2} \text{ d}^{-1}$ , which is  $7.6 \times$  higher than the annual long-term average ( $0.99 \text{ g m}^{-2} \text{ d}^{-1}$  from 2010–2015). Litter fall also peaked in September ( $3.21 \text{ g m}^{-2} \text{ d}^{-1}$ ), coinciding with drought conditions after tropical storm Erika.

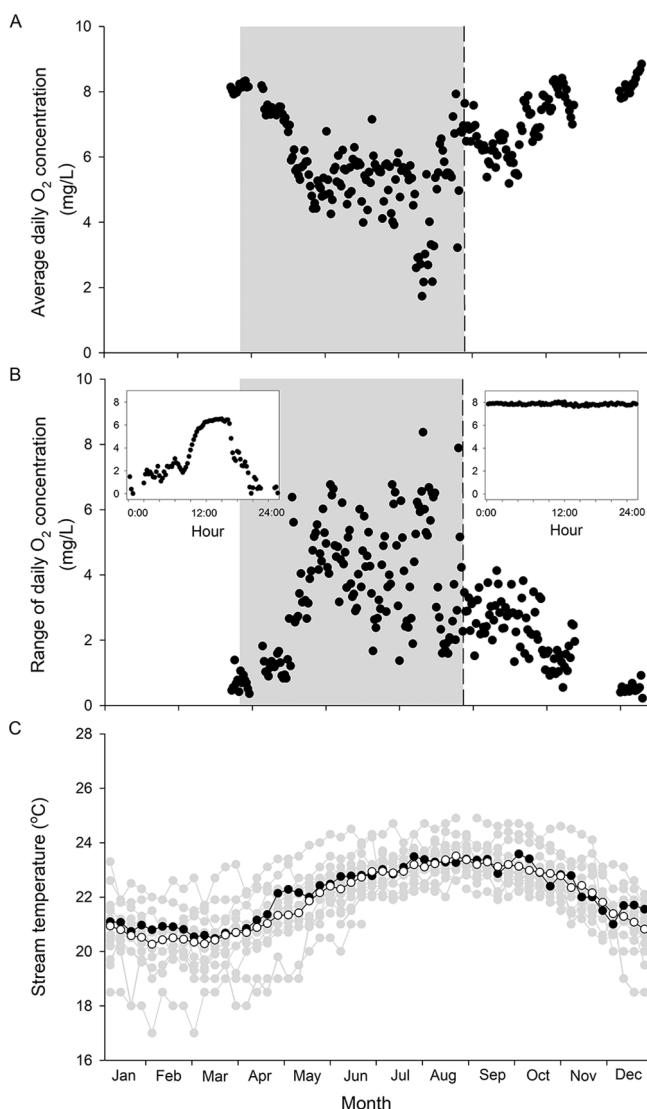


Figure 6. Average (A) and range (B) of daily oxygen concentration at the confluence pool in 2015. Gray areas represent the most severe period of the drought, and the dashed vertical lines indicates the date that tropical storm Erika struck Puerto Rico. The inset panels in B show the daily variation in a day during the peak of the drought (left panel) and a regular day without drought conditions (right panel). Weekly stream temperature in the confluence pool (C). Black circles represent 2015 automatic sensor measurements. White circles represent the long-term (2000–2014) weekly averages. Gray circles represent manual temperature readings taken from 2000 to 2014.

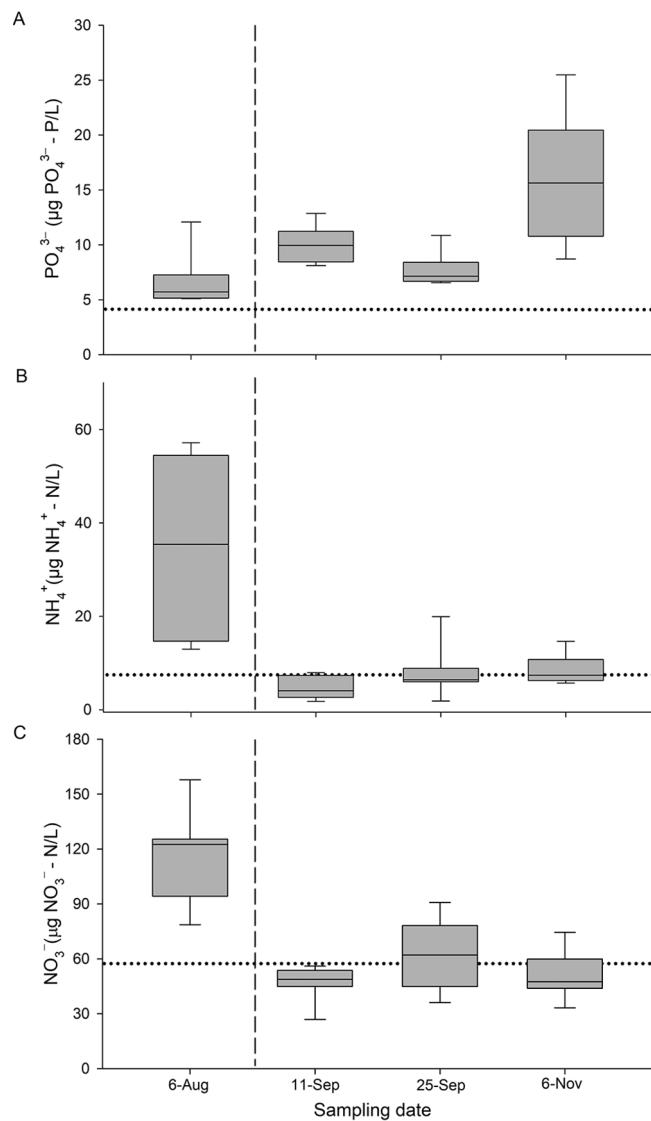


Figure 7. Average concentration of  $\text{PO}_4^{3-}$  (A),  $\text{NH}_4^+$  (B), and  $\text{NO}_3^-$  (C) in pools ( $n = 6$ ) in Prieta B. The dashed vertical line indicates the date that tropical storm Erika struck Puerto Rico. The dotted horizontal line shows long-term (2000–2014) average of the confluence pool.

#### Benthic organic matter

The May peak in leaf-litter inputs did not translate into measurable increases in organic matter in the Prieta B because CPOM and FPOM did not change consistently as leaf-litter fall increased (Table 1). CPOM averaged 41.17 g AFDM/m<sup>2</sup> in riffles and 379.67 g AFDM/m<sup>2</sup> in pools. FPOM averaged 28.73 g AFDM/m<sup>2</sup> in riffles and 166.76 g AFDM/m<sup>2</sup> in pools.

#### Epilithon

The 2015 drought appeared to strongly influence epilithon measurements. FBOM, FBIM, and Chl  $\alpha$  were 1.2

(2.60 g AFDM/m<sup>2</sup>), 2.1 (3.32 g/m<sup>2</sup>), and 14.2 $\times$  (153.19  $\mu\text{g}$  Chl  $\alpha$ /m<sup>2</sup>) lower than the long-term average of each variable (3.06 g AFDM/m<sup>2</sup>, 6.97 g/m<sup>2</sup>, and 2180.62  $\mu\text{g}$  Chl  $\alpha$ /m<sup>2</sup>, respectively). FBOM differed significantly between sampling events (Kruskal–Wallis  $\chi^2 = 7.45$ , df = 2,  $p = 0.024$ ; Fig. 9A). In contrast, FBIM did not change significantly between months during 2015 (rmANOVA:  $p > 0.05$ ; Fig. 9B). Chl  $\alpha$  was significantly lower during peak drought conditions (rmANOVA:  $F_{2,10} = 14.29$ ,  $p = 0.001$ ) but increased during the rainy September sampling period (Fig. 9C).

#### Macroinvertebrates

Macroinvertebrate assemblages were diverse, with 38 non-decapod taxa present, of which 31 were present in riffles and 24 in pools. Diptera was the most diverse macroinvertebrate order (13 taxa), followed by Trichoptera (9 taxa) and non-insects (7 taxa). The most abundant taxa were non-insect macroinvertebrates (20,015 ind/m<sup>2</sup>; mostly oligochaete worms), followed by Ephemeroptera (2069 ind/m<sup>2</sup>) and Coleoptera (1017 ind/m<sup>2</sup>) (see complete abundance list in Table S5). Non-insects also comprised most of the biomass (420 mg/m<sup>2</sup>), followed by Ephemeroptera (324 mg/m<sup>2</sup>) and Coleoptera (288 mg/m<sup>2</sup>).

Macroinvertebrate assemblages showed a strong response to the drought, with highest variability during the driest months of 2015. Taxonomic richness in riffle habitats ranged from 6 taxa/m<sup>2</sup> in February to 11 taxa/m<sup>2</sup> in July, whereas richness in pools ranged from 5 taxa/m<sup>2</sup> in September to 8 taxa/m<sup>2</sup> in February (Fig. 10A). Macroinvertebrate density in riffles ranged from 167 ind/m<sup>2</sup> in February to 554 ind/m<sup>2</sup> in June, whereas abundance in pools ranged from 623 ind/m<sup>2</sup> in September to 9421 ind/m<sup>2</sup> in July (Fig. 10B). Biomass in riffles ranged from 26 mg/m<sup>2</sup> in September to 79 mg/m<sup>2</sup> in June, whereas biomass in pools ranged from 15 mg/m<sup>2</sup> in September to 292 and 236 mg/m<sup>2</sup>

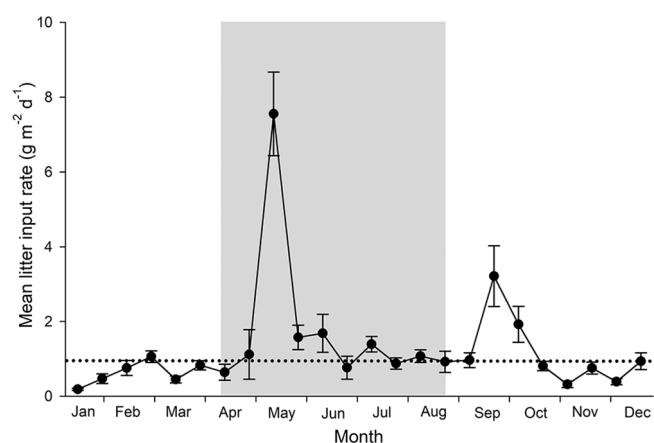


Figure 8. Mean ( $\pm\text{SE}$ ) daily litter fall inputs into Prieta B during 2015. The shaded gray area represents the most severe period of the drought. The dotted horizontal line represents the long-term (2010–2015) average of litter fall input in Prieta B.

Table 1. Mean ( $\pm$ SD) of coarse (CPOM) and fine (FPOM) particulate organic matter (g AFDM/m<sup>2</sup>) in pools and riffles of Prieta B during 2015.

Habitats	February		June		July		September		November	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<b>Pools</b>										
CPOM	554.10	239.76	204.62	64.81	455.99	208.26	10.77	5.17	672.87	594.09
FPOM	154.87	44.38	54.06	6.02	206.18	104.88	15.22	4.96	403.47	340.61
<b>Riffles</b>										
CPOM	14.03	4.44	163.01	43.04	11.72	4.20	11.88	6.64	5.22	2.21
FPOM	12.24	1.96	40.38	11.71	30.81	8.95	52.09	31.24	8.13	1.96

in June and July, respectively (Fig. 10C). Overall, macroinvertebrate richness, density, and biomass for both habitats were highest in June and July (i.e., during the peak of the drought) but lowest in February for riffles and September for pools.

Macroinvertebrate functional group composition varied widely among sampling dates but was dominated by scrapers in riffles and collector-gatherers in pools. Collector-gatherers comprised 80% of the total density in pools but only 31% in riffles. Density of Oligochaeta, the dominant collector-gatherer in pools, increased greatly in this habitat during the peak of the drought, from 1513 ind/m<sup>2</sup> in February to 7596 and 8655 ind/m<sup>2</sup> in June and July, respectively (Table S5). Scrapers comprised only 7% of the total density in pools but 47% in riffles. Scrapers in riffles also increased in density during the drought. *Cloeodes* (Baetidae:Ephemeroptera) increased from 8 ind/m<sup>2</sup> in February to 339 ind/m<sup>2</sup> in June (Table S5). Overall, collector-gatherers increased by ~10% in pools whereas scrapers increased by 17% in riffles during peak drought (i.e., June and July). The opposite trend occurred for filterers, predators, and shredders, which generally decreased in density during the drought. In the months following the peak of the drought, the density of collector-gatherers in pools and scrapers in riffles decreased (Table 2).

### Shrimp

Weekly shrimp abundance varied among the sampled pools. The confluence pool had the highest abundances (range: 53–155 ind/CPUE) and the 2 upstream pools in Prieta A had lower abundances (21–137 ind/CPUE). Shrimp abundance in the confluence pool and in the high pool did not change significantly over time ( $p > 0.05$ ), whereas the abundance in the middle pool increased slightly over time (M-K = 0.27,  $p = 0.005$ , Sen's slope = 0.6; Fig. 11A–C). The Pettitt test revealed that the abundance in the middle and high pools had a change point early in the drought (wk 14 and 23, respectively), but only the change point in the middle pool was significant ( $p < 0.001$ ; Fig. 11A, B). We detected a non-significant change point in the confluence pool near the end of the drought (wk 43; Fig. 11C).

### DISCUSSION

Here we provide the first documentation of the multiple abiotic and biotic effects of a severe drought in a wet, aseasonal tropical stream ecosystem. This event was the 2<sup>nd</sup> most severe drought in the long-term precipitation record (42 y) for the El Verde Field Station (Fig. 3A), and the reduced precipitation created physicochemical conditions that differed markedly from normal conditions in our focal streams. During this drought, one of our focal streams became a series of unconnected pools and received large pulses of leaf litter from riparian vegetation. Together, these changes impacted all trophic levels in the ecosystem.

The complex and devastating effects of drought on stream ecosystems are best represented in a hierarchical framework, as outlined in Figure 1. Our conceptual model considers the linkages and interactions among components of the aquatic and terrestrial ecosystems that could influence the response to drought of the whole-stream ecosystem. Drought affects stream ecosystems both by decreasing stream flow and affecting riparian vegetation. Flow reduction decreases longitudinal connectivity along the channel, increases isolation among stream habitats, and alters water physicochemical characteristics (point 1 in Fig. 1). In riparian areas, water-stressed vegetations lose more leaves than normal, increasing inputs of organic matter and allowing more sunlight to reach the stream channel (point 2 in Fig. 1). Ecosystem responses to drought (point 3 in Fig. 1) are variable but include increases in grazing and early emergence, particularly of sensitive taxa, and decreases in the decomposition of organic matter that causes accumulation of organic matter in isolated habitats. Highly mobile taxa such as shrimp begin to move freely among pools. It is expected that changes in biological activity and biogeochemical processes during drought increase the production of greenhouse gases. As drought conditions prolong, or if their frequency increases, as predicted by climate change models, stream ecosystems could be expected to start experiencing more dramatic conditions (point 4 in Fig. 1). Our model proposes decreases in survival, in particular of shrimp and riparian seedlings. In addition, species interactions should increase and a general change in assemblage

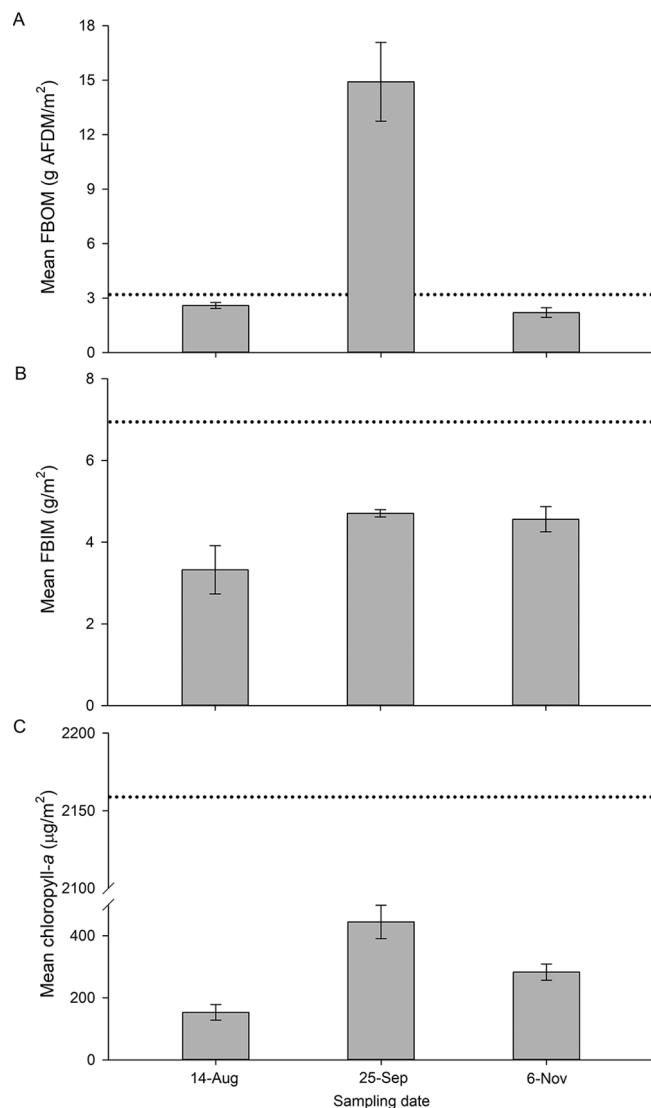


Figure 9. Mean ( $\pm$ SE) of organic matter (FBOM, A), inorganic mass (FBIM, B), and chlorophyll- $\alpha$  (C) in pools ( $n = 6$ ) in Prieta B during 3 sampling periods in 2015. The dotted horizontal line shows the long-term (2002–2016) average of each component of the epilithon in Quebrada Prieta.

composition is expected. Understanding drought impacts is particularly important for wet tropical ecosystems, where rainfall variability is expected to be high and organisms might be poorly adapted to the lack of water. As far as we know, our study is the first effort to assess how multiple components of a tropical stream ecosystem respond to a severe drought.

Several studies have examined the effects of seasonal drying in neotropical, dry-forest ecosystems where organisms and resource availability are expected to change (e.g., Rincón and Cressa 2000, Montoya et al. 2006, Longo et al. 2010), but almost no information exists about the effects of droughts on wet tropical mountain streams (but see Covich and Crowl

2002, Covich et al. 2003, 2006). The 2015 drought caused severe water shortages across the Caribbean and Puerto Rico. As occurred during the 1994 drought (Larsen 2000, Crook et al. 2009), the Puerto Rico Aqueduct and Sewage Authority was unable to meet the demand for municipal potable water supplies provided by streams draining the El Yunque National Forest. During peak periods of the 1994 and 2015 droughts, lower reaches of the Río Espíritu Santo (which is the receiving river of our focal study streams) were completely dry for periods of up to several weeks because of water abstraction. This lack of stream connectivity with the ocean results in mortality of both larval shrimp traveling downstream and shrimp juveniles migrating upstream (Pringle 1997, Benstead et al. 1999, Crook et al. 2009).

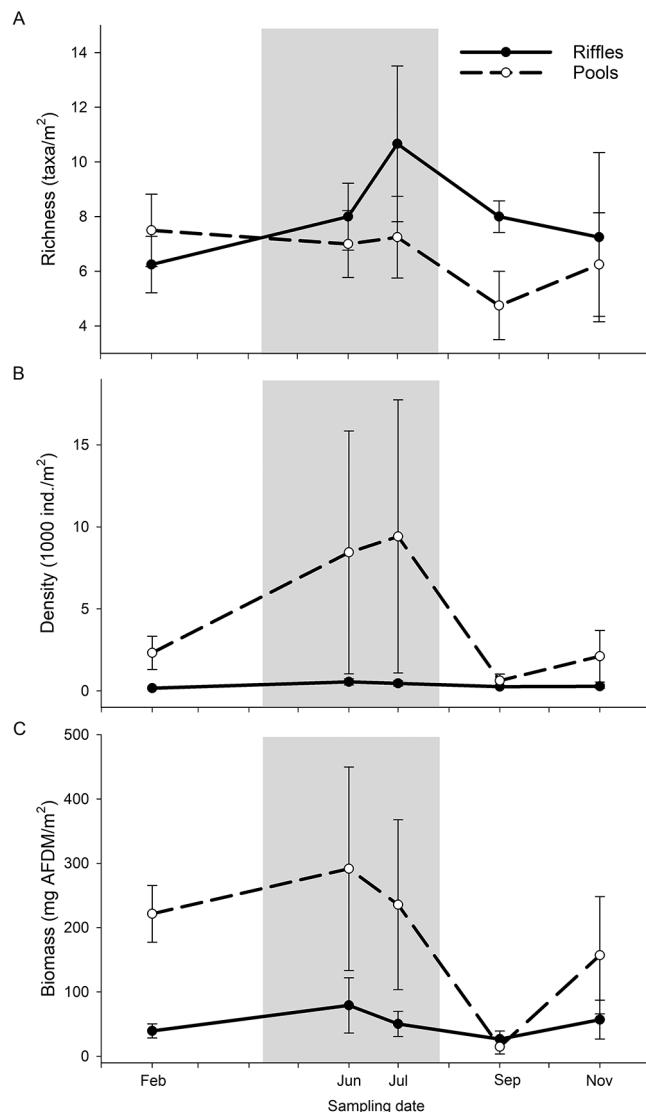


Figure 10. Macroinvertebrate richness (A), density (B), and biomass (C) in riffles ( $n = 4$ , solid line) and pools ( $n = 4$ , dashed line) in Prieta B during 2015. The shaded gray area represents the most severe period of the drought.

Table 2. % density of functional feeding groups (FFG) per sampling month during 2015.

Habitats	FFG	February	June	July	September	November
Pools	Collector–Gatherer	83.5	92.7	93.0	51.3	82.2
	Grazer–Scraper	5.2	6.1	4.4	10.3	8.3
	Filterer	4.8	0.5	0.9	16.7	1.1
	Predator	3.4	0.5	0.8	21.8	6.4
	Shredder	3.1	0.2	0.9	0.0	1.9
Riffles	Collector–Gatherer	41.9	18.0	26.4	41.9	24.3
	Grazer–Scraper	45.2	71.7	53.5	25.7	39.8
	Filterer	4.8	5.9	10.9	1.4	7.8
	Predator	4.8	3.9	8.5	24.3	26.2
	Shredder	3.2	0.5	0.8	6.8	1.9

During drought, stream chemistry can be modified by changes in direct precipitation, overland flow, shallow subsurface flow, and groundwater flow (e.g., Caruso 2002, van Vliet and Zwolsman 2008). Peak drought conditions isolated stream pools in Prieta B, which caused each independent pool to develop a unique chemical signature. Nutrient concentrations were high in the small pools of Prieta B, but not in the larger pool at the confluence of Prieta A and B, which was probably diluted by flow from Prieta A. The increased nutrient levels probably occurred because of the low algal biomass (Fig. 9C), reduction of dilution capacity, and longitudinal channel fragmentation that prevented the normal transport of nutrients downstream in Prieta B. Moreover, an increase in nutrient retention efficiency (i.e., short uptake length), as well as anaerobic nutrient transformations (i.e., denitrification), could explain low nutrient concentrations in the confluence pool.

Specific conductance and dissolved oxygen also responded markedly to drought conditions. Increases in specific conductance can result from evapo-concentration and less dilution by groundwater inputs (Mosley 2015). For example, concentrations of  $\text{Ca}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^-$ , and  $\text{SiO}_2$  in 2 Puerto Rican streams were diluted by the increase in streamflow after the 2015 drought (Clark et al. 2017). Similarly, dilution of most solutes with increasing flow has also been described for the long-term behavior of multiple streams in the Luquillo Mountains (Shanley et al. 2011, Wymore et al. 2017). In our study, the specific conductance was high during the peak of the drought, but it never reached levels likely to affect organic matter processing (e.g.,  $>500 \mu\text{S}/\text{cm}$ ; Sauer et al. 2016), algae growth (e.g.,  $1344\text{--}3531 \mu\text{S}/\text{cm}$ ; Silva et al. 2000), or macroinvertebrate assemblages (e.g.,  $>300 \mu\text{S}/\text{cm}$ ; Cormier et al. 2013).

High oxygen concentrations and lack of diel periodicity measured in the confluence pool during non-drought periods indicate that oxygen is mostly near saturation during normal flow conditions. Thus, during non-drought conditions, oxygen concentrations are probably controlled by ex-

changes with the atmosphere because of the steep topography and consequent turbulent flow and re-aeration in riffles between pools. The declining stream flow caused decreases in mean daily oxygen concentrations as the drought progressed. This led to extreme diel periodicity in oxygen concentrations (Fig. 6A, B), which indicated primary productivity was high despite low algal standing crops.

Stream temperature in the confluence pool was unaltered by drought, as evidenced by the lack of extreme fluctuation throughout the year and overall similarity with long-term patterns (Fig. 6C). Altered thermal regimes have been observed during extensive low flows, but microclimatic and microhabitat features could be important in determining temperature fluctuations in streams without human disturbance (e.g., Arismendi et al. 2012). Here, the riparian shadow and large size of the confluence pool may have acted as a thermal buffer and could explain the stability in water temperature during the drought.

The riparian vegetation in Prieta B appeared to undergo physiological stress during the drought. We saw litter fall increase  $7.6 \times$  during the most severe part of the drought (Fig. 8). The peak in leaf-litter fall occurs from April to June in LEF (Zalamea and González 2008) and the 2015 drought may have amplified this peak by reducing the flow and lowering the water table, which induces water stress in plants and leads to leaf senescence and abscission (e.g., Amlin and Rood 2003). Increases in litter fall during drought have been observed in other tropical riparian forests (e.g., Larned 2000). In our study site, those large inputs of riparian litter and reduced stream flow did not result in increases in benthic organic matter. Most litter fell into the stream during a single peak in May and was composed primarily of leaves that were rapidly processed or exported downstream with small changes in discharge. Residence time of organic material is strongly influenced by the demand of organic material in the ecosystem, timing of the inputs, and the hydrological regime (e.g., González and Pozo 1996, Pozo et al. 1997, Webster and Meyer 1997, Tank et al. 2010). Leaf loss and

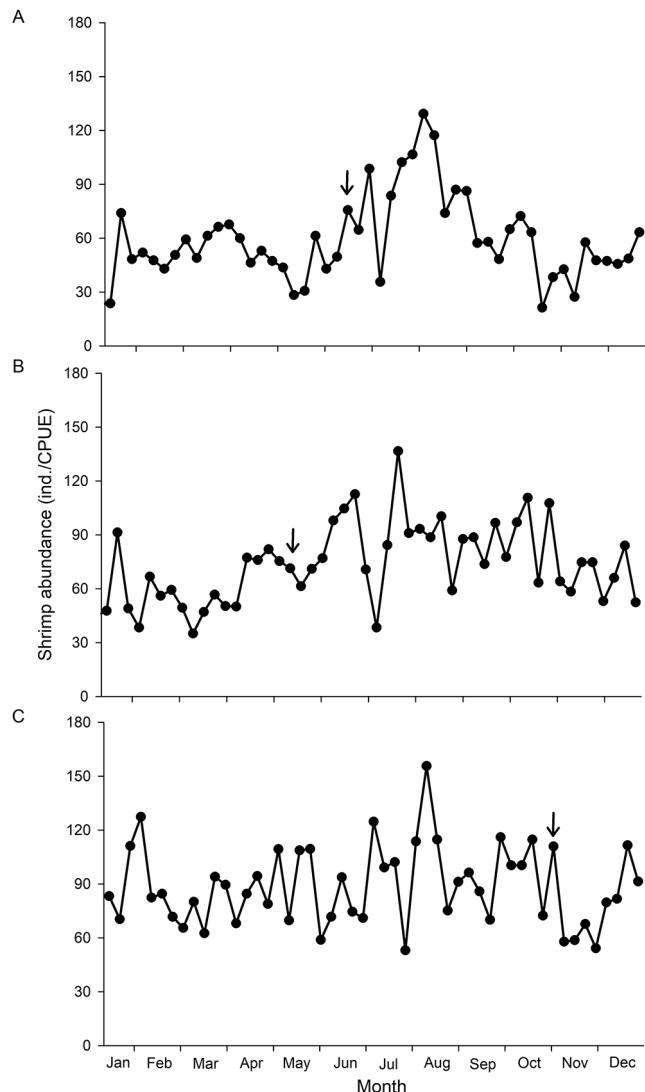


Figure 11. Weekly shrimp abundance as catch/unit effort (CPUE) in the high (A) and middle (B) pools of Prieta A and the low (C) pool (i.e., confluence pool) during 2015. The arrows indicate the change point in the data set (i.e., point in the time series at which shrimp abundance is divided in 2 sets because of a discontinuity in the data) that was identified by the Pettitt test. Note: Change point was only significant in the middle-elevation pool.

associated increases in light, combined with high nutrient levels, did not result in an increase in algal standing crop. Overall, we attribute low algal standing crop to greater top-down control by shrimp populations and insects concentrated in pools of diminishing volume.

Algal standing crop ( $\text{Chl } a$ ) recovered slightly after the rains began and stream flow was restored (Fig. 9C), but this increase was still much lower than the long-term average. Stream biofilm can be negatively affected by drying (e.g., Stanley et al. 2004, Timoner et al. 2012, Sabater et al. 2016), but biofilms are often able to recover quickly (e.g., hours) from

drying by producing resistant structures, extracellular mucilage to facilitate cellular water retention, or intracellular osmotic adjustments (Davis 1972, Peterson 1996, Robson 2000).

Macroinvertebrate responses to drought can be variable and reflect both resource availability and stream environmental conditions. Taxa with low oxygen requirements may be favored during moderate hypoxia (e.g., Connolly et al. 2004). In our study, large increases in the density of tolerant taxa, such as oligochaetes and chironomids, probably occurred in response to marked changes in stream physicochemistry. Previous studies suggest that Oligochaeta resist droughts by retreating to hyporheic areas (Otermin et al. 2002). Chironomids have rapid growth rates and continuous reproduction that allow them to recover quickly during and after drought (Otermin et al. 2002). We attribute the reduction of epilithic algae ( $\text{Chl } a$ ) and FBOM during peak drought conditions to an increase in insect grazers such as *Cloeodes*.

We did not observe an increase in shrimp abundance, unlike during the 1994 drought, when *A. lanipes* abundance was 3× higher than during pre-drought conditions in the uppermost headwater pools (22 vs 75 ind./m<sup>2</sup> of pool area; Covich et al. 2003). Pool contraction was the mechanism attributed to increases in *A. lanipes* at that time because abundances returned to pre-drought conditions when pool volume increased following the drought (Covich et al. 2003). In contrast, during the 2015 drought, shrimp abundances remained relatively similar in one branch of our focal study stream (Prieta A) and were absent in the branch that became fragmented into extremely small pools (Prieta B). The change in shrimp abundance at the beginning of the drought reflected that the middle and high pools were possibly the first to shrink. Meanwhile, abundance in the low pool decreased at the end of the drought, when rainfall resumed and pool area increased.

Future climate projections for Puerto Rico predict a decline in precipitation ranging from 130 to 1397 mm by the end of the century (Henareh-Khalyani et al. 2016). Further, an increase of 66% in the annual maximum number of consecutive dry days (measure of drought extremes) and 21% in total dry days (measure of drought intensity) are expected by that time (Henareh-Khalyani et al. 2016). For some of the wetter regions of Puerto Rico, especially in the Luquillo Mountains where mean annual rainfall is >3500 mm, decreases in precipitation are expected to occur earlier than in other regions of the island. Precipitation during the wettest months (i.e., April–July) is expected to decrease from the long-term average of 1042 to 771 mm at mid-century, which is a decline of 26% (Ramseyer et al. 2019). These declines in rainfall will probably cause stream ecosystems to desiccate, which will severely impact their habitat and ecosystem function. Our study provides an example of how multiple ecosystem components might respond to those conditions.

## ACKNOWLEDGEMENTS

Author contributions: All authors (PEGF, AR, CMP, PJT, WHM, AC, TC, and OP) participated equally in the conception or design of this study; as well as in the acquisition, analysis and interpretation of the data. Authors contributed substantially to drafting the work or revising it critically for important intellectual content.

We thank Samuel Matta, David Stoker, Roberto Reyes, and all the volunteers and students that contributed with data collection. Thanks to Jamarys Torres Diaz and Christopher Nytch for their aid in the preparation of the map and to Aura M. Alonso-Rodríguez for revising earlier drafts of the manuscript. This study was funded by the Luquillo Long-Term Ecological Research program funded by the US National Science Foundation (DEB-1546686).

## LITERATURE CITED

Amlin, N. M., and S. B. Rood. 2003. Drought stress and recovery of riparian cottonwoods due to water table alteration along Willow Creek, Alberta. *Trees* 17:351–358.

APHA (American Public Health Association). 1998. Standard methods for the examination of water and wastewater. 20<sup>th</sup> edition. American Public Health Administration, American Water Works Association, Water Environment Federation, Washington, DC.

Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert. 2012. The paradox of cooling streams in a warming world: Regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* 39:L10401.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308–343.

Benstead, J. P., J. G. March, C. M. Pringle, and F. N. Scatena. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications* 9:656–668.

Boulton, A. J., and P. S. Lake. 2008. Effects of drought on stream insects and its ecological consequences. Pages 81–102 in J. Lancaster and R. A. Briers (editors). *Aquatic insects: Challenges to populations*. CABI, Wallingford, UK.

Caruso, B. S. 2002. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology* 257:115–133.

Clark, K. E., J. B. Shanley, M. A. Scholl, N. Perdrial, J. N. Perdrial, A. F. Plante, and W. H. McDowell. 2017. Tropical river suspended sediment and solute dynamics in storms during an extreme drought. *Water Resources Research* 53:3695–3712.

Cormier, S. M., G. W. Suter, and L. Zheng. 2013. Derivation of a benchmark for freshwater ionic strength. *Environmental Toxicology and Chemistry* 32:263–271.

Connolly, N. M., M. R. Crossland, and R. G. Pearson. 2004. Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates. *Journal of the North American Benthological Society* 23:251–270.

Covich, A. P., and T. A. Crowl. 2002. Reorganization of benthic stream food webs in response to drought-altered population densities: Effects on rainforest streams. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen* 28:1172–1175.

Covich, A. P., T. A. Crowl, and T. Heartsill-Scalley. 2006. Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society* 25:99–107.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* 48:1199–1206.

Covich, A. P., and W. H. McDowell. 1996. The stream community. Pages 433–459 in D. P. Reagan and R. B. Waide (editors). *The food web of a tropical rain forest*. University of Chicago Press, Chicago, Illinois.

Crook, K. E., C. M. Pringle, and M. C. Freeman. 2009. A method to assess longitudinal riverine connectivity in tropical streams dominated by migratory biota. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:714–723.

Davis, J. S. 1972. Survival records in the algae, and the survival role of certain algal pigments, fat, and mucilaginous substances. *The Biologist* 54:52–93.

DRNA (Departamento de Recursos Naturales y Ambientales). 2016. Informe sobre la sequía de 2014–2016 en Puerto Rico. División Monitoreo Plan de Aguas, Departamento de Recursos Naturales y Ambientales, San Juan, Puerto Rico.

Dudgeon, D. 1993. The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshwater Biology* 30:189–197.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U. S. Virgin Islands. Forest Service Research Paper ITF-18. US Department of Agriculture, Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico.

García-Martinó, A. R., G. S. Warner, F. N. Scatena, and D. L. Civco. 1996. Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 32: 413–424.

González, E., and J. Pozo. 1996. Longitudinal and temporal patterns of benthic coarse particulate organic matter in the Agüera stream (northern Spain). *Aquatic Sciences* 58:355–366.

González, G., D. J. Lodge, B. A. Richardson, and M. J. Richardson. 2014. A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. *Forest Ecology and Management* 332:32–46.

Henareh-Khalyani, A., W. A. Gould, E. Harmsen, A. Terando, M. Quinones, and J. A. Collazo. 2016. Climate change implications for tropical islands: Interpolating and interpreting statistically downscaled GCM projections for management and planning. *Journal of Applied Meteorology and Climatology* 55:265–282.

Herrera, D., and T. Ault. 2017. Insights from a new high-resolution drought atlas for the Caribbean spanning 1950–2016. *Journal of Climate* 30:7801–7825.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.

IPCC (Intergovernmental Panel on Climate Change). 2014. AR5 climate change 2014: Impacts, adaptation, and vulnerability.

Summaries, frequently asked questions, and cross-chapter boxes. A Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Page 1132 in C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L.L. White (editors). Cambridge University Press, New York, New York.

Jury, M., B. A. Malmgren, and A. Winter. 2007. Subregional precipitation climate of the Caribbean and relationships with ENSO and NAO. *Journal of Geophysical Research: Atmospheres* 112: e10.1029.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573–592.

Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology* 48:1161–1172.

Lake, P. S. 2011. Drought and aquatic ecosystems: Effects and responses. Wiley-Blackwell, Chichester, UK.

Larned, S. T. 2000. Dynamics of coarse riparian detritus in a Hawaiian stream ecosystem: A comparison of drought and post-drought conditions. *Journal of the North American Benthological Society* 19:215–234.

Larsen, M. C. 2000. Analysis of 20<sup>th</sup> century rainfall and streamflow to characterize drought and water resources in Puerto Rico. *Physical Geography* 21:494–521.

Loeb, S. L. 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. *Limnology and Oceanography* 26:394–399.

Longo, M., H. Zamora, C. Guisande, and J. J. Ramírez. 2010. Dinámica de la comunidad de macroinvertebrados en la quebrada Potrerillos (Colombia) respuesta a los cambios estacionales de caudal. *Limnetica* 29:195–210.

Lynch, D. T., and D. D. Magoulick. 2016. Effects of pulse and press drying disturbance on benthic stream communities. *Freshwater Science* 35:998–1009.

Merritt, R. W., K. M. Cummins, and M. Berg. 2008. An introduction to the aquatic insects of North America. 4<sup>th</sup> edition. Kendall/Hunt, Dubuque, Iowa.

Michiels, P., D. Gabriels, and R. Hartmann. 1992. Using the seasonal and temporal precipitation concentration index for characterizing the monthly rainfall distribution in Spain. *Catena* 19:43–58.

Montoya, J. V., D. L. Roelke, K. O. Winemiller, J. B. Cotner, and J. A. Snider. 2006. Hydrological seasonality and benthic algal biomass in a neotropical floodplain river. *Journal of the North American Benthological Society* 25:157–170.

Mosley, L. M. 2015. Drought impacts on the water quality of freshwater systems: Review and integration. *Earth-Science Reviews* 140:203–214.

Mote, T. L., C. A. Ramseyer, and P. W. Miller. 2017. The Saharan air layer as an early rainfall season suppressant in the eastern Caribbean: The 2015 Puerto Rico drought. *Journal of Geophysical Research: Atmospheres* 122:10966–10982.

O’Gorman, P. A., and T. Schneider. 2009. The physical basis for increases in precipitation extremes in simulations of 21<sup>st</sup>-century climate change. *Proceedings of the National Academy of Sciences* 106:14773–14777.

Oliver, J. E. 1980. Monthly precipitation distribution: A comparative index. *Professional Geographer* 32:300–309.

Otermin, A., A. Basaguren, and J. Pozo. 2002. Re-colonization by the macroinvertebrate community after a drought period in a first-order stream (Agüera Basin, Northern Spain). *Limnetica* 21:117–128.

Pearson, R. 2014. Dynamics of invertebrate diversity in a tropical stream. *Diversity* 6:771–791.

Pendergrass, A. G., and D. L. Hartmann. 2014. Changes in the distribution of rain frequency and intensity in response to global warming. *Journal of Climate* 27:8372–8383.

Pérez-Reyes, O., T. A. Crowl, P. J. Hernández-García, R. Ledesma-Fuste, F. A. Villar-Fornes, and A. P. Covich. 2013. Freshwater decapods of Puerto Rico: A checklist and reports of new localities. *Zootaxa* 3717:329–344.

Peterson, C. G. 1996. Response of benthic algal communities to natural physical disturbance. Pages 375–402 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal Ecology*. Academic Press, San Diego, California.

Pettitt, A. N. 1979. A non-parametric approach to the change-point problem. *Applied statistics* 28:126–135.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and Team, R. C. 2018. *nlme*: Linear and nonlinear mixed effects models. R package version 3.1-128.

Pohlert, T. 2018. *trend*: Non-parametric trend tests and change-point detection. R package version 1.1.1.

Pozo, J., E. González, J. Díez, and A. Elosegi. 1997. Leaf-litter budgets in two contrasting forested streams. *Limnetica* 13:77–84.

Pringle, C. M. 1997. Exploring how disturbance is transmitted upstream: Going against the flow. *Journal of the North American Benthological Society* 16:425–438.

Ramírez, A., and P. E. Gutiérrez-Fonseca. 2014. Functional feeding groups of aquatic insect families in Latin America: A critical analysis and review of existing literature. *Revista de Biología Tropical* 62:155–167.

Ramírez, A., P. E. Gutiérrez-Fonseca, S. P. Kelly, A. C. Engman, K. Wagner, K. G. Rosas, and N. Rodríguez. 2018. Drought facilitates species invasions in urban streams: Results from a long-term study of tropical island fish assemblage structure. *Frontiers in Ecology and Evolution* 6:115.

Ramseyer, C. A., P. W. Miller, and T. L. Mote. 2019. Future precipitation variability during the early rainfall season in the El Yunque National Forest. *Science of the Total Environment* 661:326–336.

Rayner, T. S., B. J. Pusey, and R. G. Pearson. 2008. Seasonal flooding, instream habitat structure and fish assemblages in the Mulgrave River, north-east Queensland: Towards a new conceptual framework for understanding fish-habitat dynamics in small tropical rivers. *Marine and Freshwater Research* 59:97–116.

Rincón, J., and A. P. Covich. 2014. Effects of insect and decapod exclusion and leaf litter species identity on breakdown rates in a tropical headwater stream. *Revista de Biología Tropical* 62:143–154.

Rincón, J., and C. Cressa. 2000. Temporal variability of macroinvertebrate assemblages in a neotropical intermittent stream in Northwestern Venezuela. *Archiv für Hydrobiologie* 148:421–432.

Robson, B. J. 2000. Role of residual biofilm in the recolonization of rocky intermittent streams by benthic algae. *Marine and Freshwater Research* 51:725–732.

Sabater, S., X. Timoner, C. Borrego, and V. Acuña. 2016. Stream biofilm responses to flow intermittency: From cells to ecosystems. *Frontiers in Environmental Science* 4:14.

Sauer, F. G., M. Bundschuh, J. P. Zubrod, R. B. Schäfer, K. Thompson, and B. J. Kefford. 2016. Effects of salinity on leaf breakdown: Dryland salinity versus salinity from a coalmine. *Aquatic Toxicology* 177:425–432.

Sen, P. K. 1968. Estimates of the regression coefficient based on Kendall's tau. *Journal of the American Statistical Association* 63:1379–1389.

Shanley, J. B., W. H. McDowell, and R. F. Stallard. 2011. Long-term patterns and short-term dynamics of stream solutes and suspended sediment in a rapidly weathering tropical watershed. *Water Resources Research* 47:W07515.

Silva, E. I. L., A. Shimizu, and H. Matsunami. 2000. Salt pollution in a Japanese stream and its effects on water chemistry and epilithic algal chlorophyll-*a*. *Hydrobiologia* 437:139–148.

Smakhtin, V. U. 2001. Low flow hydrology: A review. *Journal of Hydrology* 240:147–186.

Stanley, E. H., S. G. Fisher, and J. B. Jones Jr. 2004. Effects of water loss on primary production: A landscape-scale model. *Aquatic Sciences* 66:130–138.

Stekhoven, D. J. 2013. *missForest*: Nonparametric missing value imputation using random forest. R package version 1.4.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29:118–146.

Timoner, X., V. Acuña, D. von Schiller, and S. Sabater. 2012. Functional responses of stream biofilms to flow cessation, desiccation and rewetting. *Freshwater Biology* 57:1565–1578.

van Vliet, M. T. H., and J. J. G. Zwolsman. 2008. Impact of summer droughts on the water quality of the Meuse river. *Journal of Hydrology* 353:1–17.

Webster, J. R., and J. L. Meyer. 1997. Organic matter budgets for streams: A synthesis. *Journal of the North American Benthological Society* 16:141–161.

Wehrtmann, I. S., A. Ramírez, and O. Pérez-Reyes. 2016. Freshwater decapod diversity and conservation in Central America and the Caribbean. Pages 267–301 in T. Kawai and N. Cumberlidge (editors). *A global overview of the conservation of freshwater decapod crustaceans*. Springer, Berlin, Germany.

Wilhite, D. A. 2000. Drought as a natural hazard: Concepts and definitions. Pages 3–18 in D. A. Wilhite (editor). *Drought: A global assessment*. Routledge, London, UK.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2093–2106.

Wymore, A. S., R. L. Brereton, D. E. Ibarra, K. Maher, and W. H. McDowell. 2017. Critical zone structure controls concentration-discharge relationships and solute generation in forested tropical montane watersheds. *Water Resources Research* 53:6279–6295.

Zalamea, M., and G. González. 2008. Leaf fall phenology in a subtropical wet forest in Puerto Rico: From species to community patterns. *Biotropica* 40:295–304.

Zimmerman, J. K. H., and A. P. Covich. 2007. Damage and recovery of riparian Sierra palms after Hurricane Georges: Influence of topography and biotic characteristics. *Biotropica* 39:43–49.

Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. *Journal of Tropical Ecology* 23:231–251.