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ARTICLE

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Hurricane disturbance drives trophic changes in neotropical mountain stream food webs

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Abstract

Food webs are complex ecological networks that reveal species interactions and energy flow in ecosystems. Prevailing ecological knowledge on forested streams suggests that their food webs are based on allochthonous carbon, driven by a constant supply of organic matter from adjacent vegetation and limited primary production due to low light conditions. Extreme climatic disturbances can disrupt these natural ecosystem dynamics by altering resource availability, which leads to changes in food web structure and functioning. Here, we quantify the response of stream food webs to two major hurricanes (Irma and María, Category 5 and 4, respectively) that struck Puerto Rico in September 2017. Within two tropical forested streams (first and second order), we collected ecosystem and food web data 6 months prior to the hurricanes and 2, 9, and 18 months afterward. We assessed the structural (e.g., canopy) and hydrological (e.g., discharge) characteristics of the ecosystem and monitored changes in basal resources (i.e., algae, biofilm, and leaf litter), consumers (e.g., aquatic invertebrates, riparian consumers), and applied Layman's community-wide metrics using the isotopic composition of ^{13}C and ^{15}N. Continuous stream discharge measurements indicated that the hurricanes did not cause an extreme hydrological event. However, the sixfold increase in canopy openness and associated changes in litter input appeared to trigger an increase in primary production. These food webs were primarily based on terrestrially derived carbon before the hurricanes, but most taxa (including *Atya* and *Xiphocaris* shrimp, the consumers with highest biomass) shifted their food source to autochthonous carbon within 2 months of the hurricanes. We also found evidence that the hurricanes dramatically altered the structure of the food web, resulting in shorter (i.e., smaller food-chain length), narrower (i.e., lower diversity of carbon sources) food webs, as well as increased trophic species packing. This study demonstrates how hurricane disturbance can alter stream food webs, changing the trophic base from allochthonous to autochthonous resources via changes in the physical environment (i.e., canopy defoliation). As hurricanes become more frequent and severe due to climate change, our findings greatly contribute to our understanding of the mechanisms that maintain forested stream trophic interactions amidst global change.

KEYWORDS
Bayesian mixing model, disturbances, food webs, hurricanes, neotropical streams, stable isotopes

INTRODUCTION

Natural disturbances are an integral part of ecosystem dynamics, occurring as relatively discrete events that change the structure, composition, and function of ecosystems, thereby influencing food web dynamics (White & Pickett, 1985). While disturbances often drive mortality, they can also release resources that were previously not available for consumers (Novais et al., 2018; Schowalter & Ganio, 1999). In this sense, disturbances can cause both positive (e.g., increased availability of food for herbivorous insect populations) and negative shifts in ecosystems (Dornelas, 2010). As future climate change scenarios predict an increase in the frequency and severity of disturbances (Christensen et al., 2013), it is imperative to understand how ecosystems will respond to these events (Seidl et al., 2017; Turner, 2010). This is especially true for tropical and subtropical regions, which support a high diversity of organisms with complex trophic relationships and where extreme events are anticipated to be more severe and frequent than in other regions of the globe (Beaumont et al., 2011; Donat et al., 2016).

Food web approaches have been widely used to evaluate the trophic basis of ecosystems (e.g., Byrnes et al., 2011; Ledger et al., 2012) and their response to disturbance, providing valuable information on energy fluxes and species interactions. In this context, stable isotope analysis has become a key technique to assess the trophic structure and dynamics of food webs by quantifying differences in the carbon and nitrogen stable isotope composition of both food resources and consumers (Layman et al., 2012). The resulting multidimensional space occupied by consumers in a food web, based on their stable isotopic values, is referred to as the isotopic niche space (Layman et al., 2012; Newsome et al., 2007). Stream food webs are typically supported by two main resources: epilithic algae (an autochthonous carbon source), which is attached to different bottom substrates, and terrestrially derived organic detritus (an allochthonous carbon source), mostly in the form of leaf litter input from riparian vegetation. The relative contribution of autochthonous versus allochthonous carbon (C) sources to consumers and the conditions that control their use has long been the focus of trophic studies (Rounick et al., 1982). The River Continuum Concept (Vannote et al., 1980) provides theoretical support for a switch in the use of terrestrial C as primary fuel for food webs in small shaded streams to algal C in midsize sunnier streams. Furthermore, recent studies have shown that the type of C utilization may be influenced by resource quality and animal needs (Marcarelli et al., 2011). Disturbance events can substantially alter resource utilization, with unpredictable consequences for food web dynamics (e.g., consumer-resource interactions) and structure (e.g., trophic length, trophic niche breath). For example, a historic flood in Colorado streams caused a shift toward greater reliance on allochthonous resources (Larson et al., 2018), while wildfires increased utilization of autochthonous food sources in Montana streams, together with decreased reliance on allochthonous food sources (Spencer et al., 2003). Likewise, low flow disturbance can shorten food chains mainly by limiting the abundance of secondary consumers in fish diets in New Zealand streams (McHugh et al., 2010). Given the increase in extreme events driven by climate change, food web studies that specifically assess the complex dynamics of food use in response to climatic disturbances are warranted.

Tropical cyclones (e.g., hurricanes) dominate the disturbance regimes of many tropical ecosystems (Lugo, 2008). These windstorm events represent large-scale natural disturbances with long-lasting effects on ecological processes and forest structure and composition (Zimmerman et al., 1996). Hurricanes cause immediate changes in forest canopy structure, not only by damaging branches and stems but also by increasing tree mortality (Brokaw & Walker, 1991). Resulting canopy openings allow the passage of sunlight to the forest floor, stimulating seed germination and plant growth. Sunlight availability also promotes the growth of epilithic algae in headwater streams, where primary production is limited by low-light conditions (Pringle et al., 1993; Pringle, 1996). Moreover, hurricanes influence stream runoff and nutrient dynamics due to the high rainfall they deliver (McDowell et al., 2013; Schaefer et al., 2000).

Hurricane disturbances are relatively common, yet we still lack a comprehensive understanding of their impacts (Patrick et al., 2022). In the Luquillo Mountains of northeastern Puerto Rico, where this study was conducted, a major hurricane passes at an average recurrence interval of 50–60 years (Scatena & Larsen, 1991). Hurricanes Hugo (1989) and Georges (1998) provided the opportunity to improve our understanding of how hurricanes affect forests and terrestrial animal communities (Gannon & Willig, 1994; Reagan, 1991; Schowalter, 1994; Vilella & Fogarty, 2005; Waide, 1991; Willig & Camilo, 1991; Wunderle, 1995). However, less is known about hurricane effects on freshwater ecosystems, as most studies have focused on the response of a single taxonomic group (shrimp; Covich et al., 1991). Covich et al. (1991) observed that a hurricane caused a temporary displacement of shrimp downstream, resulting in approximately 50% fewer shrimp, but a rapid increase in numbers occurred shortly after the hurricane. This increase may be associated with the combination of rapid algae growth and a continuous supply of leaf litter. Nevertheless, no studies have evaluated how hurricanes impact trophic interactions, trophic basis, and the overall stream food web.

In this study, we evaluate the effects of two hurricanes on changes in stream food web dynamics over a 2-year period: 6 months before hurricanes and then 2, 9, and 18 months after hurricanes. We predict that (1) stream food webs will shift their energy base from mostly allochthonous C (leaf litter) before disturbance to autochthonous C (algae and epilithic biofilm) after disturbance; (2) reliance on autochthonous resources will persist until riparian tree canopy recovers, then food webs will shift back to an allochthonous resource base; and (3) the isotopic niche of the stream consumer community will contract (i.e., a reduction in trophic diversity as indicated by a smaller total area occupied by communities in isotopic niche space) due to reduced basal resource breadth.

MATERIALS AND METHODS

Study area

This study was conducted in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18°19′ N, 65°45′ W). The elevation gradient in the LEF ranges from 100 to 1075 m above sea level (asl) (Brown et al., 1983). Long-term mean annual precipitation (1975–2016) is 3676 mm at 350 m asl and ranged from 1405 mm year^{-1} in 1994 to 5567 mm year^{-1} in 2010 (Gutiérrez-Fonseca et al., 2020). Rainfall is weakly seasonal, with a dryer season between December and March, and the wettest periods from April to May and September to November (García-Martinó et al., 1996). The climate is characterized as humid tropical maritime and is influenced by both easterly trade winds and local orographic effects (Granger, 1985). Precipitation patterns are also influenced by the North Atlantic Oscillation and El Niño–Southern Oscillation (Jury et al., 2007). Diurnal and mean annual air temperatures above the canopy are 21°C–25°C (McDowell et al., 2012). Temperature declines with elevation from 26.5°C at the coast to around 20°C at the mountain top (González & Luce, 2013).

Our study streams were Prieta A and Prieta B, first- and second-order streams, respectively. Channels in both streams are ~2 m wide and 0.75 m deep, with steep topography. Channel substrata consist of boulders, large cobbles, and pebbles, with sand and silt deposited in pools. Study streams are tributaries within the larger Espiritu Santo River drainage and eventually join to form a single channel. Canopy cover without disturbances is dense and dominated by tabonuco trees (*Dacryodes excelsa*) and sierra palms (*Prestoea montana*). There is continuous leaf litter input throughout the year, except for a slight increase from March to June and a second increase in September (Zalamea & González, 2008), which provides a constant source of food for stream detritivores (~1 g m^{-2} day^{-1}; Gutiérrez-Fonseca et al., 2020). Heavily shaded conditions similar to our headwater streams result in limited primary production (<70 g O^2 m^{-2} year^{-1}) compared to the reaches that are more exposed to solar radiation (canopy cover: 39%–40%, production: 453–634 g O^2 m^{-2} year^{-1}) (Ortiz-Zayas et al., 2005).

Macroinvertebrate assemblages are diverse and include Ephemeroptera, Odonata, Trichoptera, Lepidoptera, Coleoptera, and Diptera (Gutiérrez-Fonseca et al., 2020; Ramírez & Hernández-Cruz, 2004). Eight species of decapods occur in our study streams, although the total number of species varies among years. Two shrimp species consistently dominate decapod density and biomass: *Atya lanipes* (Atyidae) and *Xiphocaris elongata* (Xiphocarididae), which represent >90% of the total shrimp density and biomass collected (Cross et al., 2008). The green stream goby, *Sicydium plumieri* (Gobiidae), is the only fish species above waterfalls in LEF streams.

The hurricane events

In September 2017, Puerto Rico was impacted by two major hurricanes, Irma and María, Category 5 and 4, respectively (Saffir-Simpson hurricane wind scale). Hurricane Irma passed through northeastern Puerto Rico with a highest measured wind speed of 287 km/h (Cangialosi et al., 2018). Two weeks later, Hurricane María crossed the island with a highest wind speed of 250 km/h, just below the intensity threshold of a Category 5 hurricane (Pasch et al., 2018). Initial studies based on spectral mixture analysis using Landsat 8 images to estimate changes in nonphotosynthetic vegetation indicated that Hurricane María might have caused mortality and severe damage to 23–31 million trees across the island (Feng et al., 2018). Consequently, annual litter production in the Luquillo Mountains increased by 62% (Liu et al., 2018).

Sample collection and isotope analyses

We used environmental variables from our ongoing research to determine hurricane impacts on stream ecosystem structure. The variables were recorded daily (water level, as a proxy for discharge), biweekly (leaf litter), or monthly (canopy openness, benthic periphyton, and benthic organic matter [BOM]) along a 100-m reach from January 2017 to June 2019. The procedure described here was performed separately in each stream. Canopy openness was measured over the middle of the stream at nine locations with a spherical densiometer following methods outlined in Lemmon (1957). Leaf litterfall was collected with 10 litter baskets (0.29 m^2 each) that were suspended at ~1 m above the channel of each stream. Samples were oven-dried at 65°C for 24 h, weighed, and reported as grams per square meter per day. BOM samples were collected from six randomly selected pools using a stovepipe benthic corer (sampling area = 314 cm^2). BOM samples were dried at 70°C for 48 h or to constant mass and weighed. Then BOM samples were ashed at 500°C for 1 h and reweighed to obtain ash-free dry mass (AFDM).

Algal standing stocks of chlorophyll *a* (chl *a*) were quantified in six randomly selected pools. In each pool, we collected six epilithon samples at randomly chosen locations with a suction device modified from Loeb (1981). The Loeb sampler was a cylinder (5.07 cm^2 area) with a brush-fitted plunger that removed epilithon from rock substrata. We combined all samples from a single pool into a slurry and kept slurries in a cooler until they could be processed at the laboratory. Epilithon samples were filtered through a glass fiber filter (Whatman GF/F, 0.7 μm) that was precombusted at 500°C for 1 h. Filters were frozen and then analyzed for chl *a* fluorometrically according to standard methods (American Public Health Association, 2012).

To determine a potential shift in food web structure and diet of consumers, isotope samples were collected from each stream at four time points relative to the occurrence of the two hurricanes: February 2017 (6 months before), November 2017 (2 months after), June 2018 (9 months after), and February 2019 (18 months after). We collected leaf litter and biofilm samples from a 100-m reach of each stream where the consumers (i.e., macroinvertebrates, shrimp, and terrestrial predators) were collected. Leaf litter samples (10–15 leaves) were collected by hand from the streams and then washed with distilled water to remove superficial periphyton. Biofilm (i.e., a complex of communities of algae, bacteria, fungi, protozoa, and micrometazoa embedded in a polysaccharide matrix; Lock et al., 1984) samples were collected by scrubbing the surface of five rocks with a small wire brush. Rocks were rinsed with distilled water to remove any macroinvertebrates prior to biofilm collection. We justify using biofilm as an autochthonous material due to the substrate from which it was collected and the prevailing environmental conditions, two factors that are associated with the degree of autochthony in epilithic biofilms. While Hladyz et al. (2011) found that biofilms grown on organic substrates reflected the $\delta^{13}C$ value of the substrate (leaf litter of *Eucalyptus camaldulensis*), the biofilm we used in our study was sampled from rocks, so we expected the biofilm to use a high proportion of autochthonous material. Moreover, our findings are consistent with previous research indicating that biofilm predominantly utilize autochthonous carbon under high light conditions, similar to the conditions observed following the hurricanes (Wagner et al., 2017).

We collected samples of dominant macroinvertebrates from different functional feeding groups (i.e., collectors, scrapers, shedders, and predators) by a combination of kick sampling and visual search in both streams. We also collected three species of shrimp: *Atya lanipes*, *Xiphocaris elongata*, and *Macrobrachium crenulatum*, which feed by collecting and filtering organic particles, shredding leaves and consuming algae, and preying on other organisms, respectively. In addition, we included lizards (*Anolis evermanni*) and spiders (*Leucauge regnyi*) in the analysis, given their previously documented roles as terrestrial predators in streams of LEF (Kelly et al., 2015). Collected consumers were processed after being contained in filtered stream water for a minimum of 24 h to allow their digestive systems to clear. This approach prevents contamination by unassimilated material and has been widely used in other food web analysis studies (Cashman et al., 2016; Reid et al., 2008). Samples were composites of several individuals and were not acidified to avoid confounding stable isotope analysis (Carabel et al., 2006).

All samples were dried for 48 h at 60°C within a day of collection and sent to the Center for Applied Isotope Studies at the University of Georgia, where they were homogenized with mortar and pestle into a fine powder for analysis by isotope ratio mass spectrometry. Stable isotope ratios were expressed in parts per thousand (‰) in delta (δ) notation using the equation $\delta X\ (‰) = (R_{sample}/R_{standard} - 1) \times 10^3$, where X is ^{13}C or ^{15}N, and R is the corresponding ratio of heavy to light isotope in the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The reference materials used were the international Vienna PeeDee Belemnite (PDB) standard for C and atmospheric nitrogen (N_2) for nitrogen.

Bayesian mixing model

We estimated the individual consumer assimilation of basal resources using two linked Bayesian models. The first model served to determine the $\delta^{13}C$ and $\delta^{15}N$ signature of the algal component. Accurately measuring the isotopic value of algae is difficult because it requires physical separation (e.g., density-gradient centrifugation technique) of epilithic biofilm (Hamilton et al., 2005). However, this approach has shown limitations in samples containing higher-density algae (such as diatoms), which may not be cleanly separated from detritus that is similar in density (Mcneely et al., 2007). This limitation is particularly relevant in our streams, where diatoms dominate the algae community to the extent of 90% (Pringle, 1996; Pringle et al., 1993). Alternatively, some studies used herbivores, such as Glossosomatidae, as an approximation of the isotopic signature of algae. However, Finlay (2004) suggested that this approach was more suitable for sites with an open canopy, where a strong relationship between epilithon and herbivores exists, conditions that are not prevalent in our streams. Moreover, collecting herbivores, such as Glossosomatidae and Helicopsychidae, proved to be challenging in our study area due to their patchy distribution (Ramírez & Hernández-Cruz, 2004). To address these challenges, we estimated the isotopic ratios of algae from epilithic biofilm after removing the contribution of leaf litter. To strongly constrain the possible range of values for the algae, we used informative priors from a mean and SD of 17 measurements taken from tropical streams at similar elevation, canopy cover, and stream order (Appendix S1: Table S1). In this way, informative priors reduced the algal value search from an infinite to a more plausible range (Banner et al., 2020; Ellison, 2004).

We used a hierarchical partial pooling model to determine the $\delta^{13}C$ and $\delta^{15}N$ signature of algae. Partial pooling is a technique that allows periods with small sample sizes to borrow information from other periods, improving the precision of the estimation at these periods to be closer to the overall average. Thus, more reliable estimates will be produced than if a regression model were fitted to those periods alone (i.e., no pooling). We followed the procedure of Phillips and Gregg (2001) and Gelman and Hill (2006) as follows:

$$\delta_P \sim N(\delta_A \times (1-\Phi_T) + \delta_T \times \Phi_T, \sigma),$$

where δ_P is the epilithic biofilm stable isotopic signature (i.e., $\delta^{13}C$ or $\delta^{15}N$), δ_A is the algae stable isotopic signature, Φ_T is a terrestrial fraction on epilithic biofilm, and δ_T is the leaf litter stable isotopic signature (i.e., $\delta^{13}C$ or $\delta^{15}N$). We assigned normally distributed priors of mean $= -22.64$ and SD $= 3.93$ for $\delta^{13}C$ in δ_A and of mean $= 3.68$ and SD $= 2.47$ for $\delta^{15}N$ in δ_A. Priors for both isotopes were determined by averaging the values in Table S1 from Appendix S1.

After estimating the isotopic ratios (i.e., $\delta^{13}C$ and $\delta^{15}N$) of algae with the aforementioned model, we used a second Bayesian model to determine the isotopic mixing. We followed the procedure of Vlah et al. (2018) as follows:

$$\delta_{t,c} = \delta_{t,1:s}(\Delta\delta \times L) \circ \Phi_{1:s},$$

where $\delta_{t,c}$ is the isotopic ratio of each consumer (c) with respect to each tracer (t), $\delta_{t,1:s}$ is the vector of isotopic ratios for each of its potential food sources ($1{:}s$), $\Delta\delta$ is the trophic fractionation factor by each tracer (i.e., $\delta^{13}C$ or $\delta^{15}N$), L is the trophic level of each consumer, $\circ$ represents the scalar product, and Φ is a vector of source proportions (drawn from a Dirichlet distribution hyperparameter, with $\alpha = 1$ for tracer).

$\delta_{t,1:s}$ had a prior normalized distribution with mean and SD values for leaf litter and biofilm $\delta^{13}C$ or $\delta^{15}N$ and estimated mean and SD for algae by each sampling period. Gaussian prior probabilities were used for the isotope enrichment factor ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$). We used a mean $= 0.39$ and SD $= 1.14$ for $\Delta\delta^{13}C$ and mean $= 3.4$ and SD $= 0.99$ for $\Delta\delta^{15}N$, as recommended by Post (2002). L had a uniform distribution prior probability between 0 and 10.

We fitted these models (i.e., models estimating the isotopic ratios of algae and for each mixing model) by simulating the posterior parameter distributions with the "stan()" function in the rstan package (version 2.21.2, Stan Development Team, 2021) in R program version 4.0.4 (R Core Team, 2022). Stan uses Markov chain Monte Carlo (MCMC) techniques to generate samples from the posterior distribution. We ran four parallel MCMC chains for 100,000 iterations, discarding the initial 98,000 from each chain as burn-in, and used the remaining 2000 interactions (8000 samples from the four chains) to summarize the posterior distribution. The convergence of Markov chains was ensured through visual inspection of trace plots and on the scale reduction factor ($\widehat{R}$), as suggested in Gelman et al. (2013). The $\widehat{R}$ is based on comparing the variation between the chains to the variation within the chains, given by the equation $\widehat{R} = \sqrt{\overline{\sigma}^2/W}$, where $\overline{\sigma}^2 = (1-1/n)W + (1/n)B$, with B as the weighted average of the variances between chains and W within chains. If all chains converge to the same region and behave similarly, then the variance between the chains should be approximately equal to the average variance within chains and the estimated $\widehat{R}$ will be close to 1. In our case, the visual assessment and $\widehat{R}$ values less than 1.01 indicated convergence for all parameters.

Community-wide metrics

We calculated six Layman's community-wide metrics (Layman et al., 2007) to quantify variation in trophic structure among sampling periods using the isotopic data. Our data fit well with Layman's metrics since the sampling method, level of taxonomic resolution, and linkage criteria were standardized across streams and sampling periods. The metrics considered were (1) δ^{15}N range (NR), which represents the vertical structure within the food web and is a measure of trophic length; (2) δ^{13}C range (CR), which represents the diversity of basal resources used by the consumers (it is a proxy for niche diversification at the base of the food web); (3) total area (TA), which is a convex hull enclosing the δ^{13}C–δ^{15}N biplot, representing the niche space occupied by the community; (4) the mean distance to centroid (CD), which is the average Euclidean distance of each sample to the biplot centroid, representing the average degree of trophic diversity; (5) the mean nearest-neighbor distance (MNND), which is the mean Euclidean distance from each individual (i.e., consumer) to its nearest neighbor in the δ^{13}C–δ^{15}N biplot space, where low MNND values indicate an increase in trophic redundancy of species, that is, that there are many groups with similar trophic ecologies; and (6) SD of the nearest-neighbor distance (SDNND), which reflects evenness of spatial density and packing, where low SDNND values suggest a more uniform trophic niche distribution.

Use of Layman's metrics is constrained when comparing between communities that have different sample sizes (Jackson et al., 2011). Since our data had the same number of taxa (except in February 2017), this allowed us to make a direct comparison between sampling periods. Layman's community-wide metrics were calculated with the Stable Isotope Bayesian Ellipses (SIBER) package version 2.1.7 (Jackson et al., 2011; Jackson & Parnell, 2023).

All data analyses were implemented in R version 4.0.4 (R Core Team, 2022). Data visualizations were also performed in R using the ggplot2 package (Wickham, 2016). Code and associated data for these analyses are archived on Zenodo (Gutiérrez-Fonseca et al., 2023).

RESULTS

Background environmental variables

Responses of environmental factors to hurricane impacts were variable. Water level had high variability, and the two hurricanes did not generate an extreme peak beyond those observed in either study stream prior to the hurricane (Figure 1a). Before the hurricanes, percentage of canopy openness was 11.7% and 11.1% on average (Figure 1b). Hurricane Irma slightly increased the canopy openness to 21.3% and 14.6%. However, after Hurricane María, openness increased to 89.4% and 75.3%. After 9 months, some refoliation had occurred, and openness was 51.3% and 38.6%, but 18 months after the hurricanes, the canopy remained approximately two times more open than before the hurricanes (i.e., 32.6% and 31.1%). A leaf litter peak of 5.9 and 8.4 g m^{-2} day^{-1} was recorded immediately after Hurricane Irma (Figure 1c). Following this initial pulse after defoliation, mean daily leaf litter input changed from 1.3 and 1.4 g m^{-2} day^{-1} before the hurricanes to 0.3 and 0.7 g m^{-2} day^{-1} after them. We were unable to quantify the leaf litter input immediately after Hurricane María because all the litter baskets were damaged. Mean monthly chl *a* was variable over time, with no distinct response to the hurricanes, except for a slight increase several months after the initial disturbance (Figure 1d). BOM varied widely in response to increased litter input in the initial months after the hurricanes and then was reduced in accordance with reductions in litterfall (Figure 1e).

Isotope signatures of food sources

Isotopic signatures of the basal resources (algae, biofilm, and leaf litter) were distinctly different over time (i.e., before and after the hurricanes; Figure 2). These patterns were consistent for both study streams and were most evident for the δ^{13}C values. Before the disturbances, δ^{13}C was depleted (i.e., more negative δ^{13}C values) and ranged from −32.01‰ (leaf litter) to −31.28‰ (algae) in Prieta A and from −41.01‰ (algae) to −30.03‰ (leaf litter) in Prieta B. However, after the hurricanes, the autochthonous basal resources were ^{13}C-enriched and ranged from −26.32‰ to −22.50‰ in Prieta A and from −27.45‰ to −14.51‰ in Prieta B for biofilm and algae, respectively. In contrast, the allochthonous resource remained ^{13}C-depleted in both streams (−31.57‰ in Prieta A and −32.26‰ in Prieta B). After 9 and 18 months, the autochthonous resources remained ^{13}C-enriched compared to prehurricane conditions. However, the δ^{13}C signature from the algae started returning to prehurricane values.

Regarding the δ^{15}N isotopic signature in the basal resources (Figure 2), 6 months before the hurricanes, algae was consistently more δ^{15}N-enriched (11.28‰ Prieta A and 9.45‰ in Prieta B), while the leaf litter was δ^{15}N-depleted (0.56‰ Prieta A and 2.14‰ Prieta B). Two months after the hurricanes, we observed a decrease in the δ^{15}N values in all the basal resources (except in algae from Prieta B and leaf litter from Prieta A). Remarkably, 9 months after the

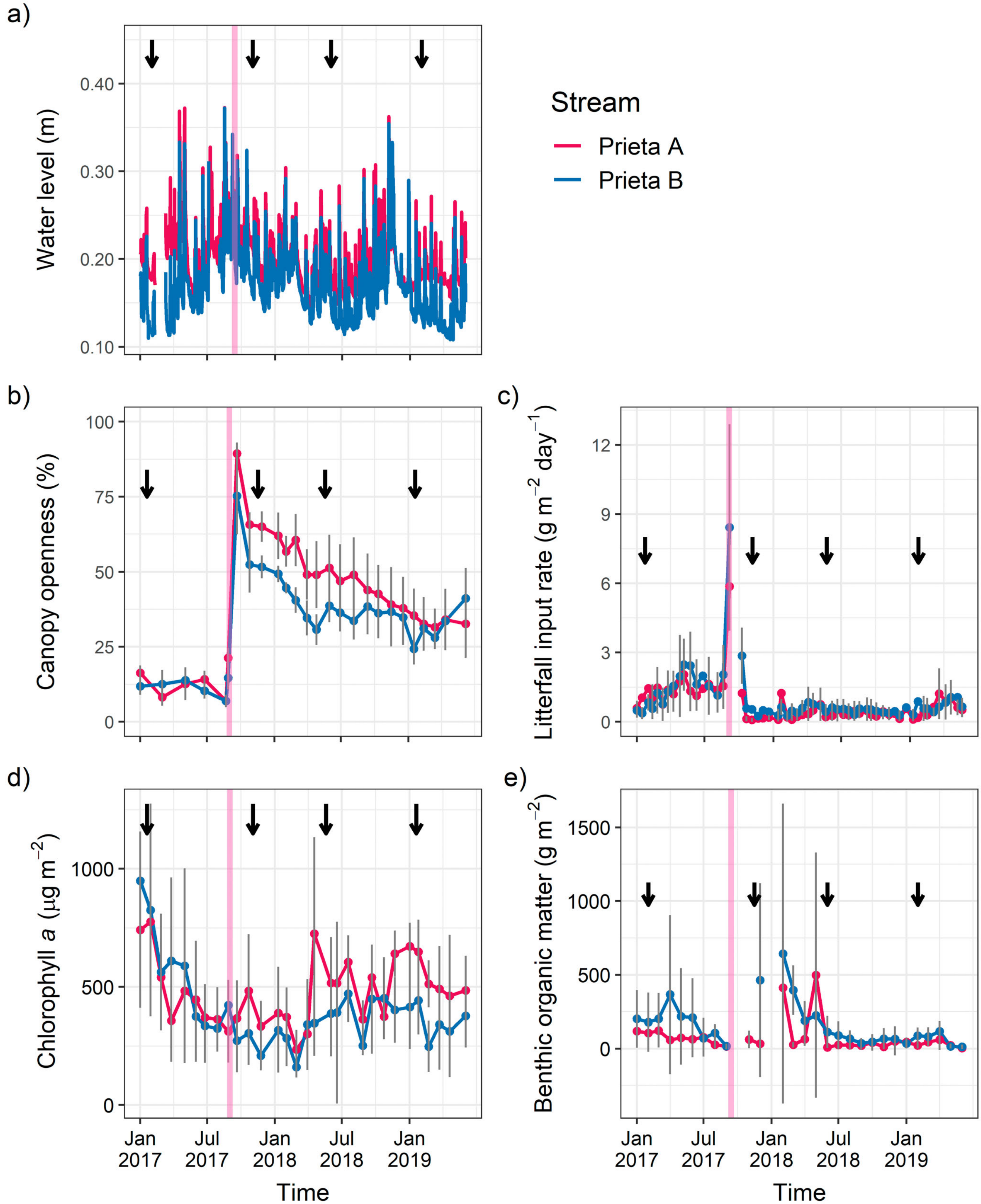

FIGURE 1 Environmental variables (mean and SD) that span a time period (from January 2017 to June 2019) before and after Hurricanes Irma and María passed over Puerto Rico, showing (a) water level (proxy for stream discharge); (b) percentage of canopy openness; (c) mean input rate of leaf litter; (d) chlorophyll *a*; and (e) benthic organic matter. The pink bar represents the 2-week period between hurricanes. Arrows represent the sampling events for stream isotope measurements (6 months before, 2 months after, 9 months after, and 18 months after the hurricanes).

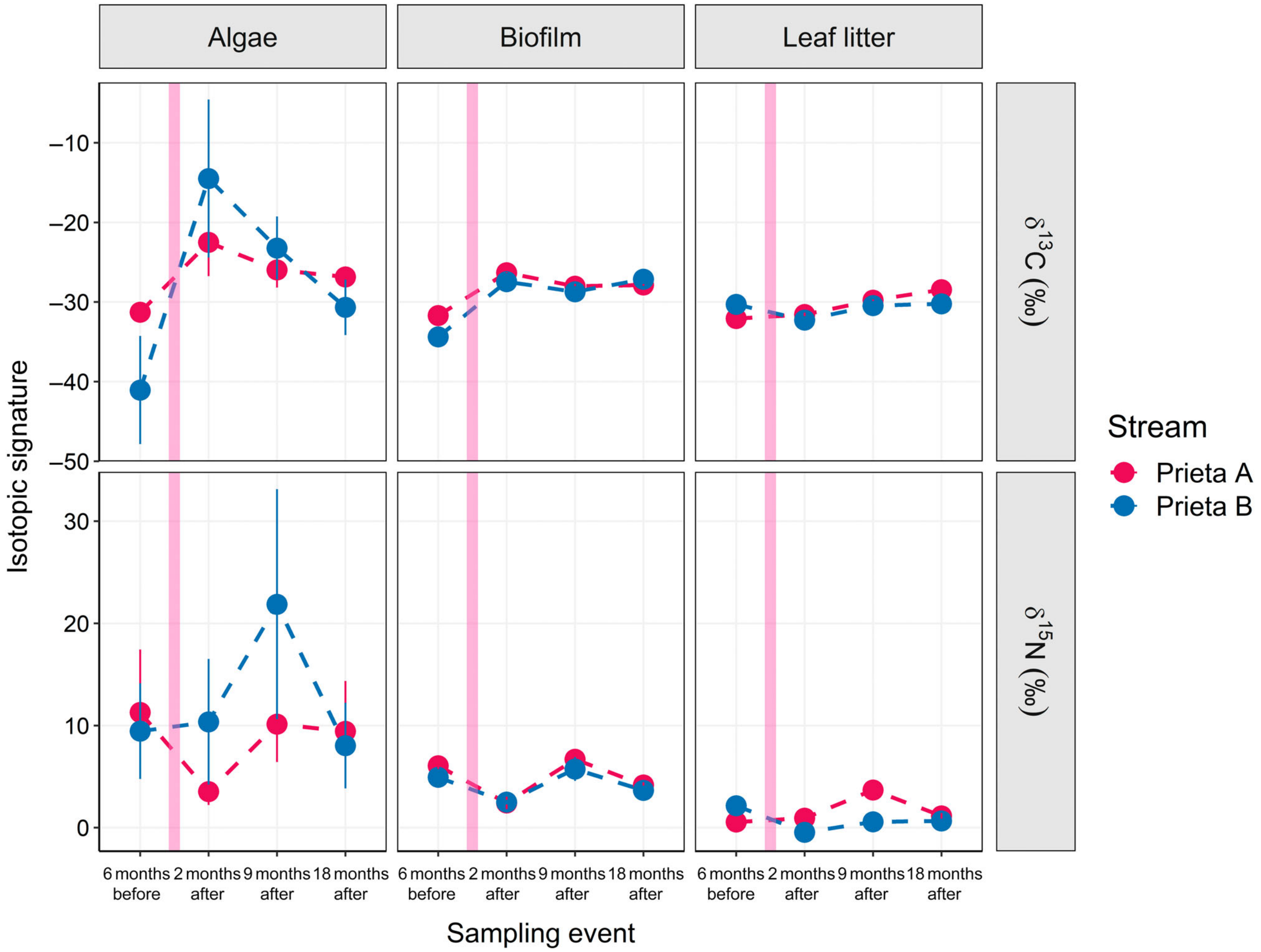

FIGURE 2 Isotopic signature (mean and SD of $\delta^{13}C$ and $\delta^{15}N$) of basal sources (algae, biofilm, and leaf litter) in the Prieta A and B study streams at different sampling times before and after the hurricanes (6 months before, 2 months after, 9 months after, 18 months after). The pink bar represents the hurricanes, delineating a before and after hurricane disturbance period.

hurricanes, the $\delta^{15}N$ exhibited an increasing trend, surpassing almost all values observed before the disturbances. These patterns clearly showed a delayed effect on the incorporation of $\delta^{15}N$ into the basal resources.

Contribution of basal C sources to consumers

Consistent with the $\delta^{13}C$ and $\delta^{15}N$ patterns observed for basal resources, the trophic basis of the food web varied widely during the study period. While terrestrially derived C was the most important energy source prior to the hurricanes (Figure 3), 2 months after the hurricanes, the resource base shifted to biofilm (i.e., consumer isotopic signatures clustered near biofilm signatures). Finally, 9 and 18 months after the hurricanes, the $\delta^{13}C$–$\delta^{15}N$ biplots demonstrated that, while biofilm-derived C continued to prevail, terrestrial C was becoming more important in both study streams (Figure 3).

With respect to the dominant shrimp macroconsumers in our two study streams (whose total biomass is orders of magnitude greater than other stream organisms, such as insects), allochthonous C generally contributed more than half of the diet prior to the hurricanes (Appendix S2: Figures S1 and S2, Appendix S3: Table S1): 0.77 in Prieta A and 0.82 in Prieta B for *A. lanipes*, 0.76 in Prieta A and 0.67 in Prieta B for *X. elongata*, and 0.69 in Prieta A and 0.46 Prieta B for *M. crenulatum*.

Remarkably, 2 months after the hurricanes, biofilm-derived C became the most important source of food, with proportions shifting to 0.50 in Prieta A and 0.81 in Prieta B for *A. lanipes*, 0.59 in Prieta A and 0.79 in Prieta B for *X. elongata*, and 0.67 in Prieta A and 0.88 in Prieta B for *M. crenulatum*. Finally, 9 months after the hurricanes, allochthonous-derived C once again

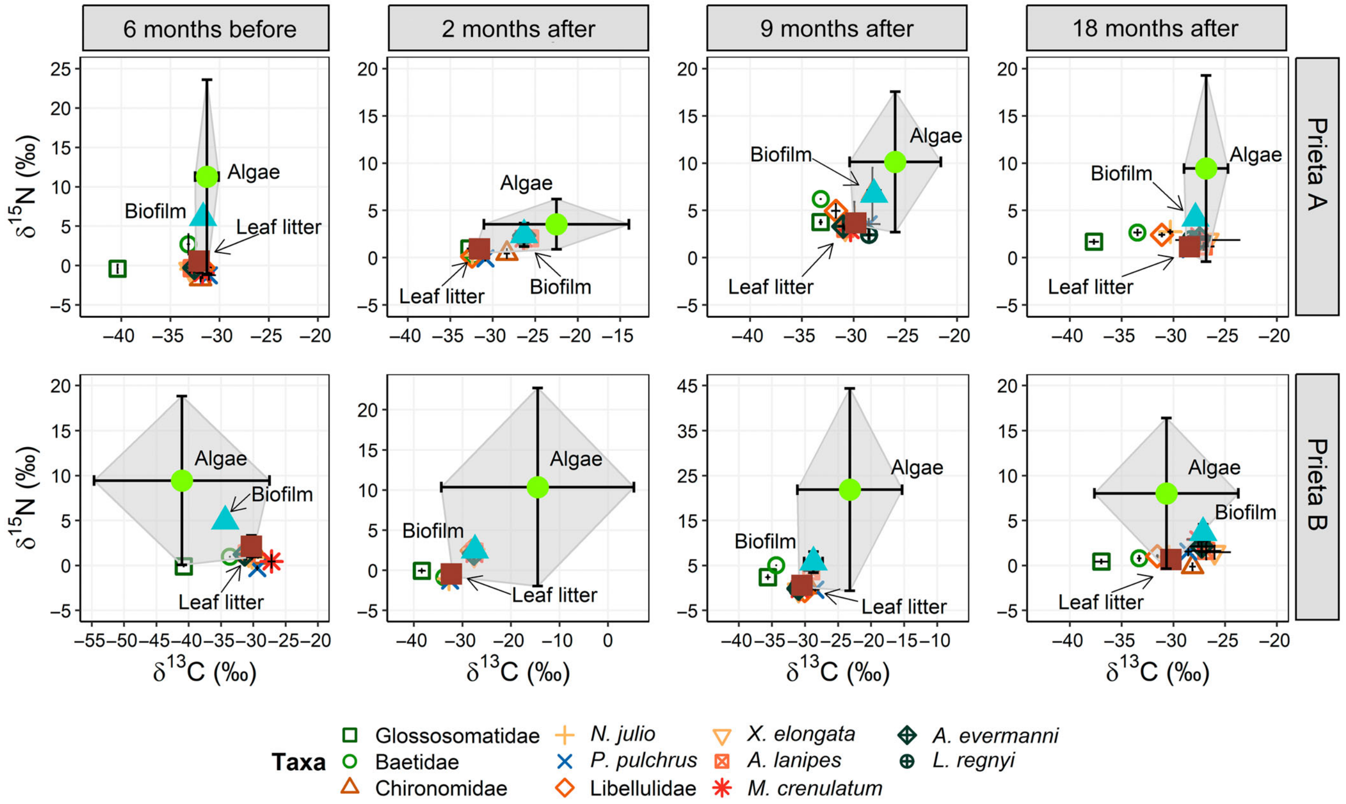

FIGURE 3 Stable isotope biplots indicating δ^{13}C and δ^{15}N values (‰) of leaf litter (brown), biofilm (blue), algae (green), and individuals of consumer taxa in the Prieta A (top) and Prieta B (bottom) study streams at different sampling times before and after the hurricane (6 months before, 2 months after, 9 months after, and 18 months after). Primary food resources are shown as means (±2 SD). Symbols represent individual consumers. Note the different scales on *y*- and *x*-axes.

became the most important energy source in the diet of *A. lanipes*, *X. elongata*, and *M. crenulatum* in both streams (except *A. lanipes* in Prieta B). Interestingly, 18 months after the hurricanes, we observed a trend in the importance of biofilm-derived C for all shrimp species in both streams (Appendix S2: Figures S3–S8, Appendix S3: Table S1).

Insect δ^{13}C signatures varied among functional feeding groups before the hurricanes (Appendix S2: Figures S1 and S2, Appendix S3: Table S1). Allochthonous plant detritus was the primary food source for all consumers, except for one family of scrapers (Baetidae), which showed an almost equal preference for both autochthonous and allochthonous C (varying between 0.22 and 0.43 the contribution of each of the resources in both streams). For the other scraper family (i.e., Glossosomatidae), allochthonous material contributed 0.53 and 0.50 in Prieta A and Prieta B, respectively. For collector taxa (Chironomidae and *N. julio*), the allochthonous contribution ranged from 0.48 in Prieta B in Chironomidae to 0.76 in Prieta A in *N. julio*. The allochthonous contribution for shredder taxa (*P. pulchrus*) ranged from 0.54 in Prieta B to 0.69 in Prieta A. For aquatic (Libellulidae) and terrestrial (*A. evermanni*) predators, the allochthonous contribution ranged from 0.72 in Prieta A in Libellulidae to 0.81 in Prieta B in *A. evermanni*.

After the hurricanes, the C contribution derived from biofilm became important for some taxa, while other consumers remained dependent on allochthonous C (Appendix S2: Figures S3 and S4, Appendix S3: Table S1). Taxa with the highest autochthonous contribution were Chironomidae with 0.41 in Prieta A and 0.81 in Prieta B, Libellulidae with 0.81 in Prieta B, and the terrestrial predators *A. evermanni*, with 0.67 in Prieta A and 0.86 in Prieta B, and *L. regnyi*, with 0.67 in Prieta A and 0.79 in Prieta B. While 9 months after the hurricanes the biofilm contribution was still significant in the diets of these taxa, 18 months later their diets returned to being dependent on terrestrially derived C (Appendix S2: Figures S5–S8, Appendix S3: Table S1). Interestingly, although terrestrial predators in Prieta B returned to reliance on terrestrial C 9 months after the hurricanes, in the following sampling event (18 months) the biofilm signature increased significantly in their diet.

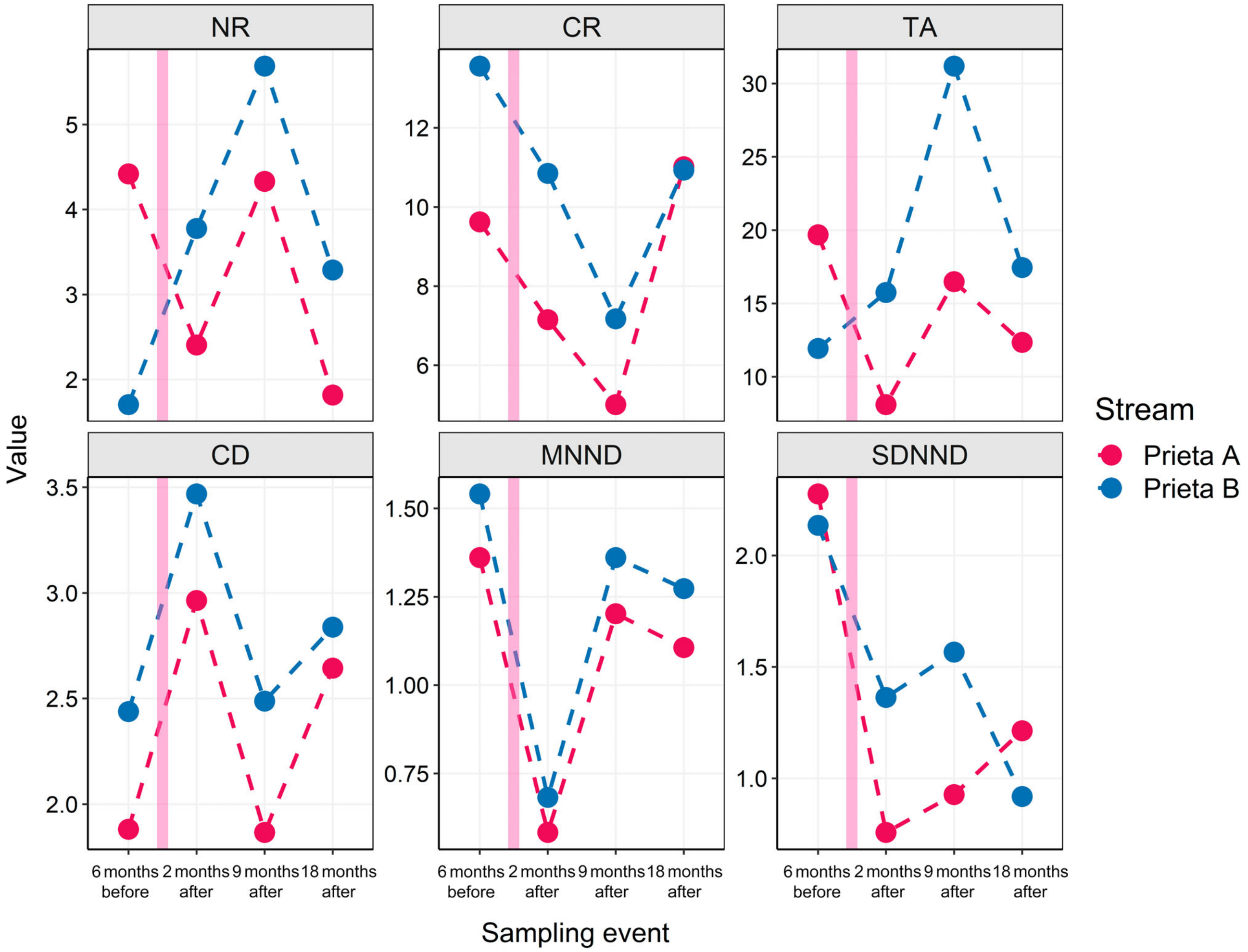

FIGURE 4 Layman's community-wide metrics for the Prieta A and B study streams, comparing sampling times before and after the hurricanes (6 months before, 2 months after, 9 months after, and 18 months after). CD, distance to centroid; CR, δ^{13}C range; MNND, mean nearest-neighbor distance; NR, δ^{15}N range; SDNND, standard deviation of nearest-neighbor distance; TA, total area. The pink bar represents the hurricanes, delineating a before and after hurricane disturbance period.

Layman's community-wide metrics

Layman's community-wide metrics varied among sampling periods in both streams (Figure 4). The trophic length (NR) decreased in Prieta A and increased in Prieta B after the hurricanes. The diversity of C sources (CR) was abruptly decreased in both streams after hurricanes. The niche breadth (TA) narrowed in Prieta A but widened in Prieta B following the trend of NR. In general, trophic diversity (CD) increased in both streams, while the density and evenness of taxon packing (MNND and SDNND, respectively) decreased 2 months after the hurricanes.

All Layman's community-wide metrics fluctuated in the same direction in both streams during the 9- and 18-month posthurricane sampling events (Figure 4). Specifically, trophic length (NR), TA, packing density (MNND), and trophic evenness (SDNND) demonstrated an increase from Month 2 to Month 9 following the hurricanes and then decreased after 18 months (except for SDNND in Prieta A). In contrast, diversity of C sources (CR) and trophic diversity (CD) declined from Month 2 to Month 9 but then exhibited an increase by the 18-month mark.

DISCUSSION

This study demonstrates how major hurricane disturbances can temporarily shift the trophic base of tropical stream food webs toward a greater reliance on autochthonous-derived C (i.e., algal resources). To our knowledge, this is the first study to examine the effects of an extreme climate event on the trophic base and the structure of a food web. When two back-to-back Category 5 and 4 hurricanes (Irma and María, respectively) struck

Puerto Rico in September 2017, almost a century had passed since a category 5 hurricane directly struck Puerto Rico (San Felipe II, 1928), providing an unprecedented opportunity to understand stream food web responses to hurricanes, which are expected to become more frequent and severe under future global warming (Collins et al., 2019).

We found that the assimilated energy of most consumer taxa in our two headwater study streams shifted, becoming much more dependent on epilithic algal resources within 2 months after Hurricanes Irma and María. Moreover, this effect remained evident in certain taxa throughout the 18-month duration of our study after the hurricanes. We found large differences in food web structure between sampling periods before and after the hurricanes. The most striking hurricane-driven shift was found in Prieta A, where both diversity of C sources (CR) and trophic length (NR) decreased, which resulted in smaller niche breadth (TA). We also observed higher trophic diversity (CD), as well as smaller packing density (MNND) and trophic evenness (SDNND), suggesting higher trophic redundancy and more compact food webs in both streams during the 2 months following Hurricanes Irma and María. These results support our expectation that the food web would be dramatically modified by the two major hurricanes.

Tropical stream food webs

This study contributes to our understanding of the trophic base of tropical stream food webs and the long-standing debate on whether they are fueled by allochthonous or autochthonous C (Dudgeon et al., 2010). We also demonstrated how major hurricane disturbances could shift the trophic base toward a greater reliance on autochthonous C. Our findings indicate that most taxa predominantly rely on terrestrial carbon sources. In small to midsized stream food webs, allochthonous C is expected to be the primary source of energy (Wallace et al., 1997, 1999), as these streams are shaded by riparian vegetation and allochthonous C can be very abundant, averaging up to three times more than the autochthonous production (Webster & Meyer, 1997). Consequently, some tropical studies suggest that terrestrial C is the main driver of secondary production in many small streams (Colón-Gaud et al., 2009; Frauendorf et al., 2013). In contrast, other studies have highlighted the importance of autochthonous C in tropical food webs (e.g., Brito et al., 2006; Bunn et al., 1999; Lau et al., 2009; Mantel et al., 2004; March & Pringle, 2003). Autochthonous matter may be preferred over allochthonous matter due to its higher nutritional quality (higher polyunsaturated fatty acid content and lower C:N ratios) and digestibility (Finlay, 2001; Lau et al., 2008; Torres-Ruiz et al., 2007), which improves the assimilation efficiency for organisms (Guo et al., 2016). This pattern is persistent in the literature even when terrestrial organic matter represents a significant fraction of the available C pool and where dense tropical vegetation creates heavily shaded conditions.

We can attempt to elucidate the debate on the significance of allochthonous and autochthonous C by examining various factors that influence ecosystem dynamics. These factors include the interaction between ecosystem physical characteristics (e.g., stream width, depth, and canopy cover), food quality, physiological requirements, and feeding plasticity (e.g., assimilation efficiency, flexibility of feeding behavior). In tropical streams where autochthony is dominant, the channels are typically open and wide (8–19 m), allowing more light to reach the streambed, potentially resulting in greater primary production. Conversely, tropical studies relying on allochthonous material as a primary food source often have narrow and shaded channels (1.6–2.5 m; García et al., 2016, this study). Our streams fall into the latter category under prehurricane conditions, characterized by a heavily shaded stream bed (~90% of canopy cover) and a high supply of leaf litter (467 g DM m^{-2} $year^{-1}$; Gutiérrez-Fonseca et al., 2020). Moreover, feeding plasticity might play a role, as flexible feeding behavior has been observed in high-elevation tropical streams (1268–-4044 masl), where taxa respond to quantity (availability of CPOM or epilithon) and quality (C:N or N:P) of resources (Atkinson et al., 2018). Similar findings were found in streams in Trinidad, where stark within-taxon variations were associated with changes in canopy cover (Collins et al., 2016). This contrasting evidence points to the high heterogeneity and complexity (with regard to both ecosystems and taxa) of tropical streams. As such, any attempts to generalize dominant energy pathways in tropical models should be made with caution.

Disturbance effects on stream trophic basis and food web

Headwater tropical streams that drain wet forests are often characterized by dense canopy cover and limited light penetration, resulting in low algal productivity and abundant detrital resources, with a constant detrital input and warm temperatures that enhance detrital breakdown (Colón-Gaud et al., 2008; Pringle et al., 1993). However, our findings reveal that hurricane disturbance disrupts these conditions, causing an initial pulse of leaf litter into streams, followed by reduced detrital inputs as the denuded canopy refoliates. Contrary to expectations of enhanced algal primary production due to increased light penetration, algal standing crop remained at low levels, similar to prehurricane conditions. These might be explained by omnivorous shrimp (*A. lanipes* and *X. elongata*), which have been shown to exert extremely high grazing pressure given their relatively large size and abundance (Cross et al., 2008; Pringle & Blake, 1994). Shrimp assemblages (in our study streams and other headwater streams located in the Espiritu Santo watershed) have been shown to rapidly reduce algal standing crop, species richness, and structural complexity (Pringle, 1996; Pringle et al., 1993).

Our findings indicate that dominant shrimp macroconsumers can opportunistically shift to feed primarily on algae given diminished detrital resources following hurricanes. This adaptive strategy plays an important role in their persistence in highly dynamic mountain stream ecosystems in Puerto Rico, which are prone to natural disturbance (particularly droughts and tropical storms). The presence of specialized scraping and filtering setae is the primary mechanism that allows this flexible feeding behavior (Felgenhauer & Abele, 1983). Several lines of evidence from previous studies in Puerto Rico suggest that algae are often a preferred food resource in open channel streams. In previous stream experiments in Puerto Rico (also conducted in the Espiritu Santo watershed), when algae-covered rocks were introduced into heavily shaded stream pools (dominated by shrimp feeding at relatively equidistant locations from each other), shrimp immediately congregated on the rock to consume the attached algae, denuding the rock within 30 min (Pringle et al., 1993).

Flexible feeding strategies were also found in some insect groups, which were capable of opportunistic diet shifts from decomposing leaves to algae. For example, the nonbiting midge (Chironomidae), a facultative collector with an allochthonous-based diet, had a high δ^{13}C biofilm signature 2 months after the hurricanes. The high body mass and predominance of Chironomidae in harsh glacier-fed streams (Niedrist & Füreder, 2017, 2018) has also been attributed to the extremely flexible feeding strategies of Chironomidae. In our streams, this group showed the highest turnover rate ($P/B = 61\ \text{year}^{-1}$; Rosas et al., 2020), potentially mobilizing large amounts of energy within streams (as prey for shrimp) and toward terrestrial ecosystems.

Disturbance effects on food web structure

The difference between pre- and posthurricane ecosystem conditions were clearly evident in the food web structure of both streams. The decrease in resource variability, food web length, and trophic niche after the hurricanes was evidenced by low values of CR, NR, and TA (except in Prieta B). These results indicate that the diversity of resources was reduced (i.e., small short-term diet breadth), leading to a narrower isotopic variation among consumers (Figure 3). We also observed lower MNND and SDNND values after the hurricanes, which suggested that more species exploited similar resources, resulting higher trophic redundancy. Our findings support our hypothesis that the isotopic niche of the stream consumer community would contract due to the reduced breadth of basal resources. Previous studies demonstrated that disturbances, such as degradation of forest quality and cover (Kemp et al., 2023), increased sedimentation (Burdon et al., 2020), and changes in the hydrological regime (Ru et al., 2020), could significantly alter food web characteristics, including the compression of the trophic niche.

The higher NR value observed in the Prieta B study stream (Figure 4), which caused a wide trophic niche, can be attributed to high nitrogen concentration following the hurricanes and the larger channel width that allows for nutrient retention. Nitrate (NO_3–N) concentration increased in streams in the LEF after Hurricane Hugo over a period of 18 months (McDowell et al., 2013). The high NO_3–N may be incorporated into food resources, leading to changes in the δ^{15}N available in consumers and food webs (Parreira de Castro et al., 2016). Notably, despite a narrower δ^{13}C (CR) range, we observed an increase in the mean trophic diversity (CD) in both streams. This decreased range in δ^{13}C was primarily caused by the variation in the δ^{13}C values of Glossosomatidae. Unlike other metrics (e.g., TA or CR), CD is less susceptible to outliers (Layman et al., 2007). Therefore, our finding of higher CD suggests that the prehurricane food web was mainly based on allochthonous food resources, while consumers were able to expand their diet to include both autochthonous and allochthonous matter following the hurricanes, consequently reducing trophic overlap.

Ecosystems and food web resilience

The resilience of ecosystems is primarily influenced by local conditions such as the disturbance regime and pre- and postdisturbance conditions (e.g., dry or wet condition after a hurricane). Additionally, topography, forest characteristics (e.g., species composition, age), and storm attributes (e.g., amount of rain, wind velocity and direction, storm duration) play an important role in ecosystem resilience (Zimmerman et al., 2021). As a result, several ecosystem characteristics may return to prehurricane conditions in different periods of time. Initial assessments using Landsat imagery data demonstrated that vegetation greenness in the Luquillo mountains recovered significantly within 2 months after Hurricane María (Feng et al., 2020), whereas mangroves in Australia and Japan recovered approximately 1 year after the impact of Category 3 and 4 hurricanes (Peereman et al., 2022). Our findings suggest that recovery of stream ecosystems is a slow and complex process, and we are only beginning to understand postdisturbance responses through the lens of food web structure. After the massive canopy loss associated with the hurricanes, riparian trees began the slow process of producing new leaves and resprouting. However, 18 months after the hurricanes, canopy cover over the stream had only reached 71%. The limited canopy recovery observed at our research sites in comparison to the findings of Feng et al. (2020) might be due to Lidar measurements being primarily focused on lower canopy layers, which may not capture the slower recovery of taller canopy trees. A previous study conducted in two watersheds near our study area indicated that litterfall in the stream recovered more slowly than in upslope areas (Vogt et al., 1996). This slow recovery may be attributed to the fact that tree branches, which support many additional leaves, take even more time to grow, which delays canopy regeneration. Moreover, fine root damage affects the ability of trees to absorb the pulse of nutrients typically observed after a hurricane disturbance (Lodge et al., 1991), further contributing to delayed canopy recovery.

Consumer diets also reflect a relatively slow return to prehurricane conditions over many months. We observed that, although autochthonous-derived C was the resource in the immediate aftermath of the hurricanes, most taxa returned to reliance on allochthonous-derived C after 18 months. To our knowledge, this is the first study to show how the diet of stream consumers switched from an allochthonous to an autochthonous resource base in response to a major disturbance—to eventually return to a primarily allochthonous resource base as the forest recovered from hurricane damage.

Climate change, disturbance, and food webs

Future climate scenarios predict an increase in hurricane activity by the end of the 21st century, characterized by a significant increase in lifetime maximum intensity, precipitation rates, and incidence of very intense (Category 3 or higher) hurricanes (Emanuel, 2013; Knutson et al., 2013). Our study provides baseline information on how these extreme climatic phenomena might change the physical habitat, trophic interactions, and energy flow in tropical stream ecosystems. Moreover, as climate change progresses and disturbance frequency increases, this study, along with our previous findings on drought effects (Gutiérrez-Fonseca et al., 2020), suggests shifts in food web dynamics as consumers switch back and forth between allochthonous and autochthonous basal resources. This ecological dynamic has already been observed in temperate watersheds, where a severe flood event with a low probability of recurrence (1 in 50 to 1 in 500 years) caused a temporary shift in the stable isotope signatures of consumers toward more reliance on allochthonous resources (Larson et al., 2018).

The findings presented here illustrate how hurricane disturbances can dramatically shift stream trophic dynamics by altering the resource base. The predicted increases in the frequency of severe defoliation events (both hurricanes and droughts) as climate change progresses will require evaluation of the cumulative effects of repeated disturbances. It is essential that future studies consider the influence of time (i.e., since the last disturbance event) and the successional state of stream and riparian communities when assessing stream food web dynamics in the face of accelerating climate change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data (Gutiérrez-Fonseca et al., 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8364733.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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