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Hurricane-induced changes in mayfly assemblage structure, production and emergence in a tropical island stream

Cambios inducidos por los huracanes en la estructura, producción, y emergencia del ensamblaje de Ephemeroptera de una quebrada de isla tropical

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Abstract

1. Hurricanes are major disturbances with important consequences to stream ecosystems as they create major floods and remove riparian vegetation. Understanding their impacts is a priority, as hurricane intensity is expected to increase due to global climate change.
2. Mayfly assemblages in streams fill a diversity of ecological roles and functions. They are important consumers of algae by scraping benthic biofilms and detritivores associated with fine particles and leaf litter. Other taxa are filterers and even predators. Mayflies are also important prey items in aquatic and terrestrial food webs.
3. Here, we assessed the effects of two consecutive hurricanes that impacted Puerto Rico in 2017 to understand how hurricane-induced changes in the environment alter mayfly composition, secondary production and emergence.
4. The study was conducted in the Luquillo Experimental Forest, Puerto Rico. Mayflies were sampled as nymphs and emerging adults for 6 months before and 17 months after hurricanes Irma and María hit the island in September 2017. Leaf litter inputs, canopy cover and chlorophyll *a* concentrations were monitored along with mayflies.

† Deceased.

5. Mayfly assemblages were dominated by two genera of Leptophlebiidae before the hurricane, *Neohagenulus (two species: N. julio* Traver, 1938, *N. luteolus* Traver, 1938) and *Borinquena (one species: B. carmencita* Traver, 1938). Both genera decreased in density after the hurricanes and were replaced with the Baetidae *Cloeodes maculipes* Traver, 1938 as the dominant taxon. This pattern was observed in both nymph and emerging adult densities.
6. The secondary production of Leptophlebiidae species was highest before hurricane disturbance, with the Baetidae *C. maculipes* showing the opposite pattern. *Neohagenulus* had an annual production of 445 mg m^{-2} $year^{-1}$, *C. maculipes* of 153 mg m^{-2} $year^{-1}$ and *B. carmencita* of 68 mg m^{-2} $year^{-1}$.
7. Overall, the mayfly assemblages in our studied stream are vulnerable to hurricane disturbances. Expected increases in hurricane impacts might result in assemblage shifts that could change assemblage composition and alter energy flows within the ecosystem.

KEYWORDS
assemblage composition, Ephemeroptera, hurricane disturbance, secondary production, tropical streams

INTRODUCTION

Hurricanes are major climatic events that have devastating and long-lasting effects on natural ecosystems, altering community structure and food webs (Patrick et al., 2022). Heavy precipitation during a storm creates major floods in streams that, through flood disturbance, lead to displacement and increased mortality of aquatic organisms (Resh et al., 1988). Hurricane floods modify stream habitat availability by altering channel geomorphology, exporting large amounts of organic matter and creating debris dams (Wohl et al., 2019). Although flood disturbance has large negative impacts on aquatic populations (Resh et al., 1988), many species are resistant or resilient to them. For example, freshwater decapods in Puerto Rico were not severely affected by hurricane floods (Covich et al., 2006) and aquatic insects with short life cycles are expected to recover quickly from flood disturbances (Lytle, 2002).

A lasting disturbance associated with hurricanes is the damage they inflict on riparian vegetation. Hurricane winds remove leaves and small branches, defoliating riparian vegetation and creating a single large pulse of detritus (Walker et al., 1991). Most of that material is either exported downstream or temporarily trapped in debris dams (Wohl et al., 2019). Defoliation increases the amount of solar radiation reaching the stream (Fernández & Fetcher, 1991). Thus, small headwater streams that are often detritus-based ecosystems switch to alga-based ecosystems for several years after hurricane disturbance (Gutiérrez-Fonseca et al., 2024), as riparian vegetation recovery can take up to 6 years (Zimmerman et al., 2021). This change in basal resources might change aquatic insect assemblage composition, favouring herbivores over detritivores as observed in response to watershed deforestation (Benstead & Pringle, 2004). However, there is still a lack of information on how aquatic insect assemblages respond to hurricane defoliation of riparian forests (Strickland et al., 2024).

Understanding hurricane impacts on ecosystems is critical, given climate change projections. Major hurricanes impact terrestrial ecosystems annually, with some geographic locations experiencing more storms than others. However, climate change models predict increases in storm intensity, and major hurricanes are expected to become more frequent (Knutson et al., 2020; Walsh et al., 2016). Historically, major hurricane impacts on Caribbean islands are relatively infrequent. Puerto Rico, for example, was expected to experience them with a recurrence interval of 50–60 years up to the 1990s (Scatena & Larsen, 1991). This frequency has increased over the past decades. The last four major hurricanes affecting Puerto Rico were Hugo in 1989, Georges in 1998 and, more recently, Irma and María in 2017, four major hurricane impacts in only 28 years.

Mayflies (Ephemeroptera) are a dominant group of aquatic insects that play multiple roles in stream ecosystems, mostly as primary consumers (Domínguez et al., 2006). Most species of mayflies have nymphs that can be considered scrapers/grazers, which feed on algae over hard surfaces in the stream bottom, or collector gatherers, which consume fine particles by collecting them from the bottom (Ramírez & Gutiérrez-Fonseca, 2014). In Puerto Rico, where this study took place, mayflies form part of both feeding groups (Gutiérrez-Fonseca et al., 2013). Mayfly adults are short-lived, reproducing and dying soon after emerging from the aquatic environment. Even so, they are an important energy source for both aquatic and terrestrial food webs (Rosas et al., 2020). For example, riparian consumers (e.g. spiders and lizards) are well adapted to catching and consuming emerging mayflies, thus linking aquatic and terrestrial ecosystems (Kelly et al., 2015). Therefore, mayflies represent an ideal group for studying the effects of hurricane disturbance on stream ecosystems, specifically their effects on habitats and the availability of food resources, as their assemblages are composed of species that rely on detritus and others that consume algae.

Here, we assessed how hurricane impacts change environmental conditions in tropical streams and how those changes alter mayfly assemblages in a headwater stream in Puerto Rico. Our objectives were to (1) describe the effect of hurricane disturbance on mayfly assemblages, secondary production and emergence; (2) determine potential environmental drivers behind changes in mayfly assemblages; and (3) assess the relation between assemblages and time since hurricane impact using available data. We predict that changes in mayfly assemblages would be associated with hurricane defoliation of riparian forests, increases in solar radiation and algal biomass. As the studied rainforest stream floods frequently in response to heavy rains, we did not expect major changes associated with hurricane floods.

MATERIALS AND METHODS

Study site

Our study stream, Quebrada Prieta, is in the Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico (18°19′ N, 65°45′ W; Figure 1). The LEF is an aseasonal forest where heavy precipitation might occur at any point during the year (Gutiérrez-Fonseca et al., 2020). The mean annual precipitation (1975–2016) is 3676 mm at 350 m above sea level, ranging from 1405 mm year^{-1} in 1994 to 5567 mm year^{-1} in 2010 (Gutiérrez-Fonseca et al., 2020). The diurnal and mean annual air temperatures above the canopy are 21–25°C (McDowell et al., 2012).

Quebrada Prieta is a second-order stream within the Espíritu Santo watershed. Prieta has a steep channel composed of a series of pools separated by drops or steps and a few small riffles. The dominant substrates are boulders and large cobbles with gravel, sand and silt deposited in pools. We selected pools as our focal study habitat along two tributaries of Prieta (i.e. arms A and B) draining primary forests (∼400 m asl). Riparian vegetation is dominated by tabonuco trees (*Dacryodes excelsa* Vahl, Burseraceae) and sierra palms (*Prestoea acuminata* (Willd.), Arecaceae). Aquatic insect assemblages are dominated by the orders Ephemeroptera, Odonata, Trichoptera, Lepidoptera, Coleoptera and Diptera (Gutiérrez-Fonseca et al., 2020; Ramírez & Hernández-Cruz, 2004). Eight species of decapods occur in our study stream, but two omnivorous ones are dominant in density and biomass: *Atya lanipes* Holthuis, 1963 (Atyidae) and *Xiphocaris elongata* Guérin-Méneville, 1855 (Xiphocarididae; Cross et al., 2008). The green stream goby, *Sicydium* spp. (Gobiidae; there are several possible species), is the only fish taxon present in Prieta.

A previous study in Quebrada Prieta by Pescador et al. (1993) reported mayfly assemblages composed of three genera and at least

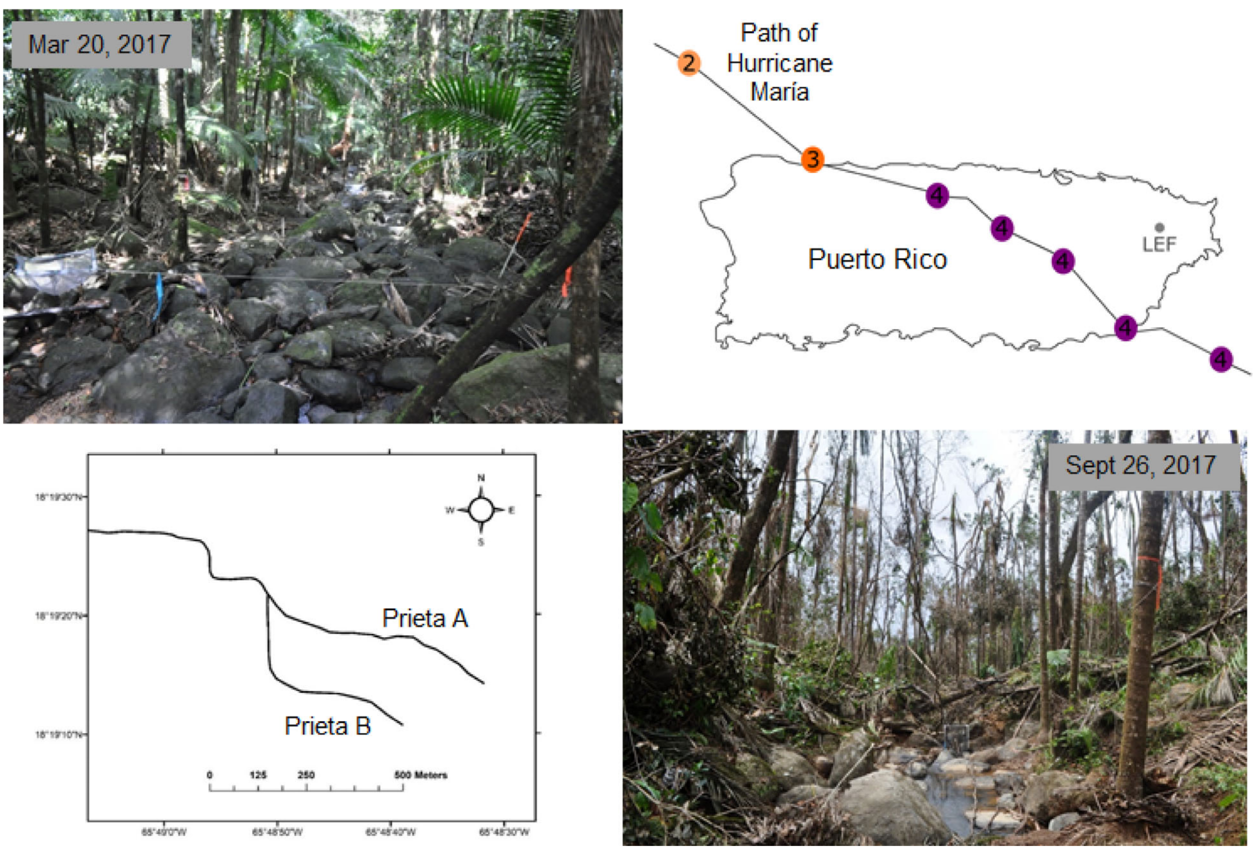

FIGURE 1 Quebrada Prieta, arms A and B, located in the Luquillo Experimental Forest (LEF) in Puerto Rico, was affected by hurricanes Irma and María in September 2017. The path of María is shown with numbers indicating hurricane intensity in the Saffir–Simpson scale. Photos contrast the stream before and after the hurricane. Photos by P. E. Gutiérrez-Fonseca.

four species. Leptophlebiidae had two species of *Neohagenulus*, *Neohagenulus julio* Traver, 1938 and *Neohagenulus luteolus* Traver, 1938, and one species of *Borinquena*, *Borinquena carmencita* Traver, 1938. In Baetidae, only the genus *Cloeodes* was found, represented by only one species, *Cloeodes maculipes* Traver, 1938.

Hurricane history at the LEF

Major hurricanes deposit large amounts of precipitation over short periods, creating floods and pulses of sediment and particles. However, the headwater streams in the LEF, like our study stream, have small watersheds and are naturally flashy. Thus, hurricane-size floods are common disturbances. In contrast, the impact of hurricane winds creates new environmental conditions in and around streams by removing the forest canopy (Leitold et al., 2022). Canopy defoliation creates a major pulse of debris (Liu et al., 2018), which have short-term impacts, as streams process or export that material within a few months (Covich et al., 1991). This initial pulse of leaf litter is followed by a post-hurricane period with minimal litter inputs that can last several years (Zimmerman et al., 2021). A more open canopy increases the amount of solar radiation reaching the stream. Stream channels that are normally heavily shaded (up to 95% canopy cover) become sunny, and their water temperature increases.

In past decades, the LEF has experienced four major hurricane impacts. Hurricane Hugo impacted the LEF in 1989 after a long period without major storm disturbances (Scatena & Larsen, 1991). Hugo reduced the canopy cover significantly, depositing major amounts of debris on the forest floor. Hurricane Georges impacted the LEF 9 years after Hugo, in 1998. Similarly, Georges reopened the canopy cover over streams. In September 2017, the LEF was struck by two major hurricanes in close succession. Hurricane Irma had minor impacts on the forest as it passed north of Puerto Rico. Hurricane María had a path closer to the LEF with major impacts on the forest and streams (Figure 1). Here, we mainly refer to María, but impacts are the combined effects of both Irma and María.

Environmental variables

Stream discharge is automatically monitored at various locations in Prieta; we are presenting data for the monitoring station located downstream from the confluence of arms A and B, as it represents the main stem of Prieta. Discharge is obtained by measuring the water level with a pressure transducer (Onset Computers, U20L-01) every 15 min and applying a gauge-discharge equation developed for the monitoring location. Canopy cover is measured with a spherical densiometer at 12 points over the 100-m reach of arms A and B. Measures were taken bimonthly before the 2017 hurricanes and monthly after the hurricanes. We are presenting canopy cover as monthly averages for both arms.

Algal chlorophyll *a* was measured by collecting monthly samples in six pools in each arm of Prieta by collecting six subsamples per pool using a modified Loeb sampler (Loeb, 1981). Subsamples were mixed, and chlorophyll was analysed using a fluorometer following extraction with ethanol, according to standard methods (APHA, 2005). Ten leaf litter baskets hanging over the channel in each of arms A and B (20 baskets total) were used to monitor the vertical inputs of leaf litter. Baskets were emptied every 2 weeks and were oven-dried at 70°C for 48 h; data are presented as grams per square metre per day. Benthic organic matter (BOM) was measured from mayfly nymph samples (see details below). BOM was dried at 70°C for 48 h and ashed at 500°C to present data as grams of ash-free dry mass (AFDM) per square metre.

Mayfly assemblages

Mayfly nymphs were sampled monthly from January 2017 to December 2018. Samples were collected in six pools along a 100-m reach in arms A and B using a corer sampler (0.0314 m^2). The corer was pushed into the substrate to a depth of 10 cm or until reaching bedrock. The benthic substrate was placed into a bucket and stirred before pouring it through a 250-μm sieve. The material retained in the sieve was placed in bags and preserved with formaldehyde (~5% solution after diluting with stream water) and later transferred to ethanol (80%).

Mayflies were separated from debris and identified using keys in Peters (1971) and Salles et al. (2018). Nymphs of the two species of *Neohagenulus* are difficult to separate and are reported at the genus level. The individual length was measured to the nearest 0.5 mm, and biomass was obtained by applying the length–mass regressions from Benke et al. (1999). Although regressions in Benke et al. (1999) are biased towards organisms from temperate regions, we currently lack these relations for most tropical taxa. Mayfly density and biomass were expressed as number of individuals per square metre and milligrams of AFDM per square metre, respectively. Secondary production was estimated by applying the instantaneous growth method (Benke & Huryn, 2017) using growth rates from Rosas et al. (2020). Mayfly production was expressed as milligrams of AFDM per square metre per month.

Adult emergence was sampled monthly from February 2017 to December 2018 using emergence traps placed over pools. Traps are pyramid-shaped with a sampling area of 0.50 m^2 and were deployed monthly for four consecutive days, allowing for the collection of subimagos and imagos. After that period, specimens remaining in the net were removed using an aspirator and added to the sample container. Samples were preserved in 80% ethanol, and specimens were identified to the species level using Traver (1938) and Peters (1971). Individual length was measured to the nearest 0.5 mm, and biomass was obtained by applying the length–mass regressions from Sabo et al. (2002). The density of emerging adults was expressed as individuals per square metre per day.

Comparisons with previous hurricane impacts were possible using mayfly emergence data from previous studies. Data for post-hurricane Hugo were available from Pescador et al. (1993). They collected mayfly emergence during 1990, starting 6 months after Hurricane Hugo hit Puerto Rico in 1989. In a second study, the lead author collected data for post-hurricane Georges in 2003, 5 years after Georges hit Puerto Rico in 1998 (Ramírez, unpublished data). Mayflies were collected in arm B monthly for 1 year. Traps were sampled continuously, and sampling containers were cleaned once a month. Considering that different data sets used different sampling efforts, we compared only the per cent contribution of each mayfly species to the total assemblage.

Statistical analysis

Pre- versus post-hurricane comparisons of nymph and adult densities and biomass were assessed using a *t*-test or Wilcoxon signed-rank test depending on whether the data were normally distributed or not using the Shapiro–Wilk test. We used regression analysis to relate changes in environmental variables (i.e. canopy, leaf litter inputs) with mayfly density and biomass. Analyses were run in R version 4.1.3 (R Core Team, 2022).

RESULTS

Hurricane impacts

Quebrada Prieta has a flashy hydrograph that reflects its aseasonal environment (Figure 2a,b). Stream hydrographs suggest that floods produced by heavy precipitation during Hurricane Irma were within the range of those observed during other times of the year, as either average daily discharge (Figure 2a) or maximum daily discharge (Figure 2b). During Hurricane María, our gauge was briefly damaged by debris falling from riparian trees, and our measure of peak discharge may be an underestimation. Hurricane winds defoliated most

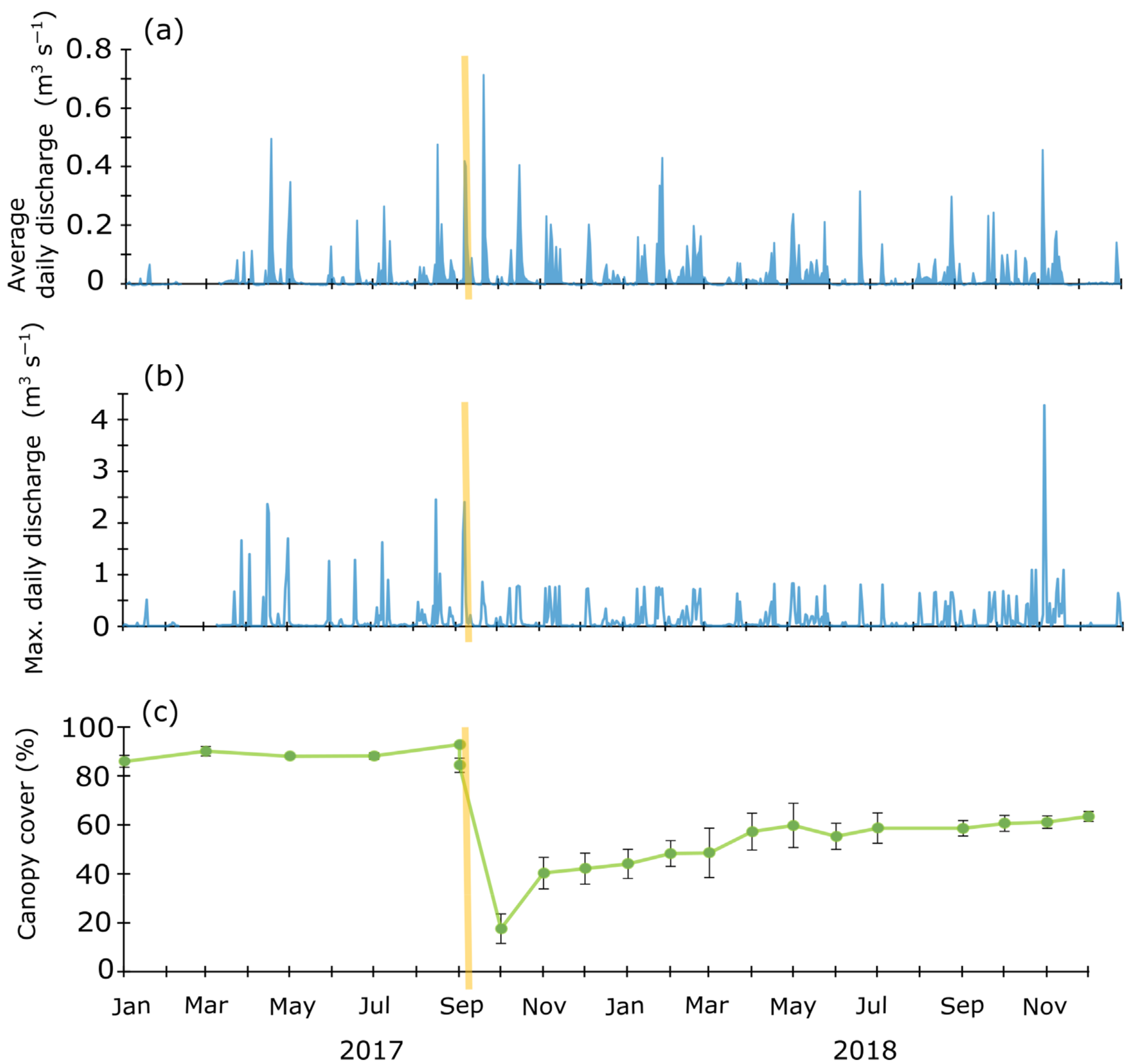

FIGURE 2 Daily average (a) and maximum (b) stream discharges and canopy cover (c) over Quebrada Prieta for the duration of the study, from January 2017 to December 2018. Points in panel (c) are monthly averages and standard error. The vertical yellow line indicates the impact of Hurricane María.

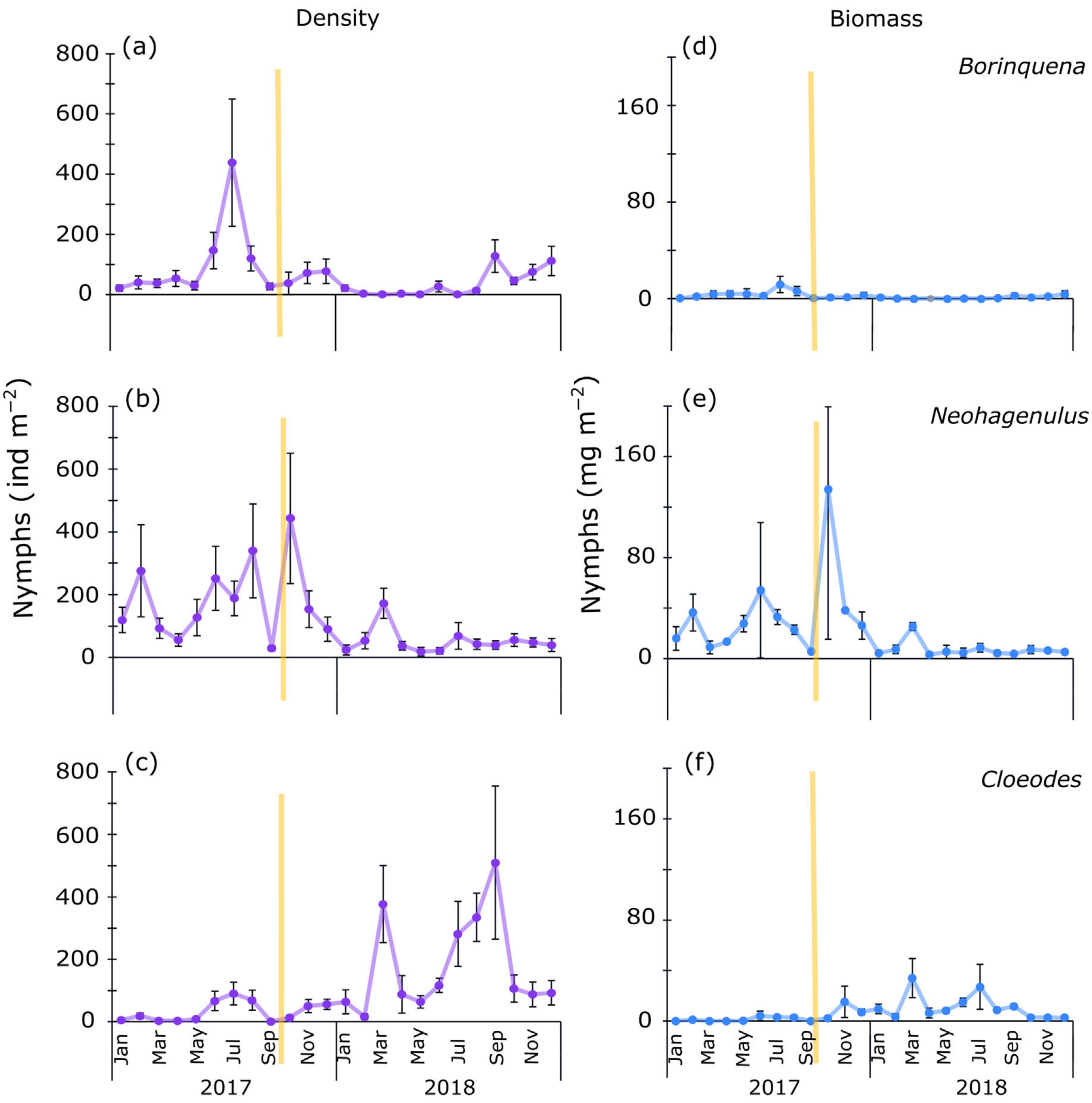

FIGURE 3 Mayfly nymph density and biomass at Quebrada Prieta for *Borinquena carmencita* (a, d), *Neohagenulus* spp. (b, e) and *Cloeodes maculipes* (c, f). The vertical yellow line indicates the impact of Hurricane María. Points are monthly averages and standard errors.

of the riparian forest, and canopy cover went from ~85% before the hurricanes to about 20% after the hurricanes (Figure 2c). Recovery was evident, and canopy cover reached ~60% by the end of our study (Figure 2c).

Assemblages and temporal trends

We found two families and four species of mayflies in Quebrada Prieta (Figure 3). In the family Leptophlebiidae, *N. julio* was the most frequently found species, with a few individuals of *N. luteolus* present. Separating small individuals of these two taxa as nymphs is difficult, we refer to the group as *Neohagenulus*, and it was the most abundant taxon (monthly nymph density ranged from 18 to 443 ind m^{-2}), followed by *B. carmencita* (nymph density: 0–437 ind m^{-2}). In Baetidae, the only species present was *C. maculipes* with nymph densities ranging from 0 to 510 ind m^{-2} (Table 1).

Leptophlebiidae were abundant before the hurricane and decreased considerably after (Table 2). Nymphs of *B. carmencita* had a peak in density and biomass during July 2017 and then remained at low values for the remainder of the study period (Figure 3a,d). *Neohagenulus* density and biomass fluctuated before the hurricane and presented a peak right after the hurricane (October 2017), and then values remained low for the entire post-hurricane study period (Figure 3b,e). The Baetidae *C. maculipes* had the opposite pattern. Density and biomass were low before the hurricane and peaked a few months after, returning to low values in the last 3 months of our study period (Figure 3c,f). Means and ranges for density and biomass are presented in Table 1.

TABLE 1 Density, biomass, secondary production and biomass turnover (production/biomass [P/B]) for each major taxon in Quebrada Prieta.

	Density (individuals m^{-2})		Biomass (mg m^{-2})		Production	
Nymphs	**Mean**	**Range**	**Mean**	**Range**	**(mg m^{-2} $time^{-1}$)[a]**	**P/B**
Borinquena						
Pre	101.15	21.23–437.93	3.78	0.40–11.10	11.19	
Post	40.69	0.00–111.47	1.02	0.00–3.69	3.37	
Annual	63.37		2.05		68.50	33.30
Neohagenulus						
Pre	164.55	29.19–339.73	22.72	5.31–52.15	48.71	
Post	87.23	18.58–443.25	18.31	3.07–132.53	33.33	
Annual	116.23		19.96		444.82	22.28
Cloeodes						
Pre	29.20	0.00–90.24	1.17	0.00–3.74	2.97	
Post	150.40	13.27–509.60	9.20	1.82–29.40	18.83	
Annual	104.95		6.19		153.16	24.74

	Density (ind m^{-2} day^{-1})		Biomass (mg m^{-2} day^{-1})	
Emergence	**Mean**	**Range**	**Mean**	**Range**
Borinquena				
Pre	0.53	0.00–1.63	0.35	0.00–0.79
Post	0.50	0.00–1.98	0.29	0.00–1.16
Annual	0.51		0.31	
Neohagenulus				
Pre	2.93	0.61–6.78	2.41	0.45–5.39
Post	1.51	0.51–6.29	1.09	0.27–4.40
Annual	2.02		1.58	
Cloeodes				
Pre	0.52	0.00–1.14	0.25	0.00–0.55
Post	2.25	0.64–5.19	1.13	0.37–2.69
Annual	1.62		0.81	

Note: Values for pre- and post-hurricane are monthly means; annual values are per year.
[a]Pre- and post-hurricane production is presented as monthly (mg m^{-2} $month^{-1}$); annual production is presented as per year (mg m^{-2} $year^{-1}$).

TABLE 2 Before–after hurricane effects on mayfly nymphs and adults in Quebrada Prieta.

	Density		Biomass		Production	
	W	***p*-Value**	***W***	***p*-Value**	***W***	***p*-Value**
Nymphs						
Borinquena	41.50	ns	24.00	0.01	15.00	0.01
Neohagenulus	30.50	0.03	31.00	0.03	24.00	0.03
Cloeodes	113.00	0.01	124.00	<0.01	105.00	<0.01
Emergence						
Borinquena	46.00	ns	47.00	ns		
*Neohagenulus**	26.00	0.05	25.00	0.04		
Cloeodes	109.00	<0.01	108.00	<0.01		

Note: See Figure 5 for direction of changes. All effects were evaluated with Wilcoxon tests (*W*), except for *Neohagenulus*, which was evaluated with *t*-tests (indicated by *). ns = not significant.

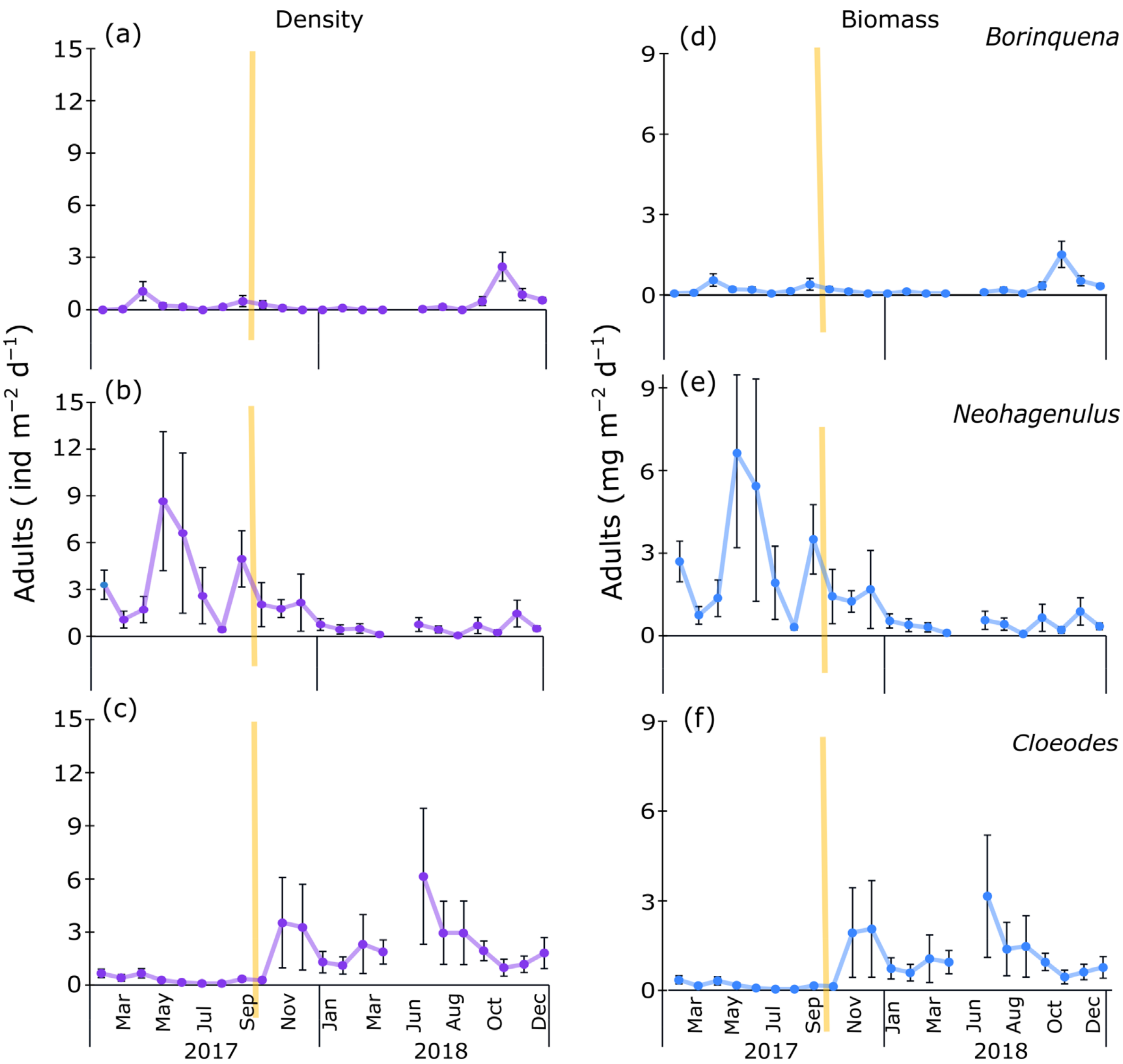

FIGURE 4 Mayfly adult emergence density and biomass at Quebrada Prieta for *Borinquena carmencita* (a, d), *Neohagenulus* spp. (b, e) and *Cloeodes maculipes* (c, f). The vertical yellow line indicates the impact of Hurricane María. Points are monthly averages and standard errors.

Adult emergence followed the same general temporal patterns described for nymphs, except that *B. carmencita* was always present at low densities and biomass (Figure 4a,d). *Neohagenulus* had a peak in emergence during May and June and then in December 2017 (Figure 4b,e). *Cloeodes maculipes* emergence followed a pattern similar to that of the nymphs, with low values during pre-hurricane months and then increasing during post-hurricane, with a return to low values during the last months of our sampling period (Figure 4c,f). Means and ranges for density and biomass are presented in Table 1.

Comparing pre- and post-hurricane periods, we found the same patterns described for monthly samples (Figure 5, Table 2). *Neohagenulus* had significantly higher density, biomass, production and emergence before the hurricane. In contrast, *B. carmencita* showed higher variability and only differences in biomass and production were significantly higher during the pre-hurricane period (Table 2). *Cloeodes maculipes* followed the opposite pattern. It was significantly more abundant after the hurricane (Figure 5; Table 2). In the case of *C. maculipes*, pre versus post differences were large, with values after the storm up to two to three times higher than pre-hurricane (Figure 5).

Neohagenulus was the most productive taxon during all periods, and the highest production was during the pre-hurricane period (average monthly production: 48.71 mg m^{-2} month^{-1}; Table 1). The lowest monthly production was for *C. maculipes* during the pre-hurricane period (average monthly production: 2.97 mg m^{-2} month^{-1}; Table 1). Calculating production based on the calendar year resulted in annual production values that ranged from 444.82 mg m^{-2} year^{-1} for *Neohagenulus* and 68.50 mg m^{-2} year^{-1} for *B. carmencita*, with *C. maculipes* falling in the middle with 153.16 mg m^{-2} year^{-1} (Table 1). Corresponding production/biomass (P/B) ratios based on annual production ranged from 22.28 (*Neohagenulus*) to 33.30 (*B. carmencita*) and 24.74 for *C. maculipes* (Table 1).

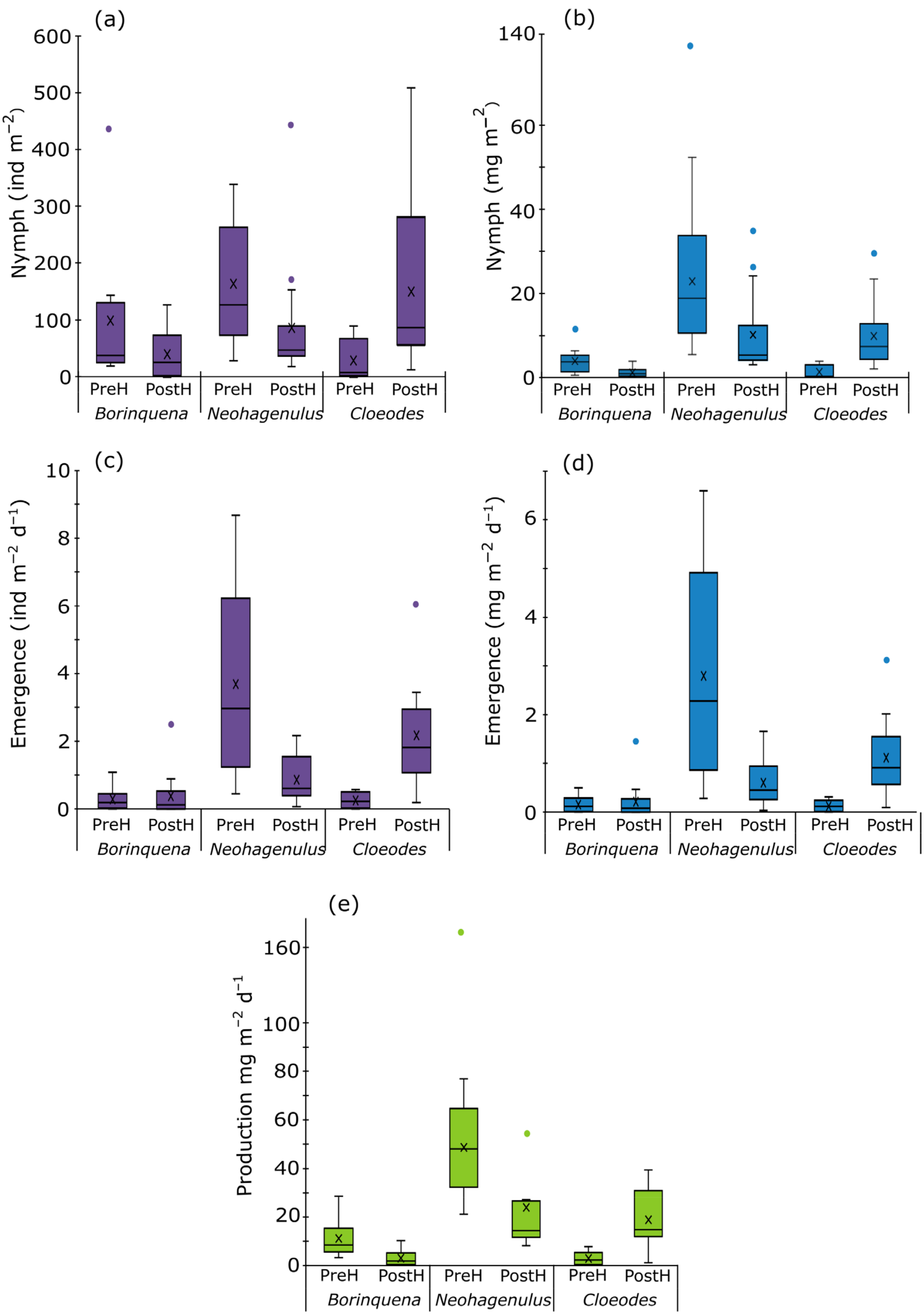

FIGURE 5 Hurricane impacts on mayfly assemblages in Quebrada Prieta. (a) Nymph density, (b) nymph biomass, (c) adult emergence density, (d) adult emergence biomass and (e) secondary production. PostH, post-hurricane; PreH, pre-hurricane. Points indicate outliers.

Only two environmental variables were significantly related to nymph or adult density or biomass. Leaf litter inputs were positively related to *Neohagenulus* and *B. carmencita* nymph density and biomass (Table 3). Leaf litter was negatively related to *C. maculipes* adult emergence (Table 3). Similarly, the ratio between chlorophyll *a* concentration and leaf litter inputs was

TABLE 3 Regression analysis between Ephemeroptera taxa and environmental variables.

	Leaf litter	Chlorophyll/leaf litter	Canopy cover
Borinquena			
Nymph density	0.61	0.59	ns
Nymph biomass	0.69	0.71	ns
Adult density	ns	ns	ns
Adult biomass	ns	ns	ns
Secondary production	0.21	0.17	ns
Neohagenulus			
Nymph density	0.61	0.59	ns
Nymph biomass	0.69	0.71	ns
Adult density	ns	ns	ns
Adult biomass	ns	ns	ns
Secondary production	0.37	0.43	ns
Cloeodes			
Nymph density	ns	ns	ns
Nymph biomass	ns	ns	−0.30
Adult density	−0.17	ns	−0.46
Adult biomass	ns	ns	−0.46
Secondary production	−0.21	−0.15	−0.33

Note: Only significant relations at $p < 0.05$ are presented; values are regression coefficients. ns = not significant.

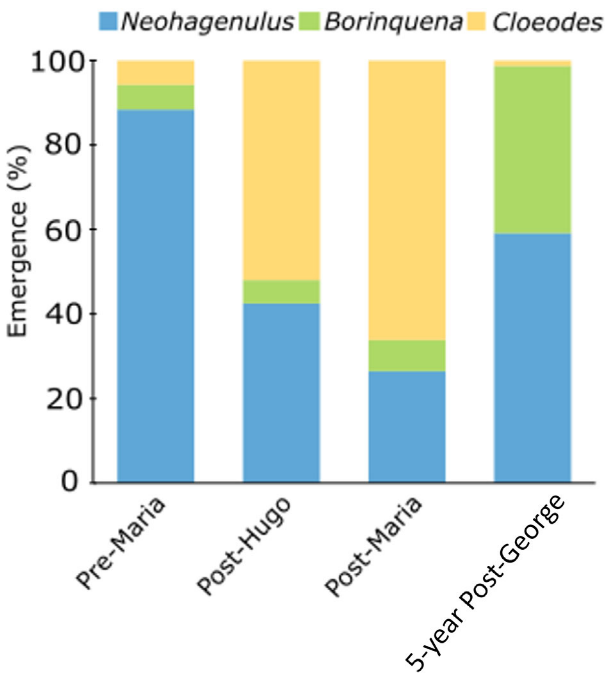

FIGURE 6 Mayfly adult emergence composition in Quebrada Prieta in relation to recent hurricane disturbances: Hugo in 1989, Georges in 1998 and María in 2017. The vertical axis shows the proportion of individuals per genus during each period.

significantly related to *Neohagenulus* and *B. carmencita* nymph density and biomass, but not to their adults or nymphs and adults of *C. maculipes* (Table 3). *Cloeodes maculipes* nymph biomass and adult density and biomass were all negatively related to canopy cover (Table 3).

Past hurricanes and emergence

Our samples from pre-hurricane María represent stream conditions from a period of ~20 years without a major hurricane impacting Puerto Rico. Samples collected post-Hugo and those from post-María represent periods immediately after a major hurricane impact. Our 5-year post-Georges data are representative of post-recovery of hurricane disturbance (Figure 6).

Leptophlebiidae dominated mayfly assemblages during periods without hurricane disturbance (i.e. pre-María and the 5-year post-Georges), with a larger number of *B. carmencita* in the recovery period post-Georges (Figure 6). In contrast, both post-hurricane periods (i.e. post-María and post-Hugo) have dominance by *C. maculipes* and reduced proportions of *Neohagenulus*, with *B. carmencita* contributing a small fraction (Figure 6).

DISCUSSION

Our study found low mayfly taxon richness in the studied stream similar to that previously reported for our area (Pescador et al., 1993). Puerto Rico is an oceanic island with low species richness relative to that of continental areas, including few aquatic insect taxa (Gutiérrez-Fonseca et al., 2013). The families recorded, Leptophlebiidae and

Baetidae, are species-rich and abundant in streams globally (Barber-James et al., 2007). We expected these two families to display similar responses to hurricane disturbance. Our findings support the expected change in assemblage abundance, biomass and secondary production following the hurricane, but the contrasting responses by different taxa were unexpected.

The most significant changes in mayfly assemblages are likely associated with shifts in habitat and energy resources. Leptophlebiidae were predominantly found in microhabitats with leaf litter and at the underside of rocks, whereas Baetidae were common on hard substrates lacking detritus (AR's and JEG's personal observations). Hurricanes significantly reduce leaf litter inputs after an initial pulse during the storm and increase solar radiation, increasing algal productivity (Wohl et al., 2019). This pulse of leaf litter is short-lived, as most are quickly exported downstream during floods, with the remaining portion rapidly consumed or decomposed. Leptophlebiidae appears to respond to leaf litter availability, as they had a short-lived peak in density, biomass and emergence in the months following the hurricane and then decreased to low values (e.g. Figure 2). In contrast, Baetidae responses were more closely associated with the increase in solar radiation, with nymphs peaking 6 months after the hurricane, but adult emergence began even early. Changes in energy resources further explain differences in the response of these mayflies to hurricane disturbance. Stable isotope analysis indicates that both mayfly families continued relying on allochthonous carbon as their primary energy source after the hurricane (Gutiérrez-Fonseca et al., 2024). Meanwhile, freshwater shrimps, the dominant consumer in the studied stream, shifted their diets towards algae (Gutiérrez-Fonseca et al., 2024), potentially intensifying competition and predation pressure on mayflies.

The impact of hurricanes Irma and María profoundly changed terrestrial and aquatic ecosystems in our study area. The change in resource availability that we observed (leaf litter vs. epilithic algae) and changed mayfly assemblages are similar to findings reported for terrestrial insect assemblages. In seasonal tropical dry forests, changes in the relative abundance of different groups of consumers occurred after hurricane defoliation of forest canopy. Several taxa of herbivorous insects and one of predatory beetles increased in density after hurricane disturbance in Mexico (Novais et al., 2018). Canopy insects in Puerto Rico have complex responses to hurricane disturbance that result from the interaction between the plant host and the environmental conditions (Schowalter & Ganio, 1999). In our study, effects were indirect, via changes in leaf litter availability and solar radiation over the stream channel.

Hurricanes impact stream ecosystems also via heavy precipitation and flooding. In montane areas, like our study region, hurricane precipitation is often intense and results in major floods. However, our stream discharge monitoring highlights that major floods occur frequently in these headwater streams and are not exclusively associated with hurricanes (see Figure 2a). North-eastern Puerto Rico is the wettest part of the island, with trade winds carrying moisture from the Atlantic Ocean and tropical storms affecting the island during the hurricane season. Mayflies in Prieta appear well adapted to flooding, and although the hurricane flood potentially impacted them, those impacts were not evident during our study. Although our monthly sampling might have missed some peaks in nymph density or adult emergence, the overall pattern was clear.

Secondary production of both families was within or above the range reported by previous studies in Luquillo for streams under closed canopy. For instance, the annual production of *N. julio* ranged from 425 to 556 mg m^{-2} year^{-1} (Rosas et al., 2020). In contrast, the same authors recorded lower production of *C. maculipes* (41–58 mg m^{-2} year^{-1}) compared with our results, which are most likely a result of hurricane effects. This is the first time that secondary production of *B. carmencita* was measured (68 mg m^{-2} year^{-1}). Secondary production of tropical aquatic insects tends to be lower than reports from temperate streams. One exception is Leptophlebiidae mayflies that have similar production in both regions (Rosas et al., 2020). Turnover ratios (P/B) are good indicators of biomass turnover over a time period (Benke, 1984). In our study area, both *Neohagenulus* and *Cloeodes* can be expected to have ratios around 20, indicating that populations replace their biomass 20 times per year (Rosas et al., 2020). We measured similar ratios in our annual estimates, ranging between 22 for *Neohagenulus* and 25 for *Cloeodes*, respectively, and even higher for *Borinquena* (P/B = 33). The responses to hurricane disturbance were similar in terms of production and densities. Both Leptophlebiidae genera decreased their productivity, whereas that of *Cloeodes* increased. The higher variability observed in the response of *Neohagenulus* could be associated with the short-lived pulse of leaf litter following the hurricane.

Disturbances that remove riparian vegetation and increase solar radiation over streams, like hurricanes, often increase the productivity of grazers to the detriment of detritivorous macroinvertebrates. For example, selective logging that removed tree cover in the margins of an Appalachian stream increased Baetidae secondary production by up to 17 times that of a reference forest stream (Wallace & Gurtz, 1986). Through gut content analysis, the same study found the increase in productivity to be associated with higher diatom availability. Similarly, in tropical streams in Madagascar, deforestation enhances the biomass of a few collector-gatherer taxa that can take advantage of enhanced algal resources, whereas most forest-associated taxa are absent from streams that lack leaf litter resources (Benstead & Pringle, 2004). Those findings agree with ours, indicating that changes in riparian vegetation are important drivers of assemblage composition and productivity.

Long-term hurricane impacts

The mayfly assemblages in our study stream were shown to be vulnerable to hurricane disturbances, via their effects on riparian forests. The observed changes in mayfly assemblages were significant and lasted for over a year following the hurricane. Species in our study stream are multivoltine and have relatively short life cycles (Rosas et al., 2020); thus, hurricane disturbance impacted several generations. It can be expected that populations will return to pre-disturbance conditions once riparian vegetation recovers from defoliation and re-establish leaf litter inputs into the stream. However, forest recovery is slow and takes more than 5 years (Brokaw et al., 2012; Zimmerman et al., 2021). As mayflies are among the most abundant aquatic insects in the LEF (Ramírez & Hernández-Cruz, 2004) and in streams in general (Domínguez et al., 2006), we suggest that changes in their abundance could cascade into other compartments of the ecosystem, including aquatic (e.g. dragonflies and shrimps) and terrestrial predators (e.g. spiders and anoles lizards).

Projections of an increase in hurricane frequency and intensity, with more intense storms affecting the Caribbean islands and coastal regions of North America expected in the coming years (Knutson et al., 2020; Walsh et al., 2016), may result in long-term changes in insect assemblages. An increase in hurricane disturbance could delay riparian recovery and extend the duration of hurricane impacts on aquatic populations. Based on mayfly responses, increases in hurricane disturbance frequency could result in a shift in community composition and a potentially change in the energy flow. Similar changes in insect assemblages have been reported for other hurricane impacted aquatic (Strickland et al., 2024) and terrestrial ecosystems (Novais et al., 2018), highlighting the importance of understanding how recurrent disturbances might result in new ecosystem dynamics.

AUTHOR CONTRIBUTIONS

Alonso Ramírez: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis; project administration; data curation; supervision; visualization. **Ana M. Meza-Salazar:** Investigation; writing – review and editing; writing – original draft; formal analysis. **Jesús E. Gómez:** Writing – original draft; investigation; methodology; writing – review and editing; data curation. **Pablo E. Gutiérrez-Fonseca:** Conceptualization; writing – original draft; methodology; writing – review and editing; formal analysis; investigation; data curation. **José Sánchez-Ruiz:** Writing – original draft; writing – review and editing; formal analysis; investigation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the EDI Data Portal at https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.227.2.

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