

Long-term climate and hydrologic regimes shape stream invertebrate community responses to a hurricane disturbance

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Abstract

1. Disturbances can produce a spectrum of short- and long-term ecological consequences that depend on complex interactions of the characteristics of the event, antecedent environmental conditions, and the intrinsic properties of resistance and resilience of the affected biological system.
2. We used Hurricane Harvey's impact on coastal rivers of Texas to examine the roles of storm-related changes in hydrology and long-term precipitation regime on the response of stream invertebrate communities to hurricane disturbance.
3. We detected declines in richness, diversity and total abundance following the storm, but responses were strongly tied to direct and indirect effects of long-term aridity and short-term changes in stream hydrology. The amount of rainfall a site received drove both flood duration and flood magnitude across sites, but lower annual rainfall amounts (i.e. aridity) increased flood magnitude and decreased flood duration. Across all sites, flood duration was positively related to the time it took for invertebrate communities to return to a long-term baseline and flood magnitude drove larger invertebrate community responses (i.e. changes in diversity and total abundance). However, invertebrate response per unit flood magnitude was lower in sub-humid sites, potentially because of differences in refuge availability or ecological-evolutionary interactions. Interestingly, sub-humid streams had temporary large peaks in invertebrate total abundance and diversity following recovery period that may be indicative of the larger organic matter pulses expected in these systems because of their comparatively well-developed riparian vegetation.
4. Our findings show that hydrology and long-term precipitation regime predictably affected invertebrate community responses and, thus, our work underscores the important influence of local climate to ecosystem sensitivity to disturbances.

KEY WORDS

aridity, community dynamics, flood, precipitation regime, recovery, resistance, tropical cyclone

1 | INTRODUCTION

Understanding the roles disturbances play in ecosystem structure and function is a critical goal of ecology (Lindenmayer et al., 2010), however, ecologists still struggle to predict how communities will respond to current and future disturbance events. Ecological disturbances can rapidly and strongly disrupt the dynamics of biological systems (Pickett & White, 1985), but not every disturbance has powerful or negative impacts. The specific characteristics of an individual disturbance (e.g. intensity) are part of what determines its impact, but context matters as well. The frequency and predictability of occurrence (Jentsch & White, 2019), antecedent environmental conditions immediately prior to an occurrence (e.g. Feller et al., 2015; Johnstone et al., 2016) and spatial variation in environmental conditions (e.g. Cavanaugh et al., 2019) have all been shown to affect spatial and temporal patterns of responses of an ecosystem to a disturbance. This multi-faceted context-dependency in disturbance ecology explains why apparently similar ecological systems can respond differently to similar disturbances (see Peters et al., 2011). Case study responses of individual systems to disturbance are common in the literature, but this makes it challenging to advance our general understanding of why ecosystems respond as they do because no two disturbances happen in precisely the same context and with the same characteristics (Buma, 2021). However, comparisons among multiple ecosystems along a well-understood environmental gradient and affected by a single large-scale disturbance allows for quantification of the mechanisms driving variation in ecosystem responses (Gaiser et al., 2020). Here, we present a unique opportunity to conduct this type of study leveraging a hurricane disturbance that affected multiple stream ecosystems along an aridity gradient.

The study of stream ecosystems has historically been at the forefront of disturbance ecology (see Resh et al., 1988; Stanley et al., 2010) because hydrological disturbance is a constant driving force behind their community structure (e.g. Lake, 2000; Suren & Jowett, 2006). For most streams, hydrology, both long-term dynamics and day-to-day variation, is largely driven by rainfall, and differences in long-term precipitation regimes lead to predictable dissimilarities in ecosystem structure and function. For instance, semi-arid streams generally are hydrologically flashy with cycles of flash flooding and dry riverbeds (Hawley & Bledsoe, 2011) and often have sparse canopy cover resulting in high solar insolation and low allochthonous input (Benfield, 1997). Semi-arid streams also have lower species richness and greater stochasticity in production rates compared to sub-humid streams (Lamberti & Steinman, 1997; Sheldon et al., 2002). In contrast, sub-humid streams typically experience predictable seasonal rainfall patterns resulting in more stable hydrological regimes (Dodds et al., 2015). These wetter streams are characterized by seasonal changes in riparian vegetation and canopy cover leading to higher temporal β -diversity (Tonkin et al., 2017) and seasonal production rates that are more stable than semi-arid systems. Furthermore, sub-humid streams, in comparison to semi-arid streams, may have higher availability of refugia created by additions of structural large woody debris from the comparably well developed riparian zones (Entrekin et al., 2009).

Hurricanes can be a severe disturbance to stream ecosystems. High winds can strip leaves from riparian vegetation and cause branches, limbs, and other debris to fall into the stream channel, changing light conditions (e.g. Vogt et al., 1996), and altering organic matter dynamics (e.g. Chen et al., 2019). Rainfall drives flooding that leads to scour, dislodgment and resuspension of organic matter and sediment (e.g. Resh et al., 1988), as well as redistributes flora and fauna (e.g. van Vrancken & O'Connell, 2010). While major flow disturbances are well-studied in stream ecosystems, there are relatively few studies of hurricane impacts on stream communities and even fewer investigations focused on evaluating disturbance effects along an aridity gradient. In the era of anthropogenic climate change, an increased ecological understanding of these dynamics is particularly important because hurricane frequency and intensity is predicted to increase (Balaguru et al., 2018), while long-term climate patterns including annual rainfall are simultaneously shifting with some regions getting wetter while others become more arid (Webster et al., 2005).

Here, we evaluate the impact of Hurricane Harvey (August 2017) on benthic invertebrate communities in multiple stream ecosystems distributed along an aridity gradient on the Texas Gulf coast. The aridity gradient present among the impacted sites provides an ideal case study to determine how local climate constrains ecosystem response to a severe disturbance. Across this gradient, we assessed and quantified diversity, richness and community composition immediately after the hurricane and documented each community's recovery time and trajectory. Our goal was to determine the environmental and hydrological parameters affecting the dynamics of benthic invertebrate stream communities following a major storm disturbance.

We hypothesized that semi-arid stream invertebrate communities would exhibit quick return times to a baseline following the storm event because these communities regularly experience more extreme flow conditions and, as a result, have higher richness and abundance of fast colonizers and strong dispersers (see Carvalho et al., 2022; Kinard et al., 2021). In contrast, communities in sub-humid streams were expected to have slower recovery times because these streams typically experience longer flood durations with more gentle rising and falling limbs (Dodds et al., 2015). However, invertebrate communities in sub-humid streams may exhibit smaller immediate negative responses to the disturbance because of higher availability of refuge habitats compared to semi-arid streams. Furthermore, sub-humid streams with well-developed canopies are more likely to receive large amounts of allochthonous organic matter inputs from the storm driven by debris from dense riparian vegetation, potentially fuelling post-storm bumps in productivity in these sites.

2 | MATERIALS AND METHODS

2.1 | Study area

We sampled nine streams across 350 km of coastline in Texas, USA (Figure 1) monthly from August 2017 to November 2018 and conducted additional sampling events in Fall of 2016 at four

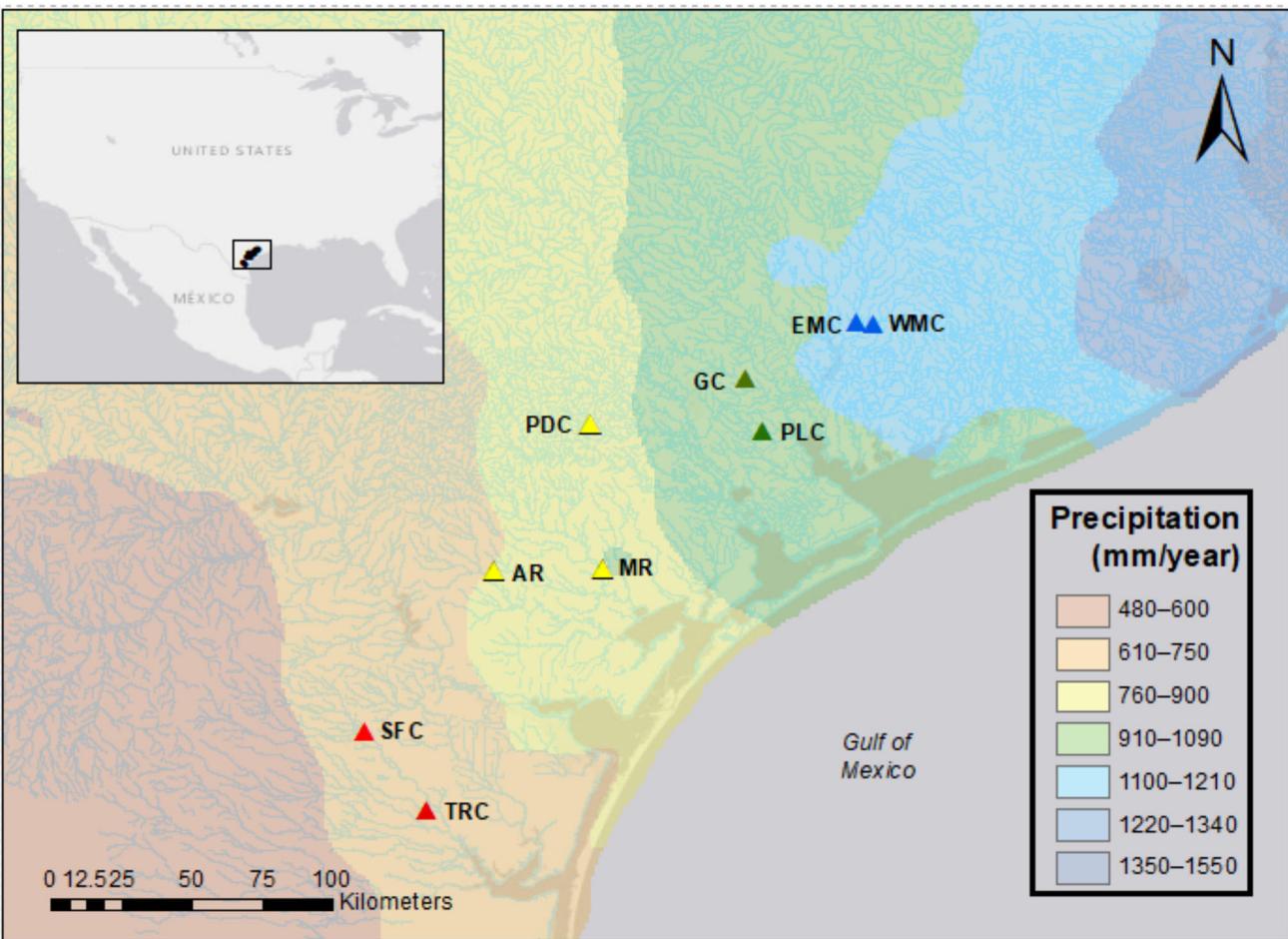


FIGURE 1 Map showing location of nine study streams across Texas, USA. Site labels are abbreviated. Semi-arid streams receiving less than 750 mm/year are Tranquitas Creek (TRC), San Fernando Creek (SFC), Aransas River (AR) and Mission River (MR). Sub-humid streams are Perdido Creek (PDC), Placedo Creek (PLC), Garcitas Creek (GC) and West Mustang Creek (WMC) and East Mustang Creek (EMC).

of the sites, March 2017 at seven of the sites, and at all of the sites in March 2019. Across the region, average precipitation increases at a rate of nearly 2.5 mm/km from western semi-arid conditions (~550 mm/year) to eastern sub-humid climate (~1350 mm/year) (Falcone, 2011). We characterized four sites as semi-arid (<750 mm/year) and five as sub-humid streams (Critchfield, 1974). The region is otherwise similar, exhibiting comparable elevation (14–62 m a.s.l.), soil geology (Quaternary and sedimentary), and air temperatures (21–22°C) (Carvallo et al., 2022; Falcone, 2011). All streams had mixed upstream land-cover land-use mainly comprised of forests, grasslands, and agricultural production. Riparian vegetation varied among sites with a general pattern of transition from short (~5–10 m tall) narrow leaf species such as honey mesquite (*Prosopis glandulosa*) in semi-arid sites to tall (30–40 m) broad leaf species such as sycamore (*Platanus occidentalis*) in sub-humid sites. All sites were wadable and had a U.S. Geological Survey (USGS) flow gauge within 200 m of the sampling area. Previous work on this study system revealed that rainfall driven variation in hydrology and environmental conditions is the dominant driver of stream invertebrate community structure (Carvallo et al., 2022; Kinard et al., 2021).

2.2 | Hurricane Harvey

Hurricane Harvey made landfall at San Jose Island near Rockport, Texas on 26 August 2017 as a Category 4 (Saffir-Simpson) hurricane and afterward stalled for 4 days bringing high winds and high rainfall of over 1500 mm to coastal Texas (Blake & Zelinsky, 2018). Hurricane Harvey was the most significant rainfall event, in terms of peak rainfall and its spatial extent, associated with a tropical cyclone in the prior United States meteorological record (Blake & Zelinsky, 2018).

2.3 | Environmental data

We acquired annual rainfall and air temperature for each site from climate data obtained from the WorldClim database by using the *dismo* package in R (Hijmans et al., 2020). We also calculated storm rainfall for each site representing the total rainfall received from the hurricane from 24 August to 30 August 2017 recorded by the National Weather Service at the nearest station (Patrick et al., 2020). Upstream drainage basin size for each site was taken from the USGS GAUGES II database (Falcone, 2011).

To determine hydrological conditions and changes related to the hurricane, we downloaded the last 20 years of daily discharge data from the USGS web data portal (United States Geological Survey, 2019). Twenty years was chosen as a reasonable time period to capture dynamics (Carvallo et al., 2022). Using daily discharge data, we calculated the median flow for the entire time series at each site on that date and considered this 'baseline flow'. We also calculated mean discharge in the week preceding the pre-storm and the peak discharge during the storm driven floods. We assessed the time in days after the storm for streamflow to return to baseline flow. We also computed the log-response ratio of the change by taking the natural log of the maximum post-storm value divided by the baseline value. This variable describes the relative flood magnitude at each site caused by the storm.

2.4 | Invertebrate sampling and processing

The 75-m stream reach was divided into four stations (0, 25, 50, 75 m) to capture spatial micro-benthic variability across the reach. We used two methods to sample benthic invertebrate communities monthly: quantitative benthic samples (corer or surber sampler) and kick/sweep sampling. A benthic core sample (75 mm diameter \times 50 mm deep) was taken at each sampling station ($n=4$) at each site to provide a quantitative estimate of communities and compare changes in abundance over time. We placed quantitative benthic samples into a 500 mL whirl-pak, put on ice, and added 95% ethanol to preserve the sample within 8 h of sampling. Kick sampling was used to capture rarer taxa and determine diversity and community composition. During each sampling event at a site, we performed 20 individual 0.1 m² samples by kicking riffle sediment and sweeping through structural habitat upstream of a d-frame net fitted with 250 μ m mesh. We distributed our 20 samples across the representative best available habitat within the channel of the 75-m stream reach including large woody debris, root wads, debris dams, riffles and overhanging vegetation (Southerland et al., 2007). All 20 samples were pooled in the field, sorted to remove large debris and placed on ice. In the lab, we fixed and submerged the sample with 95% ethanol within 8 h of sampling.

Benthic core and surber samples were rinsed in a 500 μ m sieve and sorted completely. Kick samples were processed using the Texas Commission for Environmental Quality Surface Water Quality Monitoring Protocol (Texas Commission on Environmental Quality, 2014). Each sample was processed separately by being rinsed in a 500 μ m sieve and spread evenly across a gridded sorting tray. Grid cells were randomly selected and sequentially picked for all invertebrates in each cell until the total count at the time of a cell completion was greater than 175 individuals. All invertebrates were counted and identified to the lowest possible taxonomic resolution, typically genus (Merritt et al., 2009; Thorp & Covich, 2016).

To validate the use of our baseline metric as a comparison point (see Section 2.5), we used pre-storm samples collected as part of

exploratory sampling from four of the nine sites in Fall 2016 and seven of the nine sites in Spring 2017. Replicate benthos samples from Fall 2016 were taken as surber samples (0.092 m², 250 μ m mesh) disturbed to 5 cm depth for 60 s. These samples were volumetrically large with sand and fine gravel making them difficult to process so they were not taken in spring 2017, which only included kick samples. Following assessment, quantitative benthos samples via cores were introduced in Fall 2017 sampling. Other than noted differences, sample collection and processing methods were identical in Fall 2016 and Spring 2017 to later sampling methods. Due to the incompleteness of sampling sites and sample types, pre-storm data were only used for comparison and were not included in the overall analyses.

2.5 | Data analyses

We calculated total abundance across taxa, species richness and Shannon diversity for each sampling event at a site using the *vegan* package in R (Oksanen et al., 2019). Total abundance from kick samples was not used for abundance analyses because of the subsampling process potentially introducing bias in densities. To provide a basis for comparing variation in community responses after the storm, we calculated 'baseline' values as the long-term average value of each metric across the entire post-storm sampling period through Fall 2019. A simple average was deemed appropriate because prior work found weak to non-existent seasonality in the invertebrate communities of these streams (Carvallo et al., 2022) and a review of rainfall and temperature records shows high intra/interannual stochasticity in weather patterns. We then validated our long-term post hurricane baseline via comparison to pre-storm data where available. To do this, we used paired t-tests to compare richness and abundance values of comparable pre-storm samples to the calculated baseline value. We also compared each value to sampling dates from the same month >1 year after the storm. To estimate time of recovery post-disturbance, we sequentially compared community metric values through time following the storm to the baseline using paired t-tests until we identified when each metric no longer differed from baseline values. We then calculated length of time until recovery, which we refer to as return time, based on recovery time of total abundance. Total abundance was chosen for this calculation because it allows for mitigation of changes in community composition that would affect diversity and richness values. To estimate the magnitude of storm impact on community responses, we calculated log-response ratios (LRR), the natural log of the maximum change created by the storm divided by the baseline value, for each of the metrics.

In our study, limitations in spatial coverage and availability of pre-storm data led us to use a baseline derived from long-term monitoring that could be calculated for all nine sites rather than pre-storm community states. These baselines were compared to pre-storm data, where possible, to validate the estimates. Furthermore, given the high degree of variability that exists in all stream communities,

but particularly in sandy-bottomed coastal rivers, a time-integrated measure of the stable basin of attraction for communities is more appropriate than our small sample size of pre-storm sampling events even if it were complete. There are few examples of complete state changes in stream communities following hydrologic disturbance (but see Vieira et al., 2004) and we have high confidence from our comparisons to available pre-storm samples that no such shift occurred here. Thus, we consider our measure of community deviation from long-term means an indicator of intrinsic resistance of the systems (i.e. degree a system is unchanged) and return time an indicator of intrinsic resilience of the systems (i.e. ability and rate at which a system returns to a reference state following disturbance) (see Patrick et al., 2022).

Linear regression models were used to test for hypothesized relationships between invertebrate community metrics (response) and predictors including local climate and the environmental conditions altered by the storm. Responses for separate model frameworks involved total abundance return time and log-response ratios of total abundance, diversity, and richness for each sampling method. Explanatory variables included annual rainfall, storm rainfall, flow return time (i.e. flood duration), and flow log-response ratio (i.e. relative flood magnitude). We assessed multicollinearity among explanatory variables using variance inflation factors where >5 is cause for concern (Zuur et al., 2009). None of our explanatory variables in global models were >5 so no further action was needed. All predictor variables were standardized using a Z-score standardization (mean=0, standard deviation=1) because of orders of magnitude differences in means (Gotelli & Ellison, 2013). We included an intercept only model, global model, and all combinations of effects. We used Akaike's information criterion corrected for small sample sizes (AICc) to rank models and selected competing model(s) where AICc was less than two units from the most supported model (Burnham & Anderson, 2004). All linear models were run using the *lm()* function, and multi-model inference was conducted through the *MuMIn* package in R (Barton, 2010).

To determine how time since the storm affected community metrics we performed generalized additive modelling (GAM) using the *mgcv* package in R (Wood, 2015). Time in days since the hurricane for each sampling date was calculated using 1 September 2017, as the point at which Hurricane Harvey had moved on from our sites (Blake & Zelinsky, 2018). We compared the GAMs to a linear model using an *F*-test.

To evaluate whether there was a post-storm production increase covarying with aridity, we used total abundance in cores as proxy metric and looked at the relationship between the relative increase in abundance post-storm (November–December 2017) compared to a normal year (November 2018) against annual rainfall. First, we used a paired t-test to assess whether the 2017 hurricane mean total abundance was greater than a site-level paired mean in 2018. Next, we subtracted the 2017 mean total abundance per sampling period from the 2018 value, which yielded the average difference (Δ) between the two periods. A linear model was fit with Δ as the response and annual rainfall at each site as the predictor. We also assessed

changes in community composition by comparing plots of relative abundance across taxa between three timeframes: the first sample immediately afterward the storm, sample event at time of recovery to average total abundance and for baseline averages.

To test our overall conceptual model of the interactions between, and cascading causal paths among, long-term climate and characteristics of the storm disturbance and their combined effect on community responses we employed structural equation modelling (SEM) (Grace, 2006). We fitted three separate SEM models to explain responses in total abundance, diversity and richness. All models began with a uniform concept of hypothesized relationships among immediate community response, return time to post-storm baseline community metrics, annual rainfall, storm rainfall, flood duration and flood magnitude that was informed by prior analyses. We hypothesized that flood magnitude was controlled by amount of rainfall received from the storm and the annual average rainfall at a site while flood duration depended on annual rainfall and magnitude of the flood event. Flood duration and magnitude were assumed to covary. We hypothesized that immediate community response magnitudes (log-response ratio) were influenced by flood magnitude, flood duration and local annual average rainfall (aridity). We expected that the time taken for invertebrate communities to return to baseline abundance was influenced by the flood duration and the amount of rain experienced in the storm. We also expected there to be covariance in community log-response ratios and the return time to baseline total abundance for the community (i.e. some covariation in proxies of resistance and resilience).

We multiplied log-response ratios of community responses by -1 to make them positive (e.g. larger decline equates to greater log-response ratio) to make visualization and interpretation easier as almost all storm effects were negative. We multiplied log-response ratios of diversity and richness for kick sampling by a constant of 10 to bring them to a similar magnitude of other variables to allow for matrix calculations. The final modelling frameworks were evaluated with χ^2 goodness-of-fit statistic. For these tests, the null hypothesis was that the covariance matrix of the data was not different from the covariance metric suggested by the model, hence a $p > 0.05$ rather non-intuitively indicates support for the model (e.g. the model fits the data well). All models were fit using the *lavaan* package in R (Rosseel, 2012). We used R (version 4.0.2) for all statistical analyses herein (R Core Team, 2020). We reported means with one standard deviation unless otherwise noted and used a significance level of $\alpha = 0.05$.

3 | RESULTS

Streams exhibited considerable variation in 20-year mean annual rainfall ranging from 540 to 950 mm/year (grand mean = 762 ± 147 (standard deviation) mm/year; Table S1). Sites also differed in 20-year median flow ranging from about 3–343 L/s (139 ± 137 L/s; Table S1). While all sites were affected by high winds (Patrick et al., 2020), storm rainfall varied among sites, ranging from 40 mm (~6% of the site's annual rainfall) to roughly 400 mm (~55% annual

rainfall) during the 4-day storm event (244 ± 138 mm/4-day storm event; **Table S2**). The hydrologic flow regime was also greatly affected (**Table S2**). For instance, the percent increase in flow at our sites compared to immediately before the storm ranged between only 165% to an 8,359,320% increase. Flows returned to long-term baseline on average of 11 ± 6 days.

Baseline estimates for diversity, richness, and abundance were deemed suitable targets for assessment of recovery. For the seven sites where data were available, kick invertebrate richness from pre-storm (March 2017) was found to be consistent with both the calculated baseline ($t = -1.9$, $p = 0.10$) and March of 2019 ($t = -1.5$, $p = 0.19$) (**Figure S10**). For the four sites where data were available on benthic infauna, total abundance from Fall 2016 (1-year pre-storm) did not differ from 15 months post-storm in Fall 2018 ($t = -1.3$, $p = 0.30$), and both dates were, as expected, ~ 6 times higher on average than immediately after the storm in Fall 2017 ($t = 4.66$, $p < 0.01$). Fall 2018 abundances were no different from baseline ($t = 1.8$, $p = 0.13$), but Fall 2016 abundances were on average lower than baseline ($t = 3.85$, $p = 0.01$) driven by relatively low abundances in two of four comparison sites. However, these particular sites are primarily sand and differences could be due to varying collection efficiencies between two methods (**Table S6**). Furthermore, total abundance in March 2019 (19 months

post-storm) was consistent with baseline ($t = 0.59$, $p = 0.57$) indicating it is an appropriate comparative benchmark during the post-storm recovery period.

Invertebrate communities responded differently to storm conditions among streams (**Table S3**). For instance, our driest site immediately (i.e. at our first sampling within 2 weeks after the storm) resembled baseline average abundance whereas our wettest site took more than 3 months to return to baseline. All but one of the other six sites had return times of roughly 2 months. Return time was best explained directly by a positive relationship with storm rainfall (**Figure 2a**; Adjusted $R^2 = 0.41$, $\beta = 19.9 \pm 7.9$ (SE), $p = 0.04$), but not annual rainfall or changes in flow. The return time-rainfall relationship was largely driven by the immediate recovery of our driest site and was not significant when the site was removed. The intercept only model also had a ΔAIC_c of less than two units.

Overall, kick samples yielded 185 taxa. Baseline averages were 15 ± 3 taxa. Across all sites, richness was lower by an average of 6.5 taxa immediately after the storm compared to community baseline averages ($t_7 = -4.5$, $p < 0.01$). Log-response ratios for differences in immediate richness after the storm compared to baseline averaged -0.8 ± 0.4 across all sites except one where no reduction in richness was observed (Placido Creek). Baselines for Shannon diversity averaged 1.7 ± 0.4 . In contrast to richness, across sites, there was

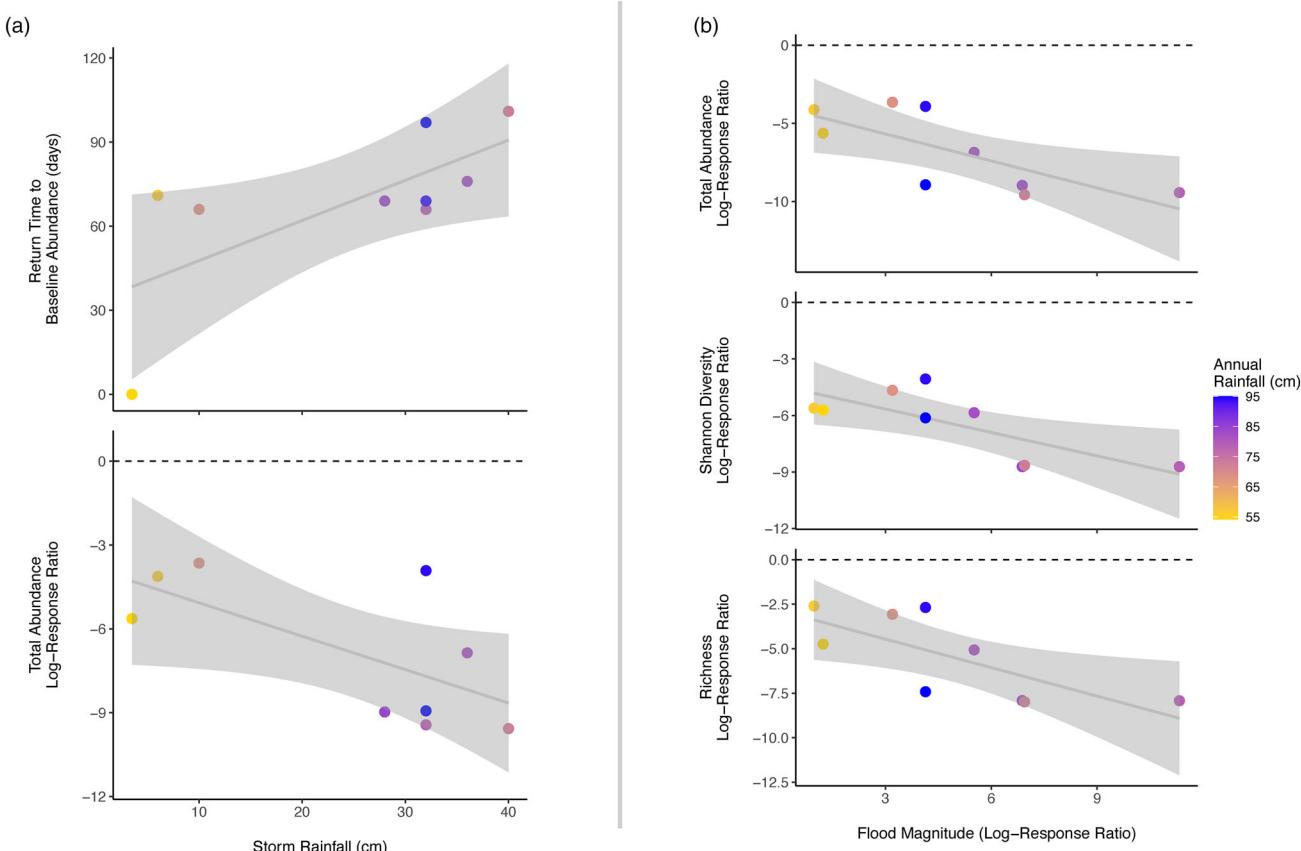


FIGURE 2 Invertebrate responses to rainfall received during Hurricane Harvey (a) and flood magnitude (b). Community responses were measured as time to return to post-storm baseline total abundance and log-response ratio of total abundance, Shannon diversity, and richness from benthic invertebrate core samples at nine streams in Texas, USA. Grey lines depict linear models ($y \sim x$) and shaded areas show 95% confidence regions.

no difference in diversity immediately after the storm ($t_7 = -0.2$, $p = 0.86$) or at recovery ($t_8 = 1.3$, $p = 0.22$) compared to baselines. For separate diversity and richness log-response ratio modelling frameworks, intercept only models had the lowest AICc for kicks (Table S4).

Core samples were less diverse than kick samples and yielded only 85 unique taxa. Baseline mean richness in cores across sites was generally only two or three taxa (2.4 ± 0.6) and mean Shannon diversity averaged 0.5 ± 0.2 . Richness and diversity in core samples declined after the storm at all sites. Average richness was $\sim 1.6 \pm 0.9$ taxa lower immediately after the storm ($t_8 = -5.1$, $p < 0.01$) and was 1.1 ± 1.2 taxa higher at recovery compared to baseline mean ($t_8 = 2.6$, $p = 0.02$). The lowest AICc model predicted greater magnitude richness responses with greater magnitude floods (Figure 2b; Adjusted $R^2 = 0.46$, $\beta = -1.7 \pm 0.6$ (standard error, SE), $p = 0.03$). The intercept only model was also in the model candidate set Δ AICc less than two. Diversity immediately after the storm was lower than baseline ($t_8 = -4.4$, $p < 0.01$), but unlike richness was similar to the baseline at time of recovery ($t_8 = 1.3$, $p = 0.23$). The lowest AICc model predicted greater drops in diversity with greater flood magnitudes (Figure 2b; Adjusted $R^2 = 0.49$, $\beta = -1.3 \pm 0.5$ (SE), $p = 0.02$). Baseline mean total abundance averaged 3400 ± 835 individuals m^{-2} . Excluding our driest site, sites exhibited lower mean total abundance immediately after the storm compared to site-specific baselines ($t_8 = -5.4$, $p < 0.01$). At the driest site, the relationship was driven by 49 individuals of the invasive snail *Melanoides tuberculata* occurring in one core and the other cores matching other sites (empty or low counts). The lowest AICc model predicted greater declines in abundance with greater flooding (Figure 2b; Adjusted $R^2 = 0.48$, $\beta = -1.9 \pm 0.6$ (SE), $p = 0.02$). The second lowest AICc model predicted greater declines in abundance with higher storm rainfall (Figure 2a; Adjusted $R^2 = 0.36$, $\beta = -1.7 \pm 0.7$ (SE), $p = 0.05$). Neither annual rainfall or flood duration enhanced the model explaining the abundance response magnitude (Table S4).

Richness, diversity, and total abundance measured in cores show a delayed peak above baseline in the months after the storm (Figure 3a; Appendix S1). Peaks in community metrics after the hurricane were observed 3–4 months (richness, abundance) and 4–5 months (diversity) later. Abundance changes were largely driven by several taxa including chironomids and dolichopodidates (see Appendix S1). Peaks in core total abundance were significantly greater than values at the same time of year one year later in 2018 ($t_8 = 2.5$, $p = 0.02$). Streams with higher annual rainfall had stronger storm-related peaks in total abundance than more arid sites (Figure 3b; Adjusted $R^2 = 0.51$, $\beta = 416 \pm 135$ (SE), $p = 0.02$).

The covariance matrices of all of the proposed structural equation models did not differ from that suggested by the data, indicating good fit (Table 1). The relationships, or numerical direction (sign) of path coefficient values, follow general patterns shown in the presented path diagram for metamodels of invertebrate total abundance and diversity in cores (Figure 4; Table S5). We observed a positive effect of storm rainfall on flood magnitude and an increase in flood duration with flood magnitude. Larger floods

and longer flood return times increased the magnitude of invertebrate response and longer flood return times also increased time for invertebrates to return to baseline. Additionally, models reveal climate operating through both direct and indirect pathways. Drier streams tended to have larger floods per unit rainfall, shorter flood durations per unit flood magnitude, and smaller invertebrate responses per unit flood magnitude. Thus, the total effect of annual rainfall (i.e. local climate) on invertebrate responses occurs not only through a direct effect, but is also mediated by cascading effects from annual rainfall through flood magnitude and flood duration down to invertebrate responses (Figure 4; Table S5). Both direct and total effects of annual rainfall on invertebrate responses were strongest for diversity and lowest for abundance (Table 1). There were slight differences across metamodels depending on sampling method (Table S5). Longer flood duration led to dampened community responses in core dataset but increased log-response of richness and diversity in kick data. All other relationships held across metamodels.

4 | DISCUSSION

In our study, invertebrate community responses and recovery times were strongly tied to climate-mediated effects. Our findings provide a compelling example of how system response to disturbance can be influenced by local context, in this case long-term rainfall regime. Local storm-rainfall was a direct predictor of responses and return times, but structural equation modelling indicates that storm rainfall effects were mediated through flood magnitude and duration, which were shaped by local climate. We also found that community responses were predictable based on their aridity and annual rainfall dynamics. Sub-humid communities showed less change in total abundance and richness after flooding, but took longer to return to post-storm baseline compared to semi-arid streams. As expected, storm flood durations were longer in sub-humid compared to semi-arid streams because they are less flashy because of greater watershed groundwater infiltration, vegetation uptake, and wider and more structurally complex floodplains and riverbeds (Dodds et al., 2015; Kingsford, 2006). We suggest that longer return times for invertebrate responses were tied to longer flood duration, which may have overridden hypothesized effects of greater refuge availability in sub-humid streams.

Across sites, the magnitude of invertebrate community responses was directly tied to the magnitude of flooding experienced after the storm. Other studies of stream invertebrates have observed greater declines as flooding intensity increases (Robinson, 2012; Suren & Jowett, 2006). This disturbance magnitude-resistance relationship is a central hypothesis of disturbance ecology (e.g. Buma, 2021; Resh et al., 1988; Woodward et al., 2015). Regular and predictable flooding events may result in relatively minor declines of richness and abundance given the adaptation of organisms to these regimes (Lytle & Poff, 2004). However, extreme events can exceed the adaptive capacity of many species and lead to severe declines and long

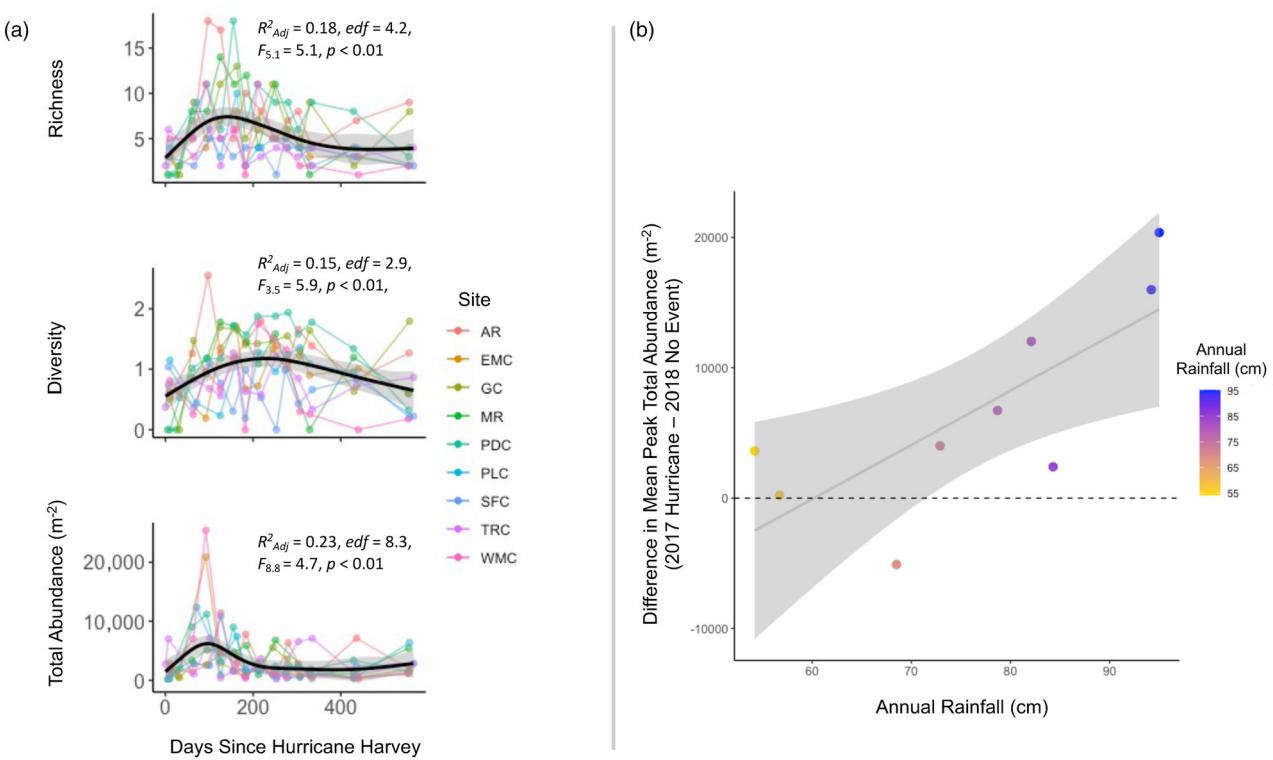


FIGURE 3 Changes in core invertebrate community metrics with days since Hurricane Harvey (a). Lines (black) represent generalized additive model fits with error (light grey). Peaks in mean total abundance of core samples were detected after the hurricane in November and early December 2017 (i.e. ~4 months after the storm) (b). Means from November 2018, when there were no storm events, were subtracted from 2017 values and modelled with annual rainfall at a site. Grey line depicts a linear model ($y \sim x$) and shaded areas show 95% confidence region.

Dataset	Response	χ^2	df	p	Total effects	
					Annual rainfall	Storm rainfall
Core	Abundance LRR	1.97	3	0.58	-0.09	0.34
	Richness LRR	1.67	3	0.64	-0.12	0.34
	Diversity LRR	1.68	3	0.64	-0.30	0.41
	Return Time	—	—	—	0.05	0.65
Kick	Richness LRR	2.72	3	0.44	-0.54	0.32
	Diversity LRR	2.72	3	0.44	-0.65	0.70
	Return Time	—	—	—	0.06	0.65

Note: Each meta-model was evaluated using the χ^2 goodness-of-fit statistic ($p > 0.05$ indicates support for the model). Number of parameters is described by 'df'. All meta-models exhibited the same structure and links, thus 'return time', calculated from core total abundance and describes how long the community took to return to baseline abundance, was included in all models. The total effects including both direct and indirect effects from mediation are presented for annual rainfall and storm rainfall. Other predictors included flood duration and flood magnitude.

TABLE 1 Structural equation models describing community responses of invertebrates in core and kick samples related to local climate and storm characteristics experienced after Hurricane Harvey at nine streams in Texas, USA.

recovery periods resulting in shifts in community assemblages (e.g. Snyder & Johnson, 2006). In our region, while we observed declines in total abundance across the study sites, recovery rate varied with local climate.

Semi-arid communities exhibited quicker return times compared to our sub-humid sites when controlling for effects of storm rainfall,

indicating that semi-arid communities may have more intrinsic adaptations at the community-level to extreme flood events. Dominant taxa in sub-humid communities may have slower population growth rates or be slower to recolonize than those in semi-arid systems, which are robustly adapted to high-energy hydrology (Mellado-Díaz et al., 2008). Carvalho et al. (2022) conducted a comparison of

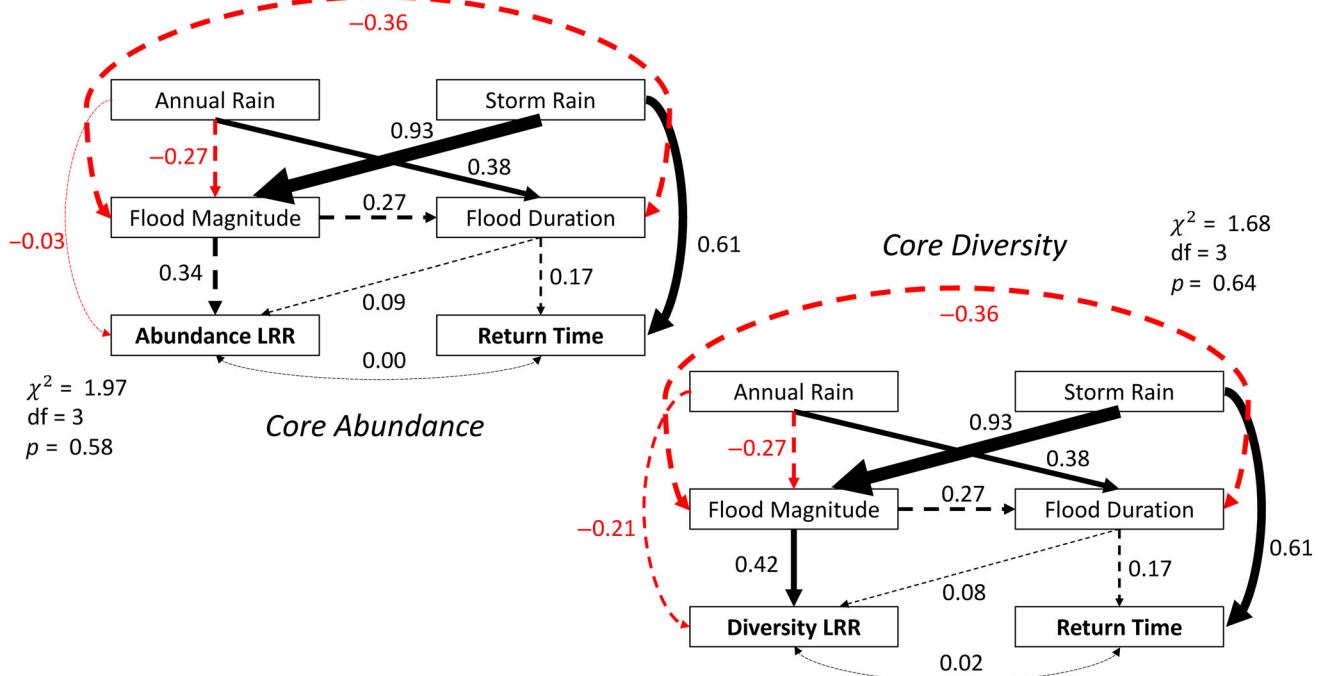


FIGURE 4 Structural equation modelling results for core total abundance and diversity metamodels. Abundance LRR is log-response ratio of change in abundance immediately after Hurricane Harvey. Return Time represents length of time after the storm the community took to return to baseline long-term post-storm abundance values. Arrow thickness is proportional to standardized path coefficients for complete model. Complete lines show significant effects whereas dotted lines are not significant. Black lines represent positive relationships whereas red lines indicate a negative relationship. Values associated with log-response ratios for abundance and diversity have been transformed for interpretability by multiplying by -1 given that log-response ratios were negative meaning values decreased after the storm.

invertebrate community traits across our same sites using a portion of the same timeseries presented here revealing that semi-arid streams have greater abundance and richness of 'rugged' taxa (e.g. chironomids, stratiomyids and thiarids) with traits such as rapid maturation, multivoltinism and strong dispersal that encourage fast recolonization and reproduction compared to wetter sites. This potentially offers an explanation for climate-mediated faster recovery times (Robinson, 2012). In contrast, as discussed in Carvallo et al. (2022) and observed here, taxa abundant in wetter sites including amphipods and mayflies (*Cloeon* spp.) are relatively slow-growing and not good dispersers; thus, would take longer to recover after a storm event.

There are examples of invertebrate populations taking multiple years to recover after a major hydrologic disturbance (Woodward et al., 2015), a stark contrast to our observed ~3-month recovery windows. Even in cases of rapid recovery of invertebrate density, taxonomic richness and composition may take longer to return to pre-disturbance conditions (Vieira et al., 2004). However, our observations match what has been observed in other arid streams (Fisher et al., 1982; Grimm & Fisher, 1989) and there are several mechanisms for rapid recovery in these systems. First, our study streams were all Strahler stream order of three or higher, indicating that they should receive a fairly high contingent of drifting colonists following disturbance as compared to more isolated headwater streams (Patrick et al., 2021; Swan & Brown, 2017). Second, in both pre- and post-hurricane samples, large-bodied taxa such shredding caddisflies

were absent, and other large taxa such as Aeshnidae were rare. Instead, the majority of taxa present at all sites were small-bodied taxa such as riffle beetles (Elmidae), midges (Chironomidae) and other dipterans, and small-bodied mayflies (Ephemeroptera) with the potential for very short generation times under ideal growing conditions. For example, multiple generations of dominant mayfly and dipteran taxa were observed within the first 30 days following a flash flood in Sycamore Creek, Arizona (Fisher et al., 1982). Third, given the region's sub-tropical climate, these taxa are able to grow and reproduce year-round. Even traditionally univoltine taxa are known to exhibit multivoltinism in sub-tropical to tropical climates. For example, *Cheumatopsyche analis* introduced to Hawaii exhibits five generations per year in contrast to its single generation per year in United States temperate regions (McIntosh et al., 2003). Furthermore, dipterans in Alabama streams, similar climatologically to our sub-humid sites, exhibit extremely high generational turnover throughout the year, with production to biomass ratios at ~200 per year (Benke, 1998).

The pattern of peaks in invertebrate total abundance, richness, and diversity observed at the time of recovery (i.e. months after the storm) appeared to be a significant deviation from normal seasonal dynamics. These peaks may indicate a temporary change in ecosystem processes after the hurricane (e.g. Chen et al., 2019; Patrick et al., 2020). Some communities at recovery were dominated by large post-storm increases in chironomids and other dipterans, but populations eventually stabilized at lower numbers



FIGURE 5 Post-storm images of downed trees, organic matter inputs and tannin-stained waters. Temporarily tannin-stained waters and treefall just upstream of sampling reach at Mission River, image taken September 2017 (a). Temporarily tannin-stained waters and treefall and impoundment just downstream of sampling reach at Garcitas Creek, image taken September 2017 (b). Complete channel obstruction and debris dam upstream of sampling reach at Placedo Creek, image taken January 2018, but obstruction was created by Hurricane Harvey (c). Temporarily tannin-stained waters and litter and debris inputs following the storm at West Mustang Creek, image taken September 2017 (d). Photo Credits: (a), (b), and (d): Christopher J. Patrick; (c): Derek J. Hogan.

of individuals (Figures S1–S9). This matches with other reports of stream taxa responding opportunistically to disturbances with large population increases for some species during recovery following extreme events, often followed by crashes. For example, community dynamics in Sycamore Creek, Arizona displayed similar patterns of rapid (~60 day) peaks in invertebrate biomass and density after flash floods which were then followed by precipitous crashes (Grimm & Fisher, 1989). Population booms may be the result of ample available resources with limited competition following disturbance, whereas the mechanisms proposed for post-boom crashes are reductions in food quality/quantity over time or trailing increases in predator populations exerting lagged control on booming primary consumer populations (Grimm & Fisher, 1989). In our study, our main invertebrate predators (Odonata) did not display a lagged recovery and a lag in invertivore fish in Poeciliidae family could be responsible for crashes, we consider it more likely that spatio-temporal variability in food quality and quantity explains the patterns we observed and suggest that this mechanism interacts with long-term climate regime.

Although we did not quantify the amount, we observed hurricane winds bringing a considerable pulse of dissolved, particulate, and large organic matter to the streams (Figure 5). For example,

observations from limited replicate monthly water sampling from August 2017 (pre-storm) through December 2017 showed dissolved organic carbon concentrations were 43% higher across sites on average the month after the hurricane in comparison to the preceding month. Furthermore, measurements in downstream estuaries revealed large pulses of organic material entering the systems (Patrick et al., 2020). This pulse of organic matter could have stimulated basal food web components and, consequently, reproduction and recruitment for aquatic invertebrates (e.g. Gutierrez-Fonseca et al., 2024; Wallace et al., 2015). Then over time, as transient organic matter resources were recycled and exported (Wohl et al., 2019), productivity returned to normal levels. Although the pattern of peaks and crashes was observable in all sites across our gradient, the magnitude of deviations in total abundance and diversity increased linearly with annual mean rainfall (Figure 3b). We hypothesize that as annual rainfall increases, riparian zones develop and such streams stand to receive larger organic matter pulses and concordantly greater increases in invertebrate production (Chen et al., 2019; Dodds et al., 2015). Compared to semi-arid streams, our well-vegetated sub-humid sites had fallen trees in the stream corridor including some within or directly adjacent to our sampling reaches, creating dams holding organic debris and litter spanning entire channels (Figure 5).

These results are of both theoretical and practical importance to our understanding of disturbance ecology. Global climate models predict shifts in both annual average rainfall and the frequency and intensity of extreme weather events (Fowler et al., 2021; Webster et al., 2005). In Texas, from 1981 to 2000, the estimated annual probability of a rain event like Hurricane Harvey was about 1%, roughly 6% in 2017, and is predicted to rise to 18% by 2081–2100 (Emanuel, 2017). This effectively means that, regionally, this disturbance type is shifting from a hundred-year storm to a once every 5 years storm within the span of a century, a rapid shift with important implications for the future of these rivers. At the same time, this particular region is expected to get both drier and hotter (Banner et al., 2010), likely shifting sub-humid stream communities to more closely resemble semi-arid communities. In this case, we might predict that these shifts will enhance stream ecosystem community resilience to extreme events, however, results are likely to play out differently in other regions of the world. Annual rainfall patterns are predicted to regionally change worldwide (Webster et al., 2005), with some areas getting wetter and others drier and these shifts need not correlate with predicted changes in disturbance intensity and frequency. In light of these changes, it is critically important to enhance our understanding of what controls ecological susceptibility to catastrophic disturbances so that we can predict and manage for ecosystem responses to future disturbance regimes. In our study, we show that local climate shapes responses of stream ecosystems to hurricanes. Thus, more broadly for all ecosystems, we demonstrate the potential importance of antecedent environmental conditions in addition to disturbance characteristics for understanding ecosystem response. Furthermore, these results suggest that in the era of climate change, as we plan for potential disruptions to important ecosystem services (Ummenhofer & Meehl, 2017), we should not only be considering the consequences of shifting disturbance regimes, but also the consequences of simultaneous shifts in the susceptibility of ecosystems to future disturbances.

AUTHOR CONTRIBUTIONS

Christopher J. Patrick, J. Derek Hogan and Bradley A. Strickland conceived the ideas and designed methodology; Christopher J. Patrick, Fernando R. Carvallo, Sean K. Kinard, Alexander T. Solis and J. Derek Hogan collected the data; Bradley A. Strickland and Christopher J. Patrick analysed the data; Bradley A. Strickland and Christopher J. Patrick led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.np5hqc01z> (Strickland et al., 2024).

ETHICS STATEMENT

Sampling activities occurred under TPWD Scientific Permit Number SPR-0716-170.

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SUPPORTING INFORMATION

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

Table S1: Site characteristics, climate, and long-term hydrological conditions of nine streams in Texas, USA.

Table S2: Effects of Hurricane Harvey on local rainfall and flow at nine streams in Texas, USA.

Table S3: Effects of Hurricane Harvey on benthic invertebrate communities from core and kick/sweep samples at nine streams in Texas, USA.

Table S4: Results from linear regression models from candidate set with delta AICc ≤ 2 (bolded) and the null and global models to describe community metrics of invertebrates in benthic core and kick samples after Hurricane Harvey at nine streams in Texas, USA.

Table S5: Structural equation models describing community responses of invertebrates in core and kick samples related to local climate and storm characteristics experienced after Hurricane Harvey at nine streams in Texas, USA.

Table S6: Effects of Hurricane Harvey on benthic invertebrate communities from core samples at nine streams in Texas, USA.

Figure S1: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Aransas River in Texas, USA.

Figure S2: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Mission River in Texas, USA.

Figure S3: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Placido Creek in Texas, USA.

Figure S4: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Perdido Creek in Texas, USA.

Figure S5: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at East Mustang Creek in Texas, USA.

Figure S6: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at West Mustang Creek in Texas, USA.

Figure S7: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Garcitas Creek in Texas, USA.

Figure S8: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at San Fernando Creek in Texas, USA.

Figure S9: Dominance-diversity curves revealing changes in community composition associated with Hurricane Harvey from benthic core sampling data at Tranquitas Creek in Texas, USA.

Figure S10: Timeseries of kick diversity (A) and richness (B) at seven sites. The first point in each timeseries shows a pre-hurricane sample.

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