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ORIGINAL ARTICLE

Structure and functional composition of macroinvertebrate communities in coastal plain streams across a precipitation gradient

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Abstract

1. Climate change is expected to alter rainfall and temperature regimes across the world. The hydrology and riparian zone vegetation of lotic ecosystems are tightly linked to rainfall and a mechanistic understanding of the effects of rainfall on lotic ecosystems is needed to forecast the ecological impacts of climate change. However, it is difficult to isolate rainfall effects from other environmental variables that covary across climates. To address this, we leveraged a unique steep rainfall gradient with few covarying changes in elevation, temperature, and geology to evaluate the effects of rainfall on stream invertebrate communities.
2. We surveyed nine streams in the Texas Gulf Coast Prairie distributed along a 550–1,350 mm/year rainfall gradient. Four sites were classified as drier semi-arid streams (<750 mm annual rainfall) and five sites were classified as wetter sub-humid streams (>750 mm annual rainfall). A suite of characteristics including benthic invertebrate community metrics, flow conditions, and water quality variables were assessed monthly for 14 months at each site to relate precipitation regime to stream structure and function.
3. Precipitation regime was observed to be a master explanatory variable. As annual rainfall increased, the flow environment became more stable within seasons and predictable across seasons, influencing spatial structure and temporal variability of invertebrate community composition. Wetter streams were dominated by slower growing taxa without adaptions for desiccation resistance and strong dispersal. Wetter sites displayed seasonal variation in community composition and species richness, whereas temporal variation in communities in drier streams was controlled by stochastic variation in flow conditions.
4. These observations show that differences in local annual rainfall correlated with major changes to community structure and functional composition. We hypothesise that this association is related to the connection of rainfall to hydrological stability, particularly the frequency of low flow disturbances, and the

subsequent effects on riparian vegetation and temporally available niches to stream invertebrates. Our work adds to evidence that alterations in precipitation patterns associated with climate change have sweeping impacts on lotic fauna.

KEYWORDS
benthic invertebrates, biodiversity, climate, functional traits, semi-arid streams

1 | INTRODUCTION

Average global temperature has exponentially increased since the industrial revolution from 0.8 to 1.2°C, causing significant changes in the frequency, intensity, and predictability of weather events now and in the future (IPCC, 2018). For instance, premature spring snow melts, increased forest fires, and increases in aridity have been documented across the globe (Seager et al., 2007; Ummenhofer & Meehl, 2017). Simultaneously, the variation in the frequency, intensity, and timing of rainfall events has become less spatially and seasonally predictable (Andrys et al., 2017; Szwed, 2019). These changes are also impacting stream ecosystems globally. For example, there have been regional changes in stream intermittency across the U.S.A. (Zipper et al., 2021) and decreased water flows and water security in Nepal (Dahal et al., 2018).

Rainfall, which drives the hydrological cycle, is a key factor shaping stream ecosystems (Lytle & Poff, 2004; Mims & Olden, 2012). Many studies have shown that macroinvertebrate community dynamics are driven by hydrological flow disturbance regimes, which is largely controlled by precipitation (Dodds et al., 2019; Lake, 2003, 2005; Mathers et al., 2019; Poff & Ward, 1989). However, forecasting specific effects of changes to precipitation patterns on stream ecosystems is challenging because unlike studies on temperature effects (Arai et al., 2015; Burgmer et al., 2006; Domisch et al., 2011; Hering et al., 2009), studies isolating rainfall effects are underrepresented in the literature (Adámek et al., 2016; Reynolds et al., 2015). What is known about how rainfall affects the structure and function of stream ecosystems comes primarily from large-scale observational studies conducted across climate gradients (e.g., Bonada et al., 2007). These studies show that arid systems receiving little annual precipitation generally lack canopy cover from riparian zone trees, leading to high solar insolation and low allochthonous input, and thus depend primarily upon autochthonous carbon from primary productivity (Benfield, 1997; Pomeroy et al., 2000). Arid stream hydrological regimes are typically flashy, with punctuated periods of dry riverbed and high energy flash floods—a common but stochastic occurrence (Jackson & Fisher, 1986). In response to these flow disturbances, arid streams tend to contain low species richness (Sheldon et al., 2002) and biomass production is stochastic through space and time, at times exceeding the secondary production of mesic (humid) systems by an order of magnitude (Grimm & Fisher, 1989; Lamberti & Steinman, 1997). The communities of arid streams have been observed to be inhabited predominantly by taxa that are better adapted for recolonisation after hydrological disturbance through faster generation time, wider dispersal ability, and greater fecundity than the taxa in the more hydrologically stable wetter systems (Bonada et al., 2007; Mellado-Díaz et al., 2007). The predominance of algae caused by high insolation also drives a higher proportion of taxa adapted for scraping and grazing algae than in wetter streams (Benfield, 1997; Grafius, 1974; Tait, 1997).

In contrast, wetter (mesic) streams are characterised by dense canopy cover provided by trees in the riparian zone. The trees decrease insolation, decreasing primary productivity, and increase allochthonous carbon input into the streams (Benfield, 1997). Due to predictable rainfall patterns and the role of terrestrial vegetation in moderating the hydrological cycle, mesic systems typically have much more stable hydrological regimes, more stable baseflow conditions and floods with more gentle rising and falling limbs occurring at predictable periods within the year (Dodds et al., 2015; Mellado-Díaz et al., 2007). These predictable and stable conditions in mesic streams can increase the success of species that depend on distinct niches in time that correspond with their life history strategies, supporting higher temporal β-diversity and more temporally stable biomass production rates than the arid streams through an increase in species turnover between seasons (Konar et al., 2013; Tonkin et al., 2017). Mesic streams in low-disturbance drainages are often inhabited by communities consisting of more specialised competitive species than rapidly colonising species (Boulton et al., 1992).

Precipitation regime determines hydrological conditions, particularly frequency of disturbance, and the identity of basal resources, which drive differences between arid and mesic stream ecosystem structure and function. For instance, a recent global meta-analysis showed that frequency of low flow disturbance events was the most important predictor of riverine benthic invertebrate secondary production after water temperature (Patrick et al., 2019). However, a challenge with interpreting the causal nature behind these patterns is the breadth of environmental variation when comparing systems across ecoregions. Observational studies that derive process from pattern (see Dodds et al., 2015) rely on a space for time substitution, but interpretations from these data are limited due to confounding environmental variables such as elevation, air temperature, and sun angle that are unavoidable in large latitudinal studies (Fukami & Wardle, 2005). To independently evaluate the effects of rainfall on stream structure and function, a study region needs to span a rainfall gradient with minimal variation in other factors (Fukami & Wardle, 2005; Liu & Schwartz, 2012).

Fortunately, the Texas Gulf Coastal Prairie (TGCP) is exactly such a region. Along the central TGCP, mean annual rainfall increases from 550 mm (semi-arid) to 1,350 mm/year (sub-humid) at a rate of 2.3 mm annual rainfall per km, making it the steepest non-montane rainfall gradient in the continental U.S.A. Along the gradient there are minimal covarying changes in underlying geology, elevation, and air temperature. Here, we report on 14 months of monthly sampling of invertebrate communities and associated environmental variables in nine streams distributed along the TGCP rainfall gradient. Our objective was to investigate how the composition, abundance, and diversity of stream invertebrate communities changed in response to interacting temporally proximate flow conditions, degrees of seasonality, and historical precipitation regimes.

Evidence suggests that greater predictability in flow regime increases temporal diversity through more specialist consumers occupying more temporally available niches and causing high temporal turnover in community composition (Tonkin et al., 2017). Thus, we predict that the abundance and diversity of invertebrates will increase with annual precipitation because wetter streams would have higher hydrological stability and seasonal predictability, supporting greater temporal diversity (Sheldon et al., 2002; Tonkin et al., 2017). This same mechanism should also drive greater seasonal shifts in invertebrate abundance and community composition in wetter sites. In contrast to the wetter streams, we predict that semi-arid sites would show stochastic temporal patterns of abundance and community composition driven by high and low flow events. We also expect semi-arid stream invertebrate communities to have greater proportions of taxa with functional adaptations to drought and flash flood disturbances including resistance to desiccation, ability to exit the water, multivoltinism, high dispersal potential, and high population turnover.

2 | METHODS

2.1 | Study region

The study sites span roughly 350 km along the coastline from Kingsville, Texas on the western edge to Ganado, Texas on the eastern edge (Table 1; Figure 1). Average annual precipitation is semi-arid (550 mm/year) on the western side and sub-humid (1,350 mm/year) on the eastern side (see Table 1). The region is characterised by constant elevation (study sites ranging from 14 to 62 m above sea level), comparable underlying geology (all Quaternary and sedimentary), and similar annual average air temperatures (20.8–22.2°C from east to west; Table 1). Land cover is a mix of forests, grasslands, and agricultural production of cattle, cotton, corn, and soy products (Chapman & Bolen, 2018). Vegetation shifts from thornwood groves in the semi-arid west to live oak forests towards the east.

2.2 | Sampling design

We chose sites on nine streams within the region that had similar mixed upstream land-cover, were wadeable, and were adjacent to a U.S. Geological Survey (USGS) daily flow gauge with a multi-year record (Falcone, 2011). Four of these sites (Tranquitas Creek, San Fernando Creek, Aransas River, and Mission River) were classified as semi-arid according to the Koppen classification system (Critchfield, 1983), whereas the other four (Perdido Creek, Placedo Creek, Garcitas Creek, West Mustang Creek, and East Mustang Creek) were classified as sub-humid. The sites were sampled monthly from August 2017 to November 2018, followed by an additional sampling event in March 2019. Monthly field surveys included the collection of habitat data, water chemistry data and samples of the macroinvertebrate communities. Surveys were conducted on 75-m reaches of each stream that were divided into four stations (0, 25, 50, and 75 m) for replicate, spatially explicit sampling.

2.3 | In-situ environmental data

On each site visit, environmental samples and measurements were collected at each of the four sampling stations distributed along the stream reach. At each station during each visit, we recorded

TABLE 1 Site environmental characteristics showing water basin size, elevation, mean temperatures, annual rainfall, and median flow rates

Site	Basin size (km^2)	Elevation (m)	20-year mean temperature (°C)	20-year mean rainfall (mm/year)	20-year mean median flow (L/s)
Tranquitas Creek	126	18	22.2	542	7.1
San Fernando Creek	193	62	22.2	567	37.4
Aransas River	77	47	21.5	685	151.5
Mission River	52	14	21.5	729	342.6
Perdido Creek	337	50	21.5	787	3.1
Placedo Creek	177	17	21.4	821	34.5
Garcitas Creek	970	20	21.2	843	56.6
West Mustang Creek	557	20	20.8	942	331.3
East Mustang Creek	190	20	20.9	950	17.6

Note: For 20-year means, we used records dating back 20 years (1997–2017) or as far back as was available. Sites are ordered from low to high precipitation levels. See *Methods* for descriptions of data sources.

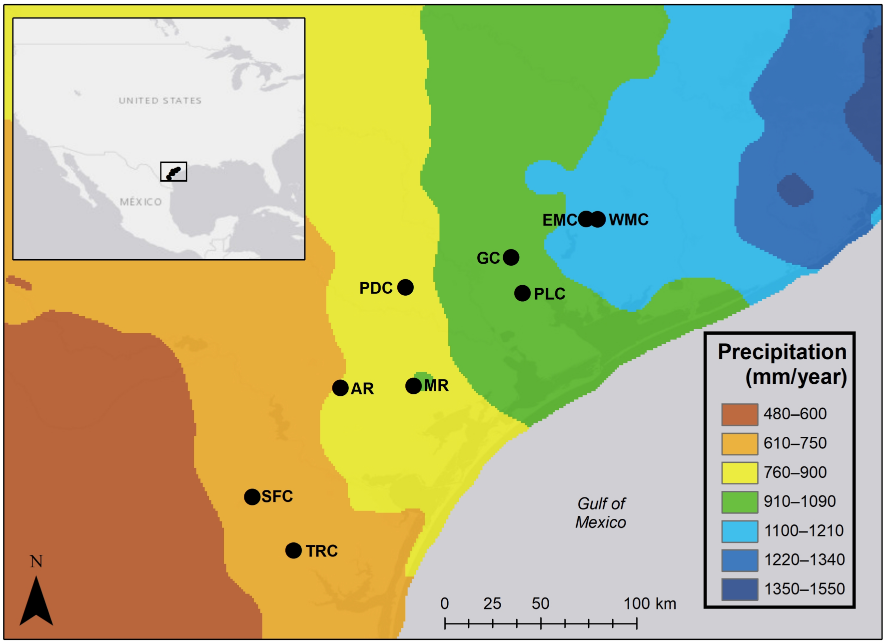

FIGURE 1 Study region in Texas, U.S.A. with sites labelled as EMC = East Mustang Creek, WMC = West Mustang Creek, PLC = Placedo Creek, GC = Garcitas Creek, PDC = Perdido Creek, MR = Mission River, AR = Aransas River, TRC = Tranquitas Creek, and SFC = San Fernando Creek. Annual precipitation (mm/year) varies across sites shown by colour gradient

channel width (m) and depth (m) in the thalweg and at each bank. Canopy cover was measured at centre channel and at each bank using a spherical densitometer. Bank slope (°) was measured on each bank using digital angle gauge. Sediment composition was recorded using a visual classification of relative proportion of surface sediment in silt/clay, sand, pebble, and cobble categories across the channel (Wentworth, 1922). Oxygen (mg/L), temperature (°C), conductivity (μcm), turbidity (NTU), and pH were measured using a YSI ProDSS multiparameter meter (YSI Incorporated). The abundance of diatoms (μg/cm^2), green algae (μg/cm^2), and cyanobacteria (μg/cm^2) were measured on natural substrate in the centre channel using a bbe BenthoTorch (bbe, Moldaenke, Germany). To characterise water column dissolved nutrients, two 60-ml water samples were collected and field filtered through 0.7 μm membrane filters, immediately placed in a cooler, and transported to the lab where they were placed in a −20°C freezer. One bottle was analysed for nitrates (NO_3^-), ammonium (NH_4^+) and orthophosphates on a Lachat Flow Injection Auto-Analyser by the Oklahoma Soil Water Forage Testing Lab. The other bottle was analysed for TN and DOC on a Shimadzu TOC Analyser (Shimadzu Corporation).

2.4 | Hydrological and catchment data

Mean annual rainfall and air temperature were estimated for each site using the bioclim dataset in the dismo library in R (Hijmans et al., 2017). The size of each upstream drainage basin (km^2) and the prevailing upstream land cover were extracted from the USGS GAUGES II database (Falcone, 2011). For all sites where it was available, 20 years of USGS water gauge daily discharge data was downloaded from the USGS (USGS, 2019). For sites with shorter records (n = 2), the maximum series length was downloaded. For each sampling date, we recorded the discharge (m^3/s) on the day of sampling, as well as the mean, median, maximum, and minimum discharge observed in the 2 weeks directly prior to sampling. The distributional characteristics (mean, median, range) of these same metrics were also calculated for those same dates across the long-term time series. Long-term records were also used to calculate flow metrics that describe the rate of change, frequency, magnitude, and duration of the flow environment (Olden & Poff, 2003). These included mean flow, median flow, 30-day maximum daily discharge, high-flow pulse percentage (% of time daily flow is more than 7 times median daily flow), low-flow pulse percentage (number of times discharge drops below the 25th percentile of flow days), variation in daily flow (mean daily flow/median daily flow), median annual maximum flow (median value of max flow observed in each year of the record), and flashiness as the Richards–Baker Index from Baker et al., (2004) (cumulative day-to-day changes in mean daily flow/cumulative mean daily flow for the entire series). We also measured the seasonality of the flow regime following the methods outlined in Tonkin et al. (2017) following Colwell's (1974) theory of quantifying periodic phenomena. Seasonality was calculated as M/P, or Colwell's contingency measure (M) divided by Colwell's within season predictability (P). This metric captures the degree to which the environment varies over the course of a year. Calculations were made using the function Colwells() in the hydrostats package in R (Bond, 2019).

2.5 | Invertebrate community samples

Invertebrate community samples were taken monthly at each site. Two methods of community sampling were employed: quantitative coring, and semi-quantitative kick and sweep sampling. To have an unbiased sampling method to compare across all sites through time, a benthic core sample (75 mm diameter × 50 mm deep) was taken on each visit at each sampling station (n = 4 per visit per site). Cores were placed into a 500-ml Whirlpak, fixed with 95% ethanol, and placed in a cooler before returning to the lab. Semi-quantitative sampling was employed to better characterise the rarer taxa present in each site, giving us a better estimate of diversity and community composition. For each site on each sampling date, we took 20 separate 0.093 m^2 samples using d-nets and kick nets distributed among the representative best available habitat in the stream channel (Southerland et al., 2007). Best available habitat included large woody debris and root wads, debris dams, riffle habitat, and overhanging vegetation. Replicate sweep and kick samples were pooled, field sorted to remove large sticks and leaves, fixed in 95% ethanol, and transported to the lab.

2.6 | Invertebrate sample processing

Semi-quantitative samples were processed using a modified version of the Texas Commission for Environmental Quality Surface Water Quality Monitoring Procedures for comparability (Texas Commission on Environmental Quality, 2019). Each sample was rinsed in a 500 μm sieve and then spread evenly across a gridded sorting tray. For each sample, grid cells were randomly selected and picked to completion until the cumulative count for the sample was >175 individuals. The total number of grid cells and the number of picked cells were recorded to later estimate the total abundance of invertebrates of each species in the sample and a rough estimate of individuals per unit area of best available habitat. Benthic core samples were also rinsed in a 500-μm sieve and then picked to completion to give a quantitative estimate of individuals/m^2.

Macroinvertebrates from both sets of sampling were enumerated and identified to lowest possible taxonomic resolution, typically genus level, using taxonomic reference guides (Merritt et al., 2008; Thorpe & Rogers, 2016). Taxa were assigned binary functional traits primarily extracted from an expanded version of the trait data published by Poff et al. (2006). Traits included the ability to breathe air, herbivore feeding mode, desiccation resistance, ability to exit the water, strong dispersal ability, multivoltinism, and we also included abundance in drift samples (see Table S1). We also assigned taxa a pollution tolerance value ranging from 0 (extremely sensitive) to 10 (very tolerant) from the U.S. Environmental Protection Agency National Aquatic Resource Survey assignments (USEPA, 2016). Additionally, we assigned each taxa the average production/biomass ratio observed for members of that family based on a meta-analytic dataset of all production values for freshwater invertebrates (Patrick et al., 2019). For genera missing from the dataset, we assigned trait values using a combination of literature review, best professional judgement, and comparison to typical traits for members of that taxonomic group.

2.7 | Data analyses

The abundance, taxonomic richness, Shannon–Wiener diversity, functional richness and Rao's quadratic entropy (*Q*; includes information about the evenness of a community's functional trait distribution), and taxonomic composition of communities were calculated among streams and through time. Calculations were made at nested spatial and temporal scales including individual samples, site level calculations for specific sampling dates, and site level calculations for the entire sampling period. Diversity calculations were made using the diversity() function in the vegan library in R (Oksanen et al., 2019). Functional diversity calculations were made using the dbFD() function in the FD library in R (Laliberté et al., 2014). Functional diversity metrics were calculated as both observed metrics and the deviation from expected values derived from null community assembly to assess the degree of environmental filtering or competitive exclusion occurring in each site (Petchey & Gaston, 2007). Null communities were assembled with an independent swap model (Gotelli, 2000) using the randomizeMatrix() function in the picante library in R (Kembel et al., 2010). Community metrics were based on aggregated kick/sweep samples while abundance calculations were based on core samples.

Multivariate analyses were conducted on community and environmental data to visualise and quantify patterns along the gradient using the Vegan library in R (Oksanen et al., 2019). Environmental data were ordinated using a principal component analysis to visualise spatial patterns in environmental data along the precipitation gradient using the rda() function. Non-metric multidimensional scaling (NMDS) was used to visualise and quantify patterns in community composition within and among streams using the metaMDS() function. In both cases, ordinations were fit using two axes for ease of interpretation and, for the NMDS, we used $n = 1{,}000$ iterations to maximise fit. Following the ordinations, we fit environmental vectors onto the ordination that maximised correlation between environmental variables and ordination using the envfit() function in the Vegan library to evaluate relationships between environmental variables and community composition (Oksanen et al., 2019).

We used generalised linear mixed models to evaluate relationships between invertebrate community metrics and environmental and climate variables. All models were ran using the lme() function in the nlme package in R (Pinheiro et al., 2018). Invertebrate community metrics (i.e., abundance, richness, diversity, functional richness, Rao's Q, NMDS axis 1 score, NMDS axis 2 score) were modelled separately as independent response variables. We treated stream identity as a random effect with an autocorrelation structure of 1 and used site-level estimates (i.e., annual averages, long-term flow metrics) as predictor variables. We used four different fixed effects modelling structures to evaluate the interactions of historical precipitation regime, seasonality, and temporally proximate flow conditions: (1) annual rainfall alone; (2) season (i.e., winter, spring, summer, autumn), climate (i.e., semi-arid vs. sub-humid), and the interaction of climate and season; (3) climate, minimum flow during the 2 weeks prior to sampling, and the interaction term; and (4) climate, maximum flow during the 2 weeks prior to sampling, and their interaction.

To assess the interaction between environment, taxa abundances, and taxa functional traits, we fit a fourth corner model to the data using the traitglm() function in the mvabund library (Wang

TABLE 2 Flow metrics for each of the stream sites (1997–2017)

Site	Flashiness	Max. 30-day daily flow (L/s)	Min. 30-day daily flow (L/s)	High-flow pulse percentage	Low-flow pulse percentage	Variation in daily flow	Median annual max. flow (L/s)	Seasonality
Tranquitas Creek	0.78	3,264	223	0.05	24.14	2.57	26,625	0.22
San Fernando Creek	0.91	3,617	21	0.09	21.14	12.57	28,639	0.22
Aransas River	1.05	1,761	21	0.07	7.55	12.06	11,565	0.18
Mission River	0.58	2,023	19	0.11	3.46	5.08	13,796	0.16
Perdido Creek	1.34	13,375	18	0.12	0.00	14.66	66,030	0.30
Placedo Creek	0.92	6,337	16	0.17	5.13	5.79	39,806	0.34
Garcitas Creek	0.81	4,251	14	0.17	4.72	6.11	18,852	0.23
West Mustang Creek	0.63	1,999	11	0.18	10.66	4.39	6,765	0.21
East Mustang Creek	0.791	1,268	19	0.28	0.00	5.22	70,335	0.29

Note: See *Methods* for descriptions of metrics and data sources. For instance, *high-flow pulse percentage* describes the % of time daily flow is above seven times median daily flow whereas *low-flow pulse percentage* denotes the number of times discharge drops below the 25th percentile of flow days. *Variation in daily flow* is the mean daily flow/median daily flow. Seasonality was essentially capturing the degree to which the hydrological environment varies over the course of a year (see Methods).

et al., 2020). The fourth corner model was fit as a generalised linear model with a least absolute shrinkage and selection operator penalty (Brown et al., 2014). Mean annual rainfall and the percentage of cobble substrate (a measure of substrate stability) were chosen as environmental predictors of species traits. We did not include additional flow variables because of their high correlation with annual rainfall, a master variable.

3 | RESULTS

3.1 | Physical and chemical characteristics of streams

Streams generally varied in their physical and chemical characteristics. Stream morphology and riparian canopy cover varied greatly among sites; however, there were no clear patterns matching the rainfall gradient (Table S2). Substrate was generally dominated by silt and sand with sites varying in smaller proportions of cobble and gravel (Table S3). Water temperature, dissolved oxygen concentrations, and pH values were also relatively consistent across sites. Conductivity was highest in the most arid stream (Tranquitas Creek) and generally decreased along the gradient to the sub-humid sites. Dissolved nutrient concentrations varied widely among streams (Table S4). Some of the highest nitrate and orthophosphate values were observed in two semi-arid streams, San Fernando Creek and Aransas River, and most other sites' concentrations were at least an order of magnitude lower. Ammonium concentrations were highest at the two driest streams, Tranquitas and San Fernando Creeks, and one of the wettest sites, West Mustang Creek, but all other sites were similar. Mean benthic algae concentrations varied greatly throughout the study region (Table S4). However, we observed that the lowest mean concentrations of all three types of algae (i.e., green algae, cyanobacteria, and diatoms) occurred in one of the wettest sites, West Mustang Creek.

Variation in hydrological characteristics among sites was largely explained by annual rainfall (Tables 2 and 3). For instance, minimum 30-day daily flows were highest in the three sites with the lowest mean annual precipitation: Tranquitas Creek (23 L/s), San Fernando Creek (21 L/s), and Aransas River (21 L/s). High-flow pulse percentage was positively related to mean annual rainfall, while minimum 30-day consecutive flow and low-flow pulse percentage were negatively related to mean annual rainfall. The linear relationship between seasonality and annual rainfall was not strong (Table 3), but the seasonality of semi-arid streams (0.20 ± 0.02 *SE*) was lower ($F_{1,7}$ = 7.0, p = 0.03) than seasonality of sub-humid streams (0.28 ± 0.02 *SE*).

3.2 | Community composition

Richness, diversity, abundance, and functional community composition varied across sites (Table 4). There were 168 different macroinvertebrate genera and 74 different families identified across all

TABLE 3 Linear relationships evaluated between mean annual rainfall (explanatory variable) and hydrologic metrics (response variables)

Response	Slope	Intercept	r^2	p
Flashiness	−0.01	1.04	0.02	0.71
Maximum 30-day daily flow	4.38	−140.79	0.16	0.28
Minimum 30-day daily flow	−0.01	1.17	0.59	**0.02**
High flow pulse percentage	0.01	−0.19	0.78	**<0.01**
Low flow pulse percentage	−0.44	42.25	0.56	**0.02**
Variation in daily flow	−0.07	12.89	0.06	0.54
Median annual maximum flow	14.30	17.54	0.07	0.51
Seasonality	0.01	0.12	0.14	0.31

Note: Bold indicates a significant *p*-value at $\alpha = 0.05$.

sites and all sampling dates (Table S5). The invertebrate communities averaged across sites were mainly predators (36% ± 3%), collector–gatherers (29% ± 2%), and filter feeders (19% ± 3%), but the relative proportions varied across sites and seasons (Table S6). The most widespread and abundant groups across sites and seasons were midges in the Chironomidae family, amphipods in genus *Hyalella*, mayflies in genus *Fallceon*, invasive snails *Melanoides tuberculata*, damselflies in genus *Argia*, and elmid beetles in genus *Stenelmis*. However, several taxa were highly abundant in one or two sites only. These included black flies in genus *Simulium*, water boatmen in genus *Trichocorixa*, caddisflies in genera *Smicridea* and *Brachycercus*, mayflies in genus *Centroptilum*, invasive Asian clams *Corbicula fluminea*, and hemipterans in genus *Rhagovelia*.

The NMDS of community composition converged after 52 iterations and had a stress value of 0.18 indicating a reasonable fit of the data. Most predictor variables were significantly correlated to the distance scores of the communities along the NMDS axes ($p < 0.05$; Table 5), especially annual temperature, precipitation, and the high and low pulse percentages. There was strong separation along the NMDS1 axis for nearly all variables (Figure 2, vector coefficients >0.80). Focusing on variables with the greatest explanatory power ($r^2 > 0.20$), we observed mean annual rainfall and mean flow to be positively associated with axis 1, and minimum 30-day daily flow, low and high flow pulse percentages, annual average temperature, and developed lands to be negatively associated with axis 1. Fewer variables displayed strong separation along the second axis. Variation in daily flow had a high negative correlation (vector = −0.91, $r^2 = 0.08$, $p = 0.02$) whereas median annual maximum flow (vector = 0.99, $r^2 = 0.10$, $p < 0.01$) and maximum 30-day daily flow (vector = 0.99, $r^2 = 0.13$, $p < 0.01$) had high positive correlations.

3.3 | Communities across flows, climate, and season

Linear mixed modelling frameworks revealed several relationships between community composition and flow, climate, and season across sites (Table S7). Average annual rainfall predicted community composition ($F_{1,7} = 10.5$, $p = 0.01$), but did not explain abundance, richness, or diversity measures. Specifically, the first ordination axis, which described community composition, was positively correlated with mean annual rainfall ($t_7 = 3.2$, $p = 0.01$, Figure 3a). Minimum antecedent flow (minimum stream flow observed during the 2 weeks prior to sampling; Figure 3b; $F_{1,67} = 10.4$, $p < 0.01$) and an interaction between minimum antecedent flow and climate predicted community composition ($F_{1,67} = 4.8$, $p = 0.03$). Community composition (position along the second ordination axis) was positively correlated with minimum antecedent flow in semi-arid, but not sub-humid sites ($t_{67} = 2.2$, $p = 0.03$). Minimum antecedent flow and climate also explained invertebrate richness (Figure 3c; $F_{1,67} = 5.5$, $p = 0.02$).

TABLE 4 Metrics describing the invertebrate communities found in each stream

Site	Functional richness	RaoQ	Richness	Shannon diversity	Abundance
Tranquitas Creek	8.4 ± 3.2	34.6 ± 4.8	12.8 ± 1.4	1.6 ± 0.1	11.8 ± 3.9
San Fernando Creek	41.2 ± 11.8	27.2 ± 4.1	12.1 ± 0.6	1.2 ± 0.1	11.5 ± 4.7
Aransas River	133.4 ± 7.6	51.5 ± 1.8	24.2 ± 0.9	2.5 ± 0.1	17.8 ± 5.3
Mission River	68.9 ± 15.5	40.4 ± 2.7	17.0 ± 2.2	1.9 ± 0.2	14.3 ± 3.2
Perdido Creek	44.7 ± 10.1	38.2 ± 4.4	18.1 ± 1.2	2.0 ± 0.2	8.3 ± 0.9
Placedo Creek	89.7 ± 19.1	45.0 ± 2.3	15.1 ± 2.3	1.9 ± 0.2	11.1 ± 4.4
Garcitas Creek	45.9 ± 8.1	40.3 ± 3.2	16.7 ± 0.6	1.7 ± 0.1	11.7 ± 2.7
West Mustang Creek	60.6 ± 12.1	40.6 ± 3.0	17.9 ± 2.2	1.8 ± 0.2	8.0 ± 2.3
East Mustang Creek	34.7 ± 8.9	32.9 ± 4.6	13.5 ± 1.5	1.6 ± 0.2	6.7 ± 1.4

Note: Values are reported as the mean ± *SE*. Sites are ordered from low to high precipitation levels.

TABLE 5 Correlations between environmental covariate data and non-metric multidimensional scaling (NMDS) axes

Predictor	NMDS1	NMDS2	r^2	*p*-value
Annual temperature	−0.98	−0.22	0.42	**<0.01**
Annual precipitation	0.95	0.31	0.41	**<0.01**
High flow pulse percentage	−0.84	0.54	0.40	**<0.01**
Low-flow pulse percentage	−0.99	−0.17	0.40	**<0.01**
Minimum 30-day daily flow	−1.00	−0.08	0.30	**<0.01**
Other-land cover	−0.96	−0.28	0.29	**<0.01**
Dev land cover	−0.95	0.30	0.27	**<0.01**
Mean daily flow	1.00	−0.07	0.24	**<0.01**
Crop land cover	0.98	0.18	0.17	**<0.01**
Maximum 30-day daily flow	0.13	0.99	0.13	**<0.01**
Median daily flow	0.96	−0.29	0.13	**<0.01**
Median annual maximum flow	−0.14	0.99	0.10	**0.01**
Forest land cover	0.98	0.21	0.10	**0.01**
Basin size	0.79	0.61	0.09	**0.02**
Variation in daily flow	−0.42	−0.91	0.08	**0.02**
Seasonality	0.84	0.55	0.03	0.27
Flashiness	−0.90	−0.43	0.02	0.32

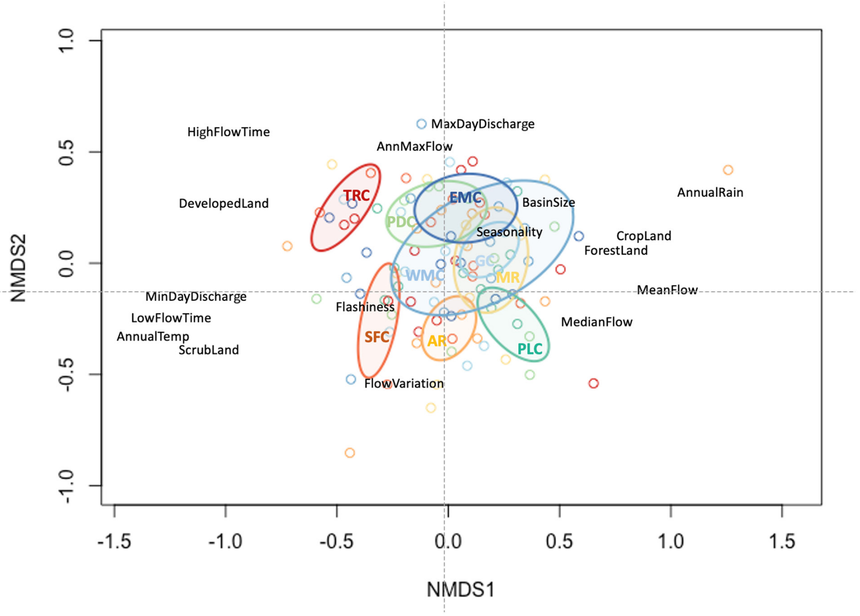

FIGURE 2 Non-metric multidimensional scaling (NMDS) of invertebrate communities. Each site, represented by a different colour ranging from highest annual rainfall (dark blue) to lowest (dark red), is characterised by points and grouped by ellipses calculated from the standard deviation. See Figure 1 for site name label descriptions. Environmental covariates are shown as black text and were fitted in the same ordination space

Higher richness was correlated with higher minimum antecedent flow rates in the samples from semi-arid sites, but not sub-humid sites ($t_{67} = -2.3, p = 0.02$). Season and local climate interacted to predict invertebrate richness (Figure 3d; $F_{3,63} = 3.3$, $p = 0.03$), but not explain richness independently. Explicitly, richness increased during summer ($t_{63} = 2.3$, $p = 0.02$) and winter ($t_{63} = 2.1$, $p = 0.04$) in sub-humid but not semi-arid sites.

3.4 | Functional traits and annual precipitation

The fourth corner analyses revealed both strong and weak correlations between invertebrate traits and the environment (Table 6; Figure 4). Species production/biomass ratio had a strong negative correlation with rainfall (−0.3), while desiccation resistance and dispersal ability had a weak negative relationship (>−0.1). Scraper–grazing/herbivory (0.3), abundance in the drift (0.3), and multivoltinism (0.2) were positively correlated with annual rainfall and pollution tolerance exhibited a weak relationship (<0.1). Proportion of cobble substrate was negatively correlated with pollution tolerance value (−0.2) and herbivory (−0.1).

4 | DISCUSSION

We evaluated the effects of annual rainfall on riverine benthic invertebrate community structure in streams distributed along a natural precipitation gradient in the Texas Gulf Coast Prairie. Matching our

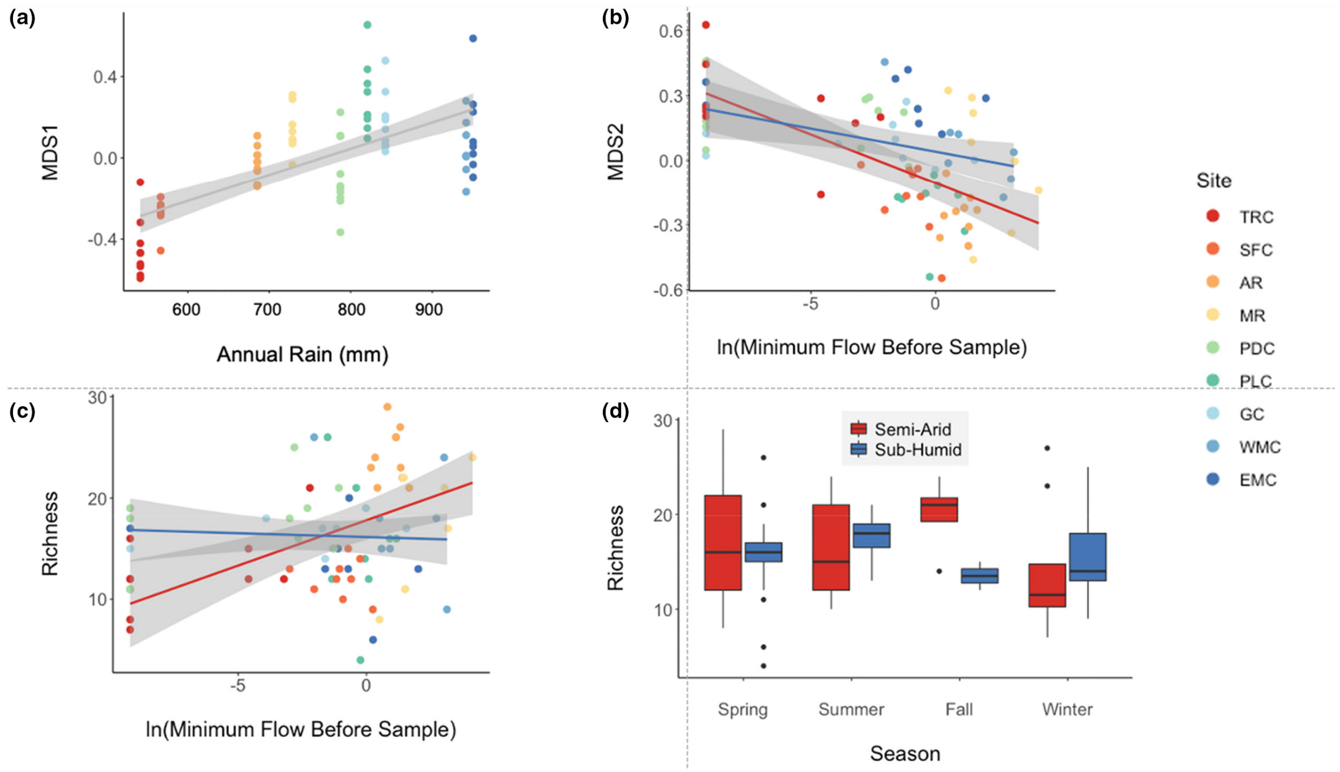

FIGURE 3 Relationships of community dynamics to environmental characteristics. Linear relationships are modelled in (a) showing the first non-metric multidimensional scaling (NMDS) axis from Figure 2 as a function of annual rainfall; (b) second NMDS and the natural log of the minimum daily flow observed in the 2 weeks before sampling; and (c) plots taxon richness and the 2-week minimum flow. (d) Uses a boxplot to show how richness varied across the seasons. In each plot, data from sub-humid streams is in blue and data from arid streams is in red. Site colours are consistent in (a), (b), and (c) and follow the key near (b) and (d)

TABLE 6 Correlations between traits and environmental data in the fourth corner analyses

Trait	Annual rainfall	% Cobble substrate
Pollution tolerance value	0.08	−0.18
Multivoltine	0.19	−0.03
Strong dispersal	−0.05	0.01
Ability to exit water	0.00	−0.01
Abundant drifter	0.31	−0.04
Desiccation tolerance	−0.05	0.02
Herbivore	0.27	−0.13
Ability to breathe air	0.00	0.00
Production/biomass ratio	−0.33	−0.03

expectations, we found that increased annual rainfall drove hydrological stability and predictability (i.e., seasonality). Semi-arid sites had a higher occurrence of unpredictable and proportionally severe low-flow disturbances and spikes in discharge matching the general observation that arid system streams tended to be more stochastic in their hydrology (Grimm & Fisher, 1989; Jackson & Fisher, 1986). However, this instability did not reduce biodiversity as we predicted. Instead, we observed significant compositional turnover along the rainfall gradient in both the identity of the resident fauna and the prevalence of dominant functional traits. We also observed that causes of temporal variation of the invertebrate communities within streams through time differed between the semi-arid and sub-humid streams. Temporal variation in community composition and taxonomic richness in the semi-arid sites was controlled by the occurrence of low-flow conditions, whereas temporal variation in taxonomic richness of the sub-humid sites varied with season. Taken together, these results support the hypothesis that rainfall is a master variable driving the local environment and the composition of the stream invertebrate communities.

Contrary to our expectations, neither biodiversity nor invertebrate abundance were related to mean annual rainfall. While the lowest mean richness, total genus richness through time, and mean Shannon–Wiener diversity indices occurred in the two stream sites at the driest end of the gradient, diversity in the remaining seven sites was variable and not in accordance with increasing precipitation. This may indicate that richness and biodiversity is higher in wetter sites, but the relationship is nonlinear and potentially operates as a threshold effect. Additional sites at the low precipitation end of the gradient would have allowed us to test this hypothesis. Abundance also ran counter to our expectations, with the lowest abundance observed on the wettest end of the gradient. Several possible explanations exist for the observed pattern. Arid sites are

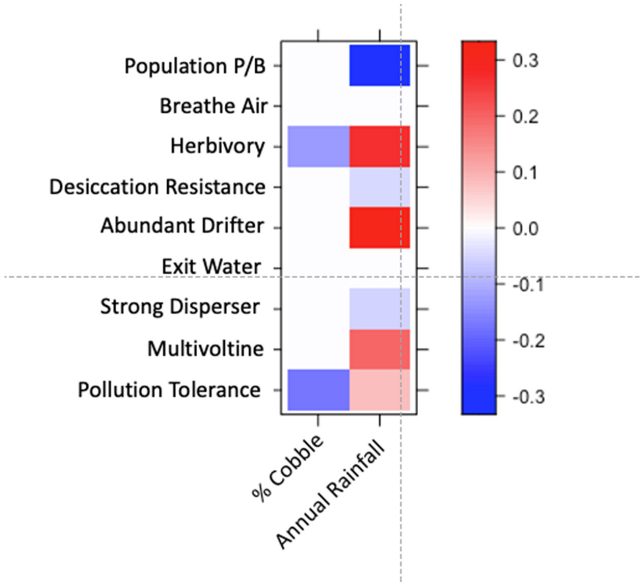

FIGURE 4 Fourth corner analysis level plot. Standardised interaction coefficient estimates for interaction terms test relationships between morphological traits and the environment while accounting for species abundances. Significant coefficient values were converted to colour scale and shown in red (positive) or blue (negative). Traits: Population P/B = population production/biomass ratio; Breathe Air = ability of the aquatic stage to breach air; Herbivory = strictly herbivorous feeding behaviour; Desiccation Resistance = adaptation to survive desiccation events; Abundant Drifter = dominance in drift samples; Exit Water = ability to exit water outside of emergence; Strong Disperser = >1 km of flight before laying eggs; Multivoltine = >1 generation per year; and Pollution Tolerance = ability to survive in low water quality. Environmental factors: % Cobble = percentage of cobble in stream bed (measure of substrate stability); and Annual Rainfall = mean annual rainfall rate over 20 years

thought to exhibit higher secondary production than temperate mesic sites (Benke & Huryn, 2010), so it may follow that biomass and abundance, which are often correlated with production, would show a similar pattern and explain low abundance at wetter sites. Another explanation is that, in similar sandy bottom streams in Alabama, the majority of invertebrate biomass and production occurs in stable substrates such as large woody debris rather than in the benthos (Benke et al., 1985; Benke & Wallace, 2014), which would not have been detected with the core sampling technique we used for quantitative analyses abundance. Therefore, given the potential higher availability of snags and woody debris in wetter sites, we may have underestimated abundance by only including benthic sampling. In general, even though all sites had predominantly sand and silt substrates, there may have been structural habitat differences across the gradient placing limits on potential abundances of benthic invertebrates (see Townsend & Hildrew, 1994).

While precipitation regime did not appear to control spatial patterns in diversity and abundance, factors controlling temporal variation within streams varied spatially across the rainfall gradient. We predicted that wetter streams would display greater seasonality of flow dynamics, which by extension would increase temporal niche availability and initiate more marked seasonal changes in benthic invertebrate communities. Matching a priori expectations, sub-humid systems had significantly higher seasonality in flow with lower day-to-day variability and repeated patterns across years in the timing of low- (winter, summer) and high- (autumn, spring) flow periods. As expected, invertebrate richness varied significantly across seasons in sub-humid but not semi-arid sites. Periods of higher richness in sub-humid streams co-occurred with seasonal lulls in flow conditions suggesting that diversity peaked during phases of relative stability (Death & Winterbourn, 1995). However, the lack of an effect of high-flow disturbances preceding sampling in sub-humid streams, indicates that these seasonal patterns are not simple responses to variation in flow conditions in the sites, but may be shaped by the long-term patterns of environmental conditions in each season including hydrology and climate (Lytle & Poff, 2004; Robinson, 2012). Similarly, low--flow events preceding sampling reduced taxonomic richness in all streams, but the effects were only significant in semi-arid streams presumably because of the relatively higher magnitudes and severity of low flow. Furthermore, these proximate flow events temporarily changed the composition of semi-arid stream communities suggesting that drier sites were more strongly shaped by day-to-day variation in flow conditions and, thus, may be selecting for a community of resilient species that can recuperate quickly from unpredictable changes (Lytle & Poff, 2004).

Multiple lines of evidence suggests that precipitation regime explains variation in the composition of invertebrate communities. Communities in the NMDS analysis were clearly oriented along the precipitation gradient and mean annual rainfall, air temperature, and high- and low-flow pulse percentages were top predictors for species composition. Hydrological variation associated with low-flow and high-flow events is strongly influenced by rainfall patterns (Dodds et al., 2015, 2019; Poff, 1996) so these can be considered a linked cluster of covariates. While mean annual air temperature was a strong predictor, it is highly correlated with mean annual rainfall and we can discount it as a major independent variable for several reasons. Mean air temperature does decrease by 1.4°C across the gradient, but the magnitude of this change is comparatively small relative to the 75% increase in mean annual precipitation. Furthermore, while air temperature changed slightly along the gradient, there was no observed change in mean annual water temperature within the sites, suggesting that there was no direct impact on the organisms in the water. Additionally, the air temperature difference may have been partially caused by the rainfall difference. There is significantly more gallery forest (as opposed to scrublands) and larger trees on the sub-humid side of the gradient due to the higher rainfall and vegetation has been shown to have a cooling effect on air temperatures (Yuan et al., 2020), absorbing rather than reflecting solar radiation and increasing evapotranspiration.

Several groups of organisms appeared as dominant taxa that responded to the rainfall gradient. On the drier side of the gradient, several invertebrate families including Chironomidae, Stratiomyidae, and Thiaridae had much higher abundances. In contrast, the relative abundance of crustaceans in genus *Hyalella* and order Decapoda increased with rainfall, as did several genera of mayflies such as *Cloeon* spp. We hypothesised that the sites on the arid side of the gradient would have a greater proportion of invertebrate taxa with functional adaptions to survive low-flow and flood disturbances. Multiple traits in the fourth-corner analysis were correlated with annual rainfall and supported this hypothesis. As expected, we found that taxa in wetter sites were slow-growing (low = population production/biomass ratio), not good dispersers, and lacked adaptations for resisting drying events (i.e., *Hyalella* sp. amphipods and *Cloeon* sp. mayflies). These traits are suggestive of taxa that have no need of rapid development during optimum conditions nor surviving or rapidly recolonising following a stream-reach drying event. This makes sense when considering that the sub-humid stream taxa would rarely experience droughts that would put them in danger of desiccation, and that arid stream taxa probably have shorter maturity times and adaptations fit for rapid recolonisation of streams post-flood (like chironomids, stratiomyids, and thiarids; Fisher et al., 1982; Gray, 1981; Grimm & Fisher, 1989; Lytle & Poff, 2004). Unfortunately, we did not measure hydrologically-driven changes in habitat availability across the precipitation gradient, but we acknowledge that both degrees of stream intermittency and spatial connectivity are important considerations in the complex relationship between invertebrate traits and drying (Cid et al., 2020; Gjerlov et al., 2003; Sánchez-Montoya et al., 2018). For instance, Mediterranean intermittent streams with dry channels were defined by organisms with life history adaptations such as short life cycles and resistant forms, but intermittent streams with pool availability were similar to perennial sites (García-Roger, 2017). The positive correlation coefficient between abundance in the drift and increasing annual rainfall rate was probably a function of the greater hydrological stability in sub-humid streams providing a fitness advantage for taxa that are actively drifting in order to avoid predation and actively seek out new resource patches (Cienciala & Hassan, 2018; Naman et al., 2016; Poff et al., 2006).

Not all significant correlations between traits and rainfall matched our expectations. The positive correlation between the herbivory trait and increasing annual rainfall, for example, was the opposite of what we expected to see since the high insolation of arid streams should have supported greater periphyton growth rates and therefore more scraper–grazer taxa (Benfield, 1997; Grafius, 1974; Pomeroy et al., 2000; Tait, 1997). Benthic algal concentrations varied greatly across sites and not in accordance with annual rainfall, which provides an explanation as to why herbivory did not decrease with increasing precipitation in our system. In addition, the regional pool of scraper–grazer taxa may not be able to tolerate the flashy flow regimes that are found on the arid side of our gradient. This corroborates with the predominance of scraper–grazer taxa such as amphipods and certain mayflies that we observed in the sub-humid sites. Our trait analysis also does not account for plasticity of individuals within a species to shift feeding tactics and vary in degrees of herbivory (Bêche et al., 2006). Future work in these streams focused on assessing diet and the tropic basis of production could quantify differences of herbivory across the gradient.

Another non-intuitive relationship was the positive relationship between multivoltine taxa and annual precipitation. Previous literature suggests that we should expect to observe greater multi-voltinism in the semi-arid stream sites as a strategy for rapidly increasing populations following hydrological disturbances (Mellado-Díaz et al., 2007). Multi-voltinism is also expected to affect biomass turnover as annual production of new biomass by multivoltine species is expected to be relatively high compared to standing biomass at any one time (Townsend & Hildrew, 1994). Contrary to this expectation, we observed decreasing rates of turnover with increasing levels of annual rainfall. This relationship may be explained by ion concentration tolerance limits of dominant multivoltine taxa. For example, the *Fallceon* spp. of baetid mayflies make up 30% of multivoltine taxa and become increasingly common in wetter sites, driving the observed relationship. While *Fallceon* spp. are more tolerant than other taxa in the order Ephemeroptera (Carlisle et al., 2007), mayflies are generally intolerant of high conductivity (Hassell et al., 2006; Merritt et al., 2008).

The proportion of cobble in the stream bed was negatively correlated with taxa with higher pollution tolerance values. Cobble substrate is excellent for a variety of mayflies and caddisflies that have comparatively low pollution tolerance values (or high sensitivity; Carlisle et al., 2007; Hering et al., 2009; Merritt et al., 2008). These findings support previous literature that found that stable environmental conditions, such as large cobble substrate, promote a greater taxonomic and functional diversity of invertebrates (Schriever et al., 2015).

5 | CONCLUSION

We have provided further evidence that rainfall is a key factor shaping stream ecosystems (Bonada et al., 2007; Lytle & Poff, 2004; Mims & Olden, 2012). Our work shows that precipitation regime influences functional composition and the spatial and temporal variation in taxonomic composition of stream macroinvertebrates. The results suggest that the impacts of precipitation regime manifest primarily through temporal variability in daily flows, particularly the frequency of low-flow disturbances. This matches with other recent work demonstrating the importance of low-flow events to ecosystem productivity (i.e., Patrick et al., 2019).

We add to a growing body of work that suggests that stream invertebrate communities are susceptible to alteration of the spatial distribution of precipitation associated with global climate change (Carey et al., 2021; Crabot et al., 2021; Vaughn, 2010), not just the effects of changing temperature (Arai et al., 2015; Burgmer et al., 2006; Domisch et al., 2011; Hering et al., 2009). Future ecological studies may be able to develop a more mechanistic understanding of the relationships between rainfall regime and community structure, which may also reveal the ecological–evolutionary consequences of changing rainfall patterns. By combining knowledge from these studies with large-scale climate models, we may be able to predict the probabilities of regional shifts in ecosystem structure related to changing climate conditions. By identifying regions most likely to undergo a community phase shift, we can facilitate the development of risk assessment and management approaches to preserve ecosystem functions and services in the face of precipitation regime changes.

AUTHOR CONTRIBUTION

Conceptualisation: F.R.C., S.K.K., B.K.R., J.D.H., C.J.P. Conducting the research: F.R.C., S.K.K., J.D.H., C.J.P. Developing methods: F.R.C., B.A.S., C.J.P. Data analysis and interpretation: F.R.C., B.A.S., C.J.P. Preparation of figures and tables: F.R.C., B.A.S., C.J.P. Writing: F.R.C., B.A.S., S.K.K., B.K.R., J.D.H., C.J.P.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article and upon request from the authors.

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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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