

STRUCTURE AND SEASONAL VARIATION OF COASTAL PRAIRIE STREAM BENTHIC
INVERTEBRATE COMMUNITIES ACROSS A PRECIPITATION GRADIENT

A Thesis

by

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This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Predicted changes in precipitation patterns associated with climate change are expected to impact flowing water ecosystems. We used a natural climate gradient to enhance our understanding of how impacts will occur. We surveyed nine streams in the Texas Gulf Coastal Prairie that were distributed across a semi-arid to mesic rainfall gradient. A suite of characteristics including benthic invertebrate community characteristics, flow conditions, and water quality variables were assessed monthly in each site to relate precipitation regime to stream structure and function. Precipitation regime was observed to be a master variable. As annual rainfall increased, the flow environment became more stable within seasons and predictable across seasons. Invertebrate community composition was significantly influenced by rainfall and correlated flow variables. Mesic sites were dominated by slower growing taxa without adaptations for desiccation resistance and strong dispersal. Sites with higher low flow pulse percentage (associated with more arid sites) were dominated by taxa with the ability to exit the water. Mesic sites displayed greater seasonal variation in composition and species richness than semi-arid sites, whereas the communities in semi-arid sites were strongly shaped by flow conditions in the weeks prior to sampling. These observations demonstrate how small changes in rainfall can drive large changes on ecosystem structure and function and suggest that climate change may have sweeping impacts on the lotic fauna of the Texas Gulf Coastal Prairie.

DEDICATION

I dedicate this thesis to my father and mother, Francisco and Yolanda Carvallo. Thank you both for your dedication to and belief in my academic success.

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I want to thank my mentor, Dr. Christopher J. Patrick for his invaluable knowledge and expertise and with whose guidance, beginning with hiring me as an undergraduate research technician in 2017, this achievement of becoming the first in my family to earn a graduate degree was made possible. I am also grateful for the support and mentorship I received from Dr. James D. Hogan, who has taken me under his wing and guided me through the intricacies of the TAMUCC Biology Master's program. I would like to especially thank Dr. Brandi Kiel Reese for inspiring me to pursue a graduate degree during my undergraduate studies and guiding me to success. I would like to thank the faculty and staff at TAMUCC for providing an excellent and supportive academic environment as I advanced through the Biology Master's Program, especially thanking Dr. Gregory Buck and Githzette Planas-Costas for providing me with my first lab experience opportunity in the Microbiology Prep Laboratory along with my academic advisor, Ronnie Emanuel, and administrative staff members Ken Brown and Suzanne Burgess. I would like to thank my colleagues and lab mates Jennifer Whitt, Alex Solis, Victoria Jenkins, Sean Kinard, Chris Groff, Don Youngberg, Roy Roberts, Hannah Berger, Colton Muller, SeanahLisa Crenshaw and Madison Hightower for all their efforts in the field and in the lab and for creating a wonderful work environment. I would also like to thank all the volunteers who helped with field and lab work including Lance De Leon and Elizabeth Ennis. I especially thank my girlfriend, , Jecilyn Luckado, for both her efforts in the field and lab as well as the encouragement and support she has shown me as I completed my program. Lastly, I express extreme gratitude to my wonderful parents, Francisco and Yolanda Carvallo, without whose support and encouragement I could not have achieved this accomplishment. This research was

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Introduction

Average global temperature has exponentially increased since the industrial revolution from 0.8-1.2°C, causing significant changes in the frequency, intensity and predictability of weather events now and in the future (IPCC, 2018). Premature spring snow melts, increased forest fires, and increases in aridity are some of the expected effects (Seager *et al.*, 2007). Simultaneously the variation in the frequency, intensity and timing of rain events is expected to become less predictable (Allan & Soden, 2008).

Rainfall, which drives the hydrologic cycle, is a key factor shaping stream ecosystems (Lytle & Poff, 2004; Mims & Olden, 2012). While temperature effects are well studied (Burgmer, Hillebrand & Pfenninger, 2006; Hering *et al.*, 2009; Domisch, Jähnig & Haase, 2011; Arai, Nukazawa, Kazama & Takemon, 2015), precipitation has largely been studied in the context of large spatial gradients as part of a suite of co-varying environmental drivers (Woodward, Perkins & Brown, 2010). Therefore, it is important that we increase our understanding of how stream ecosystems are directly affected by precipitation rates so that we can be better prepared to prevent or mitigate the catastrophic effects of climate change in the future. Forecasting the specific effects of changes to precipitation patterns on stream ecosystems is challenging because studies isolating this driver are underrepresented in the literature (Reynolds, Shafroth & Poff, 2015; Adámek, Konečná, Podhrázská, Všetická & Jurajdová, 2016). However, many studies have shown that macroinvertebrate communities are shaped by hydrologic flow regime, which is largely controlled by precipitation regime (Poff & Ward, 1989; Lake, 2003; Lake, 2005; Dodds *et al.*, 2019; Mathers, Stubbington, Leeming, Westwood & England, 2019).

Although we know that ecosystems respond to gradual changes in environmental conditions such as precipitation these responses may not be linear in nature (Scheffer, Carpenter, Foley, Folke & Walker, 2001; Carpenter, 2001). Ecosystems can sometimes rapidly shift between states in response to environmental conditions that change at a steady rate. These abrupt, significant and sometimes persistent shifts between ecosystem states are referred to as regime shifts (Ludwig, Walker & Holling, 1997; Scheffer & Carpenter, 2003). After a regime shift occurs, processes can positively reinforce the environmental conditions to maintain the changed state, often impacting human societies in negative ways (Biggs, Carpenter & Brock, 2009). Lotic systems are especially susceptible to changes in their climate and so may be particularly at risk of climate change driven regime shifts (Woodward, Perkins & Brown, 2010; Dodds, Gido, Whiles, Daniels & Grudzinski, 2015).

While communities of organisms in specific habitats are drawn from a regional pool of species that are capable of dispersing regionally among habitats, the local species pool is also filtered by environmental conditions within local habitats (Tonn *et al.*, 1990; Poff, 1997; Leibold *et al.*, 2004; Patrick & Yuan, 2017). It is this environmental filtering that can result in drastic community shifts as conditions change through space or time. In lotic systems, there are many conditions that will affect the community assemblage of a specific stream reach including stream morphology, hydrology, nutrient availability, habitat heterogeneity and biological factors like competition, predation and basal resource production (Huston, 1979; Poff & Allan, 1995). These conditions that filter riverine communities can be categorized into one of three central categories of factors affecting the stream assemblage: environmental constraints, biotic interactions and disturbances (Resh *et al.*, 1988; Mackey & Currie, 2001; Stanley, Powers & Lottig, 2010; Patrick & Swan, 2011). Common environmental gradients that have been shown to drive ecosystem

structure and function include drought/flood frequency and duration, temperature, soil types and environmental stress/rates of change (Dittmann *et al.*, 2015; Krishnadas, Kumar, & Comita, 2016). This conceptual framework is useful for evaluating the probable relationships between environmental drivers and riverine communities along precipitation gradients and is particularly important for predicting how climate change might alter the structure and function of ecosystems.

Stream ecosystem structure and function changes in predictable ways along precipitation gradients across the globe. Arid systems are characterized by high solar insolation and low allochthonous input due to a lack of canopy cover from riparian zone trees. These streams depend primarily upon autochthonous carbon from primary productivity (Benfield, 1997; Pomeroy *et al.*, 2000). Arid stream hydrologic regimes are typically flashy, with punctuated periods of dry riverbed and high energy flash floods a common but stochastic occurrence (Jackson & Fisher, 1986). Arid streams tend to contain low species richness (Sheldon, Boulton & Puckridge, 2002) and biomass production is stochastic through space and time, at times exceeding the secondary production of mesic systems by an order of magnitude (Lamberti & Steinman, 1997; Grimm & Fisher, 1989,). Mesic streams are characterized by dense canopy cover provided by a high number of 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 hydrologic cycle, mesic systems typically have much more stable hydrologic regimes, more stable baseflow conditions and floods with more gentle rising and falling limbs occurring at predictable periods within the year (Mellado-Díaz, Suárez Alonso & Vidal-Abarca, 2007; Dodds, Gido, Whiles, Daniels & Grudzinski, 2015). 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, Jason Todd, Muneeppeerakul, Rinaldo & Rodriguez-Iturbe, 2013; Tonkin, Bogan, Bonada, Rios-Touma & Lytle, 2017). The difference in hydrologic conditions, particularly frequency of disturbance, and basal resources appear to be two key factors driving differences between arid and mesic rivers. This matches with a recent meta-analytic study that showed that world-wide, frequency of low flow disturbance events was the most important predictor of riverine benthic invertebrate secondary production after water temperature (Patrick *et al.*, 2019).

Concordant with these patterns, the community composition in stream ecosystems also varies across precipitation gradients. Haddad *et al.* (2008) proposed that the autecological (functional) traits of species in a community can be a predictor of their response to disturbances. Most organisms tend to have a trade off in adaptations that favor either resistance and residence (superior competitors) or resilience and rapid succession (inferior competitors) (Mouquet & Loreau, 2003). Resistance is the ability of an environmental variable, population or community to resist change in the face of a disturbance (Harrison, 1979). Resilience is a measure of the rate at which an environmental variable, population or community recovers from a disturbance (Webster, 1983). Arid systems have been observed to be inhabited predominantly by taxa that are better adapted for recolonization through faster generation time, wider dispersal ability and larger numbers of offspring that are also more tolerant of fluctuating environmental conditions than the taxa in the more hydrologically stable humid systems (Mellado-Díaz, Suárez Alonso & Vidal-Abarca, 2007). Mesic streams in unimpacted drainages are often inhabited by communities

consisting of more specialized competitive species than rapidly colonizing species (Boulton, Peterson, Grimm & Fisher, 1992). The differences in basal resources should also drive higher proportion of scrapers and grazers, rather than shredders in the arid sites than mesic sites due to high algal production caused by high insolation (Grafius, 1974; Benfield, 1997; Tait, 1997).

A challenge with interpreting the causal nature behind prior observations is that so much changes between different ecoregions. Observational studies that derive process from pattern such as 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 air temperature and sun angle that are unavoidable in large latitudinal studies (Fukami & Wardle, 2005). Ideally the space for time approach to evaluating the effect of rainfall alone on stream structure and function would be used in a region that spans a rainfall gradient without changes in other factors such as underlying geology, elevation and temperature (Fukami & Wardle, 2005; Liu & Schwartz, 2012). Fortunately, the Texas Gulf Coastal Prairie (TGCP) is exactly such a region. Within the center of this ecoregion, mean annual rainfall increases from 55cm (semi-arid) to 120 cm/yr (mesic) with minimal covarying changes in underlying geology, elevation, and air temperature. Using the TGCP region as a study system, our primary objective was to investigate how the composition, abundance, diversity of stream invertebrate communities' changes with precipitation regime. Over a 14-month period we performed monthly sampling of invertebrate communities and associated environmental variables in nine streams distributed along precipitation gradient that transitions from semi-arid to mesic climate conditions. We predicted that the abundance and diversity of invertebrates would increase with annual precipitation because the mesic sites would have higher hydrologic stability and seasonal predictability, based on observations in the literature that arid streams have lower richness and humid streams should

support greater temporal diversity (Sheldon, Boulton & Puckridge, 2002; Tonkin, Bogan, Bonada, Rios-Touma & Lytle, 2017). Additionally, we expected that the drier sites would have greater proportions of taxa with functional adaptations to precipitation regimes marked by high intensity drought and flash flood disturbances. Those traits include resistance to desiccation, ability to exit the water, multivoltinism, high dispersal potential, and high turnover rates. We further predicted that the wetter sites should display greater seasonal shifts in invertebrate total abundance, diversity and community composition whereas the more arid sites would be more strongly structured by flow events.

Study Region

The freshwater habitats of the TGCP have not been well studied by stream-ecologists. The lack of research on the stream ecosystems in this region contributes to the value of this investigation. The study sites span roughly 350 km along the coastline from Kingsville, Texas in the western edge to Ganado, Texas in the eastern edge (Figure 1, Table 1). The region experiences a rapid and significant increase in average annual precipitation from semi-arid conditions (55 cm/yr) in the west to a sub-humid climate (135 cm/yr) in the east, giving an average rate of change in precipitation of about 0.25 cm/km from west to east (see Table 1). The region is also characterized by relatively constant elevation (18-61.6 m), underlying geology (all quaternary or sedimentary), and air temperatures (20.8 – 22.2°C) across the precipitation gradient. Within this region, we chose nine streams sites that had similar mixed upstream land-cover, were wadeable, and were adjacent to a USGS flow gauge with a multi-year daily flow record (see Table 1) (Falcone, 2011).

Materials & Methods

Sampling Design

The nine 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 75m reaches of each stream that were divided into four stations (0, 25, 50 and 75m) for replicate spatially explicit sampling.

In-Situ Environmental Data

On each site visit, environmental samples and measurements were taken at each of the four sampling stations distributed along the stream reach. At each station, oxygen (mg/L), temperature (°C), conductivity (μcm), turbidity (NTU), and pH were measured using a YSI ProDSS multiparameter meter (YSI Incorporated, Yellow Springs, OH, USA). The abundance of diatoms ($\mu\text{g}/\text{cm}^2$), green algae ($\mu\text{g}/\text{cm}^2$), and cyanobacteria ($\mu\text{g}/\text{cm}^2$) were measured using a bbe BenthosTorch (bbe, Moldaenke, Germany). Wetted channel width (m) was measured using tape measure. The proportion of sediment in the corresponding grain size categories at each station was recorded (Wentworth, 1922). Canopy cover was measured using a spherical densitometer on the left bank, right bank, and in the center channel. Water depth (m) was measured in these same three locations. Bank slope was measured for both sides of the stream at each station using a digital angle gauge. To characterize dissolved nutrients in the water 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 are placed in a -20°C freezer. One bottle was analyzed for Nitrates (NO_3^-), Ammonium (NH_4^+) and Orthophosphates on a Lachat Flow

Injection Auto-Analyzer by the Oklahoma Soil Water Forage Testing Lab. The other bottle was analyzed for TN and DOC on a Shimadzu TOC Analyzer by the Ulseth Lab at Sam Houston State University.

Hydrologic and Watershed Data

The average annual rainfall and air temperature metrics for each site were extracted from the bioclim dataset in the dismo library in R (Hijmans, Phillips, Leathwick, & Elith, 2017). The size of each upstream drainage basin (km^2) and the prevailing upstream land cover were extracted from the USGS GAGES II database (Falcone, 2011). For all sites where it was available, twenty years of USGS water gauge daily discharge data was downloaded from the USGS website (USGS, 2019). For sites with shorter records, 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 two weeks directly prior to sampling. The distributional characteristics (mean, median, range) of these same metrics were also calculated for those same dates across the 20-year time series. For example, we calculated both the average flow during the two weeks prior to sampling and the average flow during that two-week period of the year for the preceding 20 years of data. In addition to data corresponding to sampling date, we also calculated flow metrics that describe the rate of change, frequency, magnitude, and duration of the flow environment for the 20-year record (Olden & Poff, 2003). These included mean flow, median flow, 30 day maximum daily discharge, high flow pulse percentage (% of time daily flow is above 7x median daily flow), and 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 (R-B Index) from Baker, Richards, Loftus & Kramer, 2004 (cumulative day-to-day changes in mean daily flow/cumulative mean daily flow for the entire series) (Baker, Richards, Loftus & Kramer, 2004). We also measured the seasonality of the flow regime following the methods outlined in Tonkin *et al.* (2017) following Colwell's theory of quantifying periodic phenomena (1974). Seasonality is calculated as Colwell's contingency measure (M) divided by 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).

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 (7.5cm diameter x 5cm deep) was taken on each visit at each sampling station (n=4 per visit per site). Cores were placed into a 500ml whirlpak, fixed with 95% ethanol, and placed in a cooler before returning to the lab. Semi-quantitative sampling was employed to better characterize 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 m² samples using d-nets and kick nets distributed among the representative best available habitat in the stream channel (Southerland *et al.*, 2005). Best available habitat included large woody debris and root wads, debris dams, riffle habitat, and overhanging vegetation. Samples were taken by sweeping through habitat or vigorously disturbing approximate 0.093 m² of habitat just upstream of the net. Replicate samples were pooled, field sorted to remove large sticks and leaves, fixed in 95% ethanol, and transported to the lab.

Invertebrate Sample Processing

Semi-quantitative samples were processed using a modified version of the Texas Commission for Environmental Quality (TCEQ) Surface Water Quality Monitoring (SWQM) Protocol for comparability (TCEQ, 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 per 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, Cummins, & Berg 2008; Thorpe & Covich, 2016). Taxa were assigned the following binary traits: Ability to breathe air (allows organism to survive low oxygen and dry stream bed conditions that are more likely to occur in arid streams; 1 = ability to breathe air during aquatic life stage, 0 = cannot breathe air during aquatic life stage), herbivore feeding mode (Organisms who primarily feed on vegetation should be better fit for arid streams that generally have higher primary production; 1 = strictly herbivorous diet, 0 = not strictly herbivorous diet), desiccation resistance (allows organism to survive dry stream bed conditions that are more likely to occur in arid streams 1 = has adaptations to survive desiccation, 0 = lacks adaptations to survive desiccation), abundant in the drift (organisms that are more abundant in drift samples should be better fit for stable flow conditions in more humid streams; 1 = dominant occurrence in drift samples, 0 = not dominant occurrence in drift samples), ability to exit the water (allows organism

to survive low oxygen and dry stream bed conditions as well as flash floods that are more likely to occur in arid streams by moving to better habitats; 1 = can exit the water during the aquatic life stage, 0 = cannot exit the water during the aquatic life stage), strong dispersal ability (organisms can disperse their progeny over greater distances and to more habitats, which may be sparse or ephemeral in arid environments, to increase offspring success; 1 = female flies > 1 km before laying eggs, 0 = female flies < 1 km before laying eggs) and multivoltinism (organisms can reproduce multiple times within a year and thus more rapidly colonize new habitats; 1 = > 1 generation/year, 0 = < one generation/year). Binary trait data for each taxon were primarily extracted from an expanded version of the trait data published by Poff *et al.*, (2006). We also assigned taxa a pollution tolerance value ranging from 0 (extremely sensitive) to 10 (very tolerant) from the United States Environmental Protection Agency (USEPA) 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.*, unpublished). For genera missing from the dataset we assigned trait values using a combination of literature review, best professional judgment, and comparison to typical traits for members of that taxonomic group.

Statistical analyses

The abundance, taxonomic richness, Shannon-Wiener diversity, functional diversity (Rao-Q, Functional Richness), 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, Legendre & Shipley, 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.

We used both generalized and hierarchical linear models to evaluate relationships between invertebrate community metrics and environmental and climate drivers. Relationships between site level variables (annual averages, climate, long term flow metrics) were evaluated using generalized linear models. To test for the effect of climate regime on invertebrate community response variables (abundance, richness, diversity, functional richness, RaoQ, NMDS Axis 1 score, NMDS Axis 2 score), we ran mixed-effects models using the lme() function in the nlme package in R (Pinheiro *et al.*, 2018). To evaluate the effect of rainfall on invertebrate communities, annual precipitation was treated as the predictor variable and stream identity was treated as a random effect with an autocorrelation structure of 1. To evaluate the interaction between climate and flow conditions preceding sampling or climate and season of sampling, we ran three different mixed effects models against each community response variable. In each model we included one of three predictor variables: season (winter, spring, summer, fall), minimum flow during the two weeks prior to sampling, or maximum flow during the two weeks prior to sampling. We then treated climate of each site (semi-arid vs mesic) as a

fixed effect, included an interaction term between climate and other predictor, and treated stream identity as a random effect with an autocorrelation structure of 1.

Multivariate analyses were conducted on community and environmental data to visualize and quantify patterns along the gradient using the Vegan library in R (Oksanen, 2013). Environmental data were ordinated using a PCA (principal component analysis) to visualize spatial patterns in environmental data along the precipitation gradient using the `rda()` function. Non-metric multidimensional scaling (NMDS) was used to visualize 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 $n=1000$ iterations to maximize fit. Following the ordinations, we fit environmental vectors onto the ordination that maximized correlation between environmental variables and ordination using the `envfit()` function in the Vegan library to evaluate relationships between environmental drivers and community composition (Oksanen, 2013). 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 *et al.*, 2020). The fourth corner model was fit as a generalized linear model with a least absolute shrinkage and selection operator (LASSO) penalty (Brown *et al.*, 2014). Two separate fourth corner models were fit. One with only a single environmental variable, mean annual rainfall, a second with low flow pulse percentage, minimum flow during the two weeks prior to sampling, proportion of cobble substrate, and water temperature at the time of sampling. The reason for two separate analyses was the high correlation between annual rainfall, a master driver, and the flow variables. The flow variables chosen for the second analysis reflect observations of their importance for determining substrate type and water quality.

Results

Physical and Chemical Characteristics in the stream

Morphology and riparian canopy cover varied greatly among sites (Table 2). Mean depth was lowest at Aransas River (0.153 ± 0.058 m) and highest at Tranquitas Creek (1.088 ± 2.456 m). Mean width ranged from 2.94 ± 0.212 m at San Fernando Creek to 8.174 ± 1.322 m at West Mustang Creek. Mean proportion of canopy cover varied greatly from 0.094 ± 0.119 at Perdido Creek to 0.78 ± 0.145 at Tranquitas Creek.

Water chemistry metrics also varied greatly among sites (Table 2). Mean conductivity was highest in the most arid stream site (Tranquitas Creek, $3497.092 \pm 1402.629 \mu\text{S/cm}$) and generally decreased along the gradient to the mesic sites, with the lowest value at Garcitas Creek ($456.064 \pm 107.726 \mu\text{S/cm}$). Water temperature means ranged from $19.993 \pm 5.846^\circ\text{C}$ at Garcitas Creek to $22.156 \pm 6.364^\circ\text{C}$ at Mission River. Mean dissolved oxygen concentrations ranged from $5.37 \pm 5.671 \text{ mg/L}$ at Tranquitas Creek to $7.623 \pm 3.194 \text{ mg/L}$ at Placedo Creek. Mean pH values were relatively constant, ranging from $8.014 \pm 0.389 \text{ mg/L}$ at Perdido Creek to $8.428 \pm 0.897 \text{ mg/L}$ at Tranquitas Creek.

Substrate Composition

We found that substrate proportions varied greatly among sites (Table 3). Aransas river's substrate was composed of primarily gravel (0.499 ± 0.185), sand (0.243 ± 0.104) and cobble (0.188 ± 0.142). East Mustang Creek's substrate was composed of primarily silt (0.501 ± 0.171) and sand (0.411 ± 0.171). Garcitas Creek's substrate was composed of primarily. substrate was composed of primarily. substrate was composed of primarily. substrate was composed of primarily. substrate was composed of primarily. Mission River's substrate was composed

of primarily sand (0.733 ± 0.126) with some silt (0.116 ± 0.066). Perdido Creek's substrate was composed of primarily sand (0.403 ± 0.099) and silt (0.349 ± 0.147) with some boulder (0.123 ± 0.112). Placedo Creek's substrate was composed of primarily sand (0.432 ± 0.141) and silt (0.372 ± 0.16) with some cobble (0.108 ± 0.089). San Fernando Creek's substrate was composed of primarily silt (0.435 ± 0.141), gravel (0.302 ± 0.14) and sand (0.202 ± 0.124). Tranquitas Creek's substrate was composed of primarily silt (0.572 ± 0.109), gravel (0.182 ± 0.114) and sand (0.166 ± 0.104). West Mustang Creek's substrate was composed of primarily sand (0.841 ± 0.135) with some silt (0.159 ± 0.135).

Nutrient and Benthic Algae Concentrations

We also observed wide variation in concentrations of nutrients (Table 4). Nitrate concentrations were by far the highest in San Fernando Creek (12.979 ± 4.021 mg/L) with the next highest concentrations, nearly half as high, at Aransas River (6.804 ± 4.499). The rest of the sites' nitrate concentrations were much lower, ranging from 0.031 ± 0.03 mg/L at Perdido Creek to 1.727 ± 1.387 mg/L at Placedo Creek. Ammonium concentrations were lowest at Garcitas Creek (0.119 ± 0.07 mg/L) and highest at West Mustang Creek (0.379 ± 0.685 mg/L). Orthophosphate concentrations were distinctively highest at San Fernando Creek (mg/L) and Aransas River (mg/L), with the rest of the sites ranging from 0.346 ± 0.854 mg/L at East Mustang Creek to 0.106 ± 0.126 mg/L at Placedo Creek.

Mean benthic algae concentrations measured with the bbe BenthosTorch varied greatly throughout the study region (Table 4). However, we observed that the lowest mean concentrations of all three types of algae (green algae, cyanobacteria and diatoms) occurred in West Mustang Creek. The highest mean concentrations of green algae were recorded in Mission River (0.182 ± 0.349 ng/cm) and Garcitas Creek (0.175 ± 0.194 ng/cm) with the lowest at West

Mustang Creek (0.046 ± 0.11 ng/cm) followed by Tranquitas Creek (0.055 ± 0.058 ng/cm) and East Mustang Creek (0.058 ± 0.065 ng/cm). Aransas River gave the highest mean concentration of cyanobacteria at 1.306 ± 0.595 ng/cm and West Mustang gave the lowest at 0.178 ± 0.121 ng/cm. Mean diatom concentrations were highest at Placedo Creek (1.382 ± 1.179 ng/cm) and Aransas River (1.084 ± 0.682 ng/cm) and lowest at West Mustang Creek (0.321 ± 0.212 ng/cm) followed by East Mustang Creek (0.379 ± 0.235 ng/cm).

Hydrology

Flow metrics varied greatly among sites (Table 5). Flashiness ranged from a high in Perdido creek (1.338) and a low in Mission River (0.580) followed by West Mustang Creek (0.630). Maximum 30-day Daily Flow ranged from a high again in Perdido Creek (13375.437 l/s) followed by East Mustang Creek (12680.773 l/s) to lows in West Mustang Creek (1998.943 l/s) and Aransas River (1761.267 l/s). Minimum 30-day Daily Flows were highest in the three sites with the lowest mean annual precipitation: Tranquitas Creek (22.840 l/s), San Fernando Creek (21.154 l/s) and Aransas River (21.272 l/s). Minimum 30-day Daily Flows were lowest in West Mustang Creek (11.207 l/s) and Garcitas Creek (14.187 l/s). High Flow Pulse Percentage ranged from 0.049 in Tranquitas Creek to 0.277 in East Mustang Creek. Low Flow Pulse Percentage ranged from 0.000 in East Mustang Creek and Perdido Creek to 21.142 in San Fernando Creek and 24.139 in Tranquitas Creek. Variation in daily flow was lowest in Tranquitas Creek (2.571) and highest in Perdido Creek (14.659) followed closely by San Fernando Creek (12.565). Median Annual Maximum Flow was highest in East Mustang Creek (70.335) followed by Perdido Creek (66029.793) and lowest in West Mustang Creek (6764.580). Seasonality was lowest in Mission River (0.156) and highest in Placedo Creek (0.343).

Hydrologic Variation with Precipitation

We observed significant variation among sites in terms of the hydrologic characteristics (Table 5) and for several variables a significant portion of that variation was explained by mean annual rainfall (Table 6). High flow pulse percentage metrics as well as the seasonality of daily flows were positively related to mean annual rainfall (Table 6). Minimum 30-day consecutive flow and low flow pulse percentage were negatively related to mean annual rainfall (Table 6). While the linear relationship between seasonality and annual rainfall was not statistically significant at an alpha of 0.05 (Table 6), the seasonality of semi-arid streams (<75 cm/yr rainfall) was significantly lower ($F=7.031$, $df = 1,7$, $P = 0.0329$) than seasonality of humid streams. (>75 cm/yr rainfall). Semi-arid streams had a mean seasonality of daily flows of 0.196 ± 0.016 SE while humid streams had a mean seasonality of 0.276 ± 0.023 SE.

Community Composition

There were 168 different macroinvertebrate genera and 74 different families identified across all sites (Appendix A). Table 7 presents the community metrics of the stream communities in the sites. The mean in-stream Shannon-Wiener diversity varied between a low of 1.2 ± 0.1 (San Fernando Creek) and a high of 2.55 ± 0.1 (Aransas River). The same two sites had the highest and lowest average genera richness per sampling date (12.1 ± 0.6 vs 24.2 ± 0.9 genera) and total genera richness overall (50 vs 87 genera). Functional richness and Rao's Q followed different patterns. Functional richness (133.5 ± 7.6) and Rao Q (51.5 ± 1.8) were both highest in the Aransas River but the lowest functional richness occurred in Tranquitas Creek (8.5 ± 3.2) and the lowest Rao's Q occurred in East Mustang Creek (32.9 ± 4.6). Abundance (individuals per m^2) within streams ranged from a low of 6.7 ± 1.4 (East Mustang Creek) to 17.8

± 5.3 (Aransas River). Temporal β -diversity ranged from a low of 0.541 (San Fernando Creek) to a high of 0.797 (Placedo Creek).

The invertebrate communities of each stream were mainly predators ($36\% \pm 3\%$), collector gatherers ($29\% \pm 2\%$), and filter feeders ($19\% \pm 3\%$), however the relative proportions varied across sites and seasons (Appendix B). The most widespread and abundant groups were midges in the Chironomidae family, amphipods in genus *Hyaletta*, mayflies in genus *Fallceon*, invasive snails *Melanoides tuberculata*, damselflies in genus *Argia*, and elmids beetles in genus *Stenelmis*. However, a wide variety of taxa were locally abundant in one or two sites only. These included black flies in genus *Simulium*, water boatmen in genus *Trichocorixa*, caddisflies in genus *Smicridea* and *Brachycercus*, mayflies in genus *Centroptilum*, invasive Asian clams *Corbicula fluminea*, and hemipterans in genus *Rhagovelia*.

The NMDS converged after 52 iterations and had a stress value of 0.178 indicating a reasonable fit of the data. The predictor variables that were statistically significantly correlated (P -value < 0.05 ; Table 8) to the distance scores of the communities along the NMDS axes were: Annual Temperature ($R^2 = 0.422$), Annual Precipitation ($R^2 = 0.411$), High Flow Pulse Percentage ($R^2 = 0.4$), Low Flow Pulse Percentage ($R^2 = 0.396$), Minimum 30-day Daily Flow ($R^2 = 0.0301$), Median Daily Flow ($R^2 = 0.125$), Median Annual Maximum Flow ($R^2 = 0.102$), Forest Land Cover ($R^2 = 0.095$), Basin Size ($R^2 = 0.085$) and Variation in Daily Flow ($R^2 = 0.084$). 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 = -0.909, $R^2 = 0.084$, $P = 0.022$) whereas median annual maximum flow (vector = 0.990, $R^2 = 0.102$, $P = 0.005$) and maximum 30-day daily flow (vector = 0.991, $R^2 = 0.133$, $P = 0.001$) had high positive correlations.

Relationships with Flow, Climate, and Season

We observed several significant relationships between community composition and flow, climate, and season. Significant results are reported here, the complete results are reported in Appendix C. Average annual rainfall had a significant effect on community composition ($df = 1, 7$, $F = 10.49$, $P = 0.014$). Community composition, described as position along the first ordination axis, increased with increasing mean annual rainfall ($df = 7$, $t = 3.239$, $P = 0.014$, Figure 3). There was a significant interaction between sampling season and local climate on the richness of invertebrates observed in a site ($df = 3, 63$, $F = 3.33$, $P = 0.025$). Richness increased during summer ($df = 63$, $t = 2.312$, $P = 0.024$) and winter ($df = 63$, $t = 2.107$, $P = 0.039$) in the mesic but not the semi-arid sites. There was a significant interaction between minimum preceding flow (minimum stream flow observed during the two weeks prior to sampling) and climate on the richness of invertebrates in a site ($df = 1, 67$, $F = 5.47$, $P = 0.022$). Higher richness was correlated with higher minimum preceding flow rates in the samples from the semi-arid sites but not the mesic sites ($df = 67$, $t = -2.339$, $P = 0.022$). There was a significant effect of minimum preceding flow ($df = 1, 67$, $F = 10.35$, $P = 0.002$) and an interaction between minimum preceding flow and climate on position along the second NMDS axis ($df = 1, 67$, $F = 4.75$, $P = 0.033$). Community composition, described as position along the second ordination axis, was significantly correlated with minimum preceding flow in the semi-arid but not the mesic sites ($df = 67$, $t = 2.179$, $P = 0.033$).

Functional Traits and Annual Precipitation

The fourth corner analyses revealed a wide variety of significant interactions between invertebrate traits and the environment (Figure 5). Species production/biomass ratio, strong dispersal, and desiccation resistance had negative correlations with rainfall. Scraper-grazing (Herbivore) and abundance in the drift were strongly (coefficient $> |0.21|$) positively correlated with annual rainfall, while pollution tolerance value and multivoltinism also positively correlated with annual rainfall (coefficient $< |0.12|$). Water temperature was positively correlated with ability to exit the water and negatively correlated with multi-voltinism, strong dispersal, and abundance in the drift. Proportion of cobble substrate was negatively correlated with pollution tolerance value and scraper-grazer feeding mode. Minimum flow preceding sampling was positively correlated with abundance in the drift. Low flow pulse percentage was positively correlated with exit ability and negatively correlated with scraper-grazing feeding mode.

Discussion

Precipitation Regime and Hydrologic Stability

Using the TGCP as a case study region, we evaluated the effect of rainfall on riverine benthic invertebrate community structure. Matching our expectations, we found that the streams within in our study region increased in hydrologic stability and predictability, measured as seasonality, with increasing precipitation rates when categorized into arid and humid climate subgroups at the 75 cm/yr of annual rainfall level (Figure 4). Semi-arid sites had a higher occurrence of unpredictable and proportionally severe low-flow events and spikes in discharge matching the general observation that arid system streams tended to be more stochastic in their hydrology (Jackson and Fisher, 1986; Grimm and Fisher, 1989). However, this did not result in higher diversity in the more mesic sites as we predicted. Instead, we observed significant compositional turnover in both the identity of the resident fauna and the dominant functional traits prevalent in the communities. We also observed that causes of temporal variation of the invertebrate communities within streams through time differed between the semi-arid and mesic 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 mesic sites varied with season. Taken together, these results supported the idea that rainfall is a master variable driving the local environment and the composition of the stream invertebrate communities.

Community Structure Driven by Precipitation Regime

Contrary to our expectations, neither biodiversity nor invertebrate abundance were related to mean annual rainfall. The absence of a relationship with diversity could have been due to a study design issue involving a lack of sites at the arid end of the precipitation gradient. The

lowest mean richness, total genera richness through time, and mean Shannon-Wiener diversity indices occurred in the two stream sites at the driest end of the gradient, matching our expectation. Diversity in the remaining seven sites was all higher than in the two driest sites, but variable and not in accordance with precipitation. This may indicate that richness and biodiversity of the stream sites does increase with annual precipitation, but the relationship could be nonlinear, and our study design may not have included enough sites at the low precipitation end of the gradient. In contrast, abundance ran counter to our expectations that arid streams would have lower richness and diversity (Sheldon, Boulton & Puckridge, 2002; Tonkin, Bogan, Bonada, Rios-Touma & Lytle, 2017), with the lowest values observed at the wettest end of the gradient. Whereas one of these sites (EMC) bears heavy signature of agriculture land use impacts, the second site (WMC) was in a largely forested drainage. Several possible explanations exist for the counter-intuitive finding. First, all the sites were predominantly sand and silt substrates and so there may have been structural habitat limits on potential abundances of benthic invertebrates across the gradient. In similar systems, sandy bottom streams in Alabama, the majority of biomass and production has been observed to occur in stable substrates such as large woody debris rather than in the benthos (Benke, Henry, Gillespie & Hunter, 1985; Benke & Bruce Wallis, 2014), which would not have been detected with the core sampling technique we used for quantitative analyses of the communities. Second, given that arid sites were observed in the literature to have significantly higher secondary production than temperate mesic sites (Benke & Huryn, 2010), it may follow that biomass and abundance, which are often correlated with production, would show a similar pattern.

While precipitation regime did not appear to control spatial patterns in diversity and abundance, it did influence spatial variation in the identity of factors controlling temporal

variation within streams across the gradient. We predicted that mesic systems would display greater seasonality of daily flow dynamics, which by extension would drive seasonal changes in the benthic invertebrate communities. Matching *a priori* expectations, the mesic systems had significantly higher seasonality in flow patterns with lower day to day variability and repeated patterns across years in the timing of low (winter, summer) and high (fall, spring) flow periods. These patterns matched our observation that invertebrate richness varied significantly across seasons in mesic but not semi-arid sites. The periods of higher richness co-occurred with seasonal lulls in flow conditions suggesting that diversity peaks during periods of relative stability in the mesic ecosystems. However, the lack of an effect of high flow events preceding sampling in mesic systems, indicated 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 flow conditions in each season. Similarly, low flow events preceding sampling reduced taxonomic richness in all streams, but the effects were only significant in semi-arid streams (Figure 3). Furthermore, these events temporarily changed the composition of semi-arid stream communities as measured by position on the second NMDS ordination axis. This suggests that the semi-arid 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.

Multiple lines of evidence pointed to precipitation regime being a major driver of variation in the composition of macroinvertebrate communities. The communities in the NMDS analysis were clearly oriented along the precipitation gradient and mean annual rainfall, air temperature, high and low flow pulse percentages are the top predictors for species composition. Hydrologic variation associated with low flow and high flow events are driven by rainfall (Poff, 1996; Dodds, Gido, Whiles, Daniels & Grudzinski, 2015; Dodds *et al.*, 2019) so these can be

considered a linked cluster of drivers. While mean annual air temperature comes out as a significant predictor, it is highly correlated with mean annual rainfall and we can discount it as a major driver for several reasons. First, while mean air temperature does decrease by 1.4°C across the gradient, the magnitude of this change is comparatively small relative to the 75% increase in mean annual precipitation. Furthermore, while air temperature changed 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. Higher temperatures likely increased evaporation rates in the semi-arid watersheds, contributing to low flow conditions, but the relative importance of this effect when compared to the lower rates of precipitation was likely minimal. Additionally, the air temperature difference may have been partially caused by the rainfall difference. Site latitude and elevation was comparable across the gradient and sites are relatively close to one another. However, there is significantly more gallery forest (as opposed to scrublands) and larger trees on the mesic side of the gradient due to the higher rainfall. Vegetation has been shown to have a cooling effect on air temperatures (Yuan, Hamdi, Ochege, Kurban & De Maeyer, 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. Thiaridae, wholly composed of the introduced snail *Melanooides tuberculata*, was so abundant through time in semi-arid sites that it changed substrate composition. For example, in Tranquitas Creek, drifts of old *M. tuberculata* shells comprised the majority of substrate in some areas of the reach, effectively increasing sediment grain size which affects community assemblage. Work on the invasive New Zealand

Mud snail has shown that invasive snails with high secondary production rates can have big effects on nutrient cycling by sequestering most of the available carbon from primary production and other ecosystem processes (Hall, Dybdahl & VanderLoop, 2006). The invasive Asian Clam, *Corbicula fluminea*, did not display covariation with rainfall but did have similar effects on substrate. For example, in the Aransas River, old Asian clam shells were abundant throughout the reach, forming shell bars and increasing overall substrate coarseness. Asian clams, which are both filter feeders and pedal feeders, have been shown to alter the flux of material into the streambed and consume basal microorganisms such as bacteria and diatoms (Hakenkamp *et al.*, 2001). In contrast, the relative abundance of crustaceans in genus *Hyaletta* and order Decapoda increased with rainfall, as did several genera of mayflies such as *Cloeon spp.*

The functional trait analysis allowed us to interpret the meaning behind these patterns. Hydrologic analyses suggested that semi-arid streams were most strongly shaped by day to day variation in flow conditions, particularly low flow events. There were multiple species traits that were correlated with annual rainfall which supported this hypothesis. When analyzed in isolation, taxa in sites with higher rainfall were slower growing, were not good overall dispersers, and lacked adaptations for resisting drying events. These traits are suggestive of taxa that have no need of rapidly developing during optimum conditions nor living through or rapidly recolonizing following a stream reach drying event. This makes sense when considering that the mesic stream taxa would (in relation to taxa in arid streams) rarely experience droughts that would put them in danger of desiccation, and that the tendency for arid stream taxa to have shorter maturity times and adaptations fit for rapid recolonization of streams post-flood is supported well in previous literature (Gray, 1981; Fisher, Gray, Grimm & Busch 1982; Jackson & Fisher, 1986; Grimm & Fisher, 1989; Lytle, 2001 & 2002; Lytle & Poff, 2004). The large

positive correlation coefficient between abundance in the drift and increasing annual rainfall rate was likely a function of the greater hydrologic stability in mesic streams supporting an advantage in fitness for taxa that are actively drifting in order to avoid predation and actively seek out new resource patches (Poff *et al.*, 2006; Naman, Rosenfeld & Richardson, 2016; Cienciala & Hassan, 2018). Similarly, the strong positive correlation we found between preceding flow and the abundance in drift suggested that greater flow rates, like those found consistently in the mesic streams, were directly controlling the proportion of actively drifting taxa.

Not all significant correlations between traits and rainfall matched our expectations. The strong 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 (Grafius, 1974; Benfield, 1997; Tait, 1997; Pomeroy *et al.*, 2000). 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. Instead, this pattern could be explained by the negative relationship we see between herbivory and Low Flow Pulse Percentage, which suggests that the scraper/grazer taxa in this system cannot tolerate the flashy flow regimes that are found on the arid side of our gradient. This corroborates with the predominant occurrences we observed in the mesic sites of scraper/grazer taxa like amphipods and certain mayflies.

Another non-intuitive relationship was the positive relationship between multivoltine taxa and annual precipitation. Previous literature suggests that we should have observed greater multi-voltinism in the semi-arid stream sites as a strategy for rapidly increasing populations following hydrologic disturbances (Mellado-Díaz, Suárez Alonso & Vidal-Abarca, 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. Contrary to this expectation, we observed decreasing rates of turnover with increasing levels of annual rainfall ($r = -0.49$). This relationship may be explained by thermal 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 order Ephemeroptera (Carlisle, Meador, Moulton & Ruhl, 2007), mayflies are generally intolerant of warm waters and low oxygen conditions (Peeters, Brugmans, Beijer & Franken, 2006; Merrit, Cummins, & Berg 2008). Although average water temperature did not differ significantly among sites across the gradient, the minimum observed water temperatures are higher on the more arid side of the gradient. Perhaps subtle differences in the range of thermal values across the gradient are responsible for the observed pattern but more investigation is needed.

The ability for the aquatic life stage to exit the water when needed was strongly positively correlated with temperature, as well as low flow pulse percentage (LFPP). A high LFPP value is characteristic of the semi-arid streams that experience frequent dry down events (Fisher, Gray, Grimm & Busch, 1982; Sponseller, Grimm, Boulton & Sabo, 2010; Shriever *et al.*, 2015). Taxa in these conditions need traits to survive these events and, in the absence of desiccation resistance, the ability to leave the system and find other suitable aquatic habitats is a valuable trait (Poff *et al.*, 2006). Exit ability has been demonstrated to be a powerful trait for avoiding flash floods in arid land systems (Lytle, 1999).

We also observed a strong negative relationship between substrate type and taxa pollution tolerance value. Specifically, the proportion of cobble in the stream bed 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, Meador, Moulton & Ruhl, 2007; Merrit, Cummins, & Berg 2008; Hering *et al.*, 2009). These findings support previous literature that found that stable environmental conditions, like large cobble substrate, promote a greater taxonomic and functional diversity of invertebrates (Schriever *et al.*, 2015).

Conclusions

Utilizing a novel study site in the Texas Gulf Coastal Prairie region, we provide evidence that precipitation regime is a major driver of functional composition and the spatial and temporal variation in taxonomic composition of aquatic macroinvertebrates. The results suggest that the impacts of precipitation regime manifest primarily through temporal variability in daily flows, particularly the frequency of low flow events, rather than changes to riparian vegetation. This matches with other recent work demonstrating the importance of low flow events to ecosystem productivity (Patrick *et al.*, 2019). This is an important addition to the literature on the climate change impacts on lotic ecosystems, which have primarily focused on the effects of changing temperature (Burgmer, Hillebrand & Pfenninger, 2006; Hering *et al.*, 2009; Domisch, Jähnig & Haase, 2011; Arai, Nukazawa, Kazama & Takemon, 2015). The results imply that significant changes in rainfall patterns are another important factor that must be considered when evaluating risk of climate change to running water ecosystems. Our findings also demonstrate the efficacy of utilizing analyses of taxonomic and functional trait compositions to elucidate the mechanisms behind how gradients in environmental factors drive local spatial and temporal assemblages which could not be perceived using taxonomic diversity approaches alone (Poff *et al.*, 2006; Shriever *et al.*, 2015).

We have provided further evidence that rainfall is a key factor shaping stream ecosystems (Lytle & Poff, 2004; Mims & Olden, 2012), and shown how lotic systems are especially in danger of deleterious effects of predicted changes to the spatial distribution of precipitation regimes with global climate change (Allan & Soden, 2008; Vaughn, 2010). Indeed, perhaps most importantly, the basic human necessity for freshwater not only increases the urgency to protect these systems, but also increases the level of human impact on them as global population

continues to increase exponentially. We can apply the conclusions we have drawn about the effects of precipitation regimes in conjunction with climate models to characterize regional risk of ecosystems rapidly changing due to predicted changing climate conditions. By identifying regions of greatest risk and having insight into the mechanisms behind state change, we can facilitate the invention of management approaches to mitigate the effects of precipitation regime shifts on these systems.

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TABLES

Table 1 Aggregated data from the USGS on each of our stream sites (Falcone 2011). 20-year mean temperatures, rainfall rates and median flow rates are all calculated from flow records dating back 20 years or, if data dating 20 years back was not available, as far back as was available. Sites are ordered from low to high precipitation levels.

<i>Site</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Basin Size (km²)</i>	<i>20-year Mean Temperature (°C)</i>	<i>20-year Mean Rainfall (cm/yr)</i>	<i>20-year Mean Median Flow (l/s)</i>	<i>Elevation (m)</i>
Tranquitas Creek	27.521	-97.840	125.614	22.242	54.172	7.079	18
San Fernando Creek	27.773	-98.034	192.700	22.215	56.672	37.378	62
Aransas River	28.283	-97.621	76.800	21.547	68.533	151.495	47
Mission River	28.292	-97.279	51.800	21.516	72.850	342.634	14
Perdido Creek	28.752	-97.317	337.300	21.528	78.729	3.115	50
Placedo Creek	28.725	-96.769	176.896	21.363	82.051	34.547	17
Garcitas Creek	28.891	-96.819	970.400	21.209	84.251	56.634	20
West Mustang Creek	29.072	-96.468	557.400	20.787	94.171	331.307	20
East Mustang Creek	29.071	-96.417	190.200	20.908	95.025	17.556	20

Table 2 Mean water chemistry and physical characteristics for each stream site from data collected throughout the study.

<i>Site</i>	<i>Conductivity ($\mu\text{s/cm}$)</i>	<i>Water Temperature ($^{\circ}\text{C}$)</i>	<i>DO (mg/L)</i>	<i>pH</i>	<i>Proportion Canopy Cover</i>	<i>Mean Depth (m)</i>	<i>Width (m)</i>
Aransas River	1182.881 $\pm$ 476.762	20.619 $\pm$ 6.809	7.076 $\pm$ 2.071	8.421 $\pm$ 1.094	0.725 $\pm$ 0.122	0.153 $\pm$ 0.058	3.38 $\pm$ 0.301
East Mustang Creek	590.759 $\pm$ 452.638	21.368 $\pm$ 6.534	6.298 $\pm$ 2.46	8.057 $\pm$ 0.855	0.1 $\pm$ 0.112	0.31 $\pm$ 0.081	5.471 $\pm$ 0.685
Garcitas Creek	456.064 $\pm$ 107.726	19.993 $\pm$ 5.846	5.998 $\pm$ 1.983	8.115 $\pm$ 1.22	0.711 $\pm$ 0.157	0.367 $\pm$ 0.593	6.19 $\pm$ 1.424
Mission River	1604.844 $\pm$ 1008.422	22.156 $\pm$ 6.364	7.084 $\pm$ 1.927	8.32 $\pm$ 0.77	0.519 $\pm$ 0.158	0.269 $\pm$ 0.1	6.344 $\pm$ 1.194
Perdido Creek	869.235 $\pm$ 176.027	21.735 $\pm$ 6.075	6.403 $\pm$ 2.331	8.014 $\pm$ 0.389	0.094 $\pm$ 0.119	0.2 $\pm$ 0.071	4.441 $\pm$ 0.636
Placedo Creek	1425.544 $\pm$ 816.836	21.974 $\pm$ 6.98	7.623 $\pm$ 3.194	8.414 $\pm$ 1.029	0.517 $\pm$ 0.137	0.17 $\pm$ 0.098	3.293 $\pm$ 0.717
San Fernando Creek	1002.726 $\pm$ 414.08	21.958 $\pm$ 4.407	6.09 $\pm$ 1.7	8.068 $\pm$ 1.139	0.746 $\pm$ 0.133	0.333 $\pm$ 0.641	2.94 $\pm$ 0.212
Tranquitas Creek	3497.092 $\pm$ 1402.629	20.845 $\pm$ 6.355	5.37 $\pm$ 5.671	8.428 $\pm$ 0.897	0.78 $\pm$ 0.145	1.088 $\pm$ 2.456	4.796 $\pm$ 3.062
West Mustang Creek	511.849 $\pm$ 292.524	20.318 $\pm$ 6.573	6.453 $\pm$ 2.561	8.18 $\pm$ 0.836	0.775 $\pm$ 0.123	0.303 $\pm$ 0.113	8.174 $\pm$ 1.322

Table 3 Substrate characteristics for each of the streams by proportion of substrate size class. Size classes modified from Wentworth (1922). “Boulder” = 256-4096 mm, “Cobble” = 64-256 mm, “Gravel” = 2-64 mm, “Sand” = 0.0625-2 mm, Silt = less than 0.0625 mm.

<i>Site</i>	<i>Proportion Silt</i>	<i>Proportion Sand</i>	<i>Proportion Gravel</i>	<i>Proportion Cobble</i>	<i>Proportion Boulder</i>
Tranquitas Creek	0.572 ± 0.109	0.166 ± 0.104	0.182 ± 0.114	0.008 ± 0.016	0.004 ± 0.01
San Fernando Creek	0.435 ± 0.141	0.202 ± 0.124	0.302 ± 0.14	0.042 ± 0.028	0.019 ± 0.031
Aransas River	0.055 ± 0.03	0.243 ± 0.104	0.499 ± 0.185	0.188 ± 0.142	0.009 ± 0.017
Mission River	0.116 ± 0.066	0.733 ± 0.126	0.084 ± 0.051	0.024 ± 0.072	0.033 ± 0.033
Perdido Creek	0.349 ± 0.147	0.403 ± 0.099	0.075 ± 0.049	0.072 ± 0.113	0.123 ± 0.112
Placedo Creek	0.372 ± 0.16	0.432 ± 0.141	0.086 ± 0.086	0.108 ± 0.089	0.009 ± 0.015
Garcitas Creek	0.119 ± 0.078	0.788 ± 0.098	0.095 ± 0.072	0 ± 0	0 ± 0
West Mustang Creek	0.159 ± 0.135	0.841 ± 0.135	0 ± 0	0 ± 0	0 ± 0
East Mustang Creek	0.501 ± 0.171	0.411 ± 0.171	0.083 ± 0.074	0.005 ± 0.011	0 ± 0

Table 4 Nutrient and benthic algae concentrations for each stream site.

<i>Site</i>	<i>Green Algae</i> ($\mu\text{g}/\text{cm}$)	<i>Cyanobacteria</i> ($\mu\text{g}/\text{cm}$)	<i>Diatoms</i> ($\mu\text{g}/\text{cm}$)	<i>NO₃</i> (mg/L)	<i>NH₄</i> (mg/L)	<i>Orthophosphate</i> (mg/L)
Aransas River	0.05 $\pm$ 0.081	1.306 $\pm$ 0.595	1.084 $\pm$ 0.682	6.804 $\pm$ 4.499	0.152 $\pm$ 0.084	1.824 $\pm$ 0.748
East Mustang Creek	0.058 $\pm$ 0.065	0.374 $\pm$ 0.31	0.379 $\pm$ 0.235	0.806 $\pm$ 0.687	0.16 $\pm$ 0.093	0.346 $\pm$ 0.854
Garcitas Creek	0.175 $\pm$ 0.194	0.29 $\pm$ 0.188	0.61 $\pm$ 0.3	0.179 $\pm$ 0.167	0.119 $\pm$ 0.07	0.343 $\pm$ 0.596
Mission River	0.182 $\pm$ 0.349	0.247 $\pm$ 0.118	0.509 $\pm$ 0.317	0.044 $\pm$ 0.048	0.149 $\pm$ 0.082	0.168 $\pm$ 0.353
Perdido Creek	0.138 $\pm$ 0.11	0.511 $\pm$ 0.312	0.657 $\pm$ 1.226	0.031 $\pm$ 0.03	0.15 $\pm$ 0.08	0.106 $\pm$ 0.126
Placedo Creek	0.095 $\pm$ 0.212	0.468 $\pm$ 0.319	1.382 $\pm$ 1.179	1.727 $\pm$ 1.387	0.144 $\pm$ 0.064	0.064 $\pm$ 0.059
San Fernando Creek	0.097 $\pm$ 0.157	0.332 $\pm$ 0.183	0.862 $\pm$ 0.587	12.979 $\pm$ 4.021	0.215 $\pm$ 0.132	1.964 $\pm$ 0.792
Tranquitas Creek	0.055 $\pm$ 0.058	0.75 $\pm$ 1.021	0.82 $\pm$ 0.971	0.586 $\pm$ 0.84	0.248 $\pm$ 0.203	0.15 $\pm$ 0.157
West Mustang Creek	0.046 $\pm$ 0.11	0.178 $\pm$ 0.121	0.321 $\pm$ 0.212	0.344 $\pm$ 0.61	0.379 $\pm$ 0.685	0.149 $\pm$ 0.08

Table 5 Characteristic flow metrics for each of the stream sites. Calculated from flow records dating back 20 years or, if data dating 20 years back was not available, as far back as was available (Falcone 2011). Sites are ordered from low to high mean annual precipitation.

<i>Site</i>	<i>Flashiness</i>	<i>Maximum 30-Day Daily Flow (l/s)</i>	<i>Minimum 30-Day Daily Flow (l/s)</i>	<i>High Flow Pulse Percentage</i>	<i>Low Flow Pulse Percentage</i>	<i>Variation in Daily Flow</i>	<i>Median Annual Maximum Flow (l/s)</i>	<i>Seasonality</i>
Tranquitas Creek	0.775	3264.045	22.840	0.049	24.139	2.571	26624.969	0.223
San Fernando Creek	0.908	3617.108	21.154	0.089	21.142	12.565	28638.629	0.222
Aransas River	1.053	1761.267	21.272	0.067	7.547	12.059	11564.918	0.184
Mission River	0.580	2023.136	19.148	0.108	3.456	5.083	13795.687	0.156
Perdido Creek	1.338	13375.437	17.985	0.120	0.000	14.659	66029.739	0.299
Placedo Creek	0.922	6336.706	16.003	0.171	5.127	5.788	39806.060	0.343
Garcitas Creek	0.806	4250.969	14.187	0.171	4.724	6.109	18851.941	0.233
West Mustang Creek	0.630	1998.943	11.207	0.176	10.657	4.390	6764.580	0.214
East Mustang Creek	0.792	12680.773	19.400	0.277	0.000	5.221	70335.394	0.293

Table 6 Relationships between mean annual rainfall and hydrologic metrics.

<i>Response</i>	<i>Slope</i>	<i>Intercept</i>	<i>P-value</i>	<i>R²</i>
Flashiness	-0.002	1.039	0.711	0.021
Maximum 30-Day Daily Flow	4.383	-140.789	0.282	0.163
Minimum 30-Day Daily Flow	-0.007	1.166	0.016*	0.585
High Flow Pulse Percentage	0.004	-0.187	0.002*	0.780
Low Flow Pulse Percentage	-0.442	42.250	0.021*	0.555
Variation in Daily Flow	-0.069	12.891	0.540	0.056
Median Annual Maximum Flow	14.299	17.540	0.505	0.066
Seasonality	0.002	0.123	0.314	0.144

Table 7 Metrics describing the invertebrate communities found in each stream. Values are reported as the mean $\pm$ the standard error.

<i>Site</i>	<i>Functional Richness</i>	<i>RaoQ</i>	<i>Richness</i>	<i>Shannon Diversity</i>	<i>Abundance</i>
Tranquitas Creek	8.447 $\pm$ 3.245	34.607 $\pm$ 4.761	12.778 $\pm$ 1.402	1.59 $\pm$ 0.12	11.759 $\pm$ 3.859
San Fernando Creek	41.154 $\pm$ 11.826	27.171 $\pm$ 4.063	12.111 $\pm$ 0.633	1.213 $\pm$ 0.141	11.528 $\pm$ 4.738
Aransas River	133.447 $\pm$ 7.647	51.48 $\pm$ 1.767	24.2 $\pm$ 0.854	2.549 $\pm$ 0.069	17.768 $\pm$ 5.329
Mission River	68.88 $\pm$ 15.494	40.392 $\pm$ 2.717	17 $\pm$ 2.188	1.879 $\pm$ 0.154	14.289 $\pm$ 3.206
Perdido Creek	44.672 $\pm$ 10.098	38.168 $\pm$ 4.402	18.1 $\pm$ 1.169	2.012 $\pm$ 0.153	8.298 $\pm$ 0.91
Placedo Creek	89.679 $\pm$ 19.103	44.98 $\pm$ 2.292	15.125 $\pm$ 2.31	1.936 $\pm$ 0.183	11.125 $\pm$ 4.398
Garcitas Creek	45.855 $\pm$ 8.111	40.268 $\pm$ 3.2	16.667 $\pm$ 0.553	1.705 $\pm$ 0.14	11.687 $\pm$ 2.673
West Mustang Creek	60.608 $\pm$ 12.059	40.582 $\pm$ 3.045	17.857 $\pm$ 2.176	1.844 $\pm$ 0.193	8.002 $\pm$ 2.335
East Mustang Creek	34.728 $\pm$ 8.856	32.894 $\pm$ 4.643	13.5 $\pm$ 1.464	1.623 $\pm$ 0.154	6.688 $\pm$ 1.363

Table 8 Correlations between covariate data and NMDS axes

<i>Predictor</i>	<i>NMDS1 Vector</i>	<i>NMDS2 Vector</i>	<i>R²</i>	<i>P-value</i>
Annual Temperature	-0.976	-0.217	0.422	0.001
Annual Precipitation	0.952	0.307	0.411	0.001
High Flow Pulse Percentage	-0.843	0.537	0.401	0.001
Low Flow Pulse Percentage	-0.986	-0.169	0.396	0.001
Minimum 30-Day Daily Flow	-0.997	-0.083	0.301	0.001
Other-Land Cover	-0.961	-0.278	0.290	0.001
Dev Land Cover	-0.954	0.299	0.273	0.001
Mean Daily Flow	0.998	-0.068	0.235	0.001
Crop Land Cover	0.983	0.181	0.173	0.001
Maximum 30-Day Daily Flow	0.132	0.991	0.133	0.001
Median Daily Flow	0.958	-0.288	0.125	0.003
Median Annual Maximum Flow	-0.138	0.990	0.102	0.005
Forest Land Cover	0.979	0.205	0.095	0.011
Basin Size	0.791	0.612	0.085	0.019
Variation in Daily Flow	-0.418	-0.909	0.084	0.022
Seasonality	0.838	0.546	0.026	0.270
Flashiness	-0.901	-0.434	0.024	0.318

Table 9 Correlations between traits and environmental data in the fourth corner analyses.

<i>Trait</i>	<i>Annual Rainfall</i>	<i>Water Temperature</i>	<i>% Cobble Substrate</i>	<i>Minimum Preceding Flow</i>	<i>Low Flow Pulse Percentage</i>
Pollution Tolerance Value	0.124	0.000	-0.187	0.000	0.000
Multivoltine	0.225	-0.107	0.000	0.000	0.000
Strong Dispersal	-0.105	-0.119	0.000	0.000	0.000
Ability to Exit Water	0.000	0.138	0.000	0.000	0.165
Abundant Drifter	0.357	-0.136	0.000	0.158	0.000
Desiccation Tolerance	-0.107	0.000	0.000	0.000	0.000
Herbivore	0.361	0.000	-0.163	0.000	-0.116
Ability to Breathe Air	0.000	0.000	0.000	0.000	0.000
P/B	-0.391	0.000	0.000	0.000	0.000

FIGURES

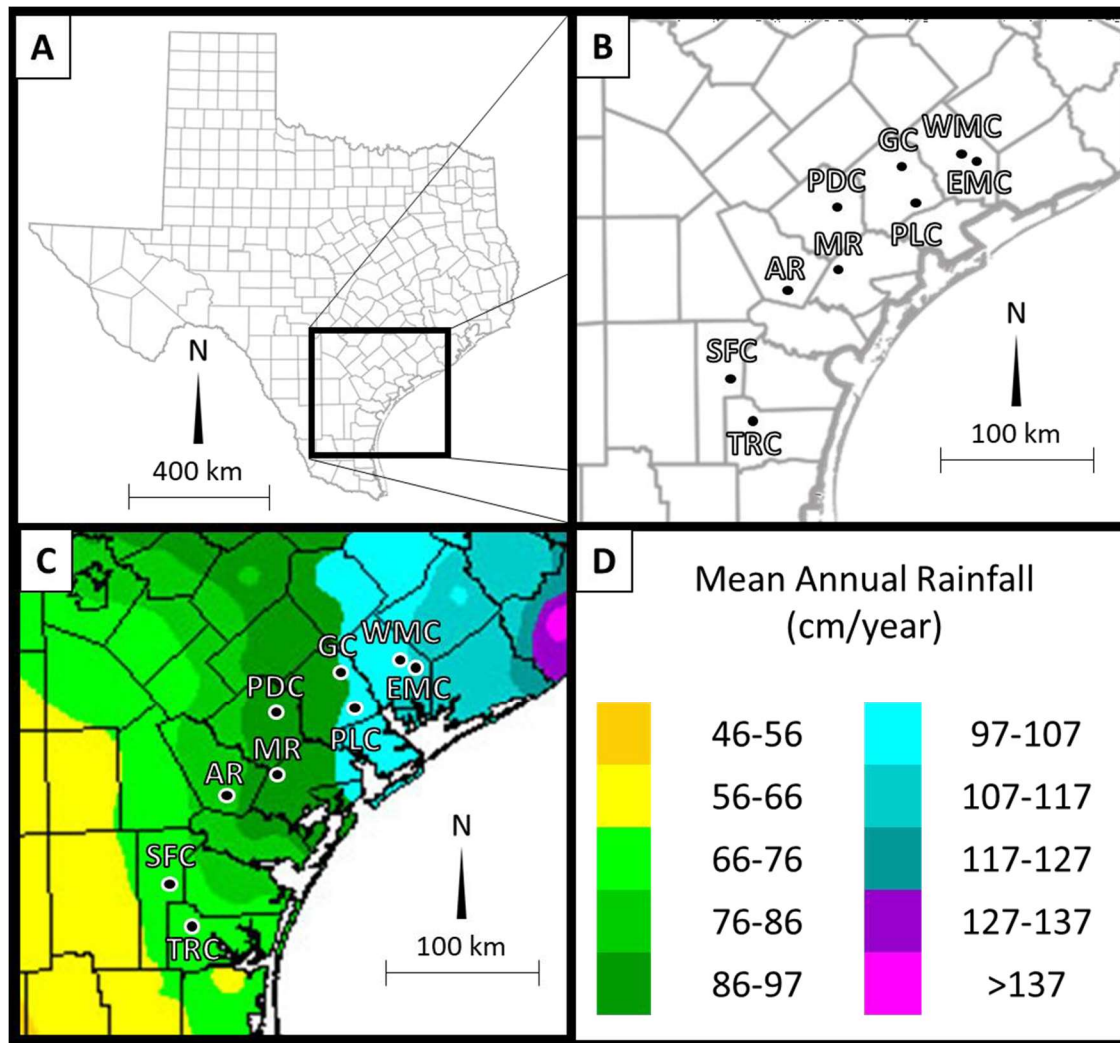


Fig. 1 Study region maps with study sites labelled. A: Plain map of Texas with a box denoting the study region. B: Plain map of study region with sites labelled. C: Map of annual rainfall rates by color within the study region with sites labelled. D: Key to colors on map in panel C. Site names: EMC= 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, SFC= San Fernando Creek.

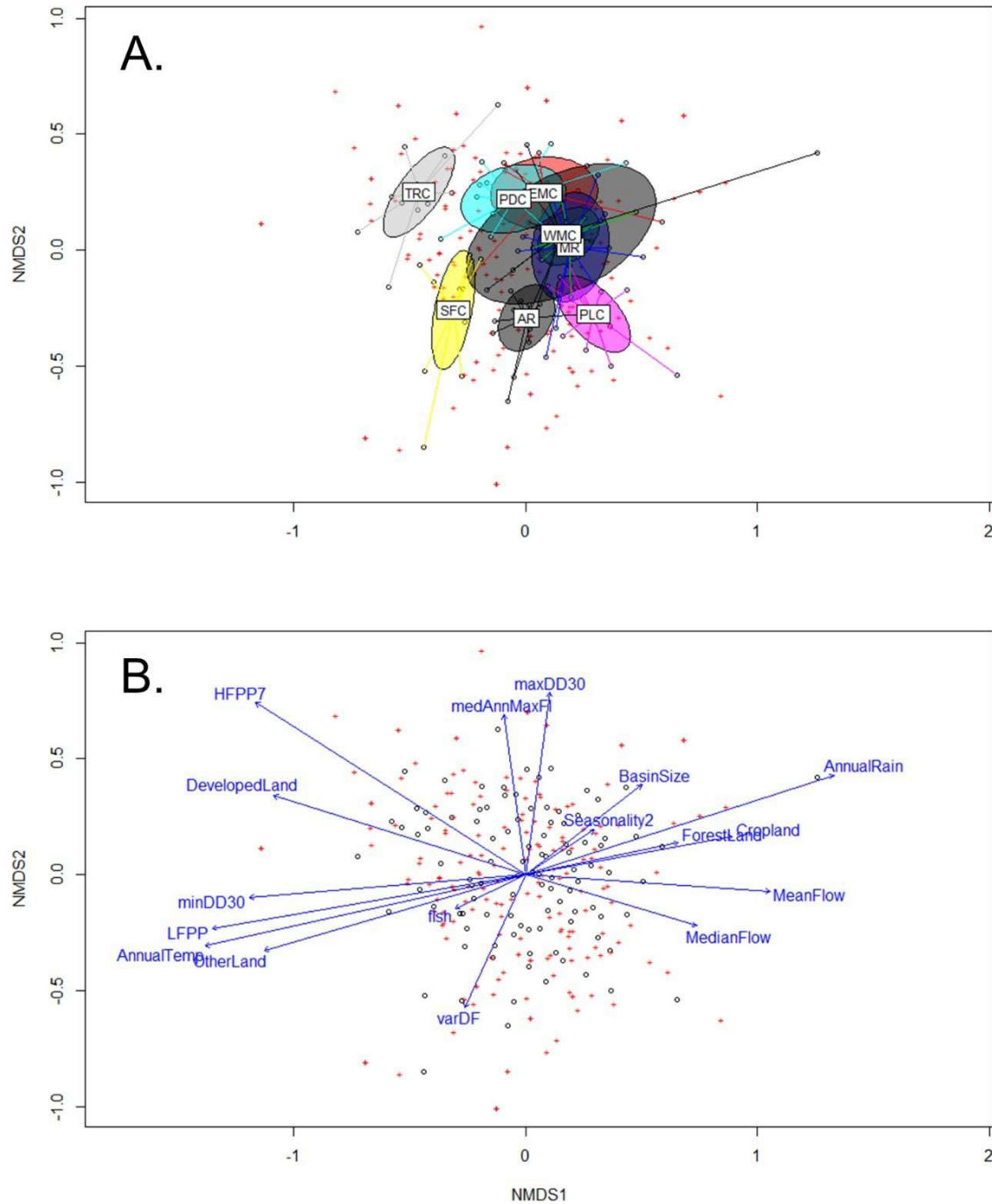


Fig. 2 Graphics of NMDS analyses. A) NMDS ordination of site taxa with the fitted environmental covariates as a vector map and with each sample site labelled and grouped with ellipses. B) Vectors of correlations between environmental variables at the site level and community composition.

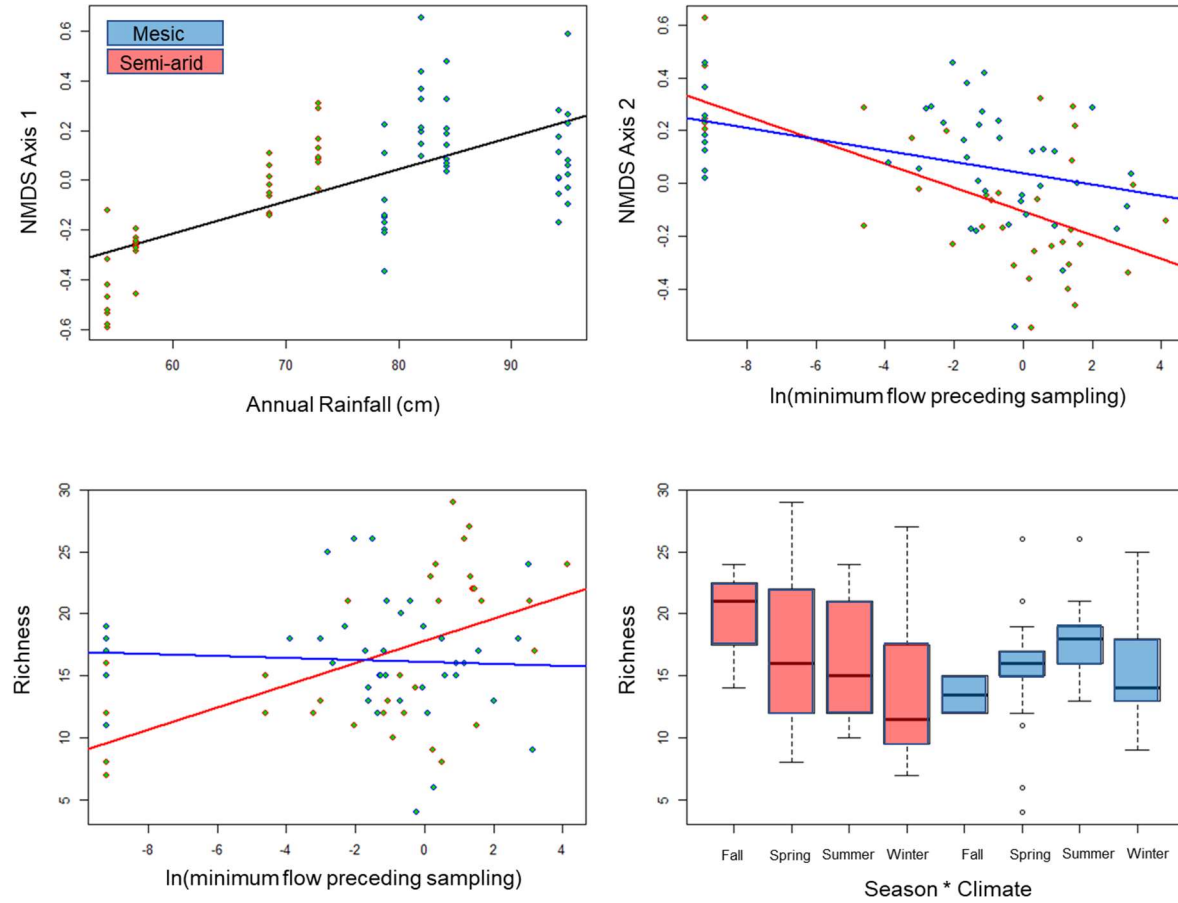


Fig. 3 Relationships from significant mixed effects models. Data from mesic streams is in blue and data from arid streams is in red. Top left: Community sample NMDS Axis 1 distance scores plotted against mean annual rainfall rates at each site/sampling event. Top right: Community sample NMDS Axis 2 distance scores plotted against the natural log of the minimum flow rate recorded two weeks before sampling at each site/sampling event. Bottom left: Richness of communities plotted against the natural log of the minimum flow rate recorded two weeks before sampling at each site/sampling event. Bottom right: Box plot illustrating variation in richness of communities as a function of season when sites are grouped by climate.

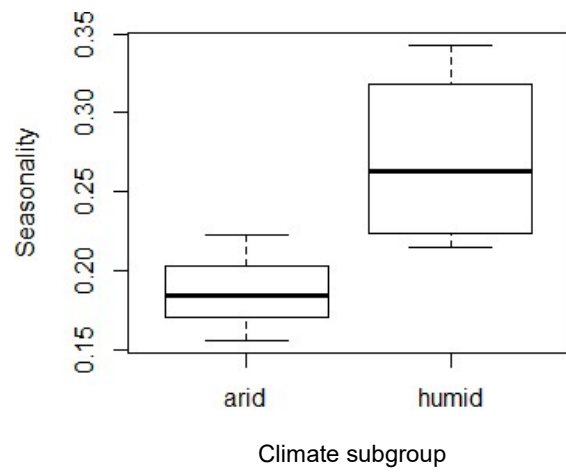


Fig. 4 Boxplot of seasonality between climate subgroups. Seasonality is calculated as Colwell's contingency measure (M) divided by within season predictability (P) (Colwell, 1974; Tonkin *et al.* 2017). This metric captures the degree to which the environment varies over the course of a year. Arid subgroup = < 75cm/yr of annual rainfall. Humid subgroup = > 75 cm/yr of annual rainfall. F-value = 4.73. P-value = 0.0816.

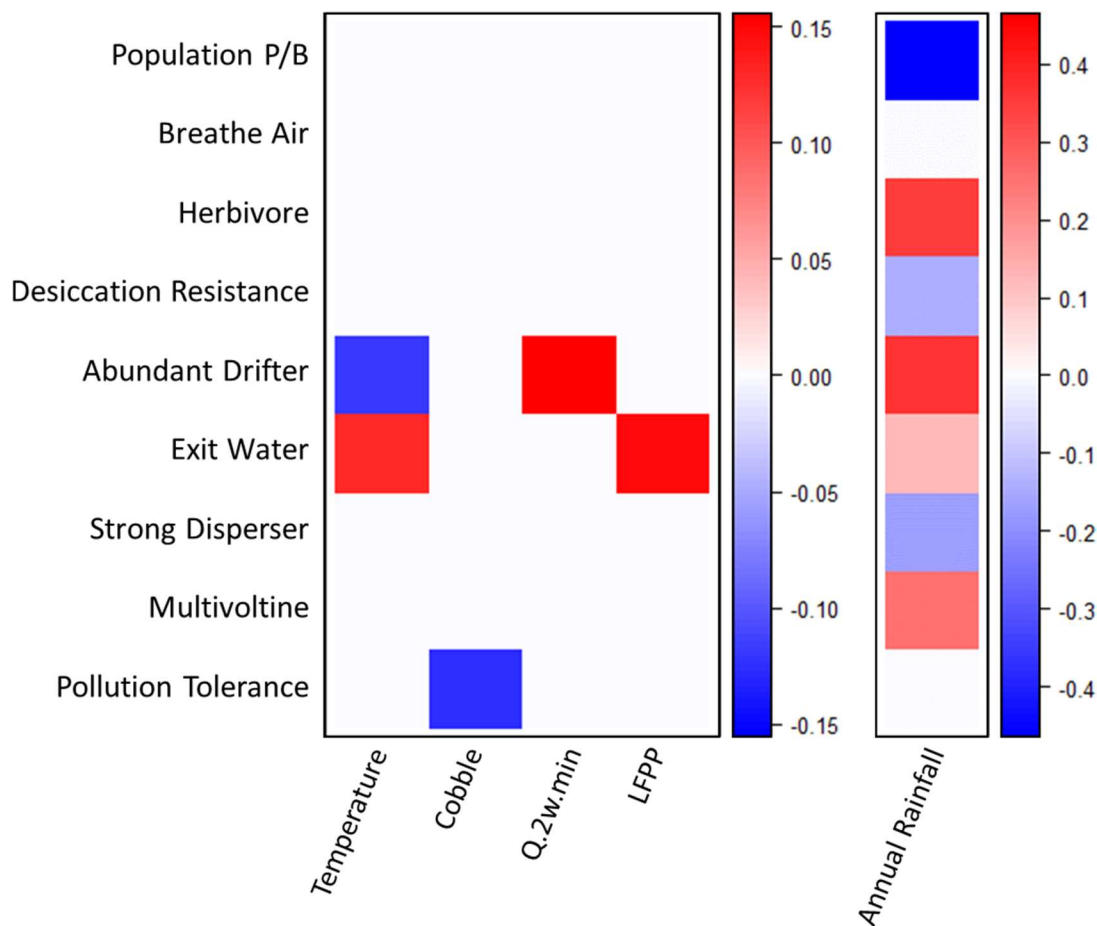


Fig. 5 Fourth corner analysis level plot. Standardized interaction coefficient estimates for interaction terms from the fourth corner analysis testing the relationship between morphological traits and the environment, accounting for species abundances.

Coefficients shown in red (positive) or blue (negative) were significant in the best model. Traits: Population P/B = Population production/biomass ratio. Breathe Air = The ability of the aquatic stage to breach air. Herbivore = strictly herbivorous feeding behavior. Desiccation Resistance = adaptation to survive desiccation events. Abundant Drifter = Dominant in drift samples. Exit Water = the ability to exit the water outside of emergence. Strong Disperser = >1km of flight before laying eggs. Multivoltine = >1 generation per year. Pollution tolerance = ability to survive in low water quality. Environmental factors: Temperature = water temperature (°C). Cobble = the proportion of cobble in the stream bed. Q.2w.min = minimum discharge rate in the preceding two weeks before sampling date (m³/s). LFPP = Low Flow Pulse Percentage (# discharge < 25th percentile of flow days). Annual Rainfall = mean annual rainfall rate over 20 years.

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APPENDIX A: Complete list of taxa that were collected.

Table 1 Presence/absence of taxa from each stream site throughout the study. 0 = absent, 1 = present. Invertebrate biota collected from August 2017 through March 2019 for this study. Site names: 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, SFC= San Fernando Creek.

CLASS	ORDER	FAMILY	GENUS	AR	EMC	GC	MR	PDC	PLC	SFC	TRC	WMC
HIRUDINEA				0	1	0	1	0	0	0	0	0
OLIGOCHAETA				1	0	1	1	0	1	1	1	1
ARACHNIDA	ARANEAE	ARANEIDAE	ARANEUS	1	0	0	0	0	0	0	0	0
ARACHNIDA	TROMBIDI-FORMES	HYDRACHNIDAE		0	0	0	0	0	0	1	0	0
BRANCHIOPODA	DIPLOSTRACA	DAPHNIIDAE	DAPHNIA	1	1	1	1	1	0	0	0	1
BRANCHIOPODA				1	1	1	1	1	0	0	0	1
COLLEMBOLA	COLLEMBOLA	ISOTOMIDAE	AXELSONIA	0	0	0	0	1	0	0	0	0
COLLEMBOLA	COLLEMBOLA	ISOTOMIDAE	ISOTOMURUS	0	1	0	0	1	0	0	1	1
COLLEMBOLA	COLLEMBOLA	SMINTHURIDAE		0	1	0	0	0	0	0	0	1
INSECTA	ODONATA	COENAGRIONIDAE	ACANTHAGRION	0	0	1	0	0	0	0	0	0
INSECTA	EPEHEMEROPTERA	BAETIDAE	ACERPENNA	0	0	1	0	0	0	0	0	0
INSECTA	COLEOPTERA	DYTISCIDAE	ACILIUS	0	0	0	0	0	0	0	1	0
INSECTA	ODONATA	AESHNIDAE	AESHNA	0	0	0	0	1	0	0	1	0
INSECTA	COLEOPTERA	DYTISCIDAE	AGABUS	0	0	1	0	0	1	0	0	0
INSECTA	TRICHOPTERA	HYDROPTILIDAE	AGRAYLEA	1	1	1	1	0	1	0	0	1
INSECTA	HEMIPTERA	NAUCORIDAE	AMBRYUS	0	0	0	1	0	0	0	0	0
INSECTA	EPEHEMEROPTERA	AMELETIDAE	AMELETUS	1	0	0	0	0	0	0	0	0
INSECTA	ODONATA	COENAGRIONIDAE	AMPHIAGRION	1	1	1	1	1	1	0	1	0
INSECTA	ODONATA	AESHNIDAE	ANAX	0	0	0	1	0	0	0	0	0
INSECTA	COLEOPTERA	ELMIDAE	ANCYRONYX	0	1	0	0	0	0	0	0	0
INSECTA	EPEHEMEROPTERA	BAETIDAE	APOBAETIS	1	0	0	0	0	0	0	0	0
INSECTA	ODONATA	COENAGRIONIDAE	ARGIA	1	1	1	1	1	1	1	1	1
INSECTA	ODONATA	GOMPHIDAE	ARIGOMPHUS	0	0	0	0	0	0	1	0	0
INSECTA	DIPTERA	CERATOPOGONIDAE	ATRICOPOGON	1	0	0	0	1	0	0	1	0
INSECTA	EPEHEMEROPTERA	BAETIDAE	BAETIS	1	0	1	0	0	1	1	0	0
INSECTA	ODONATA	AESHNIDAE	BASIAESCHNA	1	0	0	0	0	0	0	0	0
INSECTA	HEMIPTERA	BELOSTOMATIDAE	BELOSTOMA	1	1	1	1	1	0	1	0	1
INSECTA	COLEOPTERA	HYDROPHILIDAE	BEROSUS	1	1	1	1	1	1	0	1	1
INSECTA	DIPTERA	CERATOPOGONIDAE	BEZZIA	1	0	1	1	1	0	1	1	0
INSECTA	COLEOPTERA	DYTISCIDAE	BIDESSONOTUS	1	0	0	0	0	1	0	0	0
INSECTA	ODONATA	AESHNIDAE	BOYERIA	0	0	0	0	1	0	0	1	0

INSECTA	EPHEMEROPTERA	CAENIDAE	BRACHYCERCUS	1	1	1	0	1	1	1	1	1
INSECTA	COLEOPTERA	CURCULIONIDAE	BRACHYCERUS	1	1	1	1	1	1	1	1	1
INSECTA	ODONATA	LIBELLULIDAE	BRECHMORHOGA	1	0	0	0	0	0	0	0	0
INSECTA	EPHEMEROPTERA	CAENIDAE	CAENIS	0	0	0	0	0	0	1	0	0
INSECTA	EPHEMEROPTERA	BAETIDAE	CALLIBAETIS	1	0	1	1	1	1	0	1	1
INSECTA	EPHEMEROPTERA	BAETIDAE	CAMELO-BAETIDIUS	1	0	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	DYTISCIDAE	CELINA	0	0	0	0	0	1	0	0	0
INSECTA	EPHEMEROPTERA	BAETIDAE	CENTROPTILUM	0	0	1	0	0	0	0	0	1
INSECTA	DIPTERA	CERATOPOGON-IDAE	CERATOPOGON	1	0	0	0	1	0	0	0	0
INSECTA	TRICHOPTERA	HYDROPSYCHIDAE	CERATOPSYCHE	0	0	0	0	0	1	1	0	0
INSECTA	EPHEMEROPTERA	CAENIDAE	CERCOBRACHYS	0	0	0	0	0	0	0	0	1
INSECTA	TRICHOPTERA	POLYCENTRO- PODIDAE	CERNOTINA	0	0	1	0	0	1	0	0	0
INSECTA	TRICHOPTERA	HYDROPSYCHIDAE	CHEUMATO-PSYCHE	1	0	0	1	1	1	0	1	1
INSECTA	TRICHOPTERA	PHILOPOTAMIDAE	CHIMARRA	1	0	1	1	0	0	1	0	0
INSECTA	DIPTERA	CHIRONOMIDAE	CHIRONOMUS	0	0	0	0	0	1	1	0	1
INSECTA	ODONATA	COENAGRIONIDAE	CHROMAGRION	1	1	1	1	1	1	1	1	1
INSECTA	EPHEMEROPTERA	BAETIDAE	CLOEON	0	1	1	1	1	1	1	1	1
INSECTA	ODONATA	COENAGRIONIDAE	COENAGRION	0	0	0	0	0	0	0	1	0
INSECTA	COLEOPTERA	DYTISCIDAE	COPELATUS	0	0	0	1	1	1	0	1	1
INSECTA	ODONATA	AESHNIDAE	CORYPHAESCHNA	0	0	1	0	0	0	1	1	0
INSECTA	DIPTERA	CULICIDAE	CULEX	0	0	1	0	1	0	0	0	1
INSECTA	DIPTERA	CERATOPOGON-IDAE	CULICOIDES	1	1	1	1	1	0	0	0	1
INSECTA	HEMIPTERA	NEPIDAE	CURICTA	1	0	1	0	0	0	0	1	0
INSECTA	COLEOPTERA	SCIRTIDAE	CYPHON	0	1	0	1	0	0	1	1	1
INSECTA	TRICHOPTERA	POLYCENTRO- PODIDAE	CYRNELLUS	0	0	0	1	1	0	0	0	0
INSECTA	DIPTERA	CERATOPOGON-IDAE	DASYHELEA	0	0	0	0	0	0	0	1	0
INSECTA	COLEOPTERA	HYDROPHILIDAE	DERALLUS	0	0	0	1	0	0	0	0	0
INSECTA	COLEOPTERA	DYTISCIDAE	DESMOPACHRIA	0	0	0	0	1	0	0	0	0
INSECTA	ODONATA	CORDULIIDAE	DIDYMOPS	1	0	0	0	0	0	0	0	1
INSECTA	COLEOPTERA	GYRINIDAE	DINEUTUS	0	0	1	0	0	1	0	0	0
INSECTA	DIPTERA	TIPULIDAE	DOLICHOPEZA	1	0	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	ELMIDAE	DUBIRAPHIA	1	1	1	1	1	1	0	0	1
INSECTA	COLEOPTERA	SCIRTIDAE	ELODES	0	0	0	1	0	1	0	0	0
INSECTA	LEPIDOPTERA	CRAMBIDAE	ELOPHILA	0	0	0	0	1	0	0	0	0
INSECTA	ODONATA	COENAGRIONIDAE	ENALLAGMA	0	0	0	0	1	0	0	0	0
INSECTA	COLEOPTERA	HYDROPHILIDAE	ENOCHRUS	1	0	1	1	1	1	1	1	1
INSECTA	ODONATA	AESHNIDAE	EPIAESCHNA	0	0	0	0	0	0	0	0	1
INSECTA	ODONATA	GOMPHIDAE	ERPETO GOMPHUS	1	0	0	0	0	0	1	0	0
INSECTA	DIPTERA	STRATIOMYIDAE	EUPARYPHUS	0	0	0	0	0	0	0	1	0

INSECTA	EPHEMEROPTERA	BAETIDAE	FALLCEON	1	1	1	1	1	1	1	1	1	1
INSECTA	EPHEMEROPTERA	LEPTOPHEBIIDAE	FARRODES	1	0	0	0	0	0	0	0	0	0
INSECTA	DIPTERA	CERATOPOGONIDAE	FORCIPOMYIA	0	1	1	0	0	1	1	0	0	0
INSECTA	DIPTERA	SIMULIIDAE	GIGANTODAX	0	0	0	1	0	0	0	0	0	0
INSECTA	COLEOPTERA	HYDRAENIDAE	GYMNOCHTHEBIUS	1	0	0	1	0	0	0	0	0	0
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INSECTA	ODONATA	GOMPHIDAE	HAGENIUS	1	0	0	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	HYDROPHILIDAE	HELOCHARES	0	0	0	0	0	0	0	1	0	0
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INSECTA	DIPTERA	DRYOMYZIDAE	HETEROCHEILA	0	1	0	0	0	0	0	0	0	0
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INSECTA	COLEOPTERA	HYDROPHILIDAE	HYDROBIUS	1	0	0	0	0	0	0	1	0	0
INSECTA	COLEOPTERA	HYDROPHILIDAE	HYDROCHARA	0	1	0	0	1	0	0	0	0	0
INSECTA	COLEOPTERA	HYDROCHIDAE	HYDROCHUS	1	1	1	1	1	1	0	1	1	1
INSECTA	HEMIPTERA	HYDROMETRIDAE	HYDROMETRA	1	0	0	1	0	0	1	0	0	0
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INSECTA	TRICHOPTERA	HYDROPTILIDAE	HYDROPTILA	1	1	0	1	0	0	1	0	1	0
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INSECTA	ODONATA	CORDULIDAE	MACROMIA	1	1	0	0	0	0	0	1	1	0
INSECTA	HEMIPTERA	MACROVELIIDAE	MACROVELIA	0	0	0	0	0	0	1	1	0	0
INSECTA	COLEOPTERA	DYTISCIDAE	MATUS	0	0	0	0	0	0	0	1	0	0
INSECTA	DIPTERA	TIPULIDAE	MEGISTOCERA	0	0	1	0	0	0	0	0	0	0
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INSECTA	HEMIPTERA	MESOVELIIDAE	MESOVELIA	0	1	0	1	1	0	0	1	0	0
INSECTA	TRICHOPTERA	HYDROPTILIDAE	METRICHIA	0	0	0	0	0	0	1	0	0	0
INSECTA	HEMIPTERA	GERRIDAE	METROBATES	1	0	0	0	0	1	1	0	1	0
INSECTA	COLEOPTERA	SCIRTIDAE	MICROCARA	1	0	0	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	ELMIDAE	MICROCYLLOEPUS	1	1	1	0	0	1	1	0	0	0

INSECTA	HEMIPTERA	VELIIDAE	MICROVELIA	1	0	0	1	1	0	0	1	0
INSECTA	COLEOPTERA	ELMIDAE	NARPUS	1	1	1	1	1	0	0	0	0
INSECTA	ODONATA	AESHNIDAE	NASIAESCHNA	1	1	0	0	0	0	0	0	1
INSECTA	TRICHOPTERA	LEPTOCERIDAE	NECTOPSYCHE	1	0	1	1	0	1	0	0	0
INSECTA	ODONATA	COENAGRIONIDAE	NEHALENNIA	0	1	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	HYDRAENIDAE	NEOCHTHEBIUS	1	0	0	0	0	0	0	0	0
INSECTA	COLEOPTERA	ELMIDAE	NEOELMIS	1	0	1	0	0	1	1	0	1
INSECTA	HEMIPTERA	PLEIDAE	NEOPLEA	0	0	0	1	0	0	0	1	0
INSECTA	COLEOPTERA	DYTISCIDAE	NEOPORUS	0	0	1	0	0	0	0	0	0
INSECTA	TRICHOPTERA	HYDROPTILIDAE	NEOTRICHIA	0	0	0	0	0	0	0	0	1
INSECTA	HEMIPTERA	NEPIDAE	NEPA	0	0	0	0	0	1	0	0	0
INSECTA	ODONATA	CORDULIIDAE	NEUROCORDULIA	0	0	1	0	0	0	0	1	0
INSECTA	TRICHOPTERA	HYDROPTILIDAE	OCHROTRICHIA	0	0	0	1	0	0	0	0	0
INSECTA	DIPTERA	STRATIOMYIDAE	ODONTOMYIA	1	1	0	0	1	0	0	1	0
INSECTA	TRICHOPTERA	LEPTOCERIDAE	OECETIS	1	0	1	0	1	0	0	0	0
INSECTA	HEMIPTERA	MACROVELIIDAE	ORAVELIA	0	0	0	0	1	0	0	0	0
INSECTA	COLEOPTERA	ELMIDAE	ORDOBREVIEWA	1	0	1	1	0	0	0	0	0
INSECTA	DIPTERA	TIPULIDAE	ORMOSIA	0	0	1	0	0	0	0	1	1
INSECTA	TRICHOPTERA	HYDROPTILIDAE	ORTHOTRICHIA	0	0	1	0	0	0	0	0	1
INSECTA	TRICHOPTERA	HYDROPTILIDAE	OXYETHIRA	0	1	0	0	1	0	0	0	0
INSECTA	COLEOPTERA	DYTISCIDAE	PACHYDRUS	1	0	0	1	0	0	0	1	0
INSECTA	EPHEMEROPTERA	BAETIDAE	PARACLOEODES	0	1	0	0	1	0	1	1	1
INSECTA	HEMIPTERA	PLEIDAE	PARAPLEA	0	1	0	1	0	0	0	1	1
INSECTA	DIPTERA	SIMULIIDAE	PARASIMULIUM	0	0	0	1	0	0	0	0	0
INSECTA	HEMIPTERA	NAUCORIDAE	PELOCORIS	1	0	1	1	1	1	0	1	1
INSECTA	COLEOPTERA	HALIPLIDAE	PELTODYTES	1	1	1	1	1	1	0	1	1
INSECTA	DIPTERA	PSYCHODIDAE	PERICOMA	0	0	0	0	0	0	1	0	0
INSECTA	EPHEMEROPTERA	BAETIDAE	PLAUDITUS	0	1	1	1	0	0	0	0	0
INSECTA	TRICHOPTERA	HYDROPSYCHIDAE	POTAMYIA	0	0	1	0	0	1	0	0	0
INSECTA	DIPTERA	CERATOPOGONIDAE	PROBEZZIA	1	0	1	1	1	1	1	1	0
INSECTA	ODONATA	GOMPHIDAE	PROGOMPHUS	1	0	1	1	1	1	1	0	0
INSECTA	DIPTERA	PSYCHODIDAE	PSYCHODA	1	0	0	0	0	0	0	0	0
INSECTA	HEMIPTERA	NEPIDAE	RANATRA	1	1	1	1	0	1	1	1	1
INSECTA	ODONATA	AESHNIDAE	RE MARTINIA	0	0	0	1	1	0	1	1	0
INSECTA	HEMIPTERA	VELIIDAE	RHAGOVELIA	1	0	1	0	1	1	1	0	1
INSECTA	HEMIPTERA	GERRIDAE	RHEUMATOBATES	0	0	1	0	1	0	0	0	1
INSECTA	COLEOPTERA	SCIRTIDAE	SCIRTES	1	1	1	1	1	1	1	1	1
INSECTA	DIPTERA	CERATOPOGONIDAE	SERROMYIA	0	0	0	0	1	0	0	0	0
INSECTA	TRICHOPTERA	LEPTOCERIDAE	SETODES	0	1	0	0	0	0	0	0	0
INSECTA	DIPTERA	SIMULIIDAE	SIMULIUM	1	0	0	1	1	1	0	0	0

INSECTA	TRICHOPTERA	HYDROPSYCHIDAE	SMICRIDEA	1	0	0	0	0	0	0	1	0	0
INSECTA	ODONATA	CORDULIIDAE	SOMATOCHLORA	1	1	0	0	1	0	0	1	1	
INSECTA	COLEOPTERA	GYRINIDAE	SPANGLEROGYRUS	0	0	0	1	0	1	0	1	0	
INSECTA	COLEOPTERA	ELMIDAE	STENELMIS	1	1	1	1	1	1	1	1	1	
INSECTA	EPHEMEROPTERA	HEPTAGENIIDAE	STENONEMA	1	1	1	1	1	1	0	1	1	
INSECTA	DIPTERA	STRATIOMYIDAE	STRATIOMYS	0	0	0	0	0	0	0	1	0	
INSECTA	COLEOPTERA	NOTERIDAE	SUPHISELLUS	0	1	0	1	0	0	0	0	1	
INSECTA	LEPIDOPTERA	CRAMBIDAE	SYNCLITA	0	0	0	0	0	0	0	1	0	
INSECTA	ODONATA	COENAGRIONIDAE	TELEBASIS	0	0	0	0	1	0	0	0	0	
INSECTA	TRICHOPTERA	PSYCHOMYIIDAE	TINODES	1	0	0	0	0	0	0	0	0	
INSECTA	HEMIPTERA	GERRIDAE	TREPOBATES	0	0	1	0	0	0	1	0	1	
INSECTA	ODONATA	AESHNIDAE	TRIACANTHAGYNA	0	0	0	0	1	0	0	0	0	
INSECTA	TRICHOPTERA	LEPTOCERIDAE	TRIAENODES	0	1	0	0	0	0	0	0	0	
INSECTA	HEMIPTERA	CORIXIDAE	TRICHOCORIXA	0	1	1	1	0	1	0	0	1	
INSECTA	COLEOPTERA	HYDROPHILIDAE	TROPISTERNUS	0	0	0	0	1	0	1	1	0	
INSECTA	COLEOPTERA	ELMIDAE	ZAITZEVIA	0	0	0	0	1	0	0	0	0	
MALACOSTRACA	AMPHIPODA	HYALELLIDAE	HYALELLA	1	1	1	1	1	1	1	1	1	
MALACOSTRACA	DECAPODA	CAMBARIDAE	PROCAMBARUS	1	0	1	1	1	1	1	1	1	
MALACOSTRACA	DECAPODA	PALAEMONIDAE	MACROBRACHIUM	0	0	0	1	1	1	0	0	0	
MALACOSTRACA	DECAPODA	PALAEMONIDAE	PALAEMON	1	1	1	1	1	1	0	0	1	
MALACOSTRACA	MYSIDA	MYSIDAE		0	1	0	0	0	0	0	0	0	
OSTRACODA				1	1	0	0	0	0	0	0	1	
BIVALVIA	VENEROIDA	CORBICULIDAE	CORBICULA	1	1	1	1	1	1	1	0	1	
GASTROPODA	BASOMMATO-PHORA	PHYSIDAE	PHYSA	1	1	1	1	1	1	1	1	1	
GASTROPODA	NEOTAENIO-GLOSSA	THIARIDAE	MELANOIDES	1	0	0	1	1	0	1	1	1	

APPENDIX B: Relationships between functional groups and seasonal variation.

Table 1 Proportion of invertebrates in each functional feeding group organized by site and by season. Sites are ordered from low to high mean annual precipitation.

<i>Site</i>	<i>Year</i>	<i>Season</i>	<i>Filter Feeder</i>	<i>Collector-Gatherer</i>	<i>Herbivore</i>	<i>Predator</i>	<i>Shredder</i>
Tranquitas Creek	2017	Fall	0.143	0.685	0.046	0.126	0.000
	2018	Winter	0.000	0.500	0.150	0.350	0.000
	2018	Spring	0.613	0.055	0.050	0.282	0.000
	2018	Summer	0.066	0.181	0.253	0.500	0.000
San Fernando Creek	2017	Fall	0.495	0.123	0.000	0.383	0.000
	2018	Winter	0.450	0.044	0.024	0.482	0.000
	2018	Spring	0.005	0.585	0.038	0.372	0.000
	2018	Summer	0.058	0.290	0.285	0.368	0.000
Aransas River	2017	Fall	0.024	0.302	0.129	0.544	0.000
	2018	Winter	0.106	0.512	0.167	0.215	0.000
	2018	Spring	0.300	0.233	0.176	0.291	0.000
	2018	Summer	0.268	0.333	0.089	0.310	0.000
Mission River	2017	Fall	0.033	0.586	0.039	0.342	0.000
	2018	Winter	0.170	0.200	0.392	0.238	0.000
	2018	Spring	0.065	0.371	0.106	0.459	0.000
	2018	Summer	0.036	0.363	0.091	0.510	0.000
Perdido Creek	2017	Fall	0.453	0.116	0.202	0.229	0.000
	2018	Winter	0.450	0.137	0.200	0.212	0.000
	2018	Spring	0.094	0.179	0.392	0.334	0.000
	2018	Summer	0.275	0.374	0.155	0.197	0.000
Placedo Creek	2017	Fall	0.155	0.117	0.052	0.677	0.000
	2018	Winter	0.004	0.110	0.030	0.855	0.000
	2018	Spring	0.388	0.052	0.187	0.373	0.000
	2018	Summer	0.403	0.152	0.113	0.332	0.000
Garcitas Creek	2017	Fall	0.033	0.539	0.131	0.297	0.000
	2018	Winter	0.078	0.382	0.236	0.303	0.000
	2018	Spring	0.362	0.122	0.311	0.205	0.000
	2018	Summer	0.236	0.231	0.144	0.390	0.000
West Mustang Creek	2017	Fall	0.044	0.185	0.195	0.576	0.000
	2018	Winter	0.046	0.260	0.387	0.307	0.000
	2018	Spring	0.054	0.097	0.007	0.842	0.000
	2018	Summer	0.065	0.483	0.352	0.101	0.000
East Mustang Creek	2017	Fall	0.082	0.512	0.328	0.078	0.000
	2018	Winter	0.116	0.033	0.007	0.844	0.000
	2018	Spring	0.055	0.178	0.386	0.382	0.000
	2018	Summer	0.134	0.422	0.113	0.332	0.000

APPENDIX C: Results of mixed effects models.

Table 1 Results of mixed effects models presented by degrees of freedom, F-value and P-value statistics.

<i>Response Variable</i>	<i>Model Term</i>	<i>DF</i>	<i>F-value</i>	<i>P-value</i>
<i>Abundance</i>	Intercept	1,63	72.500	<.0001
	Season	3,63	2.332	0.0826
	Climate	1,7	3.351	0.1099
	Season * Climate	3,63	0.253	0.8586
<i>Functional Richness</i>	Intercept	1,63	20.749	<.0001
	Season	3,63	0.473	0.7024
	Climate	1,7	0.077	0.7899
	Season * Climate	3,63	0.895	0.4487
<i>NMDS Axis 1</i>	Intercept	1,63	0.001	0.9697
	Season	3,63	0.736	0.5343
	Climate	1,7	4.068	0.0835
	Season * Climate	3,63	0.208	0.8904
<i>NMDS Axis 2</i>	Intercept	1,63	0.137	0.7122
	Season	3,63	0.121	0.9472
	Climate	1,7	0.809	0.3983
	Season * Climate	3,63	0.796	0.5009
<i>Rao Q</i>	Intercept	1,63	233.875	<.0001
	Season	3,63	0.659	0.5801
	Climate	1,7	0.015	0.9067
	Season * Climate	3,63	0.271	0.8459
<i>Richness</i>	Intercept	1,63	152.691	<.0001
	Season	3,63	1.187	0.322
	Climate	1,7	0.025	0.8786
	Season * Climate	3,63	3.331	0.025
<i>Shannon Diversity</i>	Intercept	1,63	191.226	<.0001
	Season	3,63	0.666	0.5762
	Climate	1,7	0.002	0.9641
	Season * Climate	3,63	1.961	0.1289
<i>Abundance</i>	Intercept	1,67	59.994	<.0001
	Min Preceding Flow * Climate	1,67	0.457	0.5015
	Climate	1,7	2.893	0.1327
	Min Preceding Flow * Climate	1,67	0.969	0.3285
<i>Functional Richness</i>	Intercept	1,67	30.454	<.0001
	Min Preceding Flow	1,67	1.944	0.1678
	Climate	1,7	0.102	0.7588
	Min Preceding Flow * Climate	1,67	1.484	0.2273
<i>NMDS Axis 1</i>	Intercept	1,67	0.001	0.9794
	Min Preceding Flow	1,67	0.190	0.6641

	Climate	1,7	4.319	0.0763
	Min Preceding Flow * Climate	1,67	0.986	0.3243
<i>NMDS Axis 2</i>	Intercept	1,67	0.180	0.6729
	Min Preceding Flow	1,67	10.356	0.002
	Climate	1,7	1.029	0.3442
	Min Preceding Flow * Climate	1,67	4.749	0.0328
<i>Rao Q</i>	Intercept	1,67	224.117	<.0001
	Min Preceding Flow	1,67	1.681	0.1992
	Climate	1,7	0.072	0.7962
	Min Preceding Flow * Climate	1,67	1.263	0.2651
<i>Richness</i>	Intercept	1,67	203.221	<.0001
	Min Preceding Flow	1,67	1.449	0.2329
	Climate	1,7	0.008	0.9292
	Min Preceding Flow * Climate	1,67	5.470	0.0223
<i>Shannon Diversity</i>	Intercept	1,67	203.784	<.0001
	Min Preceding Flow	1,67	2.551	0.1149
	Climate	1,7	0.027	0.8751
	Min Preceding Flow * Climate	1,67	0.066	0.7982
<i>Abundance</i>	Intercept	1,67	61.310	<.0001
	Max Preceding Flow	1,67	0.407	0.5255
	Climate	1,7	3.168	0.1183
	Max Preceding Flow * Climate	1,67	0.123	0.727
<i>Functional Richness</i>	Intercept	1,67	22.512	<.0001
	Max Preceding Flow	1,67	2.989	0.0884
	Climate	1,7	0.103	0.7576
	Max Preceding Flow * Climate	1,67	0.117	0.7331
<i>NMDS Axis 1</i>	Intercept	1,67	0.001	0.9701
	Max Preceding Flow	1,67	0.346	0.5585
	Climate	1,7	4.148	0.0811
	Max Preceding Flow * Climate	1,67	0.938	0.3362
<i>NMDS Axis 2</i>	Intercept	1,67	0.131	0.7181
	Max Preceding Flow	1,67	1.080	0.3025
	Climate	1,7	0.864	0.3836
	Max Preceding Flow * Climate	1,67	0.338	0.563
<i>Rao Q</i>	Intercept	1,67	260.729	<.0001
	Max Preceding Flow	1,67	0.354	0.554
	Climate	1,7	0.044	0.8396
	Max Preceding Flow * Climate	1,67	0.540	0.465
<i>Richness</i>	Intercept	1,67	174.076	<.0001
	Max Preceding Flow	1,67	1.020	0.3162
	Climate	1,7	0.021	0.8889
	Max Preceding Flow * Climate	1,67	1.493	0.226
<i>Shannon Diversity</i>	Intercept	1,67	190.296	<.0001
	Max Preceding Flow	1,67	2.165	0.1459

	Climate	1,7	0.008	0.9309
	Max Preceding Flow * Climate	1,67	0.000	0.9868
<i>Abundance</i>	Intercept	1,69	58.205	<.0001
	Annual Rainfall	1,7	1.731	0.2298
<i>Functional Richness</i>	Intercept	1,69	20.683	<.0001
	Annual Rainfall	1,7	0.079	0.7863
<i>Rao Q</i>	Intercept	1,69	253.704	<.0001
	Annual Rainfall	1,7	0.419	0.5381
<i>Shannon Diversity</i>	Intercept	1,69	197.364	<.0001
	Annual Rainfall	1,7	0.299	0.6013
<i>Richness</i>	Intercept	1,69	157.855	<.0001
	Annual Rainfall	1,7	0.156	0.705
<i>NMDS Axis 1</i>	Intercept	1,69	0.002	0.9637
	Annual Rainfall	1,7	10.491	0.0143
<i>NMDS Axis 2</i>	Intercept	1,69	0.125	0.725
	Annual Rainfall	1,7	0.515	0.4962