

Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages in coastal streams

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Anthropogenic climate change is expected to increase the aridity of many regions of the world. Surface water ecosystems are particularly vulnerable to changes in the water-cycle and may suffer adverse impacts in affected regions. To enhance our understanding of how freshwater communities will respond to predicted shifts in water-cycle dynamics, we employed a space for time substitution along a natural precipitation gradient on the Texas Coastal Prairie. In the Spring of 2017, we conducted surveys of 10 USGS gauged, wadeable streams spanning a semi-arid to sub-humid rainfall gradient; we measured nutrients, water chemistry, habitat characteristics, benthic macroinvertebrates, and fish communities. Fish diversity correlated positively with precipitation and was negatively correlated with canopy cover, conductivity, and NH_4^+ . Macroinvertebrate diversity was only significantly correlated with low-flow pulse percent (a proxy for hydrologic drought), however macroinvertebrate community composition significantly changed along the gradient. Observed compositional shifts in both fish and invertebrates along the gradient are potentially indicative of both top-down and bottom-up controls on community assembly. Semi-arid sites contained salt tolerant and rapidly proliferating taxa. Sub-humid sites contained a variety of fish omnivores and piscivores, including migratory marine species which may impose top-down controls on primary consumers. These results indicate that small future changes in precipitation regime in this region may result in abrupt transitions into new community states.

Manuscript Title

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Abstract:

Anthropogenic climate change is expected to increase the aridity of many regions of the world. Surface water ecosystems are particularly vulnerable to changes in the water-cycle and may suffer adverse impacts in affected regions. To enhance our understanding of how freshwater communities will respond to predicted shifts in water-cycle dynamics, we employed a space for time substitution along a natural precipitation gradient on the Texas Coastal Prairie. In the Spring of 2017, we conducted surveys of 10 USGS gauged, wadeable streams spanning a semi-arid to sub-humid rainfall gradient; we measured nutrients, water chemistry, habitat characteristics, benthic macroinvertebrates, and fish communities. Fish diversity correlated positively with precipitation and was negatively correlated with canopy cover, conductivity, and NH_4^+ . Macroinvertebrate diversity was only significantly correlated with low-flow pulse percent (a proxy for hydrologic drought), however macroinvertebrate community composition significantly changed along the gradient. Observed compositional shifts in both fish and invertebrates along the gradient are potentially indicative of both top-down and bottom-up controls on community assembly. Semi-arid sites contained salt tolerant and rapidly proliferating taxa. Sub-humid sites contained a variety of fish omnivores and piscivores, including migratory marine species which may impose top-down controls on primary consumers. These results indicate that small future changes in precipitation regime in this region may result in abrupt transitions into new community states.

Introduction:

A warming climate necessitates a better understanding of the processes that link biological communities to long-term trends in temperature and precipitation (Wrona *et al.* 2006; Miranda, Coppola, and Boxrucker 2020). The direct ecological effects of changes in temperature have received greater attention in the literature, but rising temperatures are also expected to alter patterns of precipitation and evaporation. A warmer, more energetic atmosphere intensifies the hydrological cycle (i.e. patterns of

precipitation and evaporation), causing wet regions to become wetter and dry regions become drier (Allen and Ingram 2002), as well as increasing the frequency and intensity of extreme weather events (Held and Soden 2006). This raises concern for freshwater ecosystems which are highly sensitive to changes in water availability and contain many species with limited dispersal capabilities (Woodward, Perkins, and Brown 2010).

Streams ecosystems are shaped by flow regimes which regulate the physical extent of aquatic habitat, the water quality, sourcing and exchange rates of material, habitat connectivity and biodiversity (Rolls, Leigh, and Sheldon 2012). In addition to streamflow mechanisms, streamside vegetation mediates interactions with watershed nutrients, carbon and light inputs to streams (Schade *et al.* 2001). Precipitation regime is one of the primary regulators of both streamflow and riparian characteristics. With predicted changes in flood and drought characteristics under global warming (Hirabayashi *et al.* 2008), it is imperative to understand the mechanistic links between precipitation, streamflow, and riparian interactions with aquatic biological communities.

Hierarchical community assembly models can help us organize our hypotheses regarding impacts of climate change on stream communities (Poff 1997). Assuming organisms can disperse to a habitat, they must be able to survive in the local environment (abiotic filters) and successfully reproduce in the presence of other organisms exerting pressures (biotic interactions) such as competition and predation (Patrick and Swan 2011). Species have physiological tolerances (temperature, toxin concentrations, and salinity, etc.) which limit their distribution across environmental gradients (Whittaker, Willis, and Field 2001). If climate change alters those gradients, we can expect concordant changes in species distributions. However, understanding how the environment affects biotic interactions is more challenging due to the complex sets of interactions that govern these processes (Seabra *et al.* 2015).

Observational surveys of existing communities spatially distributed along environmental gradients can be used in a space-for-time substitution to infer how communities will change through time as environmental conditions shift. The approach allows for links to be drawn between climate drivers, local environmental conditions, and organism abundances. Species co-occurrence patterns along environmental gradients can also shed light on possible shifts in biotic interactions (D'Amen *et al.* 2018). However, the space-for-time substitution approach assumes that observed ecological differences along the spatial gradient are the sole product of corresponding changes in climate. This assumption may be unfair given that biogeographical studies have revealed that dispersal limitation, habitat heterogeneity, and local evolution can also contribute to current spatial patterns in community composition (Jacob *et al.* 2015). These studies are typically large in scale, covering vast distances (thousands of km) to capture climate gradients. These large scales make the precise mechanisms for observed biological changes difficult to ascertain due to covarying environmental variables (e.g., elevation, geology, human impacts). Thus, while current literature demonstrates that biome shifts occur across temperature and latitudinal gradients (De Frenne *et al.* 2013), the value of these observational studies for forecasting community responses to climate change is hindered by the many confounding variables. The power of using the space-for-time approach to delineate the intricacies of hydrologic cycle-ecosystem relationships is enhanced in study systems with limited confounding environmental variables (temperature, elevation, distance, and underlying geology).

The Texas Coastal Prairie (TCP) within the Western Gulf coastal grasslands is an ideal system for evaluating the effect of hydrologic climate change on ecological communities. It is located within the Western Gulf coastal grasslands which are a subtropical ecotone that spans Louisiana, Texas, and northern Mexico's coastal areas. The system encompasses the sharpest non-montane precipitation gradient in the continental United States. The climate becomes more arid as you move west, with gradual change for much of the coast and a region of rapid change located in southern Texas. In this region the annual rainfall changes from 55cm•yr⁻¹ (semi-arid) to 135 cm•yr⁻¹ (sub-humid) over a 300 km gradient, but there are minimal changes in elevation, air temperature, underlying geology, and human land use (Table 1). The region is characterized by gently rolling landscapes (slopes < 5%), afisol soils, streams with forested riparian zones, and a widespread conversion of grasslands to the agricultural production of cattle, cotton, corn, and soy products (Chapman 2018). As conditions become wetter, there is an observable ecological shift from mesquite groves in the semi-arid West to live oak and pecan forests towards the East. The TCP is an ideal study region for isolating precipitation influences on natural ecosystem processes because of the minimal impact of covarying predictors that typify climate gradient research.

Despite the intrinsic value of this region as a candidate for climate gradient research, there is limited prior biological sampling by governmental agencies of running waters in the TCP. To address this need, we conducted the first dedicated survey of streams across the climate gradient. We applied rapid bioassessment protocols to 10 USGS-gauged (U.S. Geological Survey), wadeable streams for quantification of fish, benthic macroinvertebrates, and environmental variables. Our objectives were to: 1) Identify patterns in the diversity and composition of fish and macroinvertebrates communities that correspond to changes in precipitation, and 2) identify environmental predictors that mediate the effects of climate on community processes. We expected that annual precipitation would be positively correlated with community diversity because humid precipitation regimes are expected to create more stable environmental conditions by creating habitat heterogeneity and predictable flow regimes which promote the development of greater biodiversity (Boulton *et al.* 1992; Bunn and Arthington 2002). We further expected that evapotranspiration by riparian vegetation would increase solute concentrations in semi-arid streams, particularly during base flows (Tabacchi *et al.* 2000; Lupon *et al.* 2016), creating environmental filters that limit recruitment of sensitive fish and macroinvertebrates (hereafter referred to as invertebrates).

Methods

Study Region: The Texas Coastal Prairie contains grassland prairie with forested areas occurring primarily along riverine systems. During March and April of 2017, we sampled ten, wadeable, perennial streams which span 12 counties from Kleberg County to Montgomery in South-Central Texas, USA (Fig. 1). Each study site was located within 100 meters of a USGS stream gauge which continuously monitor streamflow and climate data year-round. Study sites were chosen to maximize differences in precipitation with minimal changes in underlying geology and elevation. The annual precipitation ranges from 61-121 cm within the study region which spans a linear

distance from end to end of 378 km (Falcone 2011). The surface geology is characterized by fine clays, quaternary and sedimentary sand. The streams have similar elevations (14-62 m), substrates (quaternary), and average air temperatures (19.8-22.1°C) (Falcone 2011). Sampling was conducted by students and faculty at Texas A&M (Corpus Christi) under permit SPR-0716-170, granted by Texas Parks and Wildlife Department.

Biological Sampling: Fish communities were sampled using a Smith-Root LR-24 Backpack in a single pass survey (Lamberti 2017). Each reach length was 25 times the average stream width, in accordance with EPA rapid bioassessment protocols (US EPA 2019). Fish species were field identified to species using a field guide (Thomas *et al.* 2007) and photographed. Several specimens of each species were euthanized using tricaine mesylate (MS-222) and stored in >70% denatured ethanol as voucher specimens for lab confirmation of species identification. Fish Voucher specimens were identified using the Texas Academy of Science dichotomous key (Hubbs, Edwards, and Garrett 2008) and cross referenced with field identifications. Vertebrate sampling was permitted by the Institutional Animal Care and Use Committee, Texas A&M University Corpus Christi (AUP# 05-17).

Invertebrates were collected using a 0.305m wide D-frame net equipped with 500-µm mesh. Twenty 0.093 m² samples were collected via a combination of kick and sweep (15 s duration) sampling from a representative distribution of best available habitat (riffles, large woody debris, overhanging vegetation). Samples were pooled in a 500-µm sieve bucket where larger sticks and leaves were rinsed and removed. The captured invertebrates and remaining debris were preserved in 95% EtOH for transport to the lab. In the lab, samples were spread across a gridded sampling tray and randomly selected grid cells were picked to completion until the total count was > 300 individuals (USEPA 2015). Samples containing less than 300 individuals were picked to completion. Invertebrates were identified to lowest taxonomic resolution (typically genus) using taxonomic keys cross referenced with species observations recorded by the TCEQ's (Texas Commission on Environmental Quality) Surface Water Quality Monitoring Program (Wiggins, G. 2015; Cummins and Merritt 1996). The sum of individuals in each taxon were multiplied by the fraction of unpicked sample and reported as abundance of individuals per square meter.

Environmental Data: For each stream, we averaged values for each of the following habitat measurements that were taken at 4 cross-sections spaced 25m apart. Canopy cover was measured using a spherical densiometer. A Rosgen Index value was calculated by dividing the bank-full width by the maximum depth (Rosgen 2001). Bank height was recorded as vertical difference between water level and the height of the first bench. We estimated Sediment grain size within each cross-section using Wentworth size categories to calculate a median grain-size (d50) (Wentworth 1922). Oxygen, temperature (T_{water}), conductivity, turbidity, and pH were measured at each point using a YSI ProDSS multiparameter probe. Two 60 mL water samples were collected and filtered through a pre-combusted (500°C for 4 hours) glass fiber filter (Whatman GF/F) into acid washed amber bottles, transferred to the lab in a cooler on ice, and stored frozen (-20°C) until analysis for nutrients (NH_4^+ , NO_3^- , and PO_4^-). Water samples were

run using colorimetric methods on a latchet autoanalyzer by the Oklahoma University Soil Water and Forage Laboratory.

In addition to the habitat metrics measured in the field, we mined climate and watershed data, from the US Geologic Surveyors Geospatial Attributes of Gages for Evaluating Streamflow, version II dataset (Falcone 2011). A twenty-year continuous daily flow record was downloaded for each site (except Tranquitas Creek which only had 4 years of available data) from the USGS Water Services (<https://waterservices.usgs.gov>).

Analyses: Due to a small number of sample sites and replicates, the statistical analyses relating environmental drivers to organismal responses were restricted to seven *a priori* environmental predictors (Table 2). Annual precipitation was evaluated to identify gradient effects. The Rosgen index characterized the channel shape which is a product of flow regime, slope, substrate, and bank stability. Canopy coverage was determined by the type of vegetation which visibly shift across the study region with implications for stream insolation and basal resources. We included conductivity and NH_4^+ to evaluate water quality. Since the selected streams were deliberately chosen to be wadeable at base flow, we calculated two flow metrics to approximate the typical flow regime of each site in the context of seasonal droughts and floods, as well as overall variation in flow: Flash Index (cumulative changes in day to day daily flow / cumulative flow) and the Low-Flow Pulse Percent (LFPP = times where daily discharge drops below the 25th percentile) (Olden and Poff 2003; Patrick and Yuan 2017).

We used linear regression and Pearson correlation coefficients to identify potential confounding relationships between precipitation and each environmental predictor (Table 3). We then, used singular value decomposition of the centered and scaled data matrix in a principal component analysis with all seven environmental predictors (Fig. 2, Table 4).

For each community (fish and invertebrate) we calculated Shannon diversity and rarified taxonomic richness (Hurlbert 1971). Diversity and richness measures were calculated using the Vegan Library (Oksanen *et al.* 2019) in the ~~statistical~~ program R (R Core Team 2018). While rarified richness is reported in supplemental materials, further analyses and discussion regarding diversity utilize the Shannon-Weiner index which incorporates species evenness in addition to richness. We used linear regression to evaluate community diversity relationships with the precipitation gradient and each environmental predictor (Fig. 3, Fig. 4, Table 5). To create a predictive model of community diversity, we used multiple regression with an additive global model utilizing all seven environmental predictors and ranked them using Aikake's information criterion corrected for small sample sizes (AIC_c). All the results were compared to the best overall model by calculating the difference in AIC_c values (ΔAIC_c). Models with $\Delta\text{AIC}_c < 10$ are reported (Table 6, Table 7) and models with $\Delta\text{AIC}_c < 2$ were considered to have substantial support (Burnham and Anderson 2002).

To discern compositional shifts in fish and invertebrates across the precipitation gradient, we used Redundancy Analysis (RDA), constrained by precipitation, on Hellinger-transformed community data for each group (Pierre Legendre and Gallagher 2001; P. Legendre and Legendre 2012). We then fit the species and environmental variable vectors to each ordination by calculating the maximum correlation with the

projection of points (sites in this case). The direction of each arrow is determined by the average directional cosines and the distance to the origin is scaled by each variable's correlation coefficient, so that "weak" predictors have shorter arrows than "strong" predictors (Table 8, Table 9). Vectors were calculated using the 'envfit' function in the vegan library in the statistical program R (Oksanen et al. 2019).

Results

Site Overview: The Principal Component Analysis of the study sites displays patterns of variation among environmental predictors along the gradient (Fig. 2). The first two principal component axes, PC1 and PC2, contain 43.2% and 19.9% of the variation within the environmental predictors among the sites (Table 4). It is visually apparent that the sample sites, colored by precipitation, stratify concordantly with annual rainfall along Principal Component Axis 1 (PC1). Predictor variable vectors with similar directionality (parallel axes) can be inferred to covary. The PCA indicates that conductivity negatively covaries with precipitation and low-flow pulse % negatively covaries with flash index. A pairs regression analysis of the seven environmental variables reveals two significant (p -value < 0.05) correlations (Table 3). Conductivity negatively correlates with precipitation. NH_4^+ positively correlates with canopy coverage.

Fish Community: Eighteen fish species were identified among the surveyed sites. Proceeding from semi-arid to sub-humid sites, fish Shannon index increased from 0.64 - 1.81 and richness increased from 2 - 7 species. Regression analysis indicates that fish Shannon diversity is positively correlated with precipitation and negatively correlated with canopy coverage, conductivity, and NH_4^+ (Fig. 3, Table 5). The most plausible multivariate regression model of fish Shannon diversity includes precipitation and Low-Flow Pulse Percent (LFPP) and is 2.5 times more likely than the next-best model (Table 6). The second-best model contains a single predictor, precipitation. Across models, precipitation positively relates to Shannon diversity while LFPP is negatively related.

The Redundancy Analysis (RDA) of fish communities constrained to precipitation captures 23.6% of the overall variation in the horizontal axis (RDA1) and 25.4% in the vertical axis (PC1) (Fig. 3). Sites are stratified in ordination space horizontally according to annual rainfall; the fitted precipitation vector has a significant correlation within the ordination and is closely aligned with RDA1 (Table 8). Five statistically significant, fitted species vectors indicate that species compositions shift from small, elongate live-bearer taxa (*Poecilia latipinna*, and *Gambusia affinis*) in the most arid sites to deep-bodied, nesting centrarchids (*Lepomis megalotis* and *Lepomis macrochirus*) in the more humid sites. The remaining fitted species vector indicates that some mesic and humid stream communities are distinguished by the presence of *Cyprinella lutrensis*, a small, invasive habitat-generalist. Species found in small numbers or at singular sites fail to produce significant vectors in the RDA. Unique species found in sites on the humid side of the climate gradient include hogchoker (*Trinectes maculatus*), black bullhead catfish (*Ameiurus melas*), and blacktail shiner (*Cyprinella venusta*).

Invertebrate Community: In total, 94 invertebrate genera were identified within the surveyed sites. Invertebrate richness ranged 7–29 genera with the highest values

occurring at three sites in the middle of the precipitation gradient (Fig. 4). Regression analysis indicates that invertebrate Shannon diversity does not significantly correlate with precipitation. However, invertebrate diversity has a significant negative correlation with LFPP (Table 5). The most plausible multivariate regression model of fish Shannon diversity includes only LFPP and is 1.6 times more likely than the next-best model (Table 7). The second-best model contains a fixed random effect, and the third-best model contains LFPP and NH_4^+ as predictors. Across models, LFPP is a negatively related to invertebrate diversity, and NH_4^+ is positively related to invertebrate diversity.

The Redundancy Analysis (RDA) of invertebrate communities constrained to precipitation captures 15.4% of the overall variation in the horizontal axis (RDA1) and 16.5% in the vertical axis (PC1) (Fig. 4). Like fish, invertebrate communities are stratified in ordination space horizontally concordantly with annual precipitation; the fitted precipitation and conductivity vectors have significant correlations within the ordination and are closely aligned with RDA1 (Table 9). Eight statistically significant, fitted species vectors indicate that species compositions shift along the precipitation gradient. The most arid sites are strongly correlated with a non-native burrowing gastropod (*Melanoides tuberculata*). Mesic invertebrate communities are strongly correlated with an air-breathing gastropod (*Physa*) and a semi-aquatic Coleopteran (*Hydraena*). Mesic and humid sites separate along the vertical axis of the RDA plot and both appear to weakly correlate with the species vectors of several Ephemeroptera (*Caenis* and *Plautidius*). Humid sites correlate with a mixture of fully aquatic taxa including Crustacea (*Palaemonetes*), Amphipoda (*Hyaella*), and Trichoptera (*Cheumatopsyche*).

Discussion

Using the Texas Coastal Prairie (TCP) as a model system, our goal was to quantify patterns in the diversity and composition of stream communities along an extreme precipitation gradient to better understand how streams might respond to future changes in mean annual rainfall. We identified compositional shifts in both fish and invertebrate communities along the precipitation gradient. We also observed a positive relationship between fish diversity and mean annual rainfall, matching expectations, whereas invertebrate diversity did not exhibit the expected relationships with rainfall. Changes in water solute concentrations and flow regime appear to be additional important drivers of community responses. Below, we discuss these results, place them in the context of other literature, and make suggestions for future work.

The paucity of covarying relationships between precipitation and other environmental variables such as channel morphology and water quality support our premise that the TCP is an exemplary region to conduct space for time substitutions to make useful ecological predictions regarding climate change. We expected precipitation to covary with flow regime, water quality, canopy coverage, and stream geomorphology. However, while study sites separated horizontally in ordination space according to their annual precipitation, relatively few predictors in our analysis covaried with precipitation save for a negative relationship with water conductance (Fig. 2, Table 3). We attribute the increasing conductivity with aridity to several factors. The inherently larger water shed area that perennial arid streams have in comparison to mesic streams of similar

discharge results in greater opportunity for surface evaporation and more water contact with soils, before reaching the stream (Williams 1999).

Contrary to our predictions, flash index and Low-Flow Pulse Percent (LFPP) did not covary with annual rainfall. Hydrologic flashiness exhibited weak, negative relationships with drainage area and mean daily discharge. Smaller drainage areas often have higher flashiness due to hydrograph mixing accompanying flood routing through stream networks and other scale-dependent runoff factors (Baker *et al.* 2004). Increasing watershed size with declining annual precipitation was intentional and necessary to maintain wadeable, perennial stream habitats throughout the gradient. Unlike flashiness, LFPP showed a weak, negative relationship with the proportion of forested riparian zone which could have exacerbated low-flows during dry seasons by up-taking groundwater and evapotranspiration (Connor *et al.* 2013). Average daily discharge and the proportion of forested riparian zone represent drivers of hydrologic variation that act at the watershed scale, outside of precipitation gradient effects.

The fish communities displayed a ~~pattern of~~ increasing diversity moving from the drier to wetter sides of the survey region (Fig. 3). This may have been mediated by changes in water quality and sediment composition along the gradient. Fish Shannon diversity ~~correlated~~ positively with precipitation, but negatively with conductivity and NH_4^+ , canopy coverage and LFPP (Table 5). Elevated conductivity and NH_4^+ in semi-arid streams exhibited levels similar to urbanized streams (Hatt *et al.* 2004), creating stressful osmotic and toxic conditions for fish (Redding and Schreck 1983; Lock and Wendelaar Bonga 1991). Elevated NH_4^+ has been shown to be directly toxic to many fish (Randall and Tsui 2002) and has also fueled cytotoxic algal growth (Fetscher *et al.* 2015). Elevated solute concentrations were likely driven by evaporation, the watershed area/discharge ratio, and the greater influence of wastewater effluent on low discharge streams that typify semi-arid streams (Williams 1999; Dehedin *et al.* 2013). We also noted but did not quantify higher concentrations of silt in the semi-arid streams with prohibitive implications for nesting species (Jones *et al.* 2015). We interpreted these patterns to mean that as conditions become drier, water quality imposes abiotic filters on fish assembly which reduce overall community diversity and selects for taxa with specialized adaptations for the harsh conditions.

Communities in semi-arid streams were composed of small, live-bearing, omnivores able to tolerate high salinities including Sailfin Molly (*Poecilia latipinna*, 95 psu) and Western Mosquitofish (*Gambusia affinis*, 58.5 psu) (Page and Burr, B.M. 1991). The strongest compositional shift observed were increases in the abundance of centrarchids (sunfish) with increases in annual rainfall. Centrarchid species have 3-7 year lifespans, breed annually, build nests, and are omnivores (Cooke and Philipp 2009). Additional increases in diversity towards the wetter side of the climate gradient included the addition of black bullhead catfish (a demersal, nesting omnivore), and several shiner species (small broadcast spawning minnows). These organisms require conditions that are stable across years as well as suitable substrate for rearing young, suggesting that conditions in semi-arid sites were excluding these taxa through environmental filtering. Additionally, some of the sub-humid and mesic sites also had seasonally migrating taxa including Rio Grande Cichlid (*Herichthys cyanoguttatus*), Hogchoker (*Trinectes maculatus*), and American Eel (*Anguilla rostrata*) (Rehage *et al.*

2016; Koski 1978; Wenner, C.A. 1978). These were absent from semi-arid sites. Given the similar proximity to nearby reservoirs and estuaries, migratory taxa may have been excluded from streams with habitat fragmentation, approximated here by low flow pulse %, that typify semi-arid streams (De Jong *et al.* 2015).

Red shiners (*Cyprinella lutrensis*) were curiously absent from semi-arid sites and were only present in four mesic and sub-humid sites. In ordination space, two sites with the highest abundances of red shiner (Aransas and Placedo) separated perpendicularly from the rainfall-gradient effects and coextended with Rosgen (stream morphology) and hydrologic flashiness indices (Fig. 3). High abundances of red shiner were associated with shallow riffle habitats with gravel substrates which occurred at three sites throughout the gradient. This was peculiar since red shiner are considered to be a habitat generalist and rugged invasive throughout the United States (Marsh-Matthews and Matthews 2000; Matthews and Marsh-Matthews 2007). We suspected their apparent habitat preference was driven by competition and predation by centrarchids in nearby pool and run habitats. Although red shiners tolerate high temperatures and low oxygen, conductivity was likely excluding red shiner (salinity tolerance < 10 psu) from the arid sites (Matthews and Hill 1977). In this light, we considered hydrologic flashiness a spurious influence on red shiner distributions beyond its capacity to influence channel geomorphology.

LFPP approximated drought prevalence and was the sole significant predictor of invertebrate community diversity (Fig. 4). In addition to LFPP, the top-ranked multiple regression models also implicated NH_4^+ was an effective predictor of invertebrate diversity. These results corroborate expectations for the ramping disturbance conditions typical of droughts in which water availability and quality diminish over time. Compared to fish, invertebrates have restricted in-stream mobility and traditionally seek refuge in the hyporheic zone, interstitial spaces, and in some cases utilize desiccation-resistant life-stages (Boulton *et al.* 1992; Boulton 2003). Here, Semi-arid community compositions included a higher proportion of gastropods which are well adapted to the stresses that characterize increased LFPP. For example, *M. tuberculata* were the most abundant primary consumers in the semi-arid streams and can resist the osmotic stress imposed by drought conditions with a broad range of salinity tolerance (0-23 PSU). This species is also well-adapted to survive and reproduce throughout periodic dewatering due to its rapid maturation (21-62 days), asexual reproduction, and internal offspring gestation (Farani *et al.* 2015).

Surprisingly, while invertebrate community composition shifted with rainfall, invertebrate diversity did not correlate linearly with precipitation. Instead, invertebrate diversity peaked in the middle of the rainfall gradient. The lack of a linear correlation between invertebrate diversity and precipitation may have been caused by the inherently larger species pool for invertebrates which included more taxa with biological adaptations to drought compared to fish (Eriksson 1993). The peak likely represented the transition zone where taxa common on each side of the gradient were able to co-occur. As precipitation increased, there were three points of interest: 1) The shift in primary producers and the increased prevalence of amphipods and decapods at wetter sites implied a corresponding shift in available basal resources. Specifically, precipitation-mediated shifts in riparian vegetation from evergreen, xeric mesquite trees to deciduous hardwoods likely altered the inputs of terrestrially derived detrital inputs

and instream productivity to promote the inclusion of shredder taxa (Giling, Reich, and Thompson 2009). 2) The observed shift in primary consumers from short-lived, euryhaline dipterans and gastropods to ephemeropterans and trichopterans, environmentally sensitive species with longer lifespans, pointed towards improved water quality conditions and hydrologic stability (Rosenberg and Resh 1993; Jackson and Sweeney 1995). Taken further, this pattern alludes to trade-off between aridity tolerance and competitive specialization (Fréjaville *et al.* 2018). 3) The decreased abundance of odonate and hemipteran predators may have been due to competition with and predation by insectivorous centrarchids (Dahl and Greenberg 1998). In this way, biotic interactions at sub-humid sites presumably restricted invertebrate communities to species with anti-predator adaptations including small size, passive foraging strategies, camouflage, and armoring (Straile and Halbach 2000). Taken together, these invertebrate (and fish) community compositional patterns suggest that small changes in precipitation regime could result in abrupt ecosystem shifts (Scheffer and Carpenter 2003).

While this survey only consisted of 10 streams, it is the first published rapid bioassessment of systems along the rainfall gradient on the Texas Coastal Prairie. The results largely conform to *a priori* hypotheses indicating that the region represents a promising study region for climate research. In addition to its capacity for a space for time substitution, the TCP is poised to provide real-time data on the effects of climate change on ecosystems. Future research in this region would benefit from higher frequency sampling over a longer time period and quantification of invertebrate and fish functional traits. An in-depth time series study would allow for evaluation of how these communities change across seasons, how they respond to periodic droughts and floods, and how stable the communities are through time. More detailed quantification of the fish communities through depletion surveys and invertebrate communities via biomass cores would allow for greater characterization of the relative abundance of different taxa through time, and these could be linked to functional traits to explore the mechanisms behind some of the patterns that we observed here. A continuation of this sampling program with thorough methods will augment the analytical power, precision, and depth of this natural experiment.

Despite this study's limitations, our results highlight the breadth and far-reaching ecological consequences associated with small changes in precipitation. They warn that regions expected to become more arid, like Central and Western Texas (Jiang and Yang 2012), could expect a loss of competitive taxa with low environmental tolerances as observed here with centrarchids, ephemeropterans, and trichopterans. And that in their absence, rugged and euryhaline taxa (like livebearers, burrowing gastropods and predatory invertebrates) flourish. Furthermore, this study warrants investigation to clarify the causal relationships between the ecological constraints imposed by aridity and these observed community shifts.

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655

Figure 1

Map of South-Central Texas, where 10 USGS gaged Streams were sampled in the Spring of 2017.

An annual precipitation overlay indicates that the sample sites span a gradient from 61 cm/yr in the Southwest to 134 cm/yr in the Northeast.

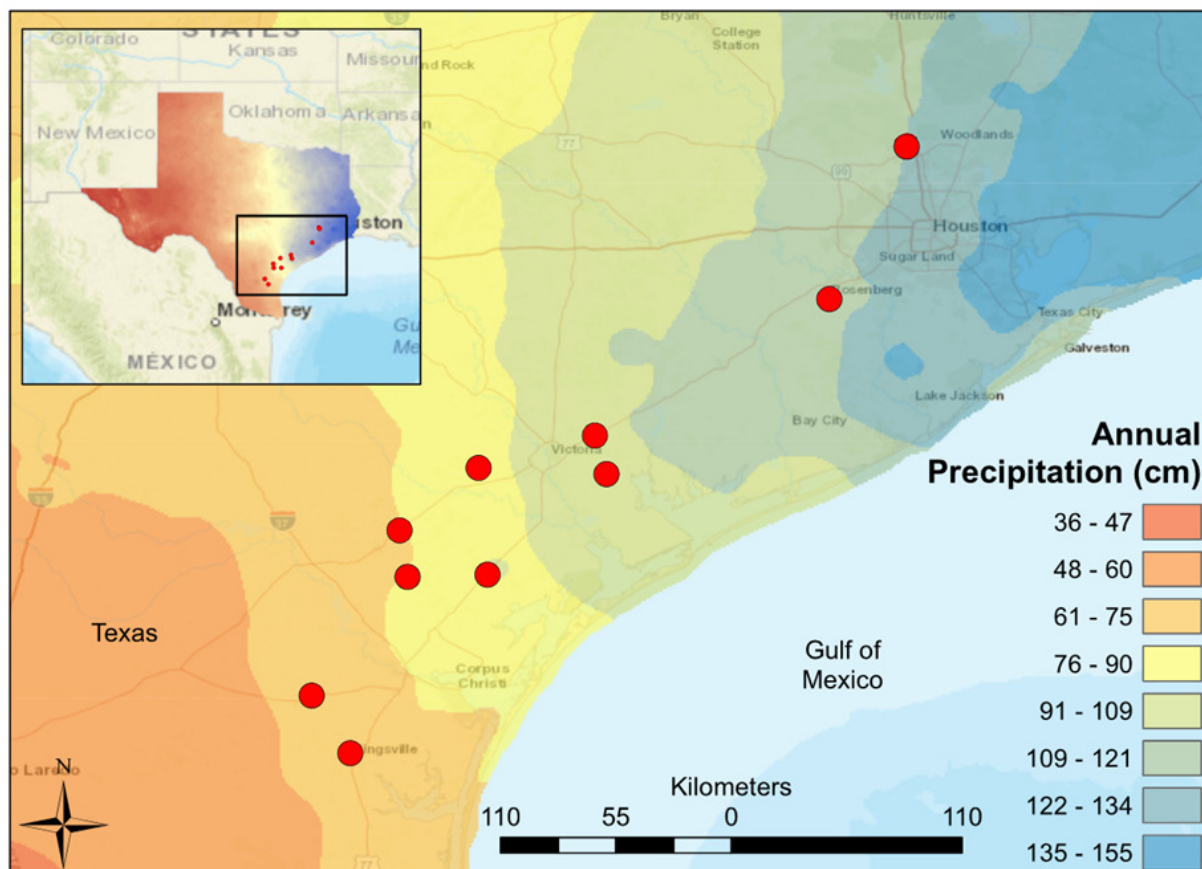


Figure 2

Principal Component Analysis of environmental predictors at 10 sites spanning a precipitation gradient along the Texas Coastal Prairie.

Circles representing sample sites are colored based on their annual precipitation. Axes labels include the percentage of variance explained by PC1 (horizontal axis) and PC2 (vertical axis).

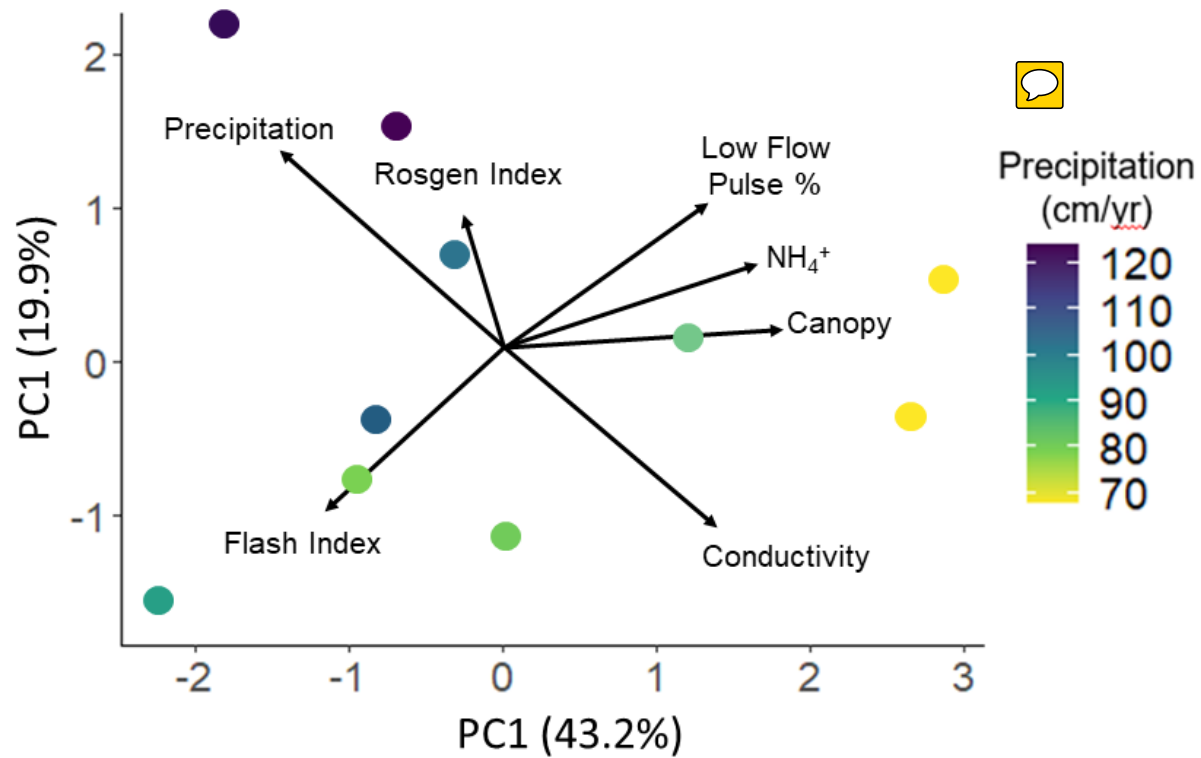


Figure 3

Fish community diversity regressions and ordinations along a precipitation gradient.

Fish diversity plotted against (a) annual precipitation (cm/yr), (b) log-transformed conductivity ($\mu\text{S}/\text{cm}$), (c) canopy cover (%), (d) NH_4^+ (mg/L). (E & F) Fish community ordinations using Hellinger transformation and redundancy analysis. Axes labels display the proportion of the variance explained as a percentage. Colored circles represent sites with color determined by annual precipitation. Arrows depict fitted vectors for (e) species and (f) environmental predictors which can be visually interpreted based on their direction. Black arrows indicate statistically significant ($p\text{-value} < 0.05$) correlations. Only significant species vectors were plotted to improve figure clarity.

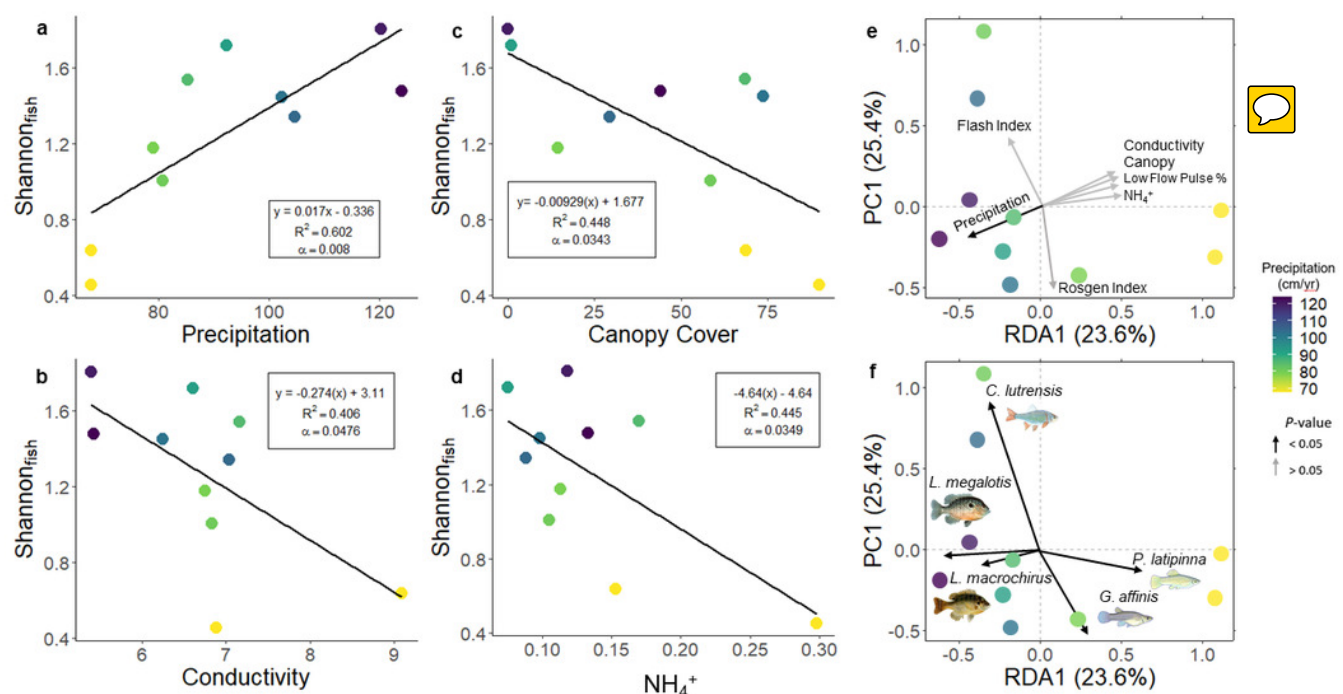


Figure 4

Invertebrate community diversity regressions and ordinations along a precipitation gradient.

Macroinvertebrate Shannon diversity plotted against (A) annual precipitation (cm/yr) and (B) Low Flow Pulse Percent. (C & D) Fish community ordinations using Hellinger transformation and redundancy analysis. Axes labels contain proportion of the variance explained as a percentage. Dots represent sites with color determined by annual precipitation. Arrows represent fitted vectors for (C) environmental predictors and (D) species which can be visually interpreted based on their direction. Black arrows indicate statistically significant (p -value < 0.05) correlations. Only significant species vectors were plotted to improve figure clarity.

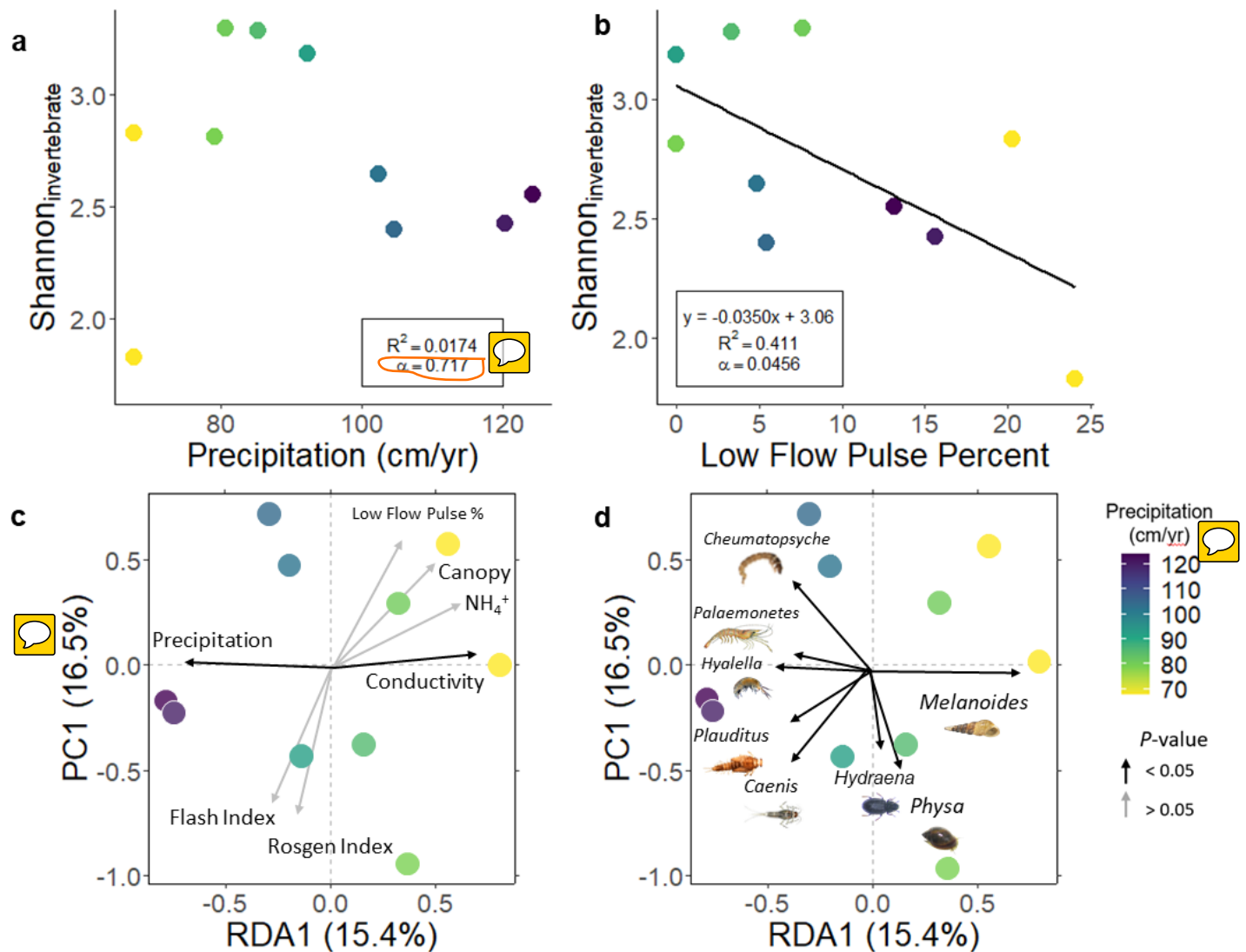


Table 1(on next page)

Mean and interquartile range values for environmental gradient features of 10 samples sites spanning the Texas Coastal Prairie.

The source data was collected from US Geologic Surveyors Geospatial Attributes of Gages for Evaluating Streamflow, version II dataset (Falcone 2011).

Environmental Feature	Mean	Interquartile
		Range
Precipitation (cm/yr)	92.5	24.6
Mean Air Temperature (°C)	21.1	0.3
Minimum Air Temperature (°C)	15.1	0.4
Maximum Air Temperature (°C)	27.5	0.8
Elevation (m)	29.9	32.0
Average Basin Slope (%)	0.7	0.8
Human Development (%)	13.3	5.8
Planted Cropland (%)	41.8	23.9
Average Clay Content (%)	30.5	4.6
Average Silt Content (%)	31.0	2.1
Average Sand Content (%)	38.5	3.9



Table 2(on next page)

Environmental predictors obtained from each sample site.

Annual precipitation, Flash Index, and Low Flow Pulse % were calculated using 30-year records provided by USGS stream gauges. Rosgen Index (stream width / stream depth), Canopy %, NH_4^+ , and Conductivity were measured in-situ in during Spring 2017 sampling.



	USGS	Precipitation		Low Flow				Conductivity
Site Name	Station ID	(cm/yr)	Flash Index	Pulse %	Rosgen Index	Canopy (%)	NH ₄ ⁺ (mg/L)	ln(μS/cm)
Aransas	8189700	80.770	1.053	7.664	11.781	58.559	0.105	6.835
Bear Branch	8068390	124.190	0.777	13.146	12.011	44.144	0.133	5.426
Big Creek	8115000	120.310	0.961	15.631	23.150	0.000	0.118	5.390
Garcitas	8164600	102.410	0.806	4.867	18.161	73.649	0.098	6.249
Medio	8189300	79.130	0.993	0.000	18.405	14.414	0.113	6.748
Mission	8189500	85.360	0.580	3.357	14.701	68.468	0.170	7.163
Perdido	8177300	92.370	1.339	0.000	15.152	0.901	0.075	6.602
Placedo	8164800	104.650	0.921	5.482	13.380	29.279	0.088	7.035
San Fernando	8211900	67.750	0.907	20.306	15.762	89.865	0.298	6.887
Tranquitas	8212300	67.750	0.781	24.060	17.988	68.769	0.153	9.096

Table 3(on next page)

Summary statistics for linear autocorrelations among environmental predictors.

* denotes a statistically significant correlation (p-value < 0.05).


	Response	Input	Sign	Slope	R ²	F-stat	df	p-value
	Conductivity	Canopy	+	0.410	0.168	1.617	2	0.239
	Flash Index	Canopy	-	0.612	0.375	4.796	2	0.060
	Low Flow Pulse %	Canopy	+	0.420	0.176	1.712	2	0.227
	NH ₄ ⁺	Canopy	+	0.643	0.414	5.649	2	0.045 *
	Rosgen Index	Conductivity	-	0.074	0.006	0.044	2	0.838
	Conductivity	Flash Index	-	0.174	0.030	0.251	2	0.630
	Low Flow Pulse %	Flash Index	-	0.309	0.096	0.847	2	0.384
	NH ₄	Flash Index	-	0.373	0.139	1.291	2	0.289
	Rosgen Index	Flash Index	+	0.007	0.000	0.000	2	0.984
	Conductivity	Low Flow Pulse %	+	0.285	0.081	0.706	2	0.425
	NH ₄ ⁺	Low Flow Pulse %	+	0.595	0.354	4.383	2	0.070
	Rosgen Index	Low Flow Pulse %	+	0.217	0.047	0.395	2	0.547
	Conductivity	NH ₄ ⁺	+	0.194	0.038	0.315	2	0.590
	Rosgen Index	NH ₄ ⁺	+	0.003	0.000	0.000	2	0.994
	Canopy	Precipitation	-	0.483	0.233	2.429	2	0.158
	Conductivity	Precipitation	-	0.785	0.616	12.817	2	0.007 *
	Flash Index	Precipitation	-	0.025	0.001	0.005	2	0.945
	Low Flow Pulse %	Precipitation	-	0.160	0.026	0.210	2	0.659
	NH ₄	Precipitation	-	0.480	0.230	2.395	2	0.160
	Rosgen Index	Precipitation	+	0.073	0.005	0.042	2	0.842
	Canopy	Rosgen.Index	-	0.301	0.091	0.798	2	0.398

Table 4(on next page)

PCA statistics for environmental predictors.

Above: Proportion of total variation captured in principle component axes 1 or 2 of environmental predictors at 10 sites spanning a precipitation gradient along the Texas Coastal Prairie. Below: Correlation coefficients for environmental predictors versus principal component axes 1 or 2.



Variation	PC1	PC2
Proportion of Variance	0.432	0.199
Cumulative Proportion	0.432	0.631
Standard deviation	1.739	1.179
Correlation (R)	PC1	PC2
Precipitation	-0.698	0.615
Conductivity	0.663	-0.550
Rosgen Index	-0.111	0.411
Canopy	0.867	0.069
NH ₄ ⁺	0.792	0.265
Flash Index	-0.553	-0.508
Low Flow Pulse %	0.633	0.456

1

Table 5(on next page)

Summary statistics for linear regressions of fish and invertebrate Shannon Index values versus environmental predictors.

* denotes a statistically significant correlation (p-value < 0.05).

Response	Input	Sign	Slope	R ²	F-stat	df	p-value
Shannon _{Fish}	Canopy	-	0.009	0.448	6.490	1	0.034 *
Shannon _{Fish}	Conductivity	-	0.274	0.406	5.464	1	0.048 *
Shannon _{Fish}	Flash Index	+	0.339	0.024	0.193	1	0.672
Shannon _{Fish}	Low Flow Pulse %	-	0.031	0.339	4.102	1	0.077
Shannon _{Fish}	NH ₄ ⁺	-	4.647	0.446	6.431	1	0.035 *
Shannon _{Fish}	Precipitation	+	0.017	0.602	12.101	1	0.008 *
Shannon _{Fish}	Rosgen Index	+	0.021	0.027	0.224	1	0.649
Shannon _{Invert}	Canopy	-	0.000	0.000	0.002	2	0.966
Shannon _{Invert}	Conductivity	-	0.134	0.802	0.091	2	0.397
Shannon _{Invert}	Flash Index	+	0.623	0.650	0.075	2	0.443
Shannon _{Invert}	Low Flow Pulse %	-	0.035	5.591	0.411	2	0.046 *
Shannon _{Invert}	NH ₄ ⁺	-	0.065	0.001	0.000	2	0.98
Shannon _{Invert}	Precipitation	-	0.003	0.141	0.017	2	0.717
Shannon _{Invert}	Rosgen Index	-	0.054	1.612	0.168	2	0.24

Table 6(on next page)

Multiple regression models predicting fish diversity along the precipitation gradient.

Predictor variables and coefficients (formula), degrees of freedom (df) , log-likelihood, Akaike's Information Criterion with the small-sample bias adjustment (AICc), difference from the best-ranked model's AICc (Δ AICc), and Akaike weights (w) for set of nonlinear, multivariate regressions predicting fish Shannon diversity.

Candidate Model Predicting Shannon _{fish}	df	Log-Likelihood	AIC _c	Δ AIC _c	Weight
+ 0.313*Precipitation - 0.210*Low Flow Pulse %	4	2.912	10.2	0.00	0.429
+ 0.346*Precipitation	3	-0.985	12.0	1.79	0.175
+ 0.263*Precipitation - 0.172*Canopy	4	+0.690	14.6	4.44	0.046
+ 0.264*Precipitation -0.171*NH4+	4	+0.688	14.6	4.45	0.046
-0.235*Conductivity - 0.252*NH4+	4	+0.649	14.7	4.52	0.045
-0.299*Canopy	3	-2.622	15.2	5.07	0.034
-0.298*NH4+	3	-2.642	15.3	5.11	0.033
- 0.284*Conductivity	3	-2.989	16.0	5.80	0.024
+ 0.301*Precipitation - 0.234*Low Flow Pulse % + 0.103*Rosgen Index	5	+4.501	16.0	5.82	0.023
random effects	2	-5.592	16.9	6.72	0.015
- 0.26*Low Flow Pulse %	3	-3.523	17.0	6.87	0.014
+ 0.348*Precipitation + 0.077*Flash Index	4	-0.594	17.2	7.01	0.013
+ 0.273*Precipitation - 0.092*Canopy - 0.177*Low Flow Pulse %	5	3.732	17.5	7.36	0.011
+ 0.343*Precipitation + 0.049*Rosgen Index	4	-0.834	17.7	7.49	0.010
- 0.219*Canopy - 0.195*Conductivity	4	-0.936	17.9	7.70	0.009
+ 0.321*Precipitation - 0.033*Conductivity	4	-0.959	17.9	7.74	0.009
- 0.195*Low Flow Pulse % - 0.229*Conductivity	4	-1.248	18.5	8.32	0.007
+ 0.357*Precipitation - 0.219*Low Flow Pulse % + 0.058*Conductivity	5	+3.082	18.8	8.66	0.006
+ 0.294*Precipitation - 0.185*Low Flow Pulse % - 0.047*NH4+	5	+3.061	18.9	8.70	0.006
- 0.230*Canopy - 0.163*Low Flow Pulse %	4	-1.510	19.0	8.84	0.005
+ 0.314*Precipitation + 0.013*Flash Index - 0.206*Low Flow Pulse %	5	+2.932	19.1	8.96	0.005
- 0.411*Canopy - 0.183*Flash Index	4	-1.568	19.1	8.96	0.005
- 0.183*Canopy - 0.180*NH4+	4	-1.669	19.3	9.16	0.004

Table 7 (on next page)

Multiple regressions predicting invertebrate diversity along a precipitation gradient.

Predictor variables and coefficients (formula), degrees of freedom (df) , log-likelihood, Akaike's Information Criterion with the small-sample bias adjustment (AICc), difference from the best-ranked model's AICc (Δ AICc), and Akaike weights (w) for set of nonlinear, multivariate regressions predicting invertebrate Shannon diversity.


Candidate Model Predicting Shannon _{invert}	df	Log-Likelihood	AIC _c	Δ AIC _c	Weight
 -0.035*Low Flow Pulse %	3	-3.236	16.5	0.00	0.299
Random Effects	2	-5.886	17.5	1.01	0.180
-0.054*Low Flow Pulse % + 4.133*NH ₄ ⁺	4	-0.967	17.9	1.46	0.144
-0.054*Rosgen Index	3	-4.968	19.9	3.46	0.053
-0.134*Conductivity	3	-5.409	20.8	4.34	0.034
+ 0.623*Flash Index	3	-5.495	21.0	4.52	0.031
+ 0.004*Canopy -0.04203*Low Flow Pulse %	4	-2.524	21.0	4.58	0.030
-0.032*Low Flow Pulse % -0.038*Rosgen Index	4	-2.538	21.1	4.60	0.030
-0.005*Precipitation -0.037*Low Flow Pulse %	4	-2.733	21.5	4.99	0.025
-0.003*Precipitation	3	-5.799	21.6	5.12	0.023
-0.000*Canopy	3	-5.885	21.8	5.30	0.021
-0.065*NH ₄ ⁺	3	-5.886	21.8	5.30	0.021
-0.022*Precipitation -0.468*Conductivity	4	-2.945	21.9	5.42	0.020
-0.033*Low Flow Pulse % -0.058*Conductivity	4	-3.103	22.2	5.73	0.017
+ 0.190*Flash Index -0.034*Low Flow Pulse %	4	-3.182	22.4	5.89	0.016
-0.020*Precipitation -0.030*Low Flow Pulse % -0.368*Conductivity	5	+0.367	24.3	7.79	0.006
-0.148*Conductivity -0.0575*Rosgen Index	4	-4.252	24.5	8.03	0.005
+ 0.630*Flash Index -0.054*Rosgen Index	4	-4.484	25.0	8.50	0.004
-0.002*Canopy -0.060*Rosgen Index	4	-4.839	25.7	9.21	0.003
-0.050*Low Flow Pulse % + 3.835*NH ₄ ⁺ -0.028*Rosgen Index	5	-0.370	25.7	9.27	0.003
+ 0.494*Flash Index -0.052*Low Flow Pulse % + 4.588*NH ₄ ⁺	5	-0.399	25.8	9.33	0.003
-0.002*Precipitation -0.053*Rosgen Index	4	-4.905	25.8	9.34	0.003
-0.057*NH ₄ ⁺ -0.054*Rosgen Index	4	-4.968	25.9	9.46	0.003
+ 0.520*Flash Index -0.116*Conductivity	4	-5.122	26.2	9.77	0.002
-0.052*Low Flow Pulse % -0.065*Conductivity + 4.174*NH ₄ ⁺	5	-0.700	26.4	9.93	0.002

Table 8(on next page)

Radial coordinates and summary statistics for fitted vectors of species and environmental predictors within the fish RDA ordination.

* denotes a statistically significant correlation (p-value < 0.05).

	Fitted Vector	axis1	axis2	R	p-value
Environment					
	Canopy	0.924	0.383	0.292	0.302
	Conductivity	0.938	0.345	0.539	0.051
	Flash Index	-0.434	0.901	0.033	0.877
	Low Flow Pulse %	0.949	0.315	0.357	0.214
	NH ₄ ⁺	0.986	0.167	0.494	0.104
	Precipitation	-0.941	-0.340	0.726	0.013 *
	Rosgen Index	0.149	-0.989	0.241	0.363
Species					
	<i>C.lutrensis</i>	-0.217	0.627	0.880	0.007 *
	<i>L.megalotis</i>	-0.407	-0.021	0.720	0.013 *
	<i>P.latipinna</i>	0.415	-0.090	0.837	0.016 *
	<i>L.macrochirus</i>	-0.240	-0.061	0.756	0.018 *
	<i>G.affinis</i>	0.188	-0.340	0.618	0.041 *

Table 9(on next page)

Radial coordinates and summary statistics for fitted vectors of species and environmental predictors within the invertebrate RDA ordination.

* denotes a statistically significant correlation (p-value < 0.05).

Vector Input	axis1	axis2	R	p-value
Environment				
Precipitation	0.976	0.001	-1.000	0.022 *
Conductivity	0.711	0.008	0.995	0.103
Rosgen Index	0.074	0.759	-0.222	-0.975 *
Canopy	0.550	0.082	0.697	0.717
NH ₄ ⁺	0.250	0.372	0.888	0.460
Flash Index	0.022	0.935	-0.389	-0.921 *
Low Flow Pulse %	0.171	0.502	0.494	0.869
Genus				
<i>Hyaella</i>	-0.168	0.005	0.780	0.007 *
<i>Cheumatopsyche</i>	-0.140	0.158	0.741	0.009 *
<i>Melanoides</i>	0.266	-0.002	0.691	0.017 *
<i>Plauditus</i>	-0.138	-0.091	0.661	0.027 *
<i>Physa</i>	0.047	-0.158	0.639	0.033 *
<i>Caenis</i>	-0.135	-0.162	0.642	0.037 *
<i>Palaemonetes</i>	-0.135	0.024	0.575	0.045 *