**Manuscript Title**

Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages

Sean Kinard1, Christopher Patrick1, Fernando Carvallo2

1. Virginia Institute of Marine Science

1370 Greate Road, Gloucester Point, Virginia 23062-1346

1. Texas A&M Corpus Christi

6300 Ocean Dr, Corpus Christi, TX 78412

Corresponding Author:

Sean Kinard1

6528 Quail Hollow Dr, Hayes VA 23072, USA

Email address: [skkinard@vims.edu](mailto:skkinard@vims.edu)

**Abstract:**

In the North American Southwest, conditions are expected to become more arid. To enhance our understanding of how freshwater communities will adjust to these shifts in water-cycle dynamics, we employed a space for time substitution along a precipitation gradient from semi-arid to sub-humid on the Texas Coastal Prairie. In the Spring of 2017, we conducted surveys of 10 USGS gauged, wadeable streams spanning a natural precipitation gradient; we measured nutrients, water chemistry, habitat characteristics, benthic macroinvertebrates, and fish community data. We observed a positive relationship between fish diversity and mean annual rainfall (*p*-value = 0.008), conductivity (*p*-value = 0.048) and surface runoff (*p*-value = 0.002). Macroinvertebrate diversity did not correlate with annual precipitation but was correlated with low flow pulse percent (*p*-value = 0.046). The compositional shifts of fish and invertebrate communities along the gradient indicate both top-down and bottom-up controls on community assembly. Semi-arid sites contain euryhaline, and rapid proliferating taxa. Sub-humid sites contain migratory euryhaline fish and fish predators which impose top-down controls on primary consumers. Proceeding from humid to arid, low-flow conditions (high solute concentrations and habitat fragmentation) restrict fish compositions. 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, Prowse et al. 2006). So far, climate change research emphasizes the direct ecological effects of changes in temperature, but rising temperatures are also expected to alter patterns of precipitation and evaporation (Held and Soden 2006). 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 et al. 2012). In addition to streamflow mechanisms, streamside vegetation mediates interactions with watershed nutrients, carbon and light inputs to streams (Schade, G. Fisher et al. 2001). Precipitation regime is the primary regulator of both streamflow and riparian characteristics. With predicted changes in flood and drought characteristics under global warming (Hirabayashi, Kanae 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 et al. 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, Wethey et al. 2015). As a result, our understanding of the role of environmental filters on community assembly is disjointed due to the vastly different spatial scales of typical biogeographical and community ecology studies (Ricklefs and Jenkins 2011).

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 (Ricklefs and Jenkins 2011). 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, Mod 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, Graae 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).

Fortunately, 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. From east to west the climate becomes more arid, 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). This 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 Thornwood groves in the semi-arid West to Live oak forests towards the East. Studying natural ecosystems that span the TCP maximizes our ability to isolate precipitation influences on natural ecosystem processes by minimizing 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 state and federal agencies of running waters in the TCP. In response, this study conducts rapid bioassessment protocols of 10 USGS-gauged, wadeable streams for 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, Peterson et al. 1992). We further expected that evapotranspiration by riparian vegetation would increase solute concentrations in semi-arid streams, particularly during base flows (Tabacchi, Lambs et al. 2000, Lupon, Bernal 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, wadable, 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℃) (Appendix-site). 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 of a 100-meter reach (Lamberti 2007). The reach length was approximately 25 times the average stream width (4.1m), in accordance with EPA rapid bioassessment protocols (Barbour, Gerritsen et al. 1999). Study sites were characterized by low variation in geomorphology and overall habitat heterogeneity resulting in high success in assessing community composition over a shorter distance. Fish species were field identified to species using a field guide (Thomas C 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 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 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. 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 2015, Merritt, Cummins et al. 2019). 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 (DL 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 (Twater), 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℃ 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℃) until analysis for nutrients (NH4+, NO3-, and PO4-). 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 (Falcone 2011).

*Analyses*: Due to a small number of sample sites and replicates, the statistical analyses are restricted to seven *a priori* environmental predictors. Annual precipitation is evaluated to identify gradient effects. The Rosgen index characterizes the channel shape which is a product of flow regime, slope, substrate, and bank stability. Canopy coverage is determined by the type of vegetation which visibly shift across the study region with implications for stream insolation, basal resourcing. We include conductivity and NH4+ 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 2). We then, used singular value decomposition of the centered and scaled data matrix in a principal component analysis with all seven environmental predictors (Figure 3, Table 3).

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, Blanchet et al. 2019) in the statistical program R (R Core Team 2019). While rarified richness is reported in supplemental appendices, 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 (Figures: 4 & 5, Tables: 4 & 7). 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 (AICc). All the results were compared to the best overall model by calculating the difference in AICc values (ΔAICc). Models with ΔAICc < 10 are reported (Tables: 6 & 8) and models with ΔAICc < 2 were considered to have substantial support (Burnham and Anderson 2002).

To discern compositional shifts across the environmental gradient, we used Redundancy Analysis (RDA), constrained by precipitation, on Hellinger-transformed community data (Pierre Legendre and Gallagher 2001; P. Legendre and Legendre 2012). we fit species and environmental variables to each ordination using the ‘envfit’ function within the VEGAN R package Oksanen, Blanchet et al. 2019). This function fits environmental vectors onto the 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 (Tables: 5 & 9). We limited species vectors to those with *p*-values < 0.05 and plotted environmental vectors separately to improve figure clarity and interpretations.

**Results**

*Site Overview:*

The Principal Component Analysis of 10 sites spanning the precipitation gradient along the Texas Coastal prairie displays patterns of variation among environmental predictors along the gradient (Figure 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 2). 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) linear relationships (Table 3). Conductivity negatively correlates with precipitation. NH4+ positively correlates with canopy coverage.

*Fish Community*: Diversity and abundance metrics are listed in appendix-fish. In total,eighteen fish species were identified within the surveyed sites. Proceeding from semi-arid to sub-humid sites, fish Shannon index increases from 0.64 - 1.81, richness increases from 2 - 7 species, and rarified richness increases from 2.09 - 5.48 species. Regression analysis indicates that fish Shannon diversity correlates positively with precipitation and it negatively correlates with canopy coverage, conductivity, and NH4+ (Figure 3 a-d & Table 4). 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 5). 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) (Figure 4 e-f). 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 6). 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 centrachids (*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 at sites at the humid side of the climate gradient include hogchoker(*Trinectes maculatus*), black bullhead catfish (*Ameirus melas*), and blacktail shiner (*Cyprinella venusta*).

*Invertebrate Community:* Diversity and abundance metrics are listed in appendix-invert.   
In total, 94 invertebrate genera were identified within the surveyed sites. Invertebrate richness ranges 7–29 genera with the highest values occurring at three sites in the middle of the precipitation gradient (Figure 5A). Regression analysis indicates that invertebrate Shannon diversity does not significantly correlate with precipitation. However, invertebrate diversity has a significant negative correlation with LFPP (Figure 5 a-b & Table 7). The most plausible multivariate regression model of fish Shannon diversity includes only Low-Flow Pulse Percent (LFPP) and is 1.6 times more likely than the next-best model (Table 5). The second-best model contains a fixed random effect, and the third-best model contains LFPP and NH4+ as predictors. Across models, LFPP is a negatively related to invertebrate diversity, and NH4+ 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) (Figure 5 c-d). 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 the euryhaline gastropod taxa (*Melanoides*). Mesic invertebrate communities are strongly correlated with an air-breathing gastropod (*Physa*) and an amphibious Coleopteran (*Hydraena*). Mesic and humid sites separate along the vertical axis of the RDA plot and appear to both weakly correlate with the species vectors of several Ephemeroptera (*Caenis* and *Plauditus*). Humid sites correlate with a mixture of fully aquatic taxa including Crustacea (*Palaemonetes*), Amphipoda (*Hyalella*), 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 understanding how streams might respond to future changes in mean annual rainfall. Our observational study identified strong 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, however, invertebrate diversity did not exhibit the expected relationships with rainfall. Environmental data collected at each site suggest several mechanistic drivers of these changes operating through water solute concentrations and flow regimes. Below, we discuss these results, place them in the context of other literature, and make suggestions for future work.

We expected precipitation to covary with flow regime, water quality, canopy coverage, and stream geomorphology. While sites separated horizontally in ordination space according to their annual precipitation, few predictors in our analysis covaried with precipitation (Figure 2). Annual Precipitation correlated negatively with conductivity (Table 4). Given similar soil types and land uses, we attribute this relationship to growing basin size to maintain similar flow conditions as conditions become drier which results in more contact with soil before reaching the stream. We also suspect surface evaporation drives solute concentrations higher in these semi-arid freshwater systems (Williams 1999). The lack of additional covarying relationships between precipitation and other environmental variables supports the assertion that TCP is an exemplary region to conduct space for time substitutions to make useful ecological predictions regarding climate change.

The fish communities displayed a pattern of increasing diversity and compositional turnover moving from the drier to wetter sides of the survey region (Fig. 3). Fish Shannon diversity correlates positively with precipitation, but negatively with water quality parameters, canopy coverage and Low-Flow Pulse Percent (LFPP) (Table 5, Table 6). Water quality was similar to polluted streams in the semi-arid streams; conductivity and NH4+ are high (Figure 4). High solute concentrations and biological waste products could limit diversity by permitting only species with specialized osmoregulatory adaptations (East, Wilcut et al. 2017). Our rapid habitat assessments failed to quantify anecdotal observations of high silt concentrations of silt in semi-arid streams with prohibitive implications for nesting species. These results suggest that as conditions become drier, water quality imposes abiotic filters on fish assembly which reduce overall community diversity in a similar fashion to pollution.

Fish communities stratified horizontally in the ordination by annual precipitation. Communities in semi-arid streams (<75 cm annual precipitation) had low species diversity and were composed of small, live-bearing, omnivores able to tolerate high salinities including Sailfin Molly (95 psu) and Western Mosquitofish (58.5 psu) (Page and Burr, B.M. 1991). The strongest compositional shift observed constituted the inclusion of centrarchids (sunfish) in communities with more humid climate; centrarchid species have 3-7 year lifespans, annual breeding, nesting strategies, and are omnivores (Cooke and Philipp 2009). Additional increases in diversity towards the wetter side of the climate gradient include the addition of black bullhead catfish (a demersal, nesting omnivore), and several shiner species (small broadcast spawning minnows). These exploratory analyses call for depletion surveys to improve abundance estimates, improve rarefaction, and enable a thorough trait-analysis across the precipitation gradient.

Lastly, Mesic and sub-humid fish communities varied in ordination space along the vertical axis which correlates strongly with flow regime metrics (Low Flow Pulse Percent and Flash Index). Only some mesic and sub-humid communities had seasonally migrating taxa including *H. cyanogutattus*, *T. maculatus,* and *A. rostrata* (Rehage et al. 2016; Koski 1978; Wenner, C.A. 1978). Given the similar proximity to nearby reservoirs and estuaries, migratory taxa may have been excluded from semi-arid streams by poor water quality (elevated NH4+) or by habitat fragmentation that typify semi-arid streams (Williams 1999; De Jong et al. 2015). To substantiate the hypothesis that low-flow hydrology restricts fish movement in the semi-arid region of the precipitation gradient, we need to conduct periodic surveys to capture temporal variability among sites throughout the gradient.

Invertebrate community compositions shifted along the climate gradient, but diversity did not correlate with precipitation. The lack of an invertebrate diversity relationship to 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. Thus, diversity as a metric, may not have been sensitive enough to capture community shifts in invertebrates within the limited scale of this study. This invertebrate study may have encountered methodological limitations. In slow currents, kick-net surveys have struggle to capture fauna in sand, clay, and silt substrates. So, in these systems, we suspect rapid bioassessment missed a substantial proportion of the available habitat to stream invertebrates. Future surveys will benefit from collections of sediment cores for invertebrate analysis.

In this study, Low flow pulse percentage (LFPP) approximated drought prevalence and was the sole significant predictor of invertebrate community diversity (Fig.5). In addition to LFPP, the top-ranked multiple regression models also implicated NH4+ was an effective predictor of invertebrate diversity. Semi-arid community compositions included a higher proportion of gastropods which are well adapted to the stresses that characterize increased LFPP (Fig 5.). 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). Droughts represent a ramping disturbance as water availability and quality diminish over time and most invertebrates are unable to escape due to restricted in-stream mobility compared to fish. aquatic invertebrates can access refuge in the hyporheic zone, interstitial spaces, and in some cases utilize desiccation-resistant life-stages (Boulton, Peterson et al. 1992, Boulton 2003).

As humidity increases, mesic invertebrate communities contain a mixture of grazers, omnivores and an abundance of predators including Odonata and Hemiptera (Fig. 5). As precipitation increases, there is a shift in primary consumers from Gastropoda to Ephemerpotera and Trichoptera; the latter species indicating enhance water quality conditions (Rosenberg and Resh 1993). Additionally, these taxa have longer life cycles (26-261days) than the prominent grazers at semi-arid sites (Jackson and Sweeney 1995). On the wet side of the gradient sites shift to include detritivores in the orders of Amphipoda and Crustacea. These results suggest that precipitation acts to regulate insect communities at the primary consumer level from the bottom up. But these analyses are exploratory and lack the sufficient thoroughness and weight of sampling effort to confidently conduct a functional feeding group analysis. Discerning the specific mechanisms of drought (intensity, duration, seasonality, and predictability) will require continuous sampling across the precipitation gradient.

The removal of one apparent outlier (Tranquitas Creek) in the invertebrate analysis would produce a negative correlation between invertebrate diversity and precipitation. Invertebrate diversity decreasing with precipitation would coincide with fish becoming more diverse across the gradient and would point towards competitive exclusion between the guilds. However, the apparent outlier had environmental predictors that were similar to our other semi-arid site (high LFPP, conductivity and NH4+, etc.), providing no hint as to the cause of the depauperate species count. With an already low number of sample sites, we retained the curious site within our analyses and call for continued sampling to investigate this potential intersection between bottom-up and top-down ecosystem processes within a natural experiment

Our results tease that deteriorating water quality due to reductions in annual precipitation prohibit larger insectivorous fish resulting in a proliferation of insect predators in mesic and semi-arid streams. Even with the confusing outlier, maximum invertebrate diversity occurred at mesic locations and the compositional shifted broadly to indicate that predation or competition played larger roles in community assembly at mesic and sub-humid sites (Dahl and Greenberg 1998). Here, we suspected fish were either superior competitors or directly consumed Hemiptera and Odonata. In this way, fish at sub-humid sites restricted invertebrate communities to species with anti-predator adaptations including small size, passive foraging strategies, camouflage, and armoring (Straile and Hälbich 2000).

Our ability to make assertions and predictions is greatly hindered by the singular sampling of only 10 streams in our rapid bioassessment of the Texas Coastal Prairie. We can confidently say these results indicate that the region represents a promising study region for climate research. In addition to its capacity for a space for time substitution, the TCP makes is poised to provide real-time data on the effects of climate change on ecosystems. The majority of Central and Western Texas are expected to become more arid as surface temperatures rise, resulting in an intensification of the existing precipitation gradient (Jiang and Yang 2012). A continuation of this sampling program with thorough methods will augment the analytical power, precision, and depth of this natural experiment.

**Acknowledgements**

Jennifer Whitt and Ian Whitt for their contributions in the field and laboratory.

**References:**

Allen, M. R. and W. J. Ingram (2002). "Constraints on future changes in climate and the hydrologic cycle." Nature **419**(6903): 224-.

Barbour, M. T., J. Gerritsen and J. B. S. B.D. Snyder (1999). Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. Washington, D.C., U.S. Environmental Protection Agency; Office of Water.

Boulton, A. J. (2003). "Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages." Freshwater Biology **48**(7): 1173-1185.

Boulton, A. J., C. G. Peterson, N. B. Grimm and S. G. Fisher (1992). "Stability of an Aquatic Macroinvertebrate Community in a Multiyear Hydrologic Disturbance Regime." Ecology **73**(6): 2192-2207.

Chapman BR, B. E. (2018). The Natural History of Texas. College Station, Texas A&M University Press.

Cooke, S. and D. Philipp (2009). Centrarchid Fishes: Diversity, Biology, and Conservation.

D'Amen, M., H. K. Mod, N. J. Gotelli and A. Guisan (2018). "Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence." Ecography **41**(8): 1233-1244.

Dahl, J. and L. A. Greenberg (1998). "Effects of fish predation and habitat type on stream benthic communities." Hydrobiologia **361**: 67-76.

De Frenne, P., B. J. Graae, F. Rodriguez-Sanchez, A. Kolb, O. Chabrerie, G. Decocq, H. De Kort, A. De Schrijver, M. Diekmann, O. Eriksson, R. Gruwez, M. Hermy, J. Lenoir, J. Plue, D. A. Coomes and K. Verheyen (2013). "Latitudinal gradients as natural laboratories to infer species' responses to temperature." Journal of Ecology **101**(3): 784-795.

DL, R. (2001). "A Stream Channel Assessment Methodology; Proceedings of 7th Federal Interagency Sedimentation Conference." 26.

East, J. L., C. Wilcut and A. A. Pease (2017). "Aquatic food-web structure along a salinized dryland river." Freshwater Biology **62**(4): 681-694.

Falcone, J. (2011). GAGES-II: Geospatial Attributes of Gauges for Evaluating Streamflow. Reston, Virginia, U.S. Geological Survey.

Farani, G. L., M. Nogueira, R. Johnsson and E. Neves (2015). "The salt tolerance of the freshwater snail Melanoides tuberculata (Mollusca, Gastropoda), a bioinvader gastropod." **10**: 212-221.

Grimm, N. B., F. S. Chapin, B. Bierwagen, P. Gonzalez and P. M. Groffman (2013). "The impacts of climate change on ecosystem structure and function." Frontiers in ecology and the environment **11**(9): 474-482.

Hagen, E. M., M. E. McTammany, J. R. Webster and E. F. Benfield (2010). "Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient." Hydrobiologia **655**(1): 61-77.

Held, I. M. and B. J. Soden (2006). "Robust responses of the hydrological cycle to global warming." Journal of Climate **19**(21): 5686-5699.

Hirabayashi, Y., S. Kanae, S. Emori, T. Oki and M. Kimoto (2008). "Global projections of changing risks of floods and droughts in a changing climate." Hydrological Sciences Journal **53**(4): 754-772.

Hubbs, C. (2008). An Annotated Checklist of the Freshwater Fishes of Texas, with Keys to Identification of Species. R. J. E. a. G. P. Garrett, Texas Academy of Science.

Jackson, J. K. and B. W. Sweeney (1995). "Egg and Larval Development Times For 35 Species of Tropical Stream Insects from Costa-Rica." Journal of the North American Benthological Society **14**(1): 115-130.

Koski, R. T. (1978). "Age, Growth, and Maturity of Hogchoker, *Trinectes* maculatus, In Hudson River, New York." Transactions of the American Fisheries Society **107**(3): 449-453.

Krumholz, L. A. (1948). "Reproduction in the Western Mosquitofish, Gambusia-Affinis-Affinis (Baird and Girard), and Its Use in Mosquito Control." Ecological Monographs **18**(1): 1-43.

Krzeminska, D., T. Kerkhof, K. Skaalsveen and J. Stolte (2019). "Effect of riparian vegetation on stream bank stability in small agricultural catchments." Catena **172**: 87-96.

Lamberti, H. (2007). Methods in Stream Ecology, Elsevier Inc.

Lupon, A., S. Bernal, S. Poblador, E. Marti and F. Sabater (2016). "The influence of riparian evapotranspiration on stream hydrology and nitrogen retention in a subhumid Mediterranean catchment." Hydrology and Earth System Sciences **20**(9): 3831-3842.

Merritt, R. W., K. W. Cummins and M. B. Berg (2019). An introduction to the Aquatic insects of North America. Dubuque, Iowa, Kendall/Hunt Pub. Co.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs and H. Wagner (2019). "vegan: Community Ecology Package."

Olden, J. D. and N. L. Poff (2003). "Toward a mechanistic understanding and prediction of biotic homogenization." American Naturalist **162**(4): 442-460.

Patrick, C. J. and C. M. Swan (2011). "Reconstructing the assembly of a stream-insect metacommunity." Journal of the North American Benthological Society **30**(1): 259-272.

Patrick, C. J. and L. L. Yuan (2017). "Modeled hydrologic metrics show links between hydrology and the functional composition of stream assemblages." Ecological Applications **27**(5): 1605-1617.

Poff, N. L. (1997). "Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology." Journal of the North American Benthological Society **16**(2): 391-409.

R Core Team (2019). R: A Language and Environment for Statistical Computing. Vienna, Austria, R Foundation for Statistical Computing.

Rehage, J. S., J. R. Blanchard, R. E. Boucek, J. J. Lorenz and M. Robinson (2016). "Knocking back invasions: variable resistance and resilience to multiple cold spells in native vs. nonnative fishes." Ecosphere **7**(6): 13.

Ricklefs, R. E. and D. G. Jenkins (2011). "Biogeography and ecology: towards the integration of two disciplines." Philosophical Transactions of the Royal Society B-Biological Sciences **366**(1576): 2438-2448.

Rolls, R. J., C. Leigh and F. Sheldon (2012). "Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration." Freshwater Science **31**(4): 1163-1186.

Rosenberg, D. M. and V. H. Resh (1993). Freshwater Biomonitoring and Benthic Macroinvertebrates. Boston, Kluwer Academic Publishers.

Schade, J., S. G. Fisher, N. Grimm and J. A. Seddon (2001). The Influence of Riparian Shrub on Nitrogen Cycling in a Sonoran Desert Stream.

Seabra, R., D. S. Wethey, A. M. Santos and F. P. Lima (2015). "Understanding complex biogeographic responses to climate change." Scientific Reports **5**.

Straile, D. and A. Hälbich (2000). "Life History and Multiple Antipredator Defenses of an Invertebrate Pelagic Predator, Bythotrephes longimanus." Ecology **81**: 150-163.

Tabacchi, E., L. Lambs, H. Guilloy, A. M. Planty-Tabacchi, E. Muller and H. Decamps (2000). "Impacts of riparian vegetation on hydrological processes." Hydrological Processes **14**(16-17): 2959-2976.

Thomas C, B. T., Whiteside BG (2007). A Field Guide: Freshwater Fishes of Texas. College Station, Texas, Texas A&M University Press.

Ward, J. H. (1963). "Hierarchical Grouping to Optimize an Objective Function." Journal of the American Statistical Association **58**(301): 236.

Wenner, C. A. (1978). Anguillidae. In W. Fischer (ed.) FAO species identification sheets for fishery purposes. W. A. F. A. 31). FAO, Rome.

Wentworth, C. K. (1922). "A scale of grade and class terms for clastic sediments." Journal of Geology **30**(5): 377-392.

Whittaker, R. J., K. J. Willis and R. Field (2001). "Scale and species richness: towards a general, hierarchical theory of species diversity." Journal of Biogeography **28**(4): 453-470.

Wiggins, G. (2015). Larvae of the North American Caddisfly Genera (Trichoptera). University of Toronto Press, Scholarly Publishing Division.

Williams, W. (2002). "Salinisation: A major threat to water resources in the arid and semi-arid regions of the world." Lakes & Reservoirs: Research & Management **4**: 85-91.

Woodward, G., D. M. Perkins and L. E. Brown (2010). "Climate change and freshwater ecosystems: impacts across multiple levels of organization." Philosophical Transactions of the Royal Society B-Biological Sciences **365**(1549): 2093-2106.

Wrona, F. J., T. D. Prowse, J. D. Reist, J. E. Hobbie, L. M. J. Levesque and W. F. Vincent (2006). "Climate change effects on aquatic biota, ecosystem structure and function." Ambio **35**(7): 359-369.