Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages (#53133)

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Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages

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In the 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 approach 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 also observed a positive relationship between fish diversity and mean annual rainfall , conductivity and surface runoff . Macroinvertebrate diversity did not correlate with annual precipitation but was correlated with low flow pulse percent. 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.

Victor Saito: You meant North-American, right?

Victor Saito: This may makes sense for north americans, but not everyone.

Victor Saito: gathered?

Victor Saito: I do not understand it.

Victor Saito: How? By the previous sentences, it is not clear.

Manuscript Title

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Abstract:

In the 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 approach 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 also 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:

Anthropogenic climate change creates an urgent need to understand the relationship between biological communities and climate (Wrona, Prowse et al. 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), and increases the frequency and intensity of extreme weather events (Held and Soden 2006). The predicted changes in precipitation patterns will have significant effects on ecosystems, especially in arid and semi-arid regions (Grimm, Chapin et al. 2013). Freshwater systems contain many species with limited dispersal capabilities which are highly sensitive to changes water temperature and availability (Woodward, Perkins et al. 2010). Global hydrological models predict region-specific changes in annual flow regime including shifts from intermittent

Victor Saito: changes in

to perennial streamflow in Arizona, New Mexico, and West Texas. However, it is unclear how the biological communities within the stream ecosystems will respond to the predicted changes to the hydrologic cycle. Therefore, clarifying mechanistic links between climate drivers and in-stream biological communities will improve our ability to predict to the effects of anthropogenic climate change on lotic ecosystems.

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 diversity (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). Abiotic filters are conceptually easy to understand. Species have physiological tolerances 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) in order 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

Victor Saito: What do you mean by hierarchical?

Victor Saito: This last sentence is disjointed from the paragraph. You are talking about abiotic and biotic drivers and close with spatial scales and biogeography.

Victor Saito: not only biogeographical studies. The whole metacommunity and priority effect studies also consider these processes.

Victor Saito: Nice!

confounding environmental variables (i.e. temperature, elevation, distance, and underlying geology).

Fortunately, the Texas Coastal Prairie (TCP) within the Western Gulf coastal grasslands is an ideal system evaluating the effect of hydrologic climate change on ecological communities. The Western Gulf coastal grasslands are a subtropical ecotone that spans Louisiana, Texas, and northern Mexico's coastal areas. From east to west to 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 (Falcone 2011), but there are minimal changes in elevation, air temperature, underlying geology, and human land use. Thus, studying natural ecosystems that span the TCP maximizes our ability to detect relationships between annual precipitation and ecosystem processes in the absence of covarying factors.

We used a section of the TCP where precipitation changes most quickly as a model system to evaluate how changes in precipitation alter stream communities. 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 (Chapman BR 2018). In addition to its value as a case study region, there is limited prior biological sampling by state and federal agencies of running waters in the TCP, so sampling efforts enhance our understanding of subtropical ecosystems (US EPA 2016). Along the rainfall gradient we surveyed 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 drivers 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 is 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) (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.

Victor Saito: If you indicate an ecotone, you should provide the phytopshysiognomies.

Victor Saito: I would rather prefer that you explain the area in terms of geology, geomorphology and general geographical terms. Saying that it spans from Luisiana to Texas is not informative for those outside US. What is the distance in km? Perhaps you don't need this much of detailing here, but only in methods.

Victor Saito: It would be important to give the exact ranges as you did for the variable of interest, at least for elevation and air temperature (in methods). As this is one important justification for your study, I would also include the coefficient of variaition showing that only rainfall varies strongly.

Victor Saito: Please, define it. (methods?)

Victor Saito: I have the impression that the last two paragraphs are mixed with methods. I would focus on the idea and general hypothesis without focusing too much in the region. I would only say that you have an outdoor natural experiment with a good range of precipitation with few confounding effects over a small spatial extent. Otherwise I have the impression that you are only giving only part of the information.

Victor Saito: Range in km.

Victor Saito: per meter?

Victor Saito: You can show the coefficient of variation to explicit the smaller variation of temperature and elevation. Or, in case the CV is higher for elevation, you could explain that this range of elevation does not affect flows too much.

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 are 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).

Victor Saito: So, every stream were sampled according to the stream width, or do you considered the value of 4.1 X 25 for all streams?

Victor Saito: Please, explain what do you mean by low.

Victor Saito: What do you mean by high. How was this evaluated? It would be clearer if you avoid subjective adjectives.

Invertebrates were collected using a 0.305m wide D-frame net equipped with 500-µm mesh. Twenty 0.093 m^2 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 and field rinsed in a 500-µm sieve bucket. After removal of rinsed larger sticks and leaves, the entire sample was preserved with the addition of 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 (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℃ 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 (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 (average annual precipitation (AP), relative humidity (RH), mean-annual potential evapotranspiration (PET), proportion of forested riparian zone (Rip.forest), and proportions of watershed forest (Bas.forest), agriculture (Bas.plant), and urban development (Bas.dev), soil permeability (Soil.Perm), soil organic content (Soil.Org), and runoff factor) 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).

In order to evaluate the typical flow regime of each site in the context of seasonal droughts, floods, and overall variation in flow, we calculated the following four variables: average daily discharge (Discharge), the flashiness index (Flash Index = cumulative changes in day to day daily flow / cumulative flow), the high flow Pulse Percentage (HFPP = Percent of time daily flow is above 3 times the median daily flow), and the low flow pulse percentage (LFPP = times where daily discharge drops below the 25th percentile) (Olden and Poff 2003, Patrick and Yuan 2017).

*Analyses***:** For each community (fish, invertebrates) 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). To evaluate the effect of rainfall on environmental variables that may influence the biota, we used linear regression to examine relationships between environmental variables and annual precipitation. We then used linear regression to evaluate the effect rainfall and environmental variables on fish and invertebrate community metrics. Prior to analyses conductivity and NO_3^- concentrations were natural log transformed to satisfy the test assumption of normality.

To evaluate how community composition changed along the gradient, we ordinated each taxa group (fish, invertebrates) across sites using non-metric multidimensional scaling (NMDS) using the 'metaMDS' within the VEGAN R package. The function runs NMDS with multiple starting configurations (n=100), compares results, and stops after finding a similar minimum stress solution. The minimum stress solution is scaled, rotated, and then species scores are added to the configuration as weighted averages (Oksanen, Blanchet et al. 2019). Using the climate data, sites were grouped using Ward's minimum variance method for hierarchical clustering (Ward 1963). Finally, we fit environmental variables to each ordination using the 'envfit' function within the VEGAN R package; this function fits environmental vectors onto the ordination and calculates the maximum correlation with the projection of points (sites in this case). To ease in visual interpretation of the plots we only retained environmental variables that were significant at an $\alpha > 0.10$ and explained > 40% of the variation. Retained environmental vectors were overlaid on top of the NMDS plots. The direction of the vector indicates the axis of the variable within the ordination space and the length of the arrow is proportional to its correlation with the projected points (Oksanen, Blanchet et al. 2019).

Results

Site Overview: Regression analysis of 26 environmental variables indicates 20 significant ($R^2 > 0.40$ and a *p*-value < 0.05) relationships reported in Appendix-regressions. We observed several significant relationships between mean annual precipitation and measured environmental variables (Appendix-regression). Surface runoff was positive related with, whereas conductivity and potential evaporation were negatively related to precipitation (Fig. 2). Increasing PET is correlated with increases in T_{water} and decreases in Soil.Org. Lastly, relative humidity correlates negatively with LFPP.

Significant environmental regressions excluding climate variables are summarized as follows (Appendix-regression); HFPP correlates negatively with PO_4^-, canopy coverage is positively correlated with NH_4^+, Rosgen Index is positively correlated with Soil.Org and turbidity, bank height is positively correlated with Soil.Perm, pH correlates positively with conductivity,

Victor Saito: Linear regression is generally used among variables with causal links. Shouldn't you use a simple correlation matrix? Or a PCA?

Victor Saito: Several linear regressions or a multiple regression?
Victor Saito: Have you tested for correlations among variables?

Victor Saito: Please, indicate the dissimilarity metric and if data was transformed.

Victor Saito: This is confusing. Is this clustering related to anything about the NMDS? You could explain the aim of each analysis.
Victor Saito: Also, indicate how you standardized data to make fair comparisons among variables.

Victor Saito: I would prefer that you refer to the statistical analysis before and R function after. I do not understand 'envfit' does.

Victor Saito: This is unusual. Could you explain the decision for alfa=0.10?

Victor Saito: Why not using direct examination of the relationship among multiple variables and a multivariate response matrix, like RDA, db-RDA?

Victor Saito: What is this again? It would be nice to remember the reader about your acronyms in each time you change section (Intro, methods, results).

turbidity is positively correlated with NO_3^- and Soil.Org, conductivity is positively colinear with pH and is negatively correlated with AP and runoff factor, NO_3^- correlates positively with turbidity and Soil.Org. Bas.dev positively correlates with Soil.Org. Bas.plant correlates negatively with Soil.Perm.

Fish Community: In total, 18 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. Rarified $Richness_{fish}$ increases with increasing Rip.forest (R^2=0.404, p=0.048) or runoff factor (R^2=0.415, p=0.044). Shannon $Index_{fish}$ decreases with increasing PET (R^2=0.518, p=0.019), conductivity (R^2=0.406, p=0.048), or NH_4^+ (R^2=0.445, p=0.035). Shannon $Index_{fish}$ increases with increasing AP (R^2=0.602, p=0.019) and runoff factor (R^2=0.716, p=0.002).

Fish abundances are found in Appendix-fish and are summarized as follows. Fish species found throughout the study region include, Red Shiner (*Cyprinella lutrensis*), Western Mosquitofish (*Gambusia affinis*), Longear Sunfish (*Lepomis megalotis*), and Bullhead minnow (*Pimephales vigilax*). Sailfin molly (*Poecilia latipinna*) was found only in Western (semi-arid) sites. Several fish species were found only in mesic sites including Rio Grande cichlid (*Herichthys cyanoguttatus*) and slough darter (*Etheostoma gracile*). Fish species found throughout the central and Eastern sites (mesic and sub-humid) include blackstripe topminnow (Fundulus notatus), green sunfish (*Lepomis cyanellus*), warmouth sunfish (*Lepomis gulosus*), bluegill sunfish (*Lepomis macrochirus*), and dollar sunfish (*Lepomis marginatus*). Fish species found only in the Eastern (sub-humid) sites include black bullhead catfish (*Ameiurus melas*), American eel (*Anguilla rostrata*), blacktail shiner (*Cyprinella venusta*), redbreast sunfish (Lepomis auritus), and orangespotted sunfish (*Lepomis humilis*).

The best solution for the NMDS ordination of fish community data had a stress value of 0.156 indicating a good fit of the data (Oksanen et al. 2019). The NMDS ordination of fish assemblages indicate compositional shifts across the precipitation gradient (Fig. 3). Hierarchical clustering resulted in 3 site groupings labeled “semi-arid” (yellow), “mesic” (green), and “sub-humid” (blue). Semi-arid fish communities are dominated by sailfin molly, western mosquitofish, and bullhead minnow. Fish communities in mesic and sub-humid climates contain a variety of sunfish species, but mesic streams uniquely contain Rio Grande cichlid. Sub-humid streams uniquely contain hogchoker (*Trinectes maculatus*), black bullhead catfish, and blacktail shiner. Significant fitted environmental variables on fish community NMDS include RH and LFPP (Appendix-ordination).

Invertebrate Community: A total of 94 invertebrate genera were identified within the study region. Invertebrate richness ranges 7–29 genera with the highest values (29, 26, and 27) occurring at three mesic sites (Aransas, Perdido and Mission respectively). Invertebrate Shannon index ranges 1.83–3.30 with higher values (3.30, 3.18 and 3.28) at three mesic sites (Aransas, Perdido, and Mission respectively) (Appendix-invert). Rarified $richness_{invertebrate}$ did not correlate significantly with environmental predictors. Shannon $Index_{invertebrate}$ decreases with increasing LFPP (R^2=0.411, p-value=0.046). Since maximum richness and Shannon index values were observed at sites in the middle of the precipitation gradient, we conducted a second order quadratic regression between Shannon $Index_{invertebrate}$ and AP (R^2=0.319, p-value=0.260) (Fig. 2).

Invertebrate community abundances are found in Appendix-invert and are summarized as follows. We identified 17 genera of coleoptera; mesic and sub-humid sites contained a variety,

Victor Saito: This information is hard to follow and summarizes. What is the key point of the regressions? A PCA would potentially summarize it better.

Victor Saito: linearly and perfectly? You can show it in scatterplots.

Victor Saito: Why some relationships are demonstrated with linear models, while others only the ranges are shown?

Victor Saito: This information is also hard to follow. Perhaps a general rank-abundance using all data would be nice to see abundance pattern at the total spatial extent.

Victor Saito: This is a bit confusing. You are mixing general biotic results with regressions and then get back again to general biotic results. I would describe the general patterns of richness, diversity and taxonomic identity first. Then, I would describe correlations with environmental variables.

Victor Saito: A rank abundance plot would do the job. You can have several colors of bars for each taxonomic group. Also, you can have one rank-abundance for each of the three climate clusters. Similarly, an old but gold Simper analysis would be informative in terms of assemblage changes with climatic changes.

but the semi-arid sites (Tranquitas and San Fernando) contain 0-1 genera (*Stenelmis*). We identified 17 genera of Ephemeroptera throughout the study region; no Ephemeroptera were identified at two semi-arid sites (Tranquitas and San Fernando) and one sub-humid site (Placedo). We identified 17 genera of Gastropoda within the study region; abundances are relatively high (exceeding 1000 per m^2) for several genera in the semi-arid and mesic sites (Tranquitas, San Fernando, and Aransas). 16 genera of Hemiptera were identified across the region; none were found in one semi-arid (Tranquitas) and three sub-humid sites (Placedo, Garcitas, and Bear Branch). 10 genera of Odonata were identified only in one semi-arid (San Fernando) and four mesic sites (Aransas, Medio, Perdido, and Mission). 10 genera of Trichoptera were identified across the study region, but one semi-arid site (Tranquitas) had none. 2 genera of Amphipoda were identified with *Hyalella* occurring at nine sites (absent at Tranquitas) and *Gammarus* only occurring at two mesic sites (San Fernando and Aransas). 2 genera of Bivalvia were identified with Corbicula occurring at six sites across the region and Pisidium only occurring at Placedo. 2 genera of Decapoda were identified with *Palaemonetes* occurring at nine sites (absent at Tranquitas) and *Orconectes* occurring at Aransas. 1 genus of Isopoda was identified (*Caecidotea*) and was only present at San Fernando.

The best solution for the NMDS ordination of the invertebrate community data had a stress value of 0.098 indicating a good fit of the data (Oksanen 2013). The NMDS ordination of invertebrate assemblages (Fig. 3) displays compositional shifts along the precipitation gradient. Invertebrate assemblages in semi-arid climate contain a variety of gastropod taxa including *Amnicola sp. Bythinia sp. And melanoides sp.* Mesic communities contain species from a greater number of taxonomic orders including Ephemeroptera, Trichoptera, Coleoptera, and Hemiptera. Sub-humid communities contain a greater proportion of Crustaceans including *Palaemonetes sp*., *Orconectes sp*., and isopods in the genus *Caecidotea*. Significant fitted environmental variables on invertebrate community NMDS include RH and LFPP, and conductivity (Appendix-ordination).

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 in the context of other literature, and make suggestions for future work.

Victor Saito: could you remove 'extreme'?

The lack of observed relationships between annual precipitation (AP) and most 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. While we did observe relationships between AP, potential evapotranspiration (PET), and runoff and water quality variables such as conductivity and nutrients as well as riparian cover, these relationships are likely causal and important mechanistic pieces of the relationships between AP and stream communities. The field-measured riparian data (canopy) proved uninformative due to outlier effects brought on by sub-urban floodway maintenance at our most humid site, Bear Creek. So,

Victor Saito: Nice!

we restrict our discussion of riparian-effects on community assembly to the watershed-level metric (Bas.forest), supplied by the USGS.

The fish communities displayed a pattern of increasing diversity, rarified richness, and compositional turnover moving from the drier to wetter sides of the survey region (Fig. 2). The wetter sites were characterized by an increase in the diversity of sunfishes and the addition of several marine migrants including hogchoker and American eel. These compositional shifts connect with quantitative relationships between environmental variables and diversity, suggesting mechanistic pathways through which precipitation is structuring the stream communities. As precipitation increases, fish communities structure diversifies to include competitive omnivores and predators. Mesic sites contain a plurality of centrarchids; species with 3-7 year lifespans, annual breeding, nesting strategies, and are omnivores (Cooke and Philipp 2009).

Sub-humid sites contain larger predator taxa including catfish, largemouth bass, warmouth sunfish, and green sunfish. Most of these species are ambush predators that reside within alcoves and woody debris, consuming a mixture of insects and small fish. These same taxa likely benefited from rainfall via an indirect effect on riparian vegetation. The relationship between canopy cover and rainfall was positive but non-significant, but Rip.forest had a strong positive relationship with fish diversity (Fig. 2). Mechanistically, riparian trees provide appropriate conditions for fish taxa via root-stabilized undercut banks or large woody debris within the channel (Krzeminska, Kerkhof et al. 2019). Large wood and bank stabilization are particularly important in these grassland prairie streams because the substrate is largely unconsolidated sand and there is little natural structure. Although not accounted for in this study, the changes in riparian vegetation from grasses to trees across this precipitation gradient may correspond to shift from autochthonous production to allochthonous production, fundamentally changing the basal resources within these aquatic systems (Hagen, McTammany et al. 2010). Further investigation of these mechanisms will require woody debris counts, bank characterizations, and stable isotope analysis of food web resources.

On the other extreme, communities in semi-arid streams (<75 cm annual precipitation) were composed of rugged species able to tolerate high salinities including Sailfin Molly (95 psu) and Western Mosquitofish (58.5 psu) (Page and Burr, B.M. 1991). The observed negative relationship between AP and conductivity, and conductivity and fish diversity point to the importance of rainfall creating low-flow hydrologic conditions (Fig. 2). Aquatic ecosystems in arid regions are prone to salinization (Williams 2002), which in conjunction with evapotranspiration and presence of agriculture contribute to base flow salinity concentrations that limit diversity by permitting only species with specialized osmoregulatory mechanisms (East, Wilcut et al. 2017). Taken together, our results indicate that regional decreasing AP restricts fish community assembly by increasing osmoregulatory stress in aquatic vertebrates.

In addition to poor water quality conditions, low-flow hydrologic regimes can limit habitat connectivity and diversity. Migratory, euryhaline species including Rio Grande cichlid (0-27.5 PSU), hogchoker (1-30 PSU), and American eel (1-36 PSU) are only found in Mesic and Sub-Humid streams (Fig. 3). Hogchoker typically reside in brackish estuaries (1-25psu) and make seasonal migrations upstream to spawn (Koski 1978). American Eel are catadromous species in which adults migrate to the Sargasso Sea to reproduce and juvenile migrate upstream to rear (Wenner 1978). Rio Grande Cichlid seek thermal refugia in deeper pools or estuaries during the winter months until temperatures rise and flows permit dispersal in late Spring (Rehage, Blanchard et al. 2016). Given the similar distances to nearby estuaries, we suspect

Victor Saito: Can you explain the mechanisms to which precipitation drives increased diversity? Does it increase habitat stability (perennial sterams)? Or is it related to stream heterogeneity (more allochtonous material and nutrients)?

Victor Saito: This paragraph is not well connected to the central topic of the study.

Victor Saito: high?

Victor Saito: A lot of discussion around taxonomic composition, but we cannot see these results in the NMDS. Perhaps a simple Simper or IndVal would help you here.

Victor Saito: What is it?

Victor Saito: Too descriptive and disconnected from the narrative. You conducted the reader to think about a precipitation in natural conditions and the impacts on community metrics, but you focus on subjectives links among individual taxa and stream habitats.

anadromous, euryhaline taxa are excluded from semi-arid streams due to increased habitat fragmentation and the unpredictability of freshets in semi-arid climate. In order to substantiate the claim that low-flow hydrology restricts fish movement in the semi-arid region of the precipitation gradient, we need to conduct seasonal surveys during wet and dry seasons.

While the invertebrate communities showed compositional shifts along the precipitation gradient, unlike fish, there was not a positive relationship with Shannon diversity. Many invertebrate taxa can mitigate the effects of drought-induced habitat fragmentation by seeking refuge in the hyporheic zone, interstitial spaces, and desiccation-resistant life-stages (Boulton, Peterson et al. 1992, Boulton 2003). The lack of diversity trends across the precipitation gradient could be attributed to the inherently larger regional pool or invertebrate species, many of which can tolerate drought conditions that typify the semi-arid region of the precipitation gradient.

Low flow pulse percentage (LFPP) was the sole significant predictor of invertebrate community diversity (Fig. 2). LFPP increases as RH decreases and indicates the prevalence of low-flow hydrologic regime in the semi-arid region of the precipitation gradient. Additionally, invertebrate community compositions shift along the precipitation gradient and these shifts coincide with changes in LFPP (Fig. 3). Semi-arid streams communities are composed of grazing Gastropoda and some predatory Hemiptera. Red-rimmed Melania (*Melanoides tuberculata*), dominate these systems, likely due to their salinity tolerance (0-23 PSU) and their ability to rapidly proliferate following dewatering due to their short life cycles, reaching sexual maturity within 21-62 days (Krumholz 1948, Farani, Nogueira et al. 2015).

On the other extreme of the gradient, sub-humid sites contain an abundance of grazer and omnivore taxa including Ephemeroptera, Amphipoda, and Trichopteran. Between these regions, mesic sites contain a mixture of grazers, omnivores and an abundance of predators including Odonata and Hemiptera. 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). These results indicate that drought also acts to regulate insect communities at the primary consumer level. Discerning the specific mechanisms of drought (intensity, duration, seasonality, and predictability) will require continuous sampling across the precipitation gradient.

Initially, the maximum invertebrate diversity in mesic sites can be attributed to overlapping dispersal from the extreme climate regions. However, the compositional shifts broadly indicate that predation and competition play larger roles in community assembly at mesic and sub-humid sites. Specifically, the distribution of fish predators has large top-down controls on invertebrate community dynamics (Dahl and Greenberg 1998). Here, we believe fish are superior insectivores compared to Hemiptera and Odonata and that fish predation at sub-humid sites restricts invertebrate communities to species with anti-predator adaptations including small size, sedentary forage strategies, and armoring (Straile and Hälbich 2000). Our results suggest that as conditions become more arid, top-down regulation by fish predators is reduced resulting in a proliferation of insect predators in mesic and semi-arid streams. A more thorough invertebrate community analysis of primary consumers will include sediment core sampling and functional trait analysis.

Acknowledgements

Victor Saito: Perhaps too speculative.

Victor Saito: I would fit this discussion considering that you found strong compositional changes, so you have losts and gains in invertebrates, but mainly losts in fishes.

To properly tackle this point I would recommend you to dicriminate compositional changes in terms of turnover and nestedness components.

Victor Saito: It would be much easier for the reader, if you write it.

Victor Saito: Too speculative with weak empirical evidence. I would not conduct the discussion in this direction. You could focus on the differences among biological groups.

Also, I would like to see a caveat paragraph. You have a very interesting natural experiment, but we I would like to know what were the challenges when analysing your data.

Victor Saito: I miss a conclusion bringing all the results together.

Jennifer Whitt and Ian Whitt

Victor Saito: In general, we indicate what we are thanking for.

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Figure 1

Victor Saito: Legends are matching the wrong figures.

Regression analysis of diversity along a precipitation gradient.

Strongest relationships between environmental variables and (a-c) Annual Precipitation, (d-h) Fish Shannon Index, (i-j) Invertebrate Shannon Index, (k-l) Invertebrate Shannon Index. Fish diversity increases with increasing precipitation and Forested Riparian. Fish diversity decreases as NH4+ increases. Invertebrate diversity correlates negatively with Low Flow (LFPP). The second order polynomial fails to corroborate visual identification of a local maximum of macroinvertebrate diversity in the climate transition-zone. Conductivity, Surface Runoff, and Potential Evapotranspiration covary with precipitation and fish diversity. Slope, R^2, F-statistics, and *p*-values are reported in Appendix-regression.

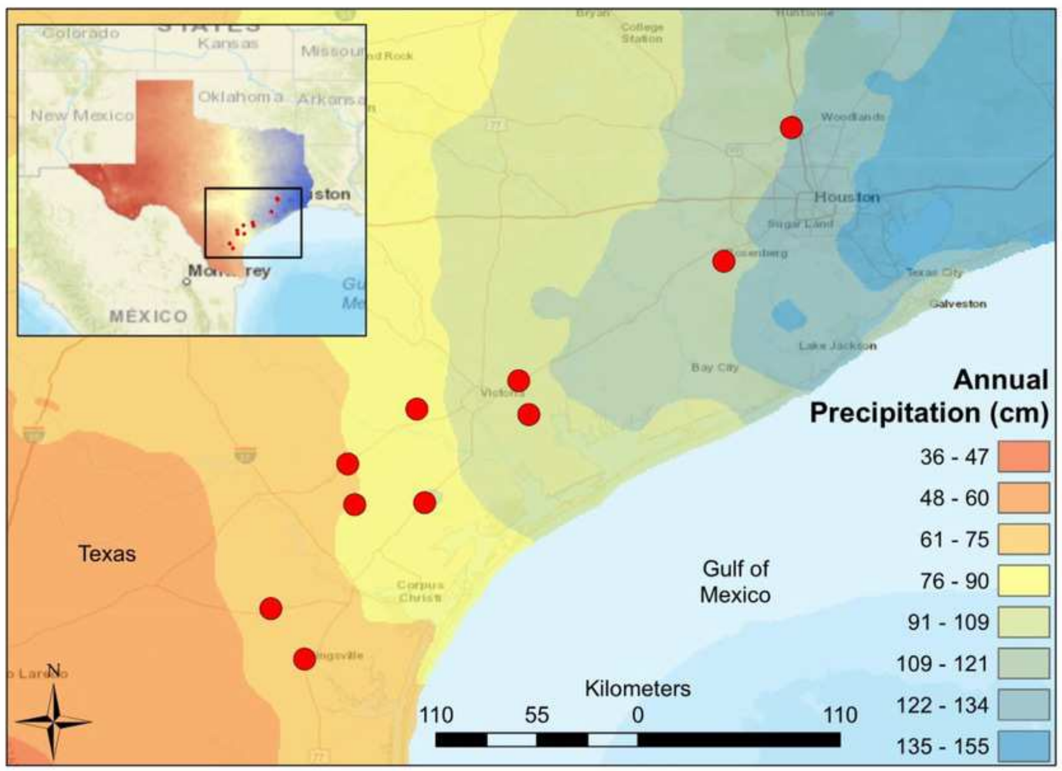
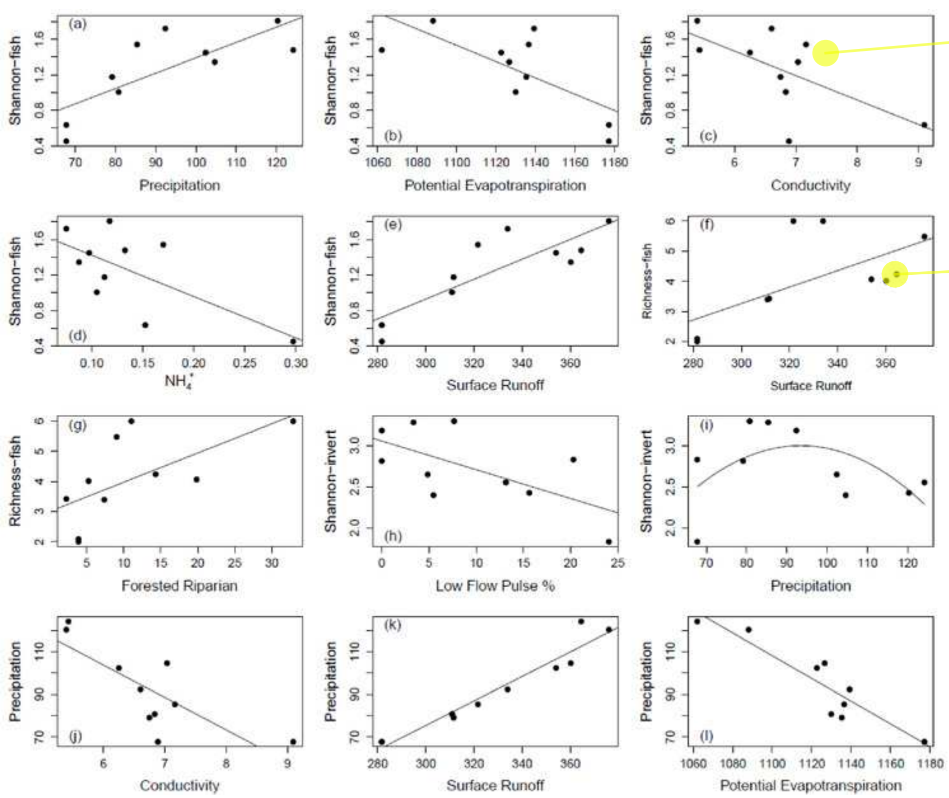


Figure 2

Map of sampling locations along the natural precipitation gradient in South-Central Texas.

10 USGS gaged Streams were sampled in the Spring of 2017. An annual precipitation overlay indicate that the sample sites span a gradient from 61 cm/yr in the Southwest to 121 cm/yr in the Northeast.



Victor Saito: Please, include P values and R square within plots.

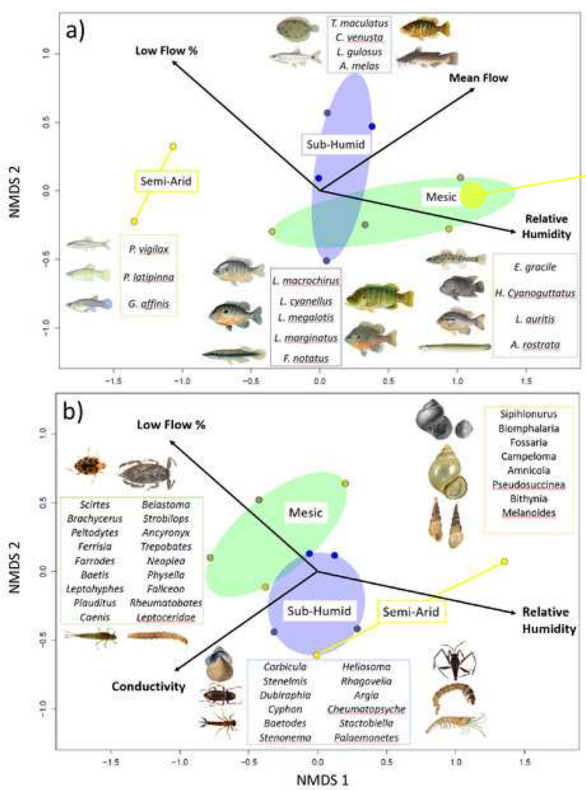
Victor Saito: Rows and collumns can be organized.

Figure 3

NMDS of (a) fish communities and (b) invertebrate communities.

Sites are grouped by precipitation regime; Semi-Arid (yellow), Mesic (green), and Sub-Humid (blue). Arrows indicate the strongest fitted environmental variables (p-value < 0.1) with length and direction corresponding to explanatory power. Semi-arid communities are dominated by livebearers and snails. Mesic and Sub-Humid communities contain a variety of sunfish, mayfly, caddisfly, true-bug, and beetle taxa. Sub-Humid communities contain different species of mayfly, caddisfly, true-bug, and beetle, but uniquely contain catfish, shrimp, and dragonfly taxa. Relative Humidity and Low Flow Pulse Percent correlates strongly with variation along the NMDS1, on which community grouping separate.

Victor Saito: Do you have a R-square?



Victor Saito: Are the taxa distributed randomly in the figure? Can't you correlate taxa, sites and environmental variables using RDA? In this way you would see which sites (type of climate) were correlated to which environmental variables, but also which species were associated to which env. variable.