**Effects of a natural precipitation gradient on fish and macroinvertebrate assemblages**

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ABSTRACT:

**Introduction:**

Anthropogenic climate change creates an urgent need to understand the relationship between biological communities and climate (Wrona, Prowse et al. 2006). As concentrations of greenhouse gases rise, the atmosphere retains more infrared radiation, resulting in rising global temperatures (IPCC 2018). A warmer atmosphere is more energetic which 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). Simultaneously, the frequency and intensity of extreme weather events are expected to increase (Held and Soden 2006). The predicted shifts in precipitation regimes will have significant effects on ecosystems, especially in arid and semi-arid regions (Grimm, Chapin et al. 2013). Freshwater systems are particularly vulnerable to changes in climate due to their fragmentation and anthropogenic stressors (Woodward, Perkins et al. 2010). Regional changes in precipitation are predicted to produce a 3-fold effect on surface runoff, and subsequent changes in the flow regimes of surface waters (Kingston and Taylor 2010, Tang and Lettenmaier 2012). However, it is unclear how these stream ecosystems will respond or adjust to the predicted changes to the hydrologic cycle. Therefore, clarifying mechanistic links between climate drivers and stream biology improves ecological predictions related to anthropogenic climate change.

Stream communities are sensitive to changes in both water chemistry and flow regime and these are directly influenced by precipitation regime (Hirabayashi, Kanae et al. 2008, Kormos, Luce et al. 2016). Precipitation also indirectly controls stream conditions by determining the streamside vegetation (riparian zone). The riparian zone regulates nutrient, carbon and light inputs to streams that fundamentally alter stream primary production and carbon cycling (Schade, G. Fisher et al. 2001). Stream ecosystems are simplistic in structure and are easily sampled. Studying stream communities under changing climate conditions maximizes our ability to predict biological responses to climate change.

Stream community assembly is constrained by abiotic and biotic filters (Poff 1997). Assuming organisms can disperse to a habitat, they must be able to survive in the local environment and successfully reproduce in the presence of other organisms exerting pressures 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). However, understanding the impact of climate change on biotic interactions is more challenging due to the complex sets of interactions that govern these processes (Seabra, Wethey et al. 2015). However, formalizing and quantifying the role of environmental filters in community assembly remains disjointed due to the vastly different spatial scales of existing biogeographical and community ecology studies (Ricklefs and Jenkins 2011). Thus, there is a need to isolate climate effects from other abiotic filters.

Observational surveys of existing community patterns along spatial 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 solely a 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. 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 for evaluating how changes to the hydrologic cycle will impact ecological communities would be enhanced if there were study systems with limited confounding environmental variables (i.e. temperature, elevation, distance, and underlying geology). Such a system would allow us to delineate the intricacies of hydrologic cycle-ecosystem relationships.

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). The TCP is a severely under-sampled region and its study enhances our understanding of subtropical ecosystems. The Texas Parks and Wildlife management surveys are spread too far apart in space and time and do not provide adequate data for a space-for-time substitution. 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.

**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. 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 48-125 cm within the study region which spans a linear distance of 378 km (Falcone 2011). The surface geology is characterized by fine clays, quaternary and sedimentary sand. The streams have similar median flows (0.02-22.09 m3⸱min-1), elevations (14-61m), substrates (quaternary), and average air temperatures (19.9-22.1℃) (Table 1).

*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). Reach length was determined by applying a modified version of the recommended standard of a length 40x the width (Reynolds, Herlihy et al. 2003). We reduced this to 25x the medium stream width (4.1m) because the 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. Data from three pass surveys collected in similar streams in the same region found that an average of 91% ± 2SE of total species are typically found in the first electrofishing pass (Patrick Lab – unpublished data). 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.

Macroinvertebrates were collected using a 0.305m wide D-frame net equipped with 500-µm mesh. Twenty 0.093m2 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 Sampling***:**  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 (DO), 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 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 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 flow regime 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), the low flow pulse percentage (LFPP = times where daily discharge drops below the 25th percentile) (Olden and Poff 2003, Patrick and Yuan 2017).

*Analyses***:** Fish and Invertebrate communities were analyzed separately. To assess community diversity we used a rarified taxa richness which provides the expected species richness in random subsamples from the community (Hurlbert 1971). To evaluate diversity and evenness, we calculated the Shannon diversity index (Shannon 1948). We used linear least-squares, linear regression analysis to examine relationships between environment and precipitation, fish diversity and environment, invertebrate diversity and environment (significant relationships had R2 > 0.4 and *p*-value < 0.05). Conductivity and NO3- concentrations were natural log transformed prior to regressions to achieve distribution 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’ function within the VEGAN R package; it 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 each site’s climate data, sites were grouped using hierarchical clustering using Ward’s minimum variance method (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). Significantly fitted environmental variables were considered to have an R2  > 0.40 and a *p*-value < 0.10, and they 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:*

Significant linear regressions are reported in table\_sp17\_Environmental\_Regressions. Significant correlations had an R2 > 0.40 and a *p*-value < 0.05. The results are summarized in the following.

Climate predictors include AP, PET and RH. AP is negatively colinear with PET, so these variables inversely share relationships with other variables. AP positively correlates with runoff factor and is negatively correlated with conductivity. However, PET uniquely correlates with Twater. RH correlates negatively with LFPP. Hydrologic predictors include HFPP, LFPP, and Av.Flow. HFPP correlates negatively with PO4-. LFPP correlates negatively with RH. Riparian predictors include canopy coverage and Rip.forest. Canopy coverage is positively correlated with NH4+. Morphologic predictors include Rosgen Index, d50, and bank height. Rosgen Index is positively correlated with Soil.Org and turbidity. Bank height is positively correlated with Soil.Perm.

Water quality predictors include Twater, DO, pH, turbidity, and conductivity. pH correlated positively with conductivity. Turbidity is positively correlated with NO3- and Soil.Org. Conductivity is positively colinear with pH and is negatively correlated with AP and runoff factor. Nutrient predictors include PO4-, NO3-, and NH4+ concentrations. NO3- correlated positively with turbidity and Soil.Org. Landscape predictors include Bas.dev, Bas.forest, Bas.plant, Soil.Org, Soil.Perm, and runoff factor. Bas.dev positively correlates with Soil.Org and it correlates negatively with PET. Bas.plant correlates negatively with Soil.Perm.

*Community Summary*: In total,18 fish species were identified within the study region. From West to East, fish Shannon index increases from 0.64 - 1.81 with an average of 1.26 and a standard deviation of 0.45. From West to East, fish species richness increases from 2 - 7 species with an average of 5.7 and a standard deviation of 2.21. Fish species rarified richness increases from 2.09 - 5.48 species with an average of 4.07 and a standard deviation of 1.44 (Table 3).

Fish community abundances are found in Table 4 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 (*Ameiurus melas*), American eel (*Anguilla rostrata*), blacktail shiner (*Cyprinella venusta*), redbreast sunfish (Lepomis auritus), and orangespotted sunfish (*Lepomis humilis*) (Table 4).

A total of 94 invertebrate genera were identified within the study region. Invertebrate richness varies across the gradient, ranging 7–29 genera (average=17.60, standard deviation=7.43) with the highest values (29, 26, and 27) occurring at three mesic sites (Aransas, Perdido and Mission respectively) containing high richness values. Invertebrate Shannon index ranges 1.83–3.30 (average=2.73, standard deviation=0.46) with higher values (3.30, 3.18 and 3.28) at three mesic sites (Aransas, Perdido, and Mission respectively) (Table 3).

Invertebrate community abundances are found in tables 3-7 and are summarized as follows. We identified 17 genera of coleoptera. Mesic and sub-humid sites contained a variety, 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 m2) 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.

*Precipitation*: Linear regressions of environmental variables with annual precipitation are reported in Table 8. Significant relationships are plotted in Figure 2 and summarized in the following. Surface runoff increases with increasing precipitation (R2 = 0.94, *p*-value = 4.00x10-6). Conductivity decreases with increasing precipitation (slope = -15.18, R2 = 0.62, *p*-value = 0.01). PET decreases with increasing precipitation (R2 = 0.87, *p*-value = 8.90x10-5).

*Diversity*: Fish rarified richness increases with increasing Rip.forest (R2=0.404, *p*=0.048) or RF (R2=0.415, *p*=0.044) (Table 9). Fish Shannon index decreases with increasing PET (R2=0.52, *p*=0.019), conductivity (R2=0.41, *p*=0.048), or NH4+ (R2=0.45, *p*=0.035). Fish Shannon index increases with increasing AP (R2=0.60, *p*=0.019) and RF (R2=0.72, *p*=0.002) (Table 10). Invertebrate rarified richness did not correlate significantly with environmental predictors (Table 11). Invertebrate Shannon index decreases with increasing LFPP (slope -0.035) (Table 12).

*Composition*: The best solutions for NMDS ordinations of fish and invertebrate community data had stress values of 0.098 and 0.156 respectively. The NMDS ordination of fish assemblages indicate compositional shifts across the precipitation gradient (Figure 4). Hierarchical clustering resulted in 3 site groupings labeled “semi-arid” (yellow), “mesic” (green), and “sub-humid” (blue). Semi-arid fish communities are dominated by *Poecilia formosa*, *Gambusia affinis*, and *Pimephales vigilax*. Fish communities in mesic and sub-humid climates contain a variety of Lepomis species, but mesic streams uniquely contain *Herichthys cyanoguttatus*. Sub-humid streams uniquely contain *Trinectes maculatus*, *Ameiurus melas*, and *Cyprinella venusta*.

Significant fitted environmental variables on fish community NMDS include RH and LFPP (Table 13).

The NMDS ordination of macroinvertebrate assemblages also display compositional shifts along the precipitation gradient (Figure 5). Macroinvertebrate 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 ln(Cond) (Table 14).

**Discussion**

*Climate-gradient*: The TCP is an exemplary region to conduct space for time substitutions to make useful ecological predictions regarding climate change. There are climate gradients of AP (67.75-124.19 cm), PET (1062.1-1177.1 mm/yr), and surface runoff (281.68-364.53 100s ft-tonf in/h/ac/yr). Field measurements reveal coincidental gradients of water parameters including log-transformed conductivity (R2=0.62, *p*=0.01) and NH4+ (R2=0.87, *p*=8.90x10-5). The field-measured riparian data (Canopy) proved uninformative due to outlier effects brought on by roadside riparian clearing at our most humid site, Bear Creek. So, we restrict our discussion of riparian-effects on community assembly to the watershed-level metric (Rip.forest), supplied by the USGS. The lack of significant relationships between AP and other variables corroborates the reduction in otherwise common confounding elevation, geologic, and land-use characteristics.

*Fish:* We expected increasing annual precipitation to correlate with increasing community diversity. Indeed, annual precipitation correlated positively with fish richness (R2 = 0.320 *p* = 0.088) (Table 3). We also hypothesized that the effects of precipitation would be mediated by flow regime and/or changes in riparian configuration. Although fish richness did not correlate with flow metrics, it did increase as Rip.forest increases (R2 = 0.404, *p* = 0.048). Forested riparian zones supply coarse woody debris (CWD) to streams which provide essential habitat and food to specific fish and invertebrates (Harmon, Franklin et al. 1986). Large woody inputs have the greatest effect on grassland stream geomorphology and consequently habitat heterogeneity (Martin, Pavlowsky et al. 2016). While an increase in the proportion of forested riparian zone may also proportionally increase CWD inputs, we suspect that a coincidental shift in tree species along the precipitation gradient causes qualitative changes in CWD from smaller shrubs to log features which create more impactful hydrologic features. In the TCP, black bullhead catfish, American eel, blacktail shiner, redbreast sunfish, and orange spotted sunfish were only present in sub-humid streams. These species prefer deep pool habitats, especially the largest predator in this study, American eel, which also inhabits undercut banks, logs and boulders (Page and Burr 2011). Rosgen Index and canopy coverage are not useful measures of instream habitat heterogeneity. So, we currently only speculate as to whether observed increases in fish richness may be related to precipitation-driven changes in riparian inputs.

We expected communities in semi-arid regions to experience greater environmental stress via drought and evapotranspiration. We also expected the constraining effects of environmental filtering to be more evident in fish communities than in invertebrates due to a limited species pool (Poff 1997). Incorporating species evenness indicates a gradual increase in diversity across the precipitation gradient. Shannon index gradually increases with increasing AP (R2 = 0.600 *p* = 0.008). Fish Shannon diversity is consequently related to variables that covary with AP; it increases with increasing surface runoff (R2=0.72, *p*=0.002) and it decreases with increasing PET (R2=0.52, *p*=0.019) and log-transformed conductivity (R2=0.41, *p*=0.048). Compositions shift along the gradient with LFPP (DATA) indicated as a significant environmental driver; Communities in semi-arid streams (<75 cm annual precipitation) were composed of rugged species able to tolerate high salinities including *Poecilia latipinna* (95 psu) and *Gambusia affinis* (58.5 psu) (Wingard, Murray et al. 2008, Chervinski 1983). These species rapidly proliferate following dewatering due to their short life cycles, reaching sexual maturity within 21-62 days (Krumholz 1948). Taken together, our results indicate that regions decreasing AP restricts fish community assembly via drought conditions (low flow and high solute concentrations).

As precipitation increases, fish communities diversify to include competitive omnivores and predators. Mesic sites contain a plurality of centrarchids; species with 3-7 lifespans, annual breeding, nesting strategies, and are omnivores (DATA). Sub-humid sites contain larger predator taxa including catfish, LMB, 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.

Although salinity tolerance is prevalent in semi-arid communities. Several euryhaline species including *Herichthys cyanoguttatum* (0-27.5 psu) and *Trinectes maculatus* (1-30 psu)*,* are only found in Mesic and Sub-Humid streams (Figures 3 & 4) (Kirby and Knowlton 1976). *T. maculatus* typically reside in brackish estuaries (1-25psu) and make seasonal migrations upstream to spawn (Koski 1978). *H. cyanoguttatum* and *P. pugio* seek thermal refugia in deeper pools or estuaries during the winter months until temperatures rise and flows permit dispersal in late Spring (Kirby and Knowlton 1976, Rehage, Blanchard et al. 2016). Although these species can tolerate high salinities, they were not found in the semi-arid sites. We attribute the absence of anadromous and euryhaline taxa in semi-arid streams to increased habitat fragmentation resulting from rare freshets in semi-arid climate (Satake and Ueno 2013).

*Invertebrates:* We expected invertebrate species diversity to increase with annual precipitation. Instead, we found that invertebrate richness and Shannon index are maximal at mesic sites and vary parabolically across the precipitation gradient (DATA). LFPP is the only significant negative predictor of macroinvertebrate Shannon index (R2 = 0.41, p < 0.05), indicating drought duration as a diversity driver (Figure 3). Even in perennial streams, prolonged droughts create physical stress via dewatering, pool isolation, and stagnation.

Invertebrate community compositions shift along the precipitation gradient and these shifts coincide with changes in LFPP (DATA). Semi-arid streams communities are dominated by grazing Gastropoda and some predatory Hemiptera. 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 contains 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 (CITATION). Additionally, these taxa have longer life cycles than the prominent grazers at semi-arid sites (DATA & CITATION). These results indicate that drought also acts to regulate insect communities at the primary consumer level.

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 (CITATION). Here, we believe fish are superior insectivores compared to Hemiptera and Odonata and that fish predation at sub-humid sites restricts invertebrate communities to small and armored grazers (CITATION). As conditions become more arid, fish predators are excluded resulting in a proliferation of insect predators in mesic and semi-arid streams.

*Conclusions:* The precipitation gradient along the TCP is unique in its capacity to deliver useful insights ecological consequences of climate change. Here, we have demonstrated the efficacy of space-for-time substitution climate gradient research in South Central Texas. We confirmed the sensitivity of fish communities to decreasing annual precipitation, mediated by drought conditions. There are compositional shifts of fish and invertebrate taxa across the gradient which indicate that as environmental filtering diminishes, trophic and competitive interactions play larger roles in community assembly. These results point towards additional pressing questions, many of which cannot be answered in this limited single-survey study. How *do* communities along the precipitation gradient respond to droughts, floods, and season? Do basal resources, their production, or consumption vary with precipitation? Do transient marine migrants play a significant role in sub-humid coastal streams?

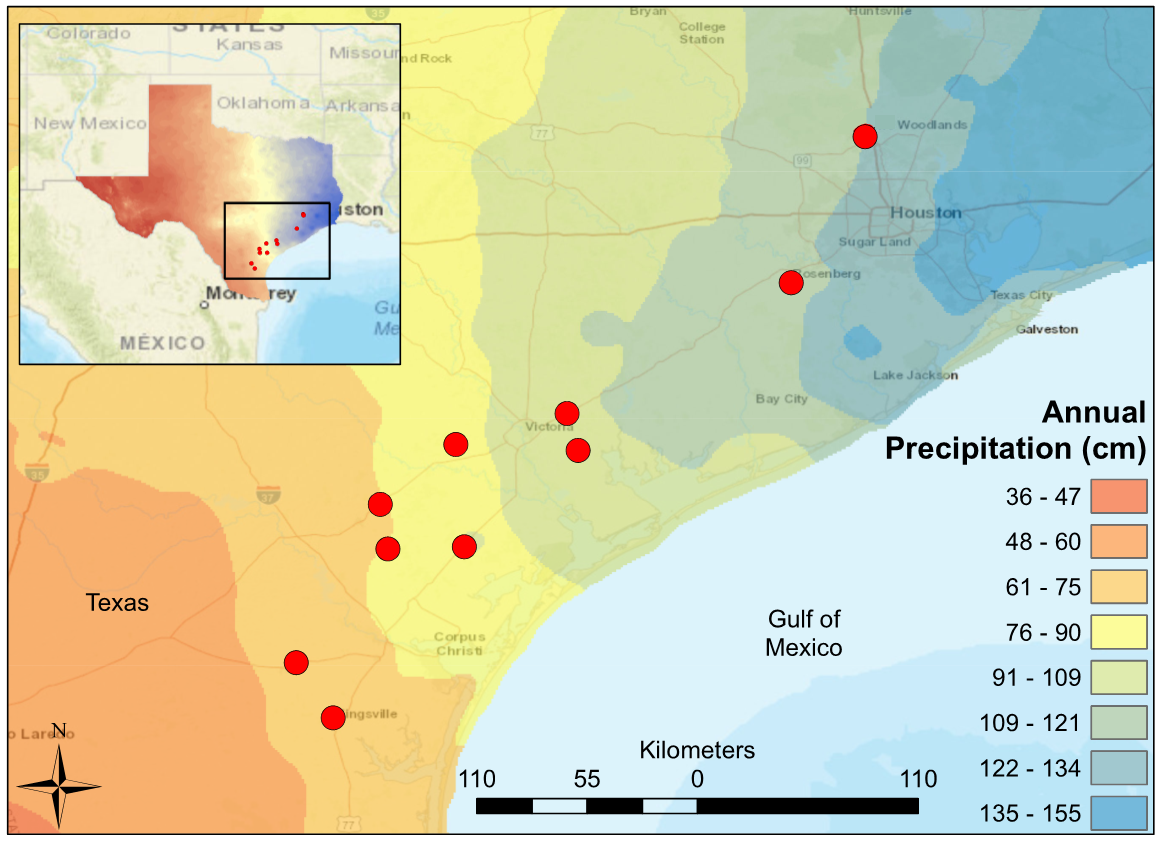


Figure 1. Map of South Central Texas, where 10 USGS gaged Streams were sampled in the Spring of 2017. An annual precipitation overlay indicate that the sample sites span a gradient from 61 cm/yr in the Southwest to 134 cm/yr in the Northeast.

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| --- | --- | --- |
| Variable | Units | Description |
| STAID | # | USGS gage station identification |
| conductivity | μS/cm | natural log-transformed conductivity |
| DO | mg/L | dissolved oxygen |
| turbidity | NTU | turbidity |
| T.water | °C | temperature water |
| pH | pH | pH |
| NH4+ | mg/L | ammonia |
| PO4- | mg/L | phosphate |
| NO3- | mg/L | natural log-transformed nitrate |
| bank height | meter | Average bank height |
| Rosgen Index | ratio | bankfull width / depth |
| d50 | mm | median grain size |
| canopy | % | canopy coverage |
| Rip.forest | % | Riparian 100m buffer "forest", 2006 era. |
| AP | cm | Watershed mean annual precipitation: from 800m PRISM data. 30 years period of record 1971-2000. |
| RH | % | Watershed average relative humidity (percent), from 2km PRISM, derived from 30 years of record (1961-1990). |
| PET | mm/yr | Mean-annual potential evapotranspiration (PET), estimated using the Hamon (1961) equation. |
| Bas.dev | % | Watershed percent "developed" (urban), 2006 era |
| Bas.forest | % | Watershed percent "forest", 2006 era |
| Bas.plant | % | Watershed percent "planted/cultivated" (agriculture), 2006 era |
| Soil.Perm | cm/hr | Average soil permeability |
| Soil.Org | % | Average value of soil organic matter content (percent by weight) |
| runoff factor | 100s ft-tonf in/h/ac/yr | Rainfall and Runoff factor ("R factor" of Universal Soil Loss Equation); average annual value for period 1971-2000 |
| Flash Index | ratio | Flashiness Index: Cumulative changes in day to day daily flow / cumulative flow for a 20 year daily flow record |
| HFPP | % | High Flow Pulse Percentage 3 : % of time daily flow is above 3 times median daily flow |
| LFPP | % | Low Flow Pulse Percentage: # times where daily discharge drops below the 25th percentile |
| Av.Flow | cfs | average daily flow based on a 20 year record for all sites except TRC which is based on a 4 year recod |

Table 1. Enviromental variables, units of measure, and descriptions. Water chemistry (conductivity, DO, turbidity, T.water, pH, NH4+, PO4- and NO3-), Morphology (bank height and Rosgen Index) and canopy coverage (canopy) were measured in the field during March and April of 2017. Forested Riparian (Rip.forest), climate metrics (AP, RH and PET), soil variables (Soil.perm and Soil.org), watershed features (Bas.dev, Bas.forest, Bas.plant, Runoff) were obtained from USGS GAGES II dataset (Falcone 2011). The flow metrics (Fash Index, HFPP, LFPP and Av.Flow) were calculated from continuous flow records from the USGS (USGS 2020).

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Variable | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Big Creek | Bear Branch |
| STAID | 8212300 | 8211900 | 8189700 | 8189300 | 8177300 | 8189500 | 8164800 | 8164600 | 8115000 | 8068390 |
| Ln(Cond) | 8923 | 979 | 929.5 | 852.25 | 736.75 | 1291 | 1135.5 | 517.75 | 219.25 | 227.13 |
| DO | 9.97 | 5.83 | 7.65 | 4.21 | 7.2 | 5.28 | 8.6 | 5.59 | 7.88 | 8.17 |
| Turbidity | 66.13 | 67.17 | 66.35 | 68.8 | 66.2 | 68.61 | 70.66 | 66.91 | 99.08 | 67.46 |
| T.water | 22.53 | 23.28 | 19.05 | 19.03 | 18.88 | 23.6 | 24.63 | 22.58 | 15.88 | 17 |
| pH | 7.99 | 6.43 | 7.08 | 6.9 | 7.18 | 7.22 | 7.31 | 7.14 | 6.96 | 6.76 |
| NH4+ | 0.15 |  | 0.11 | 0.11 | 0.08 | 0.17 | 0.09 | 0.1 | 0.12 | 0.13 |
| PO4- | 0.13 | 4.28 | 4.13 | 0.41 | 0.3 | 0.32 | 0.3 | 0.41 | 1.67 | 0.17 |
| NO3- | 0.07 | 1.8 | 0.64 | 0.01 | 0.02 | 0.04 | 0.44 | 0.05 | 2.9 | 0.02 |
| Bank.h | 0.75 | 0.59 | 0.54 | 0.69 | 0.29 | 0.46 | 0.44 | 0.34 | 0.36 | 0.89 |
| Rosgen.I | 17.99 | 15.76 | 11.78 | 18.41 | 15.15 | 14.7 | 13.38 | 18.16 | 23.15 | 12.01 |
| d50 | 2 | 2 | 32 | 2 | 2 | 2 | 25 | 2 | 2 | 2 |
| Canopy | 68.77 | 89.86 | 58.56 | 14.41 | 0.9 | 68.47 | 29.28 | 73.65 | 0 | 44.14 |
| Rip.forest | 3.92 | 3.92 | 7.41 | 2.27 | 32.9 | 11.05 | 5.28 | 19.86 | 9.06 | 14.33 |
| AP | 67.75 | 67.75 | 80.77 | 79.13 | 92.37 | 85.36 | 104.65 | 102.41 | 120.31 | 124.19 |
| RH | 69.6 | 69.6 | 74.1 | 72 | 72.1 | 73.4 | 75 | 74.2 | 71.6 | 71.4 |
| PET | 1177.1 | 1177.1 | 1129.9 | 1135.3 | 1139.2 | 1136.5 | 1126.6 | 1122.6 | 1088.1 | 1062.1 |
| Bas.dev | 4.74 | 4.74 | 8.28 | 5.24 | 2.45 | 3.72 | 11.81 | 4.28 | 10.88 | 76.71 |
| Bas.forest | 1.48 | 1.48 | 3.58 | 1.44 | 34.85 | 8.43 | 2.57 | 17.53 | 2.57 | 9.98 |
| Bas.plant | 28.01 | 28.01 | 52.39 | 40.31 | 27.41 | 35.06 | 78.16 | 50.34 | 77.35 | 0.82 |
| Soil.perm | 3.45 | 3.45 | 2.44 | 2.95 | 2.97 | 2.79 | 1.27 | 4.45 | 1.65 | 9.53 |
| Soil.Org | 0.91 | 0.91 | 0.8 | 0.95 | 0.94 | 0.82 | 0.9 | 0.75 | 2.55 | 0.48 |
| Runoff | 281.68 | 281.68 | 310.86 | 311.53 | 333.93 | 321.63 | 360.22 | 354.04 | 376.03 | 364.53 |
| Flash Index | 0.78 | 0.91 | 1.05 | 0.99 | 1.34 | 0.58 | 0.92 | 0.81 | 0.96 | 0.78 |
| HFPP | 0.31 | 0.17 | 0.11 | 0.43 | 0.29 | 0.21 | 0.26 | 0.28 | 0.24 | 0.25 |
| LFPP | 24.06 | 20.31 | 7.66 | 0 | 0 | 3.36 | 5.48 | 4.87 | 15.63 | 13.15 |
| Av.Flow | 1.76 | 13.83 | 35.04 | 3.12 | 5.41 | 115.13 | 44.72 | 43.98 | 43.54 | 25.88 |

Table 2. Environmental characteristics for 10 surveyed streams spanning a precipitation gradient throughout the Texas Coastal Prairie.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Site Name | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Big Creek |
| STAID | 8212300 | 8211900 | 8189700 | 8189300 | 8177300 | 8189500 | 8164800 | 8164600 | 8115000 |
| Fish Shannon Index | 0.64 | 0.45 | 1.01 | 1.18 | 1.72 | 1.54 | 1.34 | 1.45 | 1.81 |
| Fish Richness | 2 | 3 | 5 | 4 | 6 | 6 | 9 | 7 | 7 |
| Fish Rarified Richness | 2.00 | 2.09 | 3.39 | 3.42 | 6.00 | 6.00 | 4.02 | 4.07 | 5.48 |
| Invertebrate Shannon Index | 1.83 | 2.83 | 3.30 | 2.81 | 3.18 | 3.28 | 2.40 | 2.65 | 2.43 |
| Invertebrate Richness | 7 | 18 | 29 | 17 | 26 | 27 | 11 | 15 | 12 |
| Invertebrate Rarefied Richness | 7 | 18 | 29 | 17 | 26 | 27 | 11 | 15 | 12 |

Table 3. Calculated diversity metrics for fish and macroinvertebrate communities of ten streams spanning a precipitaiton gradient in the Texas Coastal Prairie.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Species | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Bear Branch | Big Creek |
| *A. melas* | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| *A. rostrata* | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 1 | 0 | 0 |
| *H. cyanoguttatus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *C. lutrensis* | 0 | 0 | 27 | 0 | 0 | 0 | 67 | 0 | 2 | 10 |
| *C. venusta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| *E. gracile* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *F. notatus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 5 | 0 |
| *G. affinis* | 8 | 3 | 0 | 11 | 1 | 1 | 6 | 22 | 1 | 4 |
| *L. auritis* | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *L. cyanellus* | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 2 | 0 | 6 |
| *L. gulosus* | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 1 |
| *L. humilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *L. macrochirus* | 0 | 0 | 5 | 7 | 2 | 1 | 6 | 15 | 21 | 5 |
| *L. marginatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 |
| *L. megalotis* | 0 | 0 | 3 | 0 | 3 | 5 | 17 | 30 | 29 | 8 |
| *P. latipinna* | 4 | 36 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *P. vigilax* | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 4 |
| *T. maculatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

Table 4. Electrofishing community data reported as abundance within a 75m single pass survey.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Big Creek | Bear Branch |
| Coleoptera |  |  |  |  |  |  |  |  |  |  |
| *Ancyronyx* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 91 | 0 | 0 |
| *Berosus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachycerus* | 0 | 0 | 0 | 0 | 628 | 0 | 0 | 0 | 325 | 0 |
| *Cyphon* | 0 | 0 | 0 | 0 | 0 | 381 | 392 | 91 | 0 | 0 |
| *Dubiraphia* | 0 | 0 | 1613 | 0 | 0 | 381 | 392 | 91 | 0 | 0 |
| *Elodes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 91 | 0 | 0 |
| *Gyretes* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Heterelmis* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Hydraena* | 0 | 0 | 0 | 867 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Hydrobius* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Macrelmis* | 0 | 0 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Macronychus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 91 | 0 | 0 |
| *Neoelmis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Peltodytes* | 0 | 0 | 0 | 1734 | 0 | 381 | 0 | 0 | 0 | 1158 |
| *Scirtes* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Sphaeridiinae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stenelmis* | 0 | 1512 | 3226 | 0 | 0 | 381 | 392 | 0 | 650 | 0 |
| Ephemeroptera |  |  |  |  |  |  |  |  |  |  |
| *Ameletus* | 0 | 0 | 3226 | 0 | 314 | 0 | 0 | 0 | 0 | 1158 |
| *Amelobaetidius* | 0 | 0 | 3226 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ametropus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Baetis* | 0 | 0 | 3226 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Baetodes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1158 |
| *Caenis* | 0 | 0 | 0 | 867 | 0 | 381 | 0 | 0 | 650 | 1158 |
| *Centroptilum* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cercobrachys* | 0 | 0 | 3226 | 0 | 314 | 0 | 0 | 0 | 0 | 1158 |
| *Cloeon* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Fallceon* | 0 | 0 | 0 | 0 | 628 | 0 | 0 | 91 | 325 | 1158 |
| *Farrodes* | 0 | 0 | 1613 | 0 | 314 | 381 | 0 | 0 | 0 | 0 |
| *Isonychiidae* | 0 | 0 | 3226 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Leptohyphes* | 0 | 0 | 0 | 0 | 314 | 381 | 0 | 0 | 325 | 0 |
| *Plauditus* | 0 | 0 | 0 | 0 | 314 | 381 | 0 | 0 | 325 | 1158 |
| *Procloeon* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Pseudocloeon* | 0 | 0 | 0 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Stenonema* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 182 | 0 | 0 |
| Gastropoda |  |  |  |  |  |  |  |  |  |  |
| *Amnicola* | 3328 | 756 | 0 | 0 | 0 | 0 | 392 | 182 | 0 | 0 |
| *Biomphalaria* | 3328 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bithynia* | 3328 | 0 | 1613 | 867 | 0 | 0 | 0 | 0 | 325 | 1158 |
| *Campeloma* | 3328 | 0 | 0 | 0 | 0 | 0 | 392 | 0 | 0 | 0 |
| *Fossaria* | 3328 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Gyraulus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Helicina* | 0 | 0 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Helisoma* | 0 | 0 | 0 | 0 | 628 | 0 | 392 | 0 | 0 | 0 |
| *Linisa* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Melanoides* | 9984 | 1512 | 3226 | 867 | 628 | 381 | 0 | 182 | 0 | 0 |
| *Menetus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Physa* | 0 | 0 | 0 | 867 | 628 | 381 | 0 | 0 | 0 | 0 |
| *Physella* | 0 | 0 | 1613 | 0 | 314 | 0 | 0 | 0 | 325 | 0 |
| *Planorbula* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudcosuccinea* | 3328 | 0 | 0 | 0 | 0 | 0 | 0 | 91 | 0 | 1158 |
| *Strobilops* | 0 | 0 | 0 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Valvata* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 5. Coleoptera, Ephemeroptera and Gastropoda reported as individuals per square meter.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Big Creek | Bear Branch |
| Hemiptera |  |  |  |  |  |  |  |  |  |  |
| *Belostoma* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 325 | 0 |
| *Glaenocorisa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hebrus* | 0 | 756 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Limnocoris* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Limnoporus* | 0 | 0 | 0 | 0 | 942 | 0 | 0 | 0 | 0 | 0 |
| *Lipogomphus* | 0 | 0 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Mesovelia* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Microvelia* | 0 | 0 | 0 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Morphocorixa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neoplea* | 0 | 0 | 1613 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Pelocoris* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Ranatra* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhagovelia* | 0 | 1512 | 3226 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rheumatobaetes* | 0 | 0 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Synaptonecta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Trepobates* | 0 | 0 | 0 | 0 | 628 | 381 | 0 | 0 | 0 | 0 |
| Odonata |  |  |  |  |  |  |  |  |  |  |
| *Amphiagrion* | 0 | 0 | 0 | 867 | 628 | 0 | 0 | 0 | 0 | 0 |
| *Argia* | 0 | 1512 | 3226 | 867 | 314 | 381 | 0 | 0 | 0 | 0 |
| *Brechmorhoga* | 0 | 756 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Calopteryx* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Chromagrion* | 0 | 0 | 0 | 0 | 0 | 381 | 0 | 0 | 0 | 0 |
| *Erpetogomphus* | 0 | 1512 | 3226 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Erythemis* | 0 | 0 | 0 | 867 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hetaerina* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neoneura* | 0 | 756 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Siphlonurus* | 0 | 756 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trichoptera |  |  |  |  |  |  |  |  |  |  |
| *Alisotrichia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1158 |
| *Cheumatopsyche* | 0 | 1512 | 4839 | 0 | 314 | 0 | 392 | 91 | 325 | 2316 |
| *Hydropsyche* | 0 | 0 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Leptoceridae* | 0 | 0 | 3226 | 0 | 0 | 762 | 0 | 0 | 0 | 0 |
| *Leptonema* | 0 | 756 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Metrichia* | 0 | 0 | 0 | 0 | 314 | 0 | 0 | 0 | 0 | 0 |
| *Philopotamidae* | 0 | 0 | 3226 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Potamyia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Smicridea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stactobiella* | 0 | 0 | 0 | 0 | 0 | 0 | 392 | 0 | 0 | 0 |

Table 6. Hemiptera, Odonata, and Trichoptera reported as individuals per square meter.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Tranquitas | San Fernando | Aransas | Medio | Perdido | Mission | Placedo | Garcitas | Big Creek | Bear Branch |
| Amphipoda |  |  |  |  |  |  |  |  |  |  |
| *Gammarus* | 0 | 756 | 1613 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hyalella* | 0 | 756 | 1613 | 867 | 628 | 381 | 392 | 182 | 650 | 2316 |
| Bivalvia |  |  |  |  |  |  |  |  |  |  |
| *Corbicula* | 0 | 756 | 1613 | 0 | 628 | 0 | 0 | 182 | 0 | 3474 |
| *Pisidium* | 0 | 0 | 0 | 0 | 0 | 0 | 392 | 0 | 0 | 0 |
| Decapoda |  |  |  |  |  |  |  |  |  |  |
| *Orconectes* | 0 | 756 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Palaemonetes* | 0 | 756 | 1613 | 867 | 314 | 381 | 392 | 182 | 650 | 1158 |
| Isopoda |  |  |  |  |  |  |  |  |  |  |
| *Caecidotea* | 0 | 1512 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 7. Amphipoda, Bivalvia, Decapoda and Isopoda reported as individuals per square meter.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Annual Precipitation |  |  |  |  |  |  |
| Predictor | Slope | df | R2 | F statistic | *p*-value | p < .05 |
| NO3+ | 0.27 | 8 | 0 | 0.01 | 0.94 |  |
| PO4- | -4.36 | 8 | 0.13 | 1.16 | 0.31 |  |
| RH | 3.58 | 8 | 0.11 | 1 | 0.35 |  |
| Av.Flow | 0.13 | 8 | 0.05 | 0.42 | 0.53 |  |
| Flash.I | -2.5 | 8 | 0 | 0.01 | 0.94 |  |
| HFPP | -0.1 | 8 | 0 | 0 | 1 |  |
| LFPP | -0.38 | 8 | 0.03 | 0.21 | 0.66 |  |
| Bas.Dev | 0.55 | 8 | 0.38 | 4.86 | 0.06 |  |
| Bas.forest | 0.39 | 8 | 0.04 | 0.36 | 0.57 |  |
| Bas.Plant | 0.17 | 8 | 0.04 | 0.32 | 0.59 |  |
| Rip.forest | 0.72 | 8 | 0.12 | 1.04 | 0.34 |  |
| S.runoff | 0.58 | 8 | 0.94 | 122.45 | 4.00E-06 | \* |
| Soil.Org | 11.16 | 8 | 0.1 | 0.87 | 0.38 |  |
| Soil.Perm | 7.92 | 8 | 0.13 | 1.18 | 0.31 |  |
| DO | 2.29 | 8 | 0.04 | 0.34 | 0.57 |  |
| ln(Cond) | -15.18 | 8 | 0.62 | 12.82 | 0.01 | \* |
| Ln(NO3-) | 3.82 | 8 | 0.03 | 0.29 | 0.6 |  |
| NH4+ | -150.58 | 8 | 0.23 | 2.41 | 0.16 |  |
| PET | -0.53 | 8 | 0.87 | 52.49 | 8.90E-05 | \* |
| pH | -9.95 | 8 | 0.04 | 0.34 | 0.58 |  |
| T.water | -3.28 | 8 | 0.25 | 2.63 | 0.14 |  |
| Turbidity | 1.03 | 8 | 0.27 | 2.94 | 0.12 |  |
| Bank.H | -14.13 | 8 | 0.02 | 0.16 | 0.7 |  |
| Canopy | -0.3 | 8 | 0.23 | 2.43 | 0.16 |  |
| d50 | -0.06 | 8 | 0 | 0.01 | 0.92 |  |
| Rosgen | 0.42 | 8 | 0.01 | 0.04 | 0.84 |  |

Table 8. Linear Regressions analysis of annual precipitation (AP) versus environmental predictors.

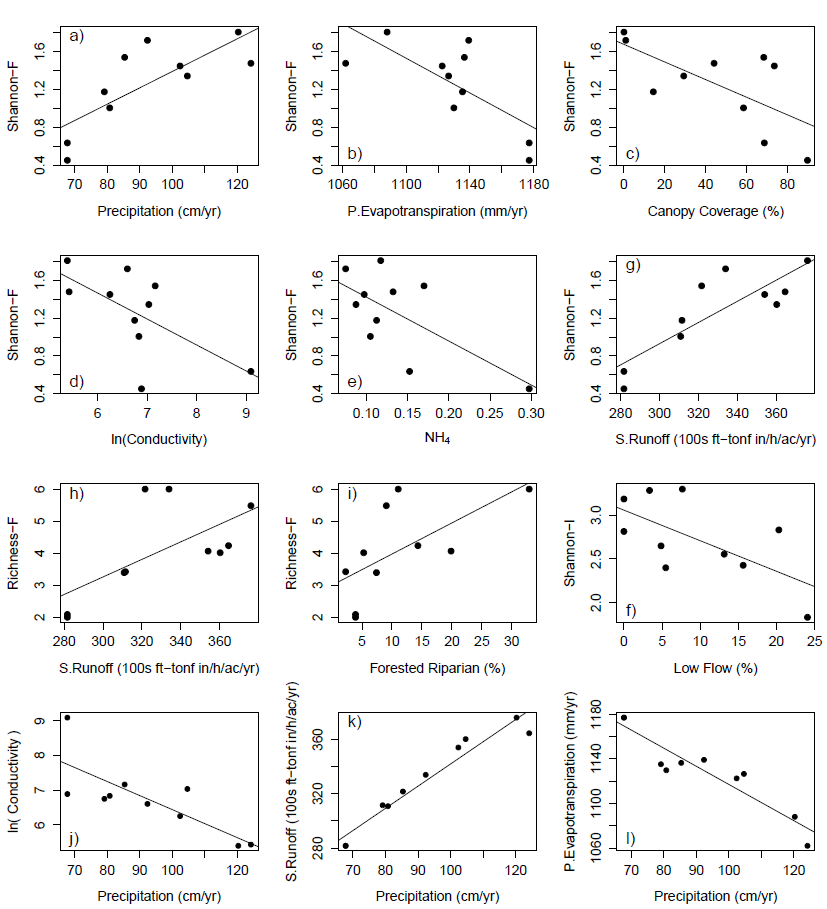


Figure 2. Strongest relationships between environmental variables (a-f) Fish Shannon Diversity, (h,i) Fish Rarified Richness, (f) Invertebrate Shannon Diversity, (j-l) Annual Precipitation.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Rarified Richness - Fish | | |  |  |  |  |
| Predictor | Slope | df | R2 | F statistic | *p-*value | *p* < .05 |
| PET | -0.021 | 8.000 | 0.268 | 2.928 | 0.125 |  |
| AP | 0.041 | 8.000 | 0.320 | 3.772 | 0.088 |  |
| RH | 0.330 | 8.000 | 0.184 | 1.808 | 0.216 |  |
| Av.Flow | 0.023 | 8.000 | 0.302 | 3.468 | 0.100 |  |
| Flash.I | 0.989 | 8.000 | 0.019 | 0.158 | 0.701 |  |
| HFPP | -0.416 | 8.000 | 0.001 | 0.005 | 0.946 |  |
| LFPP | -0.102 | 8.000 | 0.355 | 4.396 | 0.069 |  |
| Bas.dev | 0.002 | 8.000 | 0.001 | 0.012 | 0.917 |  |
| Bas.forest | 0.078 | 8.000 | 0.331 | 3.959 | 0.082 |  |
| Bas.plant | 0.010 | 8.000 | 0.027 | 0.220 | 0.651 |  |
| Rip.forest | 0.097 | 8.000 | 0.404 | 5.420 | 0.048 | \* |
| Runoff | 0.027 | 8.000 | 0.415 | 5.668 | 0.044 | \* |
| Soil.Org | 0.767 | 8.000 | 0.090 | 0.792 | 0.400 |  |
| Soil.Perm | -0.139 | 8.000 | 0.008 | 0.062 | 0.809 |  |
| DO | -0.143 | 8.000 | 0.031 | 0.257 | 0.626 |  |
| ln(Cond) | -0.707 | 8.000 | 0.260 | 2.808 | 0.132 |  |
| ln(NO3-) | 0.005 | 8.000 | 0.000 | 0.000 | 0.992 |  |
| NH4+ | -10.672 | 8.000 | 0.227 | 2.343 | 0.164 |  |
| pH | -0.160 | 8.000 | 0.002 | 0.016 | 0.901 |  |
| PO4- | -0.341 | 8.000 | 0.151 | 1.428 | 0.266 |  |
| T.water | -0.148 | 8.000 | 0.097 | 0.864 | 0.380 |  |
| Turbidity | 0.052 | 8.000 | 0.133 | 1.230 | 0.300 |  |
| Bank.H | -4.215 | 8.000 | 0.332 | 3.980 | 0.081 |  |
| Canopy | -0.025 | 8.000 | 0.308 | 3.555 | 0.096 |  |
| d50 | -0.019 | 8.000 | 0.022 | 0.178 | 0.684 |  |
| Rosgen | 0.028 | 8.000 | 0.005 | 0.038 | 0.851 |  |

Table 9. Linear regressions of fish community rarified richness versus environmental predictors.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Shannon Diversity - Fish | | |  |  |  |  |
| Predictor | Slope | df | R2 | F statistic | *p-*value | *p* < .05 |
| PET | -0.01 | 8 | 0.52 | 8.60 | 0.019 | \* |
| AP | 0.02 | 8 | 0.60 | 12.10 | 0.008 | \* |
| RH | 0.12 | 8 | 0.24 | 2.49 | 0.153 |  |
| Av.Flow | 0.01 | 8 | 0.16 | 1.56 | 0.247 |  |
| Flash.I | 0.34 | 8 | 0.02 | 0.19 | 0.672 |  |
| HFPP | 0.75 | 8 | 0.02 | 0.17 | 0.693 |  |
| LFPP | -0.03 | 8 | 0.34 | 4.10 | 0.077 |  |
| Bas.dev | 0.00 | 8 | 0.04 | 0.30 | 0.599 |  |
| Bas.forest | 0.02 | 8 | 0.27 | 2.98 | 0.123 |  |
| Bas.plant | 0.00 | 8 | 0.06 | 0.53 | 0.486 |  |
| Rip.forest | 0.03 | 8 | 0.36 | 4.55 | 0.065 |  |
| Runoff | 0.01 | 8 | 0.72 | 20.22 | 0.002 | \* |
| Soil.Org | 0.28 | 8 | 0.12 | 1.10 | 0.324 |  |
| Soil.Perm | 0.01 | 8 | 0.00 | 0.00 | 0.945 |  |
| DO | -0.02 | 8 | 0.01 | 0.06 | 0.809 |  |
| ln(Cond) | -0.27 | 8 | 0.41 | 5.46 | 0.048 | \* |
| Ln(NO3-) | 0.00 | 8 | 0.00 | 0.00 | 0.997 |  |
| NH4+ | -4.65 | 8 | 0.45 | 6.42 | 0.035 | \* |
| pH | -0.03 | 8 | 0.00 | 0.01 | 0.944 |  |
| PO4- | -0.14 | 8 | 0.26 | 2.79 | 0.133 |  |
| T.water | -0.07 | 8 | 0.20 | 1.99 | 0.196 |  |
| Turbidity | 0.02 | 8 | 0.21 | 2.10 | 0.186 |  |
| Bank.H | -1.13 | 8 | 0.25 | 2.61 | 0.145 |  |
| Canopy | -0.01 | 8 | 0.45 | 6.49 | 0.034 | \* |
| d50 | 0.00 | 8 | 0.02 | 0.13 | 0.728 |  |
| Rosgen | 0.02 | 8 | 0.03 | 0.22 | 0.649 |  |

Table 10. Linear regressions of fish community Shannon index versus environmental predictors.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Rarified Richness - Invertebrate | | | |  |  |  |
| Predictor | Slope | df | R2 | F statistic | *p-*value | *p* < .05 |
| PET | 0.016 | 8.000 | 0.006 | 0.045 | 0.838 |  |
| AP | -0.088 | 8.000 | 0.056 | 0.475 | 0.510 |  |
| RH | 1.317 | 8.000 | 0.110 | 0.984 | 0.350 |  |
| Av.Flow | 0.075 | 8.000 | 0.116 | 1.051 | 0.335 |  |
| Flash.I | 10.446 | 8.000 | 0.081 | 0.704 | 0.426 |  |
| HFPP | -38.955 | 8.000 | 0.199 | 1.994 | 0.196 |  |
| LFPP | -0.488 | 8.000 | 0.306 | 3.533 | 0.097 |  |
| Bas.dev | -0.072 | 8.000 | 0.047 | 0.399 | 0.545 |  |
| Bas.forest | 0.278 | 8.000 | 0.159 | 1.514 | 0.253 |  |
| Bas.plant | -0.046 | 8.000 | 0.022 | 0.180 | 0.683 |  |
| Rip.forest | 0.295 | 8.000 | 0.139 | 1.296 | 0.288 |  |
| Runoff | -0.039 | 8.000 | 0.032 | 0.265 | 0.621 |  |
| Soil.Org | -3.178 | 8.000 | 0.058 | 0.491 | 0.503 |  |
| Soil.Perm | -1.140 | 8.000 | 0.019 | 0.158 | 0.701 |  |
| DO | -1.899 | 8.000 | 0.204 | 2.053 | 0.190 |  |
| ln(Cond) | -0.001 | 8.000 | 0.194 | 1.926 | 0.203 |  |
| ln(NO3-) | -1.329 | 8.000 | 0.031 | 0.255 | 0.627 |  |
| NH4+ | -2.871 | 8.000 | 0.001 | 0.005 | 0.946 |  |
| pH | -5.093 | 8.000 | 0.077 | 0.671 | 0.436 |  |
| PO4- | 1.644 | 8.000 | 0.131 | 1.211 | 0.303 |  |
| T.water | -0.176 | 8.000 | 0.005 | 0.042 | 0.843 |  |
| Turbidity | -0.215 | 8.000 | 0.085 | 0.743 | 0.414 |  |
| Bank.H | -12.212 | 8.000 | 0.104 | 0.932 | 0.363 |  |
| Canopy | 0.008 | 8.000 | 0.001 | 0.009 | 0.925 |  |
| d50 | 0.166 | 8.000 | 0.063 | 0.542 | 0.483 |  |
| Rosgen | -0.959 | 8.000 | 0.201 | 2.012 | 0.194 |  |

Table 11. Linear regressions of invertebrate community rarified richness versus environmental predictors.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Shannon Index - Invertebrate | | | |  |  |  |
| Predictor | Slope | df | R2 | F statistic | *p-*value | *p* < .05 |
| PET | 0.000 | 8.000 | 0.000 | 0.003 | 0.955 |  |
| AP | -0.003 | 8.000 | 0.017 | 0.141 | 0.717 |  |
| RH | 0.095 | 8.000 | 0.150 | 1.411 | 0.269 |  |
| Av.Flow | 0.005 | 8.000 | 0.134 | 1.242 | 0.297 |  |
| Flash.I | 0.624 | 8.000 | 0.075 | 0.652 | 0.443 |  |
| HFPP | -2.083 | 8.000 | 0.149 | 1.401 | 0.271 |  |
| LFPP | -0.035 | 8.000 | 0.411 | 5.592 | 0.046 | \* |
| Bas.dev | -0.004 | 8.000 | 0.030 | 0.249 | 0.631 |  |
| Bas.forest | 0.017 | 8.000 | 0.148 | 1.388 | 0.273 |  |
| Bas.plant | -0.002 | 8.000 | 0.010 | 0.079 | 0.786 |  |
| Rip.forest | 0.018 | 8.000 | 0.131 | 1.202 | 0.305 |  |
| Runoff | -0.001 | 8.000 | 0.004 | 0.032 | 0.863 |  |
| Soil.Org | -0.175 | 8.000 | 0.046 | 0.386 | 0.552 |  |
| Soil.Perm | -0.058 | 8.000 | 0.013 | 0.105 | 0.755 |  |
| DO | -0.157 | 8.000 | 0.363 | 4.553 | 0.065 |  |
| ln(Cond) | 0.000 | 8.000 | 0.393 | 5.171 | 0.053 |  |
| ln(NO3-) | -0.058 | 8.000 | 0.015 | 0.124 | 0.734 |  |
| NH4+ | -0.044 | 8.000 | 0.000 | 0.000 | 0.987 |  |
| pH | -0.517 | 8.000 | 0.209 | 2.110 | 0.184 |  |
| PO4- | 0.098 | 8.000 | 0.123 | 1.124 | 0.320 |  |
| T.water | -0.012 | 8.000 | 0.007 | 0.053 | 0.823 |  |
| Turbidity | -0.011 | 8.000 | 0.056 | 0.471 | 0.512 |  |
| Bank.H | -0.829 | 8.000 | 0.126 | 1.149 | 0.315 |  |
| Canopy | 0.000 | 8.000 | 0.000 | 0.002 | 0.966 |  |
| d50 | 0.008 | 8.000 | 0.042 | 0.351 | 0.570 |  |
| Rosgen | -0.054 | 8.000 | 0.168 | 1.613 | 0.240 |  |

Table 12. Linear regressions of invertebrate community Shannon index versus environmental predictors.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Fitted Environmental Vectors NMDS - Fish | | | | |  | |  | |
| Predictor | NMDS1 | NMDS2 | R2 | p-value | | p < .10 | |
| PET | -0.68 | -0.73 | 0.38 | 0.19 | |  | |
| Precip. | 0.5 | 0.87 | 0.31 | 0.27 | |  | |
| RH | 0.98 | -0.21 | 0.53 | 0.08 | | \* | |
| Av.Flow | 0.83 | 0.55 | 0.45 | 0.1 | |  | |
| Flash.I | 0.04 | -1 | 0.07 | 0.81 | |  | |
| HFPP | -0.53 | -0.85 | 0.23 | 0.4 | |  | |
| LFPP | -0.75 | 0.66 | 0.51 | 0.09 | | \* | |
| Bas.Dev | 0.17 | 0.99 | 0.3 | 0.27 | |  | |
| Bas.forest | 0.43 | -0.9 | 0.22 | 0.45 | |  | |
| Bas.Plant | 0.99 | -0.15 | 0.01 | 0.96 | |  | |
| Rip.forest | 0.55 | -0.84 | 0.24 | 0.4 | |  | |
| S.runoff | 0.66 | 0.75 | 0.31 | 0.27 | |  | |
| Soil.Org | -0.95 | 0.31 | 0.01 | 0.97 | |  | |
| Soil.Perm | 0.1 | 0.99 | 0.04 | 0.93 | |  | |
| DO | -0.32 | 0.95 | 0.12 | 0.65 | |  | |
| ln(Cond) | -0.71 | -0.7 | 0.27 | 0.33 | |  | |
| Ln(NO3-) | -0.33 | 0.94 | 0.12 | 0.66 | |  | |
| NH4+ | -0.55 | 0.83 | 0.33 | 0.23 | |  | |
| pH | -0.21 | -0.98 | 0.12 | 0.66 | |  | |
| PO4- | -0.41 | 0.91 | 0 | 0.98 | |  | |
| T.water | -0.68 | 0.74 | 0.07 | 0.74 | |  | |
| Turbidity | 0.05 | 1 | 0.03 | 0.9 | |  | |
| Bank.H | -0.5 | 0.87 | 0.18 | 0.51 | |  | |
| Canopy | -1 | -0.04 | 0.04 | 0.85 | |  | |
| d50 | 0.82 | 0.58 | 0.16 | 0.62 | |  | |
| Rosgen | -0.53 | -0.85 | 0.3 | 0.28 | |  | |

Table 13. Fitted environmental variables for fish NMDS.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Fitted Environmental Vectors NMDS - Invertebrate | | | | | |  | |
| Predictor | NMDS1 | NMDS2 | R2 | p-value | p < .10 | |
| PET | -0.68 | -0.73 | 0.38 | 0.18 |  | |
| Precip. | 0.5 | 0.87 | 0.31 | 0.28 |  | |
| RH | 0.98 | -0.21 | 0.53 | 0.09 | \* | |
| Av.Flow | 0.83 | 0.55 | 0.45 | 0.1 |  | |
| Flash.I | 0.04 | -1 | 0.07 | 0.79 |  | |
| HFPP | -0.53 | -0.85 | 0.23 | 0.38 |  | |
| LFPP | -0.75 | 0.66 | 0.51 | 0.09 | \* | |
| Bas.Dev | 0.17 | 0.99 | 0.3 | 0.26 |  | |
| Bas.forest | 0.43 | -0.9 | 0.22 | 0.47 |  | |
| Bas.Plant | 0.99 | -0.15 | 0.01 | 0.96 |  | |
| Rip.forest | 0.55 | -0.84 | 0.24 | 0.43 |  | |
| S.runoff | 0.66 | 0.75 | 0.31 | 0.26 |  | |
| Soil.Org | -0.95 | 0.31 | 0.01 | 0.97 |  | |
| Soil.Perm | 0.1 | 0.99 | 0.04 | 0.93 |  | |
| DO | -0.32 | 0.95 | 0.12 | 0.65 |  | |
| ln(Cond) | -0.82 | -0.58 | 0.4 | 0.08 | \* | |
| Ln(NO3-) | -0.33 | 0.94 | 0.12 | 0.65 |  | |
| NH4+ | -0.55 | 0.83 | 0.33 | 0.24 |  | |
| pH | -0.21 | -0.98 | 0.12 | 0.64 |  | |
| PO4- | -0.41 | 0.91 | 0 | 0.97 |  | |
| T.water | -0.68 | 0.74 | 0.07 | 0.73 |  | |
| Turbidity | 0.05 | 1 | 0.03 | 0.9 |  | |
| Bank.H | -0.5 | 0.87 | 0.18 | 0.54 |  | |
| Canopy | -1 | -0.04 | 0.04 | 0.85 |  | |
| d50 | 0.82 | 0.58 | 0.16 | 0.58 |  | |
| Rosgen | -0.53 | -0.85 | 0.3 | 0.27 |  | |

Table 14. Fitted environmental variables for invertebrate NMDS.

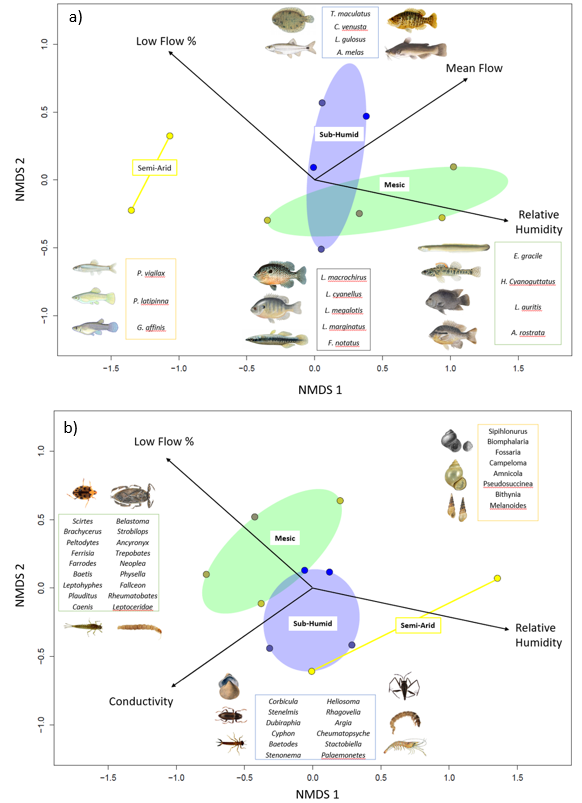


Figure 4. NMDS ordination of (a) fish and (b) invertebrate communities in ten coastal prairie streams in South Texas. Sites are grouped according to Annual Precipitation. Distances between sites are proportional to compositional differences in community. The explanatory power of environmental factors is indicated by the length and direction of the arrows. Labeled Illustrations indicate the location of various species within the ordination space.

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