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From Rain Drops To Rivers: Unraveling Aridification's Influence On Coastal Stream Ecosystem Dynamics

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From Rain Drops to Rivers: Unraveling Aridification's Influence on Coastal Stream Ecosystem Dynamics

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In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Sean Kelly Kinard
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Approval Page

This dissertation is submitted in partial fulfillment of
the requirements for the degree of
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Chapter 4:

Kinard, Sean, Christopher J. Patrick, Hannah B. Vander Zanden, Amber J. Ulseth, Christopher M. Groff, Christopher Frazier, Connor L. Brown, Matt R. Whiles, Bradley A. Strickland, J. Derek Hogan. "Proximity and Dams Restrict Upstream Nutrient-Transport in Sub-Tropical, Coastal Rivers." Intended for submission to Estuaries and Coasts

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Table of Contents

List of Tables

List of Figures

List of Appendices

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Dissertation Abstract

This dissertation addresses the escalating threat of aridification to global freshwater ecosystems due to anthropogenic climate change, focusing on South-Central Texas, USA, using a space-for-time approach along a precipitation gradient from semi-arid to sub-humid. Over the 2017-2020 survey period, I integrated community, stable isotope, climate, and hydrologic data.

In Chapter 2, my initial assessment of fish and invertebrate communities along the precipitation gradient unveiled compositional shifts and other nuanced responses. Positive correlations between fish diversity and rainfall, coupled with unexpected invertebrate diversity patterns, underscored the role of water quality in shaping fish assemblages. Drier conditions imposed abiotic filters, reducing diversity and favoring taxa with specialized adaptations, particularly in semi-arid systems with a dominance of euryhaline and live-bearing taxa.

Chapter 3 examined differences in allochthonous and autochthonous dependencies as well as overall food-web structure across the precipitation gradient. In drier climates, a shift from insect predation to herbivory was apparent, supported by stable isotope data indicating increased autochthonous assimilation, wider resource use, and reduced trophic levels. Invertebrate metrics suggested limited bottom-up effects, while niche dimensions indicated top-down control at Sub-Humid and competition at Semi-Arid and Transition sites to be important drivers of food web structure. In summary, aridification intensifies autochthonous production, fish herbivory, and invertebrate dietary overlap in semi-arid streams.

Chapter 4, exploring ecological connectivity in coastal rivers, focused on inconspicuous amphidromous species. Stable isotope analysis quantified substantial estuarine assimilation and highlighted dam impacts on connectivity. Significant downstream to upstream connectivity, driven by completely amphidromous taxa, emphasized vulnerability to interruptions by dams, urbanization, and climate change. Dominance of Fundulidae, Cyprinidontidae, and Palaemonidae families facilitated estuarine nutrient subsidies.

Chapter 5 addressed ecological impacts of hydrological disturbances, challenging prevailing notions about flood effects. Results revealed nuanced relationships influenced by long-term precipitation patterns, with varied impacts of drought events based on precipitation regimes. These findings contribute to a refined understanding of climate, hydrology, and fish communities, offering insights into how different precipitation regimes shape responses to hydrological disturbances. Specifically, my data highlighted Poeciliid resilience and reduced centrarchid abundances during hydrological droughts in hot and arid summers.

This dissertation unveils nuanced ecological dynamics within semi-arid ecosystems, where abiotic filters, influenced by water quality, shape fish communities. The prevalence of euryhaline and live-bearing taxa, along with amphidromous species, underscores the vital role of estuarine connectivity in maintaining resilient coastal rivers, especially in arid climates. My findings elucidate intricate ecological responses to floods, droughts, and seasonality, contingent upon long-term precipitation patterns. As regions teeter on the brink of transitioning from mesic to semi-arid climates, my results foreshadow analogous transformations in stream ecosystems. This scholarly pursuit represents a substantial stride in advancing ecological understanding, offering vital insights for adept stewardship amid the challenges presented by climate-induced alterations.

From Rain Drops to Rivers: Unraveling Aridification's Influence on Coastal Stream Ecosystem Dynamics

Chapter 1: Dissertation Introduction

Unraveling the Impact of Aridification on Streams

On a global scale, the escalating impacts of climate warming are altering patterns in evaporation and precipitation, presenting significant concerns for both human populations and ecosystem management. Predictions indicate an expansion of global drylands, encompassing 41% of Earth’s terrestrial surface and accommodating over one-third of the world’s population (Feng and Fu 2013). Models project wetter regions, including the tropics, becoming wetter, and drier regions, such as the subtropics, becoming even drier (Allan and Soden 2008; Trenberth 2011; Dai, Zhao, and Chen 2018). The shift towards boom-or-bust precipitation cycles, replacing frequent light rains, raises the specter of water scarcity, particularly in vulnerable regions like the Southwestern USA, Mediterranean, and Southern Africa (Seager *et al.* 2007; Vicente-Serrano *et al.* 2014; Allen *et al.* 2019). Amidst the challenges posed by climate change, it is imperative for conservation initiatives to attain a more nuanced understanding of the intricate relationship between climate dynamics and ecosystems on a global scale.

Riverine environments emerge as critical focal points within the broader context of climate change, housing a diverse array of threatened and endangered species that confront escalating threats (Vaughn 2010). As primary interfaces between terrestrial and aquatic systems, these environments exhibit intricate sensitivity to changes in rainfall, shaping not only litterfall patterns but also influencing the physical characteristics of stream environments (Dodds *et al.* 2015). In arid regions, streams undergo significant transformations, becoming extreme environments marked by high nutrient concentrations, conductivity, and low dissolved oxygen during drought periods, potentially leading to severe alterations in stream food webs (Lawrence *et al.* 2014). This heightened vulnerability is compounded by the ever-growing human demand for freshwater, necessitating intricate interactions between human activities and the delicate balance of aquatic habitats.

Global climate models predict increased aridity in many regions over the next century, underscoring the urgent need to comprehend the mechanistic links between precipitation, flow regimes, and aquatic biota (Seager *et al.* 2007). Stream ecosystems, intricately shaped by flow regimes, play a pivotal role in regulating the physical extent of aquatic habitats, water quality, material sourcing and exchange rates, and habitat connectivity (Rolls, Leigh, and Sheldon 2012). Aridification amplifies the prevalence of droughts and flash floods, disrupting local communities by imposing intolerable conditions or physically displacing individuals. Lengthening dry periods induce changes in macroinvertebrate communities, where drought-sensitive taxa are replaced by drought-tolerant species, posing challenges to the resilience of stream ecosystems (Storey 2016). In contrast, humid precipitation regimes, characterized by low interannual variability and frequent bank flooding, foster hydrological connectivity and resource exchange between aquatic and terrestrial systems, potentially enhancing the resilience of stream communities. Fish communities, responding to precipitation and temperature along continental climate gradients, become increasingly diverse (Griffiths, McGonigle, and Quinn 2014). As semi-arid regions expand, an improved understanding of the impacts of aridification on stream ecosystems becomes imperative to manage the increasing societal demands for freshwater resources.

Water scarcity resulting from arid climates restricts connectivity within aquatic systems as well as their connections to terrestrial ecosystems. Hydrologic contraction during droughts can cause streambed drying, forcing aquatic organisms into the substrates or the remaining pools. For example, in the Colorado River Delta, reduced river flows due to aridity have led to intermittent or complete drying of some reaches, affecting the connectivity between river channels and adjacent wetland habitats (Day *et al.* 2021). The drying of streambeds can impact fish migrations and alter the availability of critical habitats for aquatic organisms. Furthermore, the impacts of hydrologic drying extend beyond the immediate aquatic environment, influencing broader ecosystem dynamics. In arid regions like the Sonoran Desert, diminished river flows contribute to the fragmentation of riparian habitats, disrupting the connectivity between river corridors and adjacent upland ecosystems (Stromberg *et al.* 2007, 2013). This fragmentation affects the movement of wildlife, including migratory birds and terrestrial mammals, emphasizing the interconnectedness of hydrological patterns with terrestrial biodiversity.

Ecological Implications of Aridification and Adaptive Conservation Strategies

Case studies from semi-arid regions, such as the American Southwest and the Murray-Darling Basin in Australia, exemplify the profound impact of aridification on traditional ecological assumptions. In the American Southwest, prolonged droughts challenge classical ecological models by disrupting stable hydrological conditions, notably observed in the Colorado River Basin, where increased aridity has altered riparian ecosystems and community structures (Stromberg, Lite, and Dixon 2010). Similarly, Australia's Murray-Darling Basin has witnessed shifts in metapopulation dynamics due to unpredictable water availability, leading to changes in species distribution and abundance, challenging established ecological predictions (Balcombe *et al.* 2006; Selwood *et al.* 2017).

Conservation and management challenges intensify as aridification reshapes hydrological regimes globally. In the Murray-Darling Basin, adaptive strategies respond to prolonged droughts, emphasizing the need for balancing water needs across agriculture, human communities, and ecosystems in aridifying regions (Koehn *et al.* 2014; Prosser, Chiew, and Stafford Smith 2021). Similarly, in the Mediterranean Iberian Peninsula, recurring droughts impact aquatic ecosystems, necessitating the establishment of an environmental flow regime for water scarcity mitigation (Ibáñez and Caiola 2013). These cases highlight the imperative for integrated approaches to address diverse challenges arising from aridification, ensuring the resilience of ecosystems and the species they support.

These cases collectively highlight the imperative for adaptive and integrated conservation approaches as aridification continues to shape hydrological dynamics, emphasizing the necessity of collaborative efforts to navigate the intricate challenges posed by changing water availability. The dynamic nature of water availability in arid climates calls for comprehensive and cooperative strategies to ensure the resilience of ecosystems and the effective conservation of species affected by the evolving hydrological conditions. In this dissertation aims to address these gaps by uncovering the mechanistic relationship between precipitation patterns and community dynamics in coastal streams.

Understanding Climate-Driven Dynamics in Coastal Streams: Using a Space-for-Time Approach

The following chapters employ a space-for-time substitution approach, using observational surveys of existing communities distributed along environmental gradients. This foundational method helps infer how communities will evolve over time as environmental conditions shift. Through this approach, the research establishes links between climate drivers, local environmental conditions, and organism abundances. However, it’s crucial to recognize the assumptions and limitations of the space-for-time approach. While it assumes that observed ecological differences along the spatial gradient result solely from corresponding changes in climate, challenges arise due to factors such as dispersal limitation, habitat heterogeneity, and local evolution, as suggested by biogeographical studies (Jacob *et al.* 2015). Large-scale studies covering vast distances struggle to precisely ascertain the mechanisms for observed biological changes due to covarying environmental variables, such as elevation, geology, and human impacts.

Acknowledging these limitations, the power of the space-for-time approach is particularly pronounced in study systems with fewer confounding environmental variables. Coastal Rivers in south-central Texas emerge as an ideal domain for a space-for-time substitution, given their suitability and limited confounding variables.

Integrated with climate models, the research outcomes can pinpoint areas at varying risk levels of climate-driven state changes. This precision provides a robust foundation for targeted management strategies to mitigate impacts through interventions (Patrick *et al.* 2019).

Investigating Climate Gradients in South Texas Coastal Rivers

South Texas presents an ideal locale for addressing critical questions related to climate gradients, particularly along the coastal bend of the Gulf of Mexico. This region boasts a natural precipitation gradient, ranging from semi-arid (55 cm.yr-1) to sub-humid (135 cm.yr-1) over a 300 km span, with a consistent 0.27 cm.yr-1 per km change (Falcone 2011). Notably, this gradient occurs without significant alterations in temperature, elevation, geography, or land-use, providing a unique opportunity to isolate precipitation effects.

The rivers within the coastal plain of Texas, specifically in eco-region 34, are particularly data deficient, amplifying the value of collected riverine data for local management applications. The middle and lower coasts of Texas, climatically distinct regions with unique precipitation patterns, hydrology, flora, and fauna, are critically undersampled, identified as a priority data gap by the Texas Parks and Wildlife Department (TPWD) and Texas Commission on Environmental Quality (TCEQ). Despite robust state monitoring programs and the presence of major coastal academic programs, the coastal rivers remain unsampled mirroring a larger scale pattern of data deficiency in coastal plain systems through the United States. However, information about the geology, climate, and terrestrial communities of this region in Texas is more readily available.

The semi-arid region near Kingsville, situated within the expansive Gulf Coastal Prairie, exhibits distinct geological, botanical, and faunal characteristics attuned to arid conditions. The geology of this area is marked by well-drained soils, predominantly loamy in texture, and shaped by Quaternary deposits and sedimentary formations. As one traverses the landscape, arid-adapted flora dominates, with species like Weesatch (*Condalia hookeri*) and Mesquite (*Prosopis glandulosa*) thriving (Chapman 2018). These vegetation types showcase adaptations such as deep taproots and reduced leaf production, crucial for conserving water in the face of limited rainfall. Terrestrial fauna in this semi-arid zone includes species adept at surviving in arid environments, such as the Texas Horned Lizard (*Phrynosoma cornutum*) and the Collared Peccary (*Pecari tajacu*), reflecting a community finely tuned to the challenges of water scarcity and high temperatures.

Moving northeast towards Ganado, the Gulf Coastal Prairie undergoes a transition into a sub-humid climate, marked by distinctive geological, botanical, and faunal shifts. The geology evolves to include a mix of clayey loams and sandy loams, fostering increased water retention. Shifts in rainfall and soil moisture influences the vegetation, leading to the emergence of lush hardwood forests. Species like Pecan (*Carya illinoinensis*), Live Oak (*Quercus virginiana*), and Dogwood (*Cornus florida*) become prevalent, showcasing adaptations to higher moisture availability. The sub-humid region supports a more diverse array of terrestrial fauna, including White-tailed Deer (*Odocoileus virginianus*) and a variety of bird species that find suitable habitats in the flourishing hardwood forests. This ecological transition highlights the dynamic interplay between climate, geology, and biodiversity in shaping the Gulf Coastal Prairie.

In light of climate models predicting increased aridity in this region, transitioning from semi-arid to arid conditions (Huang *et al.* 2016; Overpeck and Udall 2020; Sun *et al.* 2018), the urgency of studying these understudied coastal rivers becomes evident. This research unravels the intricate dynamics of South Texas rivers, offering crucial insights into immediate challenges while carrying wider implications for regions with similar climates. With many semi-arid and mesic areas globally confronting escalating aridity from climate change, our findings provide a blueprint for understanding how coastal ecosystems respond to shifting precipitation patterns. This knowledge informs proactive conservation and management, crucial as the projected drying trend can impact ecosystem resilience, alter species compositions, modify hydrological dynamics, and disrupt vital ecological processes. Leveraging insights from South Texas, regions facing analogous climate challenges can proactively anticipate and navigate the repercussions of aridification, fostering a more adaptable approach to environmental stewardship. In essence, this research not only fills immediate knowledge gaps but also contributes to a global understanding of how climate-induced shifts in precipitation patterns affect ecosystems.

Dissertation Overview

The following chapters encompass intensive sampling of fish and invertebrates in coastal rivers along the South Texas precipitation gradient. Sampling occurred roughly every month over a 14-month period, with additional sampling events taking place at larger time intervals (3 to 6 months) over a 5-year period.

In Chapter 2, we explore and characterize lotic fish and invertebrate communities spanning the precipitation gradient to identify patterns in diversity and composition related to aridification. The study uses survey data from spring 2017 across 10 USGS-gauged, wadeable streams, ranging from semi-arid to sub-humid conditions. The findings reveal precipitation levels relate positively with fish diversity, negatively with fish abundance as well as driving shifts in both fish and macroinvertebrate community composition. These results emphasize the potential consequences of aridification on the loss of competitive and environmentally sensitive taxa, leading to less desirable community states.

In Chapter 3, we employ a combination of community surveys, experimental manipulations, and stable isotope analyses in three representative streams (in 2018) along the precipitation gradient. The results demonstrate that aridification leads to enhanced autochthonous production, increased herbivory, and a shortened food chain in semi-arid streams, suggesting that future aridification may drive comparable changes in stream structure and function, with potential implications for ecosystem dynamics.

In Chapter 4, we used a combination of community surveys from 2017-2020, with stable isotope collections in 2020 to quantify estuary-stream connectivity driven by inconspicuous amphidromous species and assess the impact of dams, climate, and geographic factors on this connection. Findings indicate that amphidromous species transport substantial estuarine nutrient subsidies into coastal rivers. The study underscores the dominance of these species in arid stream ecosystems, stressing their cumulative ecosystem services and vulnerability to urbanization and climate change.

In Chapter 5, we investigate the ecological impacts of drought, floods, and season on stream fish communities. Conducted from 2017 to 2020, the research integrates fish collection, environmental assessments, and statistical models, revealing nuanced relationships between antecedent maximum flows, precipitation regimes, and fish abundance or diversity. The findings challenge prevailing assumptions, highlighting the role of historic climate in mediating the ecological consequences of disturbance, and provide valuable insights for more context-sensitive conservation and management strategies.

In summary, this dissertation not only advances our comprehension of the impact of aridification on coastal rivers but also accentuates the wider ramifications for biodiversity, intricate ecosystem dynamics, and the formulation of adaptive management strategies in response to climate-induced transformations. These insights advocate for a multi-disciplinary ecological philosophy that recognizes the interconnectedness of diverse environmental factors and urges a proactive approach in safeguarding these fragile ecosystems amidst the challenges of a changing climate. As we delve into these intricate relationships, we unveil the delicate balance of nature and the imperative need for conscientious stewardship. As John Muir once eloquently stated, “When one tugs at a single thing in nature, he finds it attached to the rest of the world.”

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Chapter 2: Effects of a Natural Precipitation Gradient on Fish and Macroinvertebrate Assemblages in Coastal Streams

2.1 Abstract

Anthropogenic climate change is expected to increase the aridity of many regions of the world. Surface water ecosystems are particularly vulnerable to changes in the water-cycle and may suffer adverse impacts in affected regions. To enhance our understanding of how freshwater communities will respond to predicted shifts in water-cycle dynamics, we employed a space-for-time approach along a natural precipitation gradient on the Texas Coastal Prairie. In the Spring of 2017, we conducted surveys of 10 USGS-gauged, wadeable streams spanning a semi-arid to sub-humid rainfall gradient; we measured nutrients, water chemistry, habitat characteristics, benthic macroinvertebrates, and fish communities. Fish diversity correlated positively with precipitation and was negatively correlated with conductivity. Macroinvertebrate diversity peaked within the middle of the gradient. Semi-arid fish and invertebrate communities were dominated by euryhaline and live-bearing taxa. Sub-humid communities contained environmentally sensitive trichopterans and ephemeropterans as well as a variety of predatory fish which may impose top-down controls on primary consumers. These results warn that aridification coincides with the loss of competitive and environmentally sensitive taxa which could yield less desirable community states.

2.2 Introduction

A warming climate warrants a better understanding of the processes that link biological communities to long-term trends in temperature and precipitation (Wrona *et al.* 2006; Miranda *et al.* 2020). The direct ecological effects of changes in temperature have received greater attention in the literature, but rising temperatures are also expected to alter patterns of precipitation and evaporation. A warmer, more energetic atmosphere intensifies the hydrological cycle (patterns of precipitation and evaporation), causing wet regions to become wetter and dry regions become drier (Allen and Ingram 2002), as well as increasing the frequency and intensity of extreme weather events (Held and Soden 2006). In general, this raises concern for freshwater ecosystems which are highly sensitive to changes in water availability and contain many species with limited dispersal capabilities (Woodward *et al.* 2010).

Stream ecosystems are shaped by flow regimes which regulate the physical extent of aquatic habitats, water quality, sourcing and exchange rates of material, and habitat connectivity (Rolls *et al.* 2012). Aridification increases the prevalence of droughts and flash floods which disturb local communities by imposing intolerable conditions or physically displacing individuals. Lengthening dry periods cause changes in macroinvertebrate communities where drought sensitive taxa (Ephemeroptera, Plecoptera, and Trichoptera) are replaced by drought tolerant species (Storey 2016). In contrast, humid precipitation regimes have low interannual variability and frequent bank flooding that promotes hydrological connectivity and resource exchange between aquatic and terrestrial systems. Fish communities become increasingly diverse with precipitation and temperature along continental climate gradients (Griffiths *et al.* 2014). The expansion of semi-arid regions (Huang *et al.* 2015) warrants an improved understanding of the mechanistic links between precipitation, flow regime, and aquatic biota to manage for the increasing societal demands for freshwater resources.

Hierarchical community assembly models can help us organize our hypotheses regarding impacts of climate change on stream communities (Poff 1997). Assuming organisms can disperse to a habitat, they must be able to survive in the local environment (abiotic filters) and successfully reproduce in the presence of other organisms exerting pressures (biotic interactions) such as competition and predation (Patrick and Swan 2011). Species have physiological tolerances (temperature, toxin concentrations, and salinity, etc.) which limit their distribution across environmental gradients (Whittaker *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 *et al.* 2015).

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

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

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

2.3 Methods

***Study Region*:**

The Texas Coastal Prairie contains grassland prairie with forested areas occurring primarily along riverine systems. During March and April of 2017, we sampled ten, wadeable, perennial streams which span 12 counties from Kleberg County to Montgomery in South-Central Texas, USA (Figure 2.1). Each study site was located within 100 meters of a USGS stream gauge which continuously monitor streamflow and climate data year-round. Study sites were chosen to maximize differences in precipitation with minimal changes in underlying geology and elevation. The annual precipitation ranges from 67-124 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℃) (Falcone 2011). Sampling was conducted by students and faculty at Texas A&M (Corpus Christi) under permit SPR-0716-170, granted by Texas Parks and Wildlife Department.

Biological Sampling:

Fish communities were sampled using a Smith-Root LR-24 Backpack in a single pass survey (Lamberti 2017). Each reach length was 25 times the average stream width, in accordance with EPA rapid bioassessment protocols (US EPA 2019). Low variability in stream withs (4.9 ± .6 m) resulted in comparable catch effort across sites, so fish abundances were reported in terms of catch per sample event. Fish species were field identified to species using a field guide (Thomas *et al.* 2007) and photographed. Several specimens of each species were euthanized using tricaine mesylate (MS-222) and stored in >70% denatured ethanol as voucher specimens for lab confirmation of species identification. Fish Voucher specimens were identified using the Texas Academy of Science dichotomous key (Hubbs, Edwards, and Garrett 2008) and cross referenced with field identifications. Vertebrate sampling was permitted by the Institutional Animal Care and Use Committee, Texas A&M University Corpus Christi (AUP# 05-17).

Invertebrates were collected using a 0.305m wide D-frame net equipped with 500-µm mesh. Twenty 0.093 m^2 samples were collected via a combination of kick and sweep (15 s duration) sampling from a representative distribution of best available habitat (riffles, large woody debris, overhanging vegetation) (Southerland *et al.* 2007). Samples were pooled in a 500-µm sieve bucket where larger sticks and leaves were rinsed and removed. The captured invertebrates and remaining debris were preserved in 95% EtOH for transport to the lab. In the lab, samples were spread across a gridded sampling tray and randomly selected grid cells were picked to completion until the total count was > 300 individuals (USEPA 2015). Samples containing less than 300 individuals were picked to completion. Invertebrates were identified to lowest taxonomic resolution (typically genus) using taxonomic keys cross referenced with species observations recorded by the TCEQ's (Texas Commission on Environmental Quality) Surface Water Quality Monitoring Program (Wiggins 2015; Cummins and Merritt 1996). The sum of individuals in each taxon were multiplied by the fraction of unpicked sample and reported as abundance of individuals per square meter.

Environmental Data:

For each stream, we averaged values for each of the following habitat measurements that were taken at 4 cross-sections spaced 25m apart. A Rosgen Index value was calculated by dividing the bank-full width by the maximum depth (Rosgen 2001). Bank height was recorded as vertical difference between water level and the height of the first bench. We estimated sediment grain size within each cross-section using Wentworth size categories to calculate a median grain-size (d50) (Wentworth 1922). Oxygen, temperature (T_{water}), conductivity, turbidity, and pH were measured at each point using a YSI ProDSS multiparameter probe. Two 60 mL water samples were collected and filtered through a pre-combusted (500℃ 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 gathered climate and watershed data, from the US Geologic Surveyors Geospatial Attributes of Gages for Evaluating Streamflow, version II dataset (Falcone 2011). A twenty-year continuous daily flow record was downloaded for each site (except Tranquitas Creek which only had 4 years of available data) from the USGS Water Services (https://waterservices.usgs.gov).

Analyses:

Due to a small number of sample sites and replicates, the statistical analyses relating environmental drivers to organismal responses were restricted to six *a priori* environmental predictors. Annual precipitation was evaluated to identify gradient effects. Channel shape is a product of flow regime, slope, substrate, and bank stability and was summarized by the Rosgen index. We included conductivity and NH_4^+ to evaluate water quality. Since the selected streams were deliberately chosen to be wadeable at base flow, we calculated two flow metrics to approximate the typical flow regime of each site in the context of seasonal droughts and floods, as well as overall variation in flow: Flash Index (cumulative changes in day to day daily flow / cumulative flow) and the Low-Flow

Pulse Percent (LFPP = times where daily discharge drops below the 25th percentile) (Olden and Poff 2003; Patrick and Yuan 2017).

We used linear regression and Pearson correlation coefficients to identify potential confounding relationships between precipitation and each environmental predictor. We then, used singular value decomposition of the centered and scaled data matrix in a principal component analysis with all six environmental predictors. The environmental PCA and associated exploratory results are described in appendices 2.03.

For each community (fish and invertebrate) we estimated coverage and Hill diversity metrics (Roswell *et al.* 2021). We used coverage-based estimates of species richness, Shannon entropy and Gini-simpson index (Chao *et al.* 2014). While richness and Gini-Simpson index values are reported in appendices 2.04 and 2.05, further analyses and discussion regarding diversity utilize the Shannon Entropy because it is not overly sensitive to either rare or common species. We used univariate regression to evaluate community diversity relationships with the precipitation gradient and each environmental predictor. We also performed exhaustive multiple regression with an additive global model utilizing all six environmental predictors and ranked them using Aikake's information criterion corrected for small sample sizes (AIC_c). All the results werecompared to the best overall model by calculating the difference in AICc values (ΔAICc). Models with $\Delta AICc < 2$ were considered to have substantial support (Burnham and Anderson 2002). Diversity Hill metrics were calculated using the iNEXT package (Hsieh *et al.* 2020) in R (R Core Team 2018).

To discern compositional shifts in fish and invertebrates across the precipitation gradient, we used Redundancy Analysis (RDA) on Hellinger-transformed community data, constrained to the six environmental variables in Table 2.1 (Legendre and Gallagher 2001; Legendre and Legendre 2012). We then fit vectors to the species and environmental variables where the direction of each arrow is determined by the average directional cosines from the origin to site values within the ordination. Significant vectors had an associated p-value < 0.05. Ordination and vectors were calculated using the 'rda' and 'envfit' functions respectively in the vegan package in R (J. Oksanen *et al.* 2019, Bellier *et al.* 2012). Statistics and analytical R scripts for analyses described above are reported in the appendices.

2.4 Results

Fish Community:

Eighteen fish species were identified. Proceeding from semi-arid to sub-humid sites, Shannon entropy increased from 1.6 to 6.1 and richness increased from 2 to 9 species (Figure 2.2). Univariate regressions indicate that Shannon diversity is positively correlated with precipitation and negatively correlated with conductivity (Table 2.1). Multiple regression indicates that precipitation alone is the strongest predictor of Shannon diversity.

Communities along the precipitation gradient are stratified in ordination space with significant vector loading on NH_4^+ (Figure 2.3). The position of species and sites indicate that compositions shift from small, elongate live-bearer taxa (*Poecilia latipinna*, and *Gambusia affinis*) in the most arid sites to deep-bodied, nesting centrarchids (*Lepomis megalotis* and *Lepomis macrochirus)* in the more humid sites. Some mesic and humid stream communities are distinguished by the presence of *Cyprinella lutrensis*, a small, invasive habitat-generalist. Species found in small numbers or at singular sites fail to produce significant vectors in the RDA. Unique species found in sites on the humid side of the climate gradient include hogchoker (*Trinectes maculatus*), black bullhead catfish (*Ameirus melas*), and blacktail shiner (*Cyprinella venusta*).

Invertebrate Community:

In total, 94 invertebrate genera were identified. Invertebrate richness ranged 7–29 genera with the highest values occurring at three sites in the middle of the precipitation gradient (Figure 3.4). Regression analysis indicates that Shannon entropy does not significantly correlate with precipitation. However, multiple regression indicates that invertebrate diversity relates negatively with LFPP (Table 2.1).

Communities along the precipitation gradient stratify in ordination space along opposite/parallel axes of precipitation and conductivity. Arid communities are strongly correlated with gastropods including a non-native burrowing snail (*Melanoides tuberculata*). Mesic invertebrate communities are strongly correlated with crawling beetles (*Hydraena*) and swimming beetles (*Peltodytes*). The most humid communties correlate with several Ephemeroptera (*Caenis* and *Plauditus*), Crustacea (*Palaemonetes*), Amphipoda (*Hyalella*), and Trichoptera (*Cheumatopsyche*).

2.5 Discussion

Our goal was to quantify patterns in the diversity and composition of stream communities along an extreme precipitation gradient to better understand how streams might respond to future changes in mean annual rainfall. We identified compositional shifts in both fish and invertebrate communities along the precipitation gradient. We also observed a positive relationship between fish diversity and mean annual rainfall, matching expectations, whereas invertebrate diversity did not exhibit the expected relationships with rainfall. Changes in water solute concentrations and flow regime appear to be additional important drivers of community responses.

The fish communities displayed increasing diversity moving from the drier to wetter sides of the survey region. Fish diversity increased with precipitation but was negatively related to conductivity, NH_4^+, and canopy coverage. Elevated conductivity and NH_4^+ in semi-arid streams exhibited levels similar to urbanized streams (Hatt *et al.* 2004), creating stressful osmotic and toxic conditions for fish (J. M. Redding and Schreck 1983; Lock and Wendelaar Bonga 1991). Elevated NH_4^+ has been shown to be directly toxic to many fish (Randall and Tsui 2002) and has also fueled cytotoxic algal growth (Fetscher *et al.* 2015). Elevated solute concentrations were likely driven by evaporation, the watershed area/discharge ratio, and the greater influence of wastewater effluent on low discharge streams that typify semi-arid streams (Williams 1999; Dehedin *et al.* 2013). We interpreted these patterns to mean that as conditions become drier, water quality imposes abiotic filters on fish assembly which reduce overall community diversity and selects for taxa with specialized adaptations for the harsh conditions. The negative relationship between fish diversity and canopy coverage was attributed to incomplete leaf-emergence in deciduous canopies prior to May.

Communities in semi-arid streams were composed of small, live-bearing, omnivores able to tolerate high salinities including Sailfin Molly (*Poecilia latipinna*, 95 psu) and Western Mosquitofish (*Gambusia affinis*, 58.5 psu) (Page and Burr, B.M. 1991). The strongest compositional shift observed were increases in the abundance of centrarchids (sunfish) with increases in annual rainfall. Centrarchid species have 3-7 year lifespans, breed annually, build nests, and are omnivores (Cooke and Philipp 2009). Additional increases in diversity towards the wetter side of the climate gradient included the addition of black bullhead catfish (a demersal, nesting omnivore), and several shiner species (small broadcast spawning minnows). These organisms require conditions that are stable across years as well as suitable substrate for rearing young, suggesting that conditions in semi-arid sites were excluding these taxa through environmental filtering. Additionally, some of the sub-humid and mesic sites also had seasonally migrating taxa including Rio Grande Cichlid (*Hericthys cyanogutattus)*, Hogchoker (*Trinectes maculatus),* and American Eel (*Anguilla rostrate*) (Rehage *et al.* 2016; Koski 1978; Wenner 1978). These were absent from semi-arid sites. Given the similar proximity to nearby reservoirs and estuaries, migratory taxa may have been excluded from streams with habitat fragmentation, approximated here by low flow pulse %, that typify semi-arid streams (De Jong *et al.* 2015).

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

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

Despite relating with LFPP, invertebrate diversity did not correlate linearly with precipitation. Instead, invertebrate diversity peaked in the middle of the rainfall gradient. The lack of a linear correlation between invertebrate diversity and precipitation may have been caused by the inherently larger species pool for invertebrates which included more taxa with biological adaptations to drought compared to fish (Eriksson 1993). The peak likely represented the transition zone where taxa common on each side of the gradient were able to co-occur. Alternatively, the driest site (Tranquitas Creek) displayed uncharacteristically low diversity compared to other semi-arid sites and may constitute an outlier. When removed, invertebrate diversity correlated negatively with precipitation ($R^2 = 0.43$, *p*-value = 0.06). Regardless, the relation between precipitation and invertebrate diversity remains unclear.

Invertebrate community compositional shifts with rising precipitation invite continued assessment on the following speculative premises within the region: 1) The observed shift in primary consumers from short-lived, euryhaline dipterans and gastropods to ephemeropterans and trichopterans, environmentally sensitive species with longer lifespans, pointed towards improved water quality conditions and hydrologic stability (Rosenberg and Resh 1993; Jackson and Sweeney 1995). Taken further, this pattern alludes towards the evolutionary trade-off between aridity tolerance and competitive specialization (Fréjaville *et al.* 2018). 2) The increased prevalence of shredder-crustaceans (amphipods and crayfish) at wetter sites pointed towards a possible shift in available basal resources; precipitation-mediated shifts in riparian vegetation from evergreen, xeric mesquite trees to deciduous hardwoods could bring about increased allochthonous inputs to support more shredder taxa (Giling, Reich, and Thompson 2009). 3) The decreased abundance of odonate and hempiteran predators may have been due to competition with and predation by insectivorous centrarchids (Dahl and Greenberg 1998). In this way, top-down trophic interactions at sub-humid sites could have restricted invertebrate communities to species with anti-predator adaptations including small size, passive foraging strategies, camouflage, and armoring (Straile and Halbich 2000).

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

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

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2.7 Tables

Response	Input	Slope	R^2	F-stat	df	p-value	Multiple Regression
$\text{Shannon}_{\text{Fish}}$	Precipitation	0.056	0.576	10.885	2	0.011*	**+ ***
$\text{Shannon}_{\text{Fish}}$	Flashiness	1.430	0.038	0.316	2	0.589	**+**
$\text{Shannon}_{\text{Fish}}$	Channel Shape	0.113	0.069	0.597	2	0.462	**+**
$\text{Shannon}_{\text{Fish}}$	Low Flow Pulse %	-0.083	0.222	2.281	2	0.169	**-**
$\text{Shannon}_{\text{Fish}}$	NH_4^+	-13.221	0.326	3.877	2	0.084	**-**
$\text{Shannon}_{\text{Fish}}$	Conductivity	-0.920	0.413	5.636	2	0.045*	**-**
$\text{Shannon}_{\text{Invert}}$	Flashiness	8.651	0.061	0.517	2	0.493	**+**
$\text{Shannon}_{\text{Invert}}$	Precipitation	-0.085	0.057	0.487	2	0.505	**-**
$\text{Shannon}_{\text{Invert}}$	Low Flow Pulse %	-0.489	0.336	4.056	2	0.079	**- ***
$\text{Shannon}_{\text{Invert}}$	NH_4^+	-2.519	0.001	0.004	2	0.950	**-**
$\text{Shannon}_{\text{Invert}}$	Conductivity	-0.884	0.017	0.135	2	0.723	**-**
$\text{Shannon}_{\text{Invert}}$	Channel Shape	-0.899	0.193	1.917	2	0.204	**-**

Table 2.1: Regression Statistics

Univariate regression summary statistics and multiple regression relationships predicting fish and invertebrate Shannon Index values using environmental predictors. * denotes a p-value < 0.05 or an Δ AICc < 2.

2.8 Figures

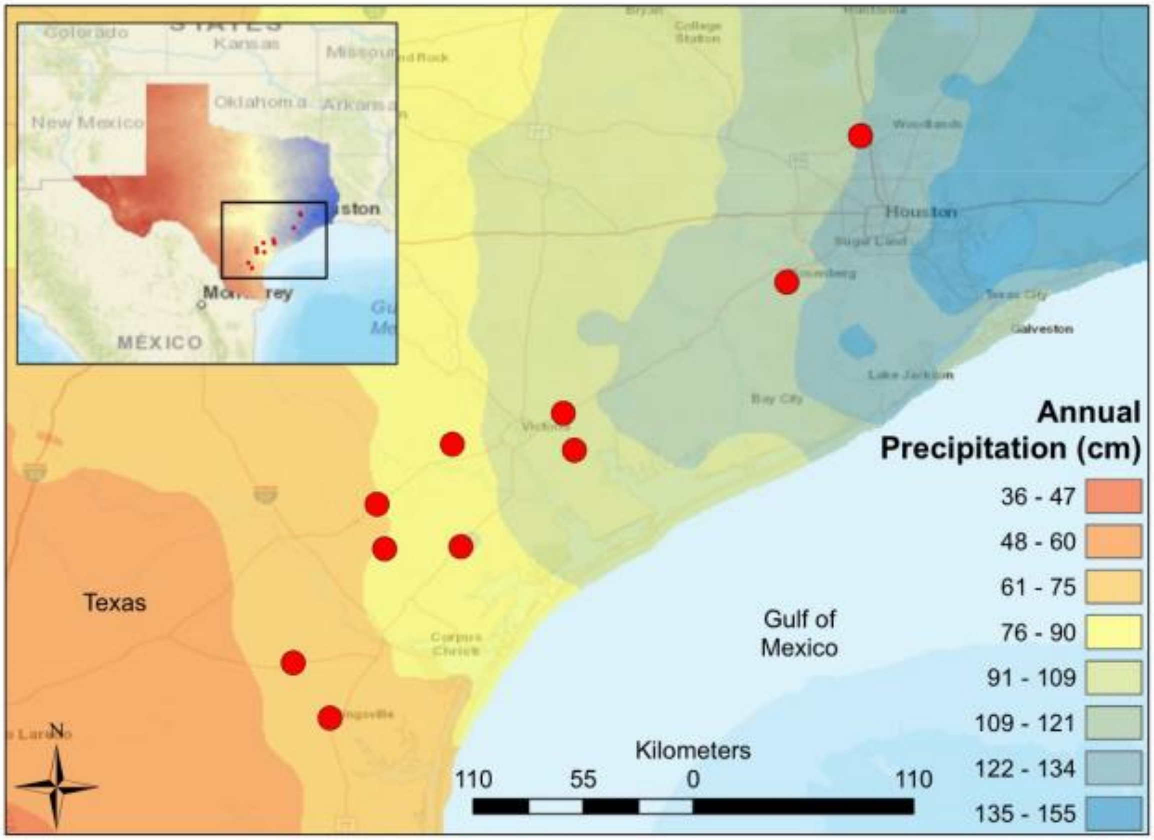


Figure 2.1: Study Region Map

Map of South-Central Texas, where 10 USGS gauged streams were sampled in the spring of 2017. An annual precipitation overlay indicates that sample sites spanned a gradient from 61 cm/yr in the Southwest to 134 cm/yr in the Northeast

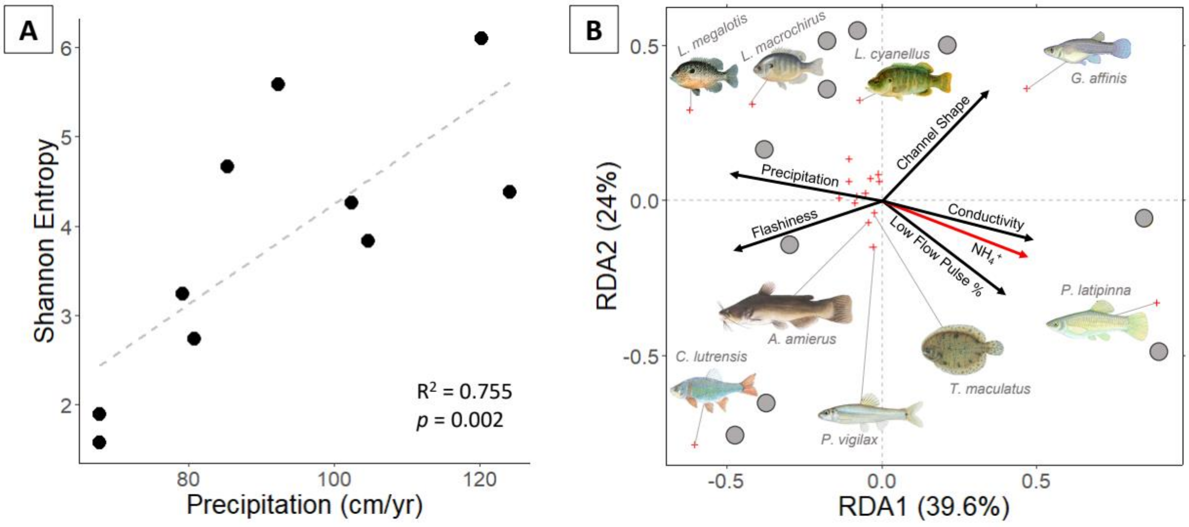


Figure 2.2: Fish Diversity and Composition (RDA)

(A) Fish Shannon-Hill diversity plotted against annual precipitation (cm/yr) (B) Fish community ordination using Hellinger transformation and redundancy analysis. Axes labels display the proportion of the variance explained as a percentage. Sites are represented by grey circles. Species are represented by red crosses, with species labels and reference images added to outer members. Environmental variables are shown in arrows and the significant ones are presented in red.

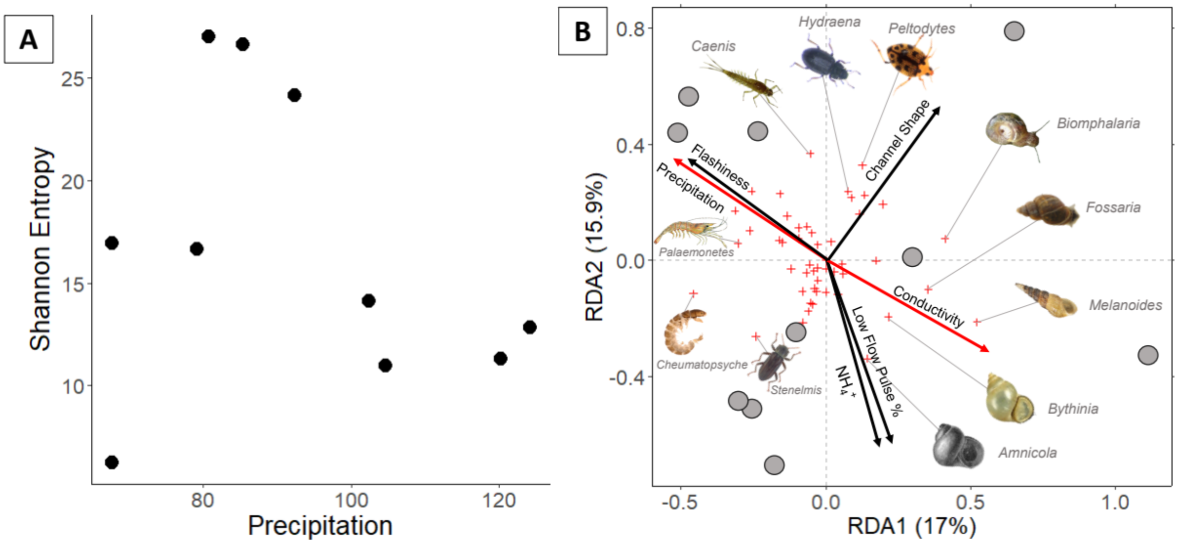


Figure 2.3: Invertebrate Diversity and Composition (RDA)

(A) Invertebrate diversity plotted against annual precipitation (cm/yr) (B) Invertebrate community ordination using Hellinger transformation and redundancy analysis. Axes labels display the proportion of the variance explained as a percentage. Sites are represented by grey circles. Species are represented by red crosses, with species labels and reference images added to outer members. Environmental variables are shown in arrows and the significant ones are presented in red.

2.9 Appendix

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

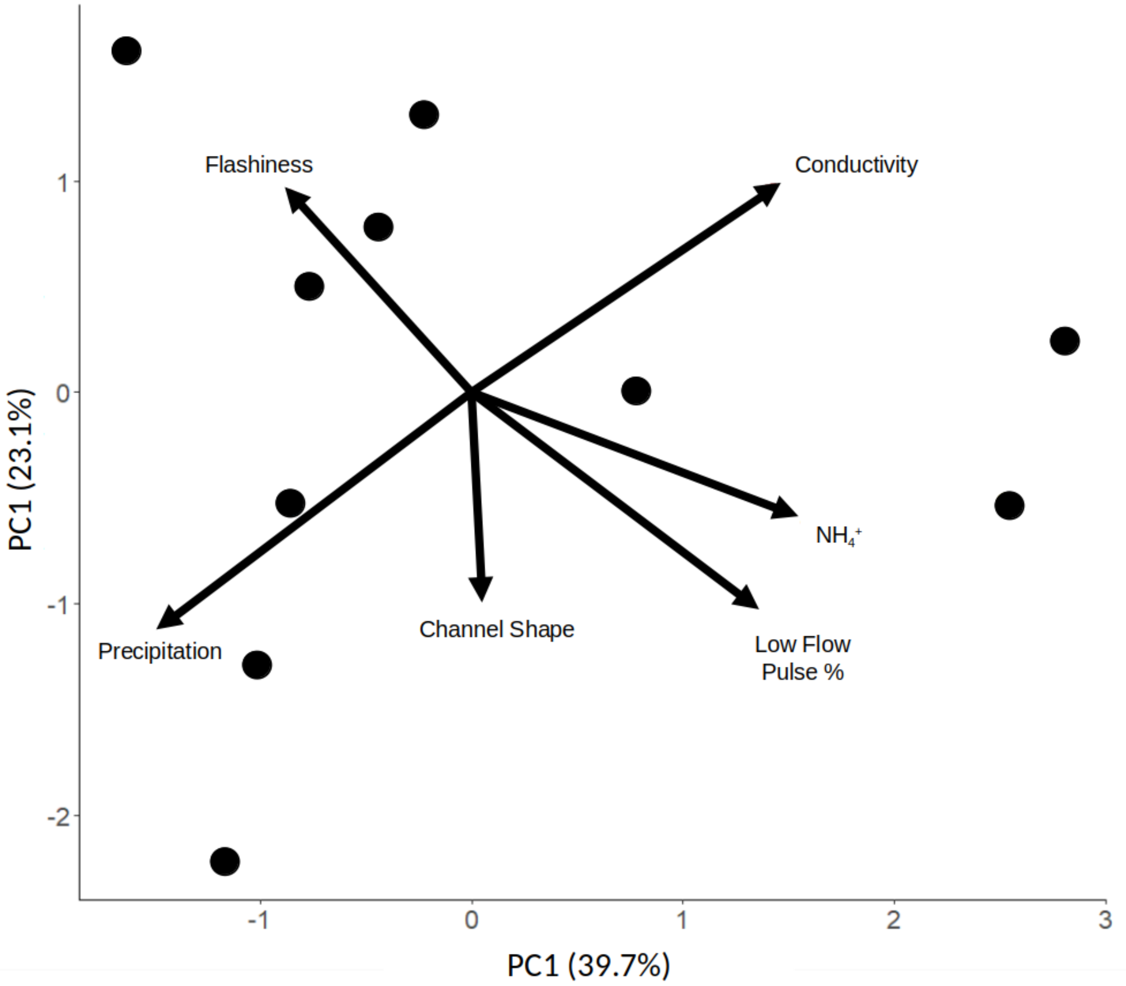
Appendix 2.01: Regional Environmental Variation Table

Mean and interquartile range values for environmental gradient features of 10 samples sites spanning the Texas Coastal Prairie. The source data was collected from US Geologic Surveyors Geospatial Attributes of Gages for Evaluating Streamflow, version II dataset (Falcone 2011).

Site Name	USGS Station ID	Rain (cm/yr)	Flashiness	Low Flow Pulse %	Channel Shape	NH4+ (mg/L)	Conductivity ln(µS/cm)
San Fernando	8211900	67.75	0.91	20.31	15.76	0.30	6.89
Tranquitas	8212300	67.75	0.78	24.06	17.99	0.15	9.10
Medio	8189300	79.13	0.99	0.00	18.41	0.11	6.75
Aransas	8189700	80.77	1.05	7.66	11.78	0.10	6.84
Mission	8189500	85.36	0.58	3.36	14.70	0.17	7.16
Perdido	8177300	92.37	1.34	0.00	15.15	0.08	6.60
Garcitas	8164600	102.41	0.81	4.87	18.16	0.10	6.25
Placedo	8164800	104.65	0.92	5.48	13.38	0.09	7.04
Big Creek	8115000	120.31	0.96	15.63	23.15	0.12	5.39
Bear Branch	8068390	124.19	0.78	13.15	12.01	0.13	5.43

Appendix 2.02: Environmental Summary Table

Environmental values for the 10 sample sites. Annual precipitation, flashiness, and Low-Flow Pulse % were calculated using 30-year records provided by USGS stream gauges. Channel shape (stream width / stream depth), NH_4^+, and conductivity were measured in-situ in during Spring 2017 sampling.

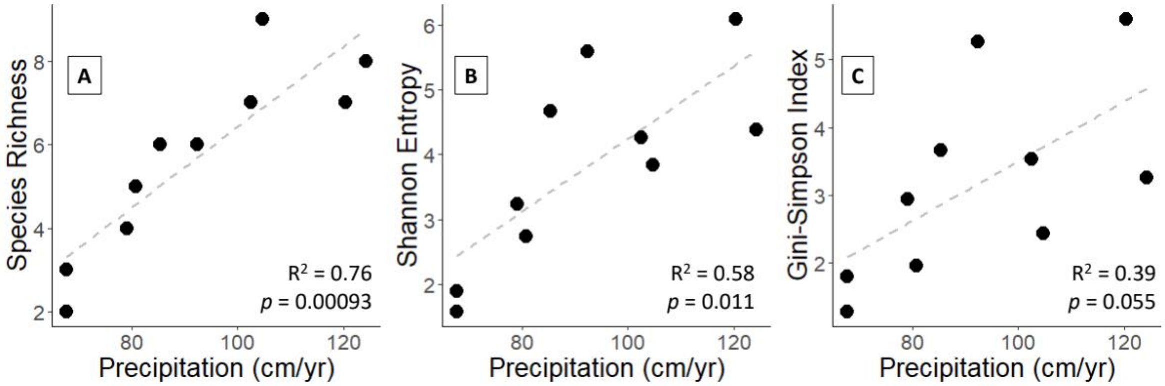


Appendix 2.03: Environmental Principle Component Analysis (PCA)

Principal Component Analysis of environmental predictors at 10 sites spanning a precipitation gradient along the Texas Coastal Prairie. Circles representing sample sites are colored based on their annual precipitation. Axes labels include the percentage of variance explained by the first principal component (horizontal axis) and the second principal component (vertical axis).

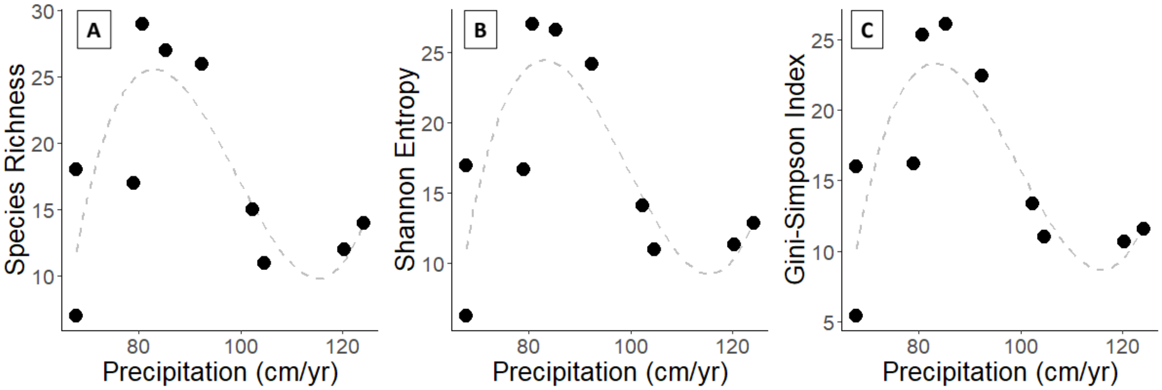
Appendix 2.04: Environmental Pairs Plot

Environmental predictors pairs plot. Scatter plots with linear regression are depicted in the upper right panels. Data point density is plotted by the blue line along the center diagonal panels. Correlation coefficients are scaled by magnitude and depicted in the lower left panels opposite of their complimentary scatterplot in the top right section.



Appendix 2.05: Fish Hill Numbers

Fish community (A) Species richness, (B) Shannon entropy, and (C) Gini-Simpson diversity plotted against annual precipitation. Dotted grey lines depict linear regressions and the associated correlation coefficients and *p*-values are printed in the lower right section of each panel.



Appendix 2.6: Invertebrate Hill Numbers

Invertebrate community (A) Species richness, (B) Shannon entropy, and (C) Gini-Simpson diversity plotted against annual precipitation. Invertebrate biodiversity does not exhibit a straightforward linear relationship with annual precipitation, but the highest invertebrate diversity was observed at sites within the middle of the rainfall gradient.

Chapter 3: Hydrogen Stable Isotopes Reveal Algal Dependency in Arid, Freshwater Food-Webs

3.1 Abstract

As climate-induced aridification becomes a pervasive global concern, our research delves into the overarching consequences on freshwater communities, shedding light on the universal interplay between precipitation variability and the structure of riverine food webs. Climate change is expected to increase aridity in subtropical regions such as the North American Southwest, areas around the Mediterranean Sea, and South Africa. To enhance our understanding of how freshwater fish and invertebrate communities will adjust to shifts in precipitation dynamics, we performed community surveys, an experimental manipulation, and multi-trophic level stable isotope analysis in three wadeable freshwater streams along an extreme precipitation gradient from semi-arid (55cm/yr) to sub-humid (85cm/yr) streams in South Central Texas. Exclosures revealed that algal standing stocks increased with aridity, and there was a marked transition from a trophic cascade mediated through fish predation on invertebrate grazers to direct herbivory. Supporting this pattern, Bayesian source-partitioning models using the stable isotopes δ^2H and δ^{13}C show increasing aquatic source assimilation (autochthony) in fish and invertebrate communities in our drier streams. Sub-Humid fish communities exhibited low autochthony (5%) compared to Transition (36%) and Semi-Arid (75%) communities. Also, the range of δ^2H values within fish communities imply resource

specialization because of greater resource breadth at the Semi-Arid (58‰) compared to Transition (43‰) and the Sub-Humid sites (41‰). Lastly, isotopic trophic levels using δ^{13}N indicate fewer steps in the food chain between primary producers and fish in the Semi-Arid site (0.7) compared to the Sub-Humid site (2.1). Our results suggest that the consequences of aridification in streams include enhanced autochthonous production, increased herbivory, and a shortened overall food chain. Our findings point towards arid stream communities being adapted to boom-or-bust production cycles that accompany the ramping stresses applied during droughts and the pulses of nutrients following flash floods. Future aridification is likely to drive comparable changes in stream food web structure and function.

3.2 Introduction

Global climate change is altering patterns in evaporation and precipitation, creating concerns for both human populations and ecosystem management (Allen *et al.* 2019). For example, global drylands currently encompassing 41% of the Earth's terrestrial surface and home to over one third of the world's population, are predicted to expand over the next century (Feng and Fu 2013). Worldwide, models indicate that wetter regions (including the tropics) will become wetter and drier regions (including the subtropics) will become drier (Allan and Soden 2008, Trenberth 2011, Dai *et al.* 2018). Climate warming is also projected to increase temporal variability in rainfall, replacing frequent light rains with boom-or-bust precipitation cycles (Konapala *et al.* 2020, Overpeck and Udall 2020). These altered precipitation regimes increase the risk of water scarcity for societal and natural systems including the Southwestern USA, Mediterranean and Southern Africa (Seager *et al.* 2007, Vicente-Serrano *et al.* 2014, Allen *et al.* 2019). The interplay between precipitation patterns, aridity, and stream ecosystems is a pressing ecological concern, with potential cascading effects on vegetation, nutrient cycles, and food webs. This study seeks to unravel the nuanced impacts of aridity on basal resource availability and consumption within stream ecosystems across a natural precipitation gradient.

Streams, as vital connectors between terrestrial and aquatic systems, exhibit a notable sensitivity to alterations in rainfall patterns, influencing watershed and riparian vegetation dynamics and, consequently, litterfall (Dodds *et al.* 2015). Rainfall dictates patterns in watershed and riparian vegetation and consequently litterfall, which provides pulses of external organic carbon and nitrogen that support aquatic, detrital food-webs. For example, persistently arid climates are characterized by sparser vegetation and incomplete riparian canopies, reducing litterfall and permitting greater solar insolation and consequent algal production (Bonada and Resh 2013). During dry seasons in tropical regions or periodic droughts, deciduous and semi-deciduous plants drop leaves to cope water stress (Zhang *et al.* 2014, Tonin *et al.* 2017). Moreover, during baseflow and droughts, especially when human modifications maintain flows (Lawrence *et al.* 2014), stream environments can become extreme. They exhibit high nutrient concentrations, temperatures, and conductivity, alongside low dissolved oxygen. Consequently, aridification has the potential to significantly alter stream food webs by affecting basal resources and water quality.

The arid hydrologic regime is another factor that controls the structure and function of dryland streams, forcing organisms to sustain or avoid the physical effects of drought and floods, while also shaping stream food webs by altering basal resource availability throughout the year. Droughts ramp up physical stresses from reduced water availability, nutrient accumulation, and hypoxia (Bernal *et al.* 2013) which serve to reduce taxonomic and functional diversity in arid fish communities (Rodrigues-Filho *et al.* 2018, Kinard *et al.* 2021). In contrast, periodic flash floods scour the benthos, exporting nutrients, detritus, biofilms, and organisms downstream (Fisher *et al.* 1982). Benthic macroinvertebrates in arid systems have adaptations such as enhanced dispersal ability, rapid proliferation (multivoltinism), and brooding capabilities (oviviviparity) to rapidly recolonize and regrow their populations following severe and unpredictable flash floods (Usseglio-Polatera and Beisel 2002, Bonada *et al.* 2007, Díaz *et al.* 2008). However, by exporting nutrients, detritus, biofilms, and organisms downstream, floods reset arid food-webs in a period of rapid (2–3 week) succession (Fisher *et al.* 1982). Rapid algal recovery following floods support swift recolonization by invertebrates and fish, making autochthonous resources pivotal for succession and perhaps the most reliable basal resource in arid food webs.

In addition to hydrologic contraction during dry periods (Bernal *et al.* 2013), aridity changes vegetation throughout the watershed and riparian zones which alters nutrient, carbon, and light inputs to streams (Mosley 2015). For instance, semi-arid riparian corridors in South-Central Texas are commonly vegetated with drought-adapted species including Live Oak (*Quercus virginiana*) and Honey Mesquite (*Prosopis glandulosa*)

(Chapman 2018). Mesquite trees obtain water from taproots reaching deep soil horizons and they conserve water-loss by reducing leaf production and shedding which subsequently deprives streams of allochthonous (terrestrial) inputs that typify forested streams (Ordoñez *et al.* 2009, Qin *et al.* 2019). Additionally, impermeable soils and slow litter decomposition lead to nutrient-rich runoff which contributes to eutrophic algal blooms following floods (Hefting *et al.* 2005, Creed *et al.* 2018). Drought modifications to watershed vegetation combined with stochastic floods render allochthonous resources scarce and unreliable. Thus, it may be necessary for arid communities to rely on autochthonous sources beyond periods of recolonization.

Stable isotope ecology, employing molecular tools (Doucett *et al.* 2007), discerns contributions of aquatic and terrestrial sources to organism tissues. These analyses exploit naturally occurring isotopic ratios shaped by predictable processes, enabling profiling with distinct molecular signatures. Mixing models estimate source contributions to a consumer's isotopic signature. In Australian inland rivers with anastomosing channels, Bunn *et al.* (2003) found algal resources to be major contributors to the aquatic food web, emphasizing the significance of autochthonous algal production over terrestrial organic matter inputs during floods. Similarly, in Atlantic rainforest streams, Brito *et al.* (2006) revealed that, despite high terrestrial carbon stocks, stable isotopes showed fauna relying primarily on algal-based carbon sources. Delong and Thorp's (2006) study in the Upper Mississippi River affirmed algal transported organic matter as the major resource for primary consumers, minimizing the role of terrestrial C3 litter. This collective research underscores algae's pivotal role in freshwater trophic dynamics, challenging conventions and emphasizing the importance of autochthonous production. Algae and biofilm prove significant contributors to stream food webs, presenting digestible and nutritious alternatives to detritus (Mantel *et al.* 2004, Kieckbusch *et al.* 2004, Lau *et al.* 2009, Brett *et al.* 2017).

Traditionally, the importance of allochthonous pathways have overshadowed autochthonous pathways in stream food web paradigms, but recent developments in stable isotope ecology reveal the substantial role of in-stream primary production on stream ecosystem functioning (Lau *et al.* 2009, Neres-Lima *et al.* 2016). The River Continuum Concept (Vannote *et al.* 1980) and the Flood Pulse Concept (Junk *et al.* 1989) were based on observations from temperate forested ecosystems and were reasoned on observable phenomena such as leaf-litter entering streams, finding terrestrial insects in fish gut contents, and changes in water quality along a longitudinal stream profile (Doretto *et al.* 2020). In contrast, the role of algal production, ingestion, and assimilation have been challenging to measure until more recently.

Study Design, Questions, & Goals:

In this study, we use a combination of fish and invertebrate surveys, stable isotope sampling, and manipulative consumer exclusion experiments in streams across a natural precipitation gradient to ascertain the effects of aridity on basal resource availability and consumption. We use stable isotopes of $\delta^{13}C$ and $\delta^{2}H$ to trace nutrient sources (allochthonous versus autochthonous) and $\delta^{15}N$ to trace isotopic trophic positions (Doucett *et al.* 2007, Finlay *et al.* 2010, Vander Zanden *et al.* 2016). We hypothesize the following:

(1) Aridity-induced changes in riparian vegetation and hydrology will enhance autochthonous production, leading to increased standing algal stocks.

(2) The impact of fish on algal standing stocks will shift from positive to negative across the rainfall gradient. In drier sites, fish will primarily graze algae, while in wetter sites, fish will predominantly control invertebrate grazers.

(3) In more arid climates, fish and invertebrates will assimilate higher amounts of carbon ($\delta^{13}C$) and hydrogen ($\delta^{2}H$) from autochthonous sources due to the prevalence and superior nutrition of algae compared to detritus.

(4) Isotopic niche width ($\delta^{2}H$ range) and height ($\delta^{15}N$ range) will positively correlate with aridity because abundant algal sources will support more generalized foraging habits in arid conditions.

In clarifying the role of aridity in controlling stream reliance on autochthonous sources, we aim to both refine expectations for the ecological ramifications of aridification as well as identify finer scale food-web characteristics to improve contemporary food-web theory for sub-tropical streams.

3.3 Methods:

Study Region

In June of 2019, we sampled three wadeable, perennial streams distributed along 180 km of the coastal plain in South-Central Texas, USA (Figure 3.1). This subtropical, risen seafloor is dominated by grasslands and forested riparian corridors. Proceeding from the Southwest to the Northeast within this coastal prairie, annual precipitation increases as dry winds from the Chihuahuan Desert give way to humid winds from the Gulf of Mexico. Riparian vegetation corresponds to changes in annual rainfall transitioning from Huisache (*Acacia smallii Isely*) and Honey Mesquite (*Prosopis glandulosa*) to Live Oak (*Quercus virginiana*) and Hickory (*Carya illinoinensis*). Sites were 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 (semi-arid ~ 55cm/yr, transition ~ 70 cm/yr, and sub-humid ~ 85 cm/yr). Additional criteria included the presence of continuous flow data from USGS stream gauges (< 100m from each gauge) and minimal variation among sites in air temperature, mean discharge, underlying geology, and elevation (Falcone 2011). The surface geology of the sites is characterized by fine clays, quaternary and sedimentary sand. The streams have similar elevations (20-62 m), substrates (quaternary), and annual mean air temperatures (21-22 °C). Mean annual precipitation and temperatures (were calculated from 1981-2010), watershed geology, and elevation were obtained from the USGS

Gauges ii dataset (Falcone 2011). Sampling was conducted under permit SPR-0716-170, granted by Texas Parks and Wildlife Department.

We selected three streams to represent the distinct communities observed in a previous rapid bio-assessment in 2017 (Kinard *et al.* 2021). The 2017 surveys implicated opposing specializations at each extreme of the rainfall gradient. Communities in drier climate contained relatively few fish and invertebrate species, most of which were dominated by euryhaline (salinity-tolerant) and/or ovoviviparous (live-bearing) taxa. The diversity, measured by Shannon Entropy, of fish exhibited a positive correlation with annual rainfall. Additionally, the dominance of *Poecilia latipinna* (Sailfin Molly) in semi-arid streams shifted to the dominance of *Lepomis megalotis* (Longear Sunfish) in more humid climates. Furthermore, streams in wetter climates harbored invertebrate species belonging to the orders Ephemeroptera (mayflies) and Trichoptera (caddisflies), which are known to be sensitive to adverse water quality conditions such as hypoxia and salinization. Diversity of invertebrates peaked in the middle of the rainfall gradient, indicating an overlap of species' distributions from either side of the rainfall gradient. Although there are fewer sampled streams, the 2018 surveys (detailed in appendices 3.13-3.20) corroborate the regional trends observed in the 2017 rapid bio-assessment and provide greater level of detail by using more thorough sampling methods.

Carvallo *et al.* (2022) describes invertebrate communities throughout 2018 at nine streams within the study region including all three sites in this study. Invertebrate mean annual abundance, species richness, and functional richness peaked at the Transition site. Looking at functional feeding groups, herbivorous invertebrates constituted incrementally larger proportions of the community from Semi-Arid (4%) to Transition (18%) to Sub-Humid (31%) sites. As the proportion of herbivores increased in the wetter climates, predators declined 17% and other groups (collector-gatherer and filterer) declined 11%. The pattern of prevalent herbivorous invertebrates at the wetter sites persisted for the majority of the year (Fall, Winter, and Spring). In summer however, herbivores constituted a larger proportion of the Semi-Arid community (28%) compared to the Transition (9%) and the Sub-Humid site (14%). Fourth-corner analysis indicated traits associated with more annual rainfall included herbivory, drift-dispersal, and multivoltinism. Traits associated with less annual rainfall included a high production-to-biomass ratio, desiccation resistance, and strong dispersal capabilities.

Environmental Data

During each site visit, we conducted thorough environmental assessments at four designated sampling stations within 75-meter reaches of each stream. Utilizing a YSI ProDSS multiparameter meter from YSI Incorporated (Yellow Springs, OH, USA), we measured critical parameters, including oxygen levels (mg/L), temperature (°C), conductivity (µcm), turbidity (NTU), and pH. Additionally, we employed a bbe BenthoTorch from bbe (Moldaenke, Germany) to assess the abundance of diatoms (ug/cm^2), green algae (ug/cm^2), and blue-green algae/cyanobacteria (ug/cm^2). Wetted channel width (m) and thalweg depth (m) were measured with a tape measure and a meter stick, respectively. Sediment composition, classified according to Wentworth's categories (1922), was determined at each station, along with water depth (m) at the same three locations. Bank slope measurements were conducted on both sides of the stream at each station using a digital angle gauge.

To characterize dissolved nutrients in the water, we collected two 60 mL water samples during each visit. These samples were field-filtered through 0.7 µm membrane filters, promptly stored in a cooler, and later transported to the laboratory. In the lab, one bottle underwent analysis for NO_3^-, NH_4^+, and SRP using a Lachat Flow Injection Auto-Analyzer at the Oklahoma Soil, Water Forage Analytical Laboratory, while the other bottle was analyzed for total nitrogen and dissolved organic carbon on a Shimadzu TOC Analyzer at the Ulseth Laboratory, Sam Houston State University. This comprehensive suite of measurements provided a detailed understanding of the ecological conditions and dynamics of the stream ecosystem. The methods employed build upon the previously described approach, ensuring a comprehensive assessment of the environmental parameters related to the stream.

Exclosure Experiment

In July 2018, we evaluated the effect of fish consumer pressure on algal growth in the three study streams. In each stream, four $1m^2$ plots were established at random locations within the 75m transect. Each plot consisted of an iron rebar post on each corner and 1cm vexar plastic mesh wrapping around the posts to create an exclosure wall. The wall was buried in the substrate and affixed with forked metal stakes placed at 0.2m intervals around the exterior. Within each plot, three 10cm x 10cm white unglazed ceramic tiles were deployed and an additional three tiles were deployed outside and adjacent to each plot as an experimental control (n=6 tiles per plot x 4 plots per stream x 3 streams = 72 tiles). After a one-month deployment, the chlorophyll (ug/cm^2) on each tile for diatoms, green algae, and blue-green algae were measured in situ using a bbe BenthoTorch (bbe, Moldaenke, Germany).

We used a 2-way ANOVA to assess the effects of exclosure (exclosure or control) and site variations (three sites) on the total standing algal stock. We implemented this analysis with the 'car' R library in R, version 4.2.3 (Team 2021, Fox and Weisberg 2019). To evaluate hydrological conditions during exclosure deployment, we obtained daily discharge data from the USGS web data portal (United States Geological Survey 2019). In the appendices 3.01-3.03, we present the median, maximum, and flooding duration, defined as the proportion of days exceeding three times the annual median. We also include measurements of canopy coverage, NO_3^-, and PO_4^- concentrations taken before and after exclosure deployment.

Community Sampling

Fish and invertebrates, described in terms of abundance, diversity, and community composition, were sampled monthly for this study between May and July of 2018. For fish sampling, block nets (3 mm mesh) were deployed at the top and bottom of the 75m reach and fish communities were sampled in a three-pass depletion using a Smith-Root LR-24 Backpack Electrofisher (Hauer and Lamberti 2017). All fish were identified to species using a field guide and dichotomous key and counted (Bonner *et al.* 2007, Hubbs *et al.* 2008). The first 20 individuals of each species were measured (total length) and one of each species were euthanize using an ice slurry and preserved in 95% ethanol as voucher specimens. After sampling was complete, the remaining fish were released back into the stream, alive. Vertebrate sampling was permitted by the Institutional Animal Care and Use Committee, Texas A&M University Corpus Christi (AUP#05-17).

Invertebrates were collected using a 0.305m wide D-frame net equipped with 500µm mesh. Twenty ~0.1m2 samples were collected via a combination of kick and sweep (15s duration) sampling from a representative distribution of best available habitat (riffles, large woody debris, overhanging vegetation) (Southerland *et al.* 2007). Samples were pooled and debris were removed on-site before transportation to the lab on ice and inundated with 95% ethanol. Samples were processed according to the Texas Commission for Environmental Quality Surface Water Quality Monitoring Protocol (TCEQ (Texas Commission on Environmental Quality) 2019). Each sample was processed separately by being rinsed in a 500µm sieve and placed evenly in a gridded sorting tray. Grid cells were randomly selected and invertebrates in each cell sorted completely until the total count at the time of a cell completion was greater than 175 individuals. The total number of cells the sample occupied and the number sorted were recorded as well. All invertebrates were counted and identified to the lowest possible taxonomic resolution, typically genus (Thorp and Rogers 2016).

Fish abundance per stream on each sampling date was estimated by applying a depletion curve to the repeated pass data to estimate total abundance per species and the dividing by transect surface area to report density of fish per m2 (Hauer and Lamberti 2007). To estimate abundances of invertebrates from the kick and sweep samples, we first scaled the 175-invertebrate count by the percent of the sample sorted to estimate individuals per taxa per sample. Then these values were divided by the total surface area sampled (1.86m2) to obtain an estimate of invertebrates per m^2.

To assess community diversity among fish and invertebrates, we employed coverage-based estimates, considering species richness, Shannon Entropy, and the Gini-Simpson index (Chao *et al.* 2014). While richness and Gini-Simpson index values are detailed in appendix, our subsequent analyses and discussions on diversity primarily focus on Shannon Entropy, given its balanced sensitivity to both rare and common species. The calculation of Diversity Hill metrics, including Shannon Entropy, utilized the iNEXT package (2016) in the R software (2018).

To examine changes in the composition of fish and invertebrates along the precipitation gradient, we applied Redundancy Analysis (RDA) to community data that had been transformed using the Hellinger method (Legendre and Gallagher 2001, Legendre and Legendre 2012). In this analysis, arrows were used to represent species and environmental variables, with each arrow's direction indicating the average trend from the origin to the values at each site within the ordination. For fish, vectors were considered significant if the associated p-value was <0.05, and for invertebrates, vectors were considered significant if the p-value was < 0.1, accounting for differences in sampling power. We conducted the ordination and vector fitting using the ‘rda’ and ‘envfit’ functions, respectively, available in the vegan package in R (Oksanen *et al.* 2013). Summary figures and tabulated statistics for fish and invertebrate community abundance, diversity, and composition are described in detail in appendices 3.13-3.20.

Stable Isotope Sampling

In May of 2019, we collected samples of primary producers (aquatic and terrestrial), fish, water, and kick-net invertebrates for stable isotope analysis. Periphyton were collected by scrubbing exposed rock surfaces with a plastic brush. The resulting slurry was taken to the lab, poured into drying tins before drying. Filamentous algae were collected from rocks vegetation and stream banks by hand. Debris was removed using tweezers prior to drying. Green leaves were collected from a variety of tree species within 10 meters of the wetted edge of the stream. Living blades of grass were collected from a variety of species along stream banks. We collected in-stream debris (detritus) including decaying leaves and wood by hand. We filtered 60mL of water through a 0.7µm membrane. Fish were collected using a Smith-Root LR-24 Backpack Electrofisher a single pass survey conducted until at least three individuals of each common taxa were acquired. Invertebrates were collected using a D-net in the same manner as the monthly surveys in 2018. Specimens were transported to the lab in coolers filled with ice. Vertebrate sampling was permitted by the Institutional Animal Care and Use Committee, Texas A&M University Corpus Christi (AUP# 05-17).

To avoid decomposition or sample contamination, stable isotope samples were kept frozen (except invertebrates) until they could be dried. To prepare samples for drying, excess fluid was poured off from periphyton and algal samples before placing them into trays. Keeping grass and trees separate, we sub-sampled several leaves into individual trays for drying. Fish samples were processed in two steps, first by removing fins, heads, internal organs, and skin before drying. After drying, skeletal muscle was extracted from the dried remains of fish with fork lengths greater than 30mm. Fish with fork lengths less than 30mm were ground whole (skeletal muscle and bone). We separated invertebrates from debris and sorted them by family into small cups, filled with filtered water, and placed them in the refrigerator overnight to purge their gut contents. We identified invertebrates to taxonomic family using taxonomic keys that were cross referenced with species observations recorded by the TCEQ's (Texas Commission on Environmental Quality) Surface Water Quality Monitoring Program (Cummins and Klug 1979, TCEQ (Texas Commission on Environmental Quality) 2019). Each sample (except frozen water) was dried in an oven at 55°C for 24 hours and ground into a homogeneous powder using a mortar and pestle.

For $\delta^{13}C$ and $\delta^{15}N$ analysis, sample powders were weighed and packed into 5x9mm tin capsules with the following target weights: animals (1.000mg) and plants (3.000mg). For $\delta^{2}H$ analysis, 0.400mg of sample powders were weighed into 4x3mm silver capsules. All samples were weighed using a microbalance (with readability up to 0.001mg). Packed capsules were placed in 96-well plates and shipped with frozen water samples to the Cornell Stable Isotope Laboratory to be analyzed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$ using a

Thermo DeltaV isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer (www.cobsil.com). Stable isotope signatures for each taxonomic group at each site are reported in appendices 3.10-3.12.

Prior to statistical analyses, δ^2H values were adjusted to compensate for environmental water contribution (17.3%) using the following equation (Solomon *et al.* 2009):

$$W_a = W_s - W_e * (1 - 0.827)^t$$

where W_a is the corrected δ^2H for assimilated solids, W_s is the original δ^2H value of the sample, W_e is the δ^2H value of the environmental water, and t is the trophic level of the sample. Primary producers were assigned a trophic level of 1, fish trophic levels were obtained from fishbase.com (based on gut-content analysis), and invertebrate trophic levels were assigned based on functional feeding group; level 2 was assigned to primary consumers and level 3 was assigned to predators. Cambaridae (crayfish) were removed prior to analyses because they contained an influential $\delta^{15}N$ signature and were unevenly sampled during stable isotopic collections; they were rare within the sites despite being widespread within the region.

Scatterplots of δ^2H vs $\delta^{13}C$ and δ^2H vs $\delta^{15}N$ were inspected visually to check the assumptions of Bayesian mixing models. δ^2H and $\delta^{13}C$ were useful tracers for source-partitioning models, but $\delta^{15}N$ was not. δ^2H provide more precise estimates because source separation was consistent across the gradient and community mixtures were within the boundaries of local sources (Dekar *et al.* 2012). History has shown that $\delta^{13}C$ source signatures can be indistinguishable which hinders source-partitioning estimates

(Finlay 2001). Here, $\delta^{13}C$ remained informative, but values for basal resources overlapped at Transition and Sub-Humid sites which made it harder to distinguish source signatures when running mixing models. Although $\delta^{15}N$ values can be used to estimate source partitioning, there was significant source overlap at multiple sites and some invertebrates at the Semi-Arid site exceeded the lower boundary of basal resource $\delta^{15}N$. We included scatterplots and summary statistics for $\delta^{2}H$ $\delta^{13}C$, and $\delta^{15}N$ samples in appendices 3.04 and 3.09 respectively.

The Bayesian mixing model, Stable Isotope Mixing Models in R (simmr) (Parnell *et al.* 2013), was used to quantify the contribution of autochthonous and allochthonous sources to stream animals. Filamentous algae and periphyton were pooled as ‘Aquatic Sources’, while green leaves and C-3 grasses were pooled as ‘Terrestrial Sources’. Mixing models were run on several scales of comparison including community, functional feeding group, and species (family for invertebrates). Species collected across the region include fish such as *Poecillia latipinna*, *Lepomis macrochirus*, *Lepomis gulosus*, and *Lepomis cyanellus*, as well as invertebrates from the taxonomic families Corbiculidae and Coenagrionidae. The 'simmr_mcmc' function in the simmr package was employed to derive individual source proportions for each comparison group in the model. The model underwent 10,000 iterations, with the initial 1,000 iterations from the burn-in period discarded. The resulting probability density function distributions determined the most likely source solutions for each comparison group. Statistical significance between sites was assessed with 95% credible intervals.

Isotopic trophic levels for fish and invertebrate communities were estimated using the formula:

$$L = \frac{N_s - (A * N_A) - (1 - A) * N_T}{f}$$

where L is the trophic level, N_s is the sample N, A is the percentage of autochthonous assimilation (ascertained from mixing models above), N_A is the mean $\delta^{15}N$ for aquatic sources, N_t is the mean $\delta^{15}N$ for terrestrial sources, and f is the trophic discrimination factor (here, 3.4‰) (Post 2002). Sample N values were calibrated to the local resources, so isotopic trophic levels represent the distance from local resources in steps of 3.4‰ $\delta^{15}N$. Comparisons between sites were carried out using bootstrap resampling. We estimated the mean and its 95% confidence intervals through 2000 iterations. The confidence intervals were derived using the normal approximation method, providing a robust assessment of the variability in the estimates.

Comparisons of community niche widths and area were conducted using Bayesian estimates of the standard ellipse area (SEA) in isotopic biplots and nearest neighbor distances (NND). Community niche width, represented by the SEA, provides a measure of the isotopic space occupied by a group of species within a community, while NND reflects the distance between different groups in isotopic space. For each community group, Bayesian bivariate normal distributions were fitted with 10,000 iterations, discarding the first 1,000, thinning 10 samples, and utilizing 2 chains. The resulting probability density function distributions identified the mean and 95% credible interval, offering insights into the overall niche characteristics. To further assess resource breadth (δ^2H range) and food chain length ($\delta^{15}N$ range), bootstrap estimates were generated with 2,000 iterations. Statistical significance was determined by comparing 95% credible intervals for these metrics between sites. All calculations were performed in R, employing the SIBER and 'boot' packages (Jackson *et al.* 2011, Canty and Ripley 2022).

3.4 Results

Exclosure Experiment

Moving from the Semi-Arid to Transition to Sub-Humid sites, the standing algal stock on tiles increased, and the exclosure effect on algae transitioned from negative to positive, as illustrated in Figure 3.2. Mean comparisons revealed that algal abundance on control plates was greatest in the Semi-Arid site (1.23 ± 0.52 ug/cm^2), intermediate at the Transition site (0.21 ± 0.11 ug/cm^2), and least in the Sub-Humid site (0.1 ± 0.03 ug/cm^2). At the Semi-Arid and Transition sites, fish exclosures positively affected mean algal stock (+125% and +85%, respectively), while exclosures reduced mean algal stock by -80% in the Sub-Humid site. Mean algal stocks inside the exclosures (2.78 ± 0.48 ug/cm^2) were significantly higher than controls (1.23 ± 0.52 ug/cm^2) at the Semi-Arid site, showed no significant difference between exclosures (0.4 ± 0.24 ug/cm^2) and controls (0.21 ± 0.11 ug/cm^2) at the Transition site, and were significantly lower in the exclosures (0.1 ± 0.03 ug/cm^2) compared to the controls (0.1 ± 0.03 ug/cm^2) at the Sub-Humid site.

During the exclosure experiment, sites with drier climates exhibited higher flow stability and nutrient concentrations. The Semi-Arid site had a moderate base flow (median discharge) of 35 l/s with low flooding (4%) and high NO_3^- (11.5 mg/l) and PO_4^- (2.3 mg/l) concentrations. The Transition site experienced higher base flow (59 l/s), more flooding (17%), and moderate NO_3^- (3.6 mg/l) and PO_4^- (1.8 mg/l) concentrations. In contrast, the Sub-Humid stream had the highest density of extremely low discharges. A histogram of daily discharges showed little evidence for a consistent 'base-flow' (median = 7 l/s), which was exceeded three-fold, 22% of the time. NO_3^- (0.2 mg/l) and PO_4^- (0.3 mg/l) concentrations were lowest at the Sub-Humid site. Canopy coverage was higher at the Transition and Sub-Humid sites compared to the Semi-Arid site, but the differences were very small (<6%).

Fish Community

RDA of fish communities constrained to 6 environmental predictors explained 51% and 19% of the variation along the first two primary axes of variation. Visually, the Semi-Arid site was separated horizontally along Axis-1 coincidentally with the only significant environmental vector of higher NO3- concentrations. In July, the Transition fish community resembled that of the Sub-Humid site but separated from the other sites vertically along Axis-2, which weakly coincided with benthic chlorophyll. Community compositions were distinct at either end of the precipitation gradient. Fish found throughout the study region included *P. latpinna*, *G. affinis* (Western Mosquitofish), *L. macrochirus*, *L. cyanellus* , and *L. gulosus*, but their proportions varied. The Semi-Arid site was dominated by the livebearer *P. latipinna* and had the greatest fish densities (1.1 ± 0.4 fish/m^2), approximately double that of the Transition or the Sub-Humid sites (*p*-values = 0.33, 0.1, respectively). Although mean comparisons were not significant, Shannon Wiener diversity was higher at Sub-Humid and Transition sites (4.8 and 4.6) compared to the Semi-Arid site (3.8). The wetter sites are dominated by larger centrarchids (sunfish and bass), including *L. macrochirus*, *L. megalotis*, *L. cyanellus*, and *Micropterus salmoides* (Largemouth Bass). The Transition site also contained mostly centrarchids, but uniquely contained *Cyprinella lutrensis* (Red Shiner) in May and June.

Invertebrate Community

Here, we describe the invertebrate kick-net communities during May through July 2018 to provide seasonal context for the stable isotope collections and results. RDA of kick-net invertebrate communities indicated Sub-Humid communities separated from the others along the horizontal axis, which coincided with the only significant environmental vector, conductivity. Semi-Arid invertebrate communities were similar to those of the Transition site in June, but in May and July varied widely along the vertical axis. Region-wide kick-net invertebrate families included Corbiculidae (clams) and Coenagrionidae (damselfly nymphs). The Sub-Humid community uniquely contained many Hyalellidae (amphipods), while Semi-Arid and Transition sites contained greater proportions of Chironomidae (non-biting midges), Melanoides (snails), and Rhagovelia (water striders). Statistical analysis revealed no significant differences in means; however, the Sub-humid site exhibited the highest invertebrate densities (1257 ± 1002 invertebrates/m^2) compared to the Semi-Arid (278 ± 66) and Transition (577 ± 137) communities. The Transition site (14.5) showed the highest mean Shannon diversity compared to Semi-Arid (5.7) and Sub-Humid (4.5) sites. The p-values for Transition vs. Semi-Arid (0.32) suggest no significant difference, while Transition vs. Sub-Humid (0.07) suggests a potential distinction with caution advised. Appendices contain complete details and statistical outputs for Spring community ordinations (3.13-3.16), abundance comparisons (3.19), and diversity comparisons (3.20-3.21).

Stable Isotopes

Exploring δ^{15}N x δ^{2}H biplots revealed shifts in community isotopic distribution from wide resource breadth and short food chain length at the Semi-Arid site to narrow resource breadth and tall food-chain length at the Sub-Humid site (Figure 3.3). Fish covered the full range of resource δ^{2}H values at the Semi-Arid site but only covered ranges of allochthonous signatures at the Transition and Sub-Humid sites. At the Semi-Arid site, invertebrate and fish signatures overlapped, and smaller poeciliids (*P. latipinna* and *G. affinis*) clustering near autochthonous source signatures separated from centrarchids (*Lepomis* and *Micropterus spp*.) and cichlids (*Herichthys cyanoguttatus*) near allochthonous source signatures, with larger fish having higher δ^{15}N. Patterns in size or species became difficult to generalize at the other sites where signatures clustered tightly along both axes within the Transition site but only along the δ^{2}H axis at the Sub-Humid site. Overall aquatic food-chain length appeared greatest at the Sub-Humid site, where there was a distinct hierarchy of δ^{15}N signatures incrementally from sources to invertebrates to fish. Within invertebrates, Corbiculiidae were narrowly clustered within each site, while gatherers and predatory taxa ranged widely. Invertebrate signatures at the Transition site appeared to resemble allochthonous resource signatures.

Autochthonous Assimilation Estimates

Mixing models using δ^{2}H and δ^{13}C indicated that in drier climates, fish incorporated a larger proportion of carbon fixed within the aquatic environment (Table 3.2). The pattern was visually apparent in Figure 3.4. Mean estimates of autochthonous assimilation for fish communities incrementally increased from Sub-Humid (5%; 1-10) to Transition (36%; 32-40) to Semi-Arid (75%; 65-87) sites. The pattern remained consistent at finer scales of comparison (species and feeding groups). *P. latipinna* (an opportunistic herbivore) autochthonous assimilation incrementally increased from Sub-Humid (18%; 3-49) to Transition (39%; 8-76) to Semi-Arid (80%; 61-96) (Table 3.2). Similarly, autochthonous assimilation increased within *L. cyanellus* (an insectivore/piscivore) from the Sub-Humid (18%; 3-45) to Transition (34%; 8-52) to Semi-Arid (62%; 22-92).

Invertebrate communities exhibited varying degrees of autochthonous assimilation (Figure 3.4B). Mean autochthonous assimilation for these communities was estimated to be relatively higher at the Semi-Arid site (57%; 38-73) compared to the Transition (28%; 20-35) and Sub-Humid (32%; 10-55) sites. In the case of invertebrate functional feeding groups, trends mirrored the overall community pattern, except for filterers, which displayed stepwise increases in aquatic source assimilation with decreasing precipitation (from 20% to 31% to 42%) (Figure 3.4B).

Linear regression indicates Isotopic trophic level related negatively with autochthonous assimilation within common fish species (R^2=0.89, $p < 0.001$), while invertebrates displayed no relationship (R^2=0.34, $p = 0.225$) (Figure 3.4).

Isotopic Trophic Levels

Overall, isotopic trophic levels demonstrated a stepwise increase from the Semi-Arid to Transition to Sub-Humid sites (Table 3.3). This trend was particularly pronounced in fish communities, with the trophic level being low at the Semi-Arid site (0.7; 0.5-0.9), intermediate at the Transition site (1.8; 1.6-2.0), and highest at the Sub-Humid site (2.1; 2.0-2.3). The consistency of this pattern held true at finer taxonomic levels (feeding group and species) across the gradient. For instance, *P. latipinna* exhibited a relatively low isotopic trophic level in the Semi-Arid site (0.4; 0.2-0.6), but higher values in the Transition (1.6; 1.1-2.1) and Sub-Humid sites (2.2; 1.9-2.7).

In invertebrate communities, mean isotopic trophic levels were lowest at the Semi-Arid site (0.2; 0.0-0.4) and relatively higher at both the Transition (1.8; 1.6-2.0) and Sub-Humid (2.1; 2.0-2.3) sites (Table 3.3). Examining finer taxonomic scales, predators reflected the community pattern with a relatively low estimate in the Semi-Arid site (0.3; 0.1-0.6) compared to the Transition (1.4; 1.0-1.8) and Sub-Humid (0.9; 0.5-1.3) sites. Filterers, exemplified by Corbiculidae, deviated from the overall community trend due to wide variation at the Transition site (0.4; 0.0-0.9), but estimates remained relatively low at the Semi-Arid site (0.0; 0.0-0.0) compared to the Sub-Humid site (0.8; 0.7-0.9). Conversely, gatherers displayed consistent isotopic trophic positions across sites.

Isotopic Community Niche Within fish, δ^2H x δ^{15}N standard ellipse area, an indicator of niche space, significantly increased from Sub-Humid to Semi-Arid sites (Figure 3.5). Observed differences in standard ellipse area were better explained by variation in δ^2H isotope ranges (indicative of resource breadth) than variation in δ^{15}N range (indicative of food chain length) (Table 3.4).

Within fish, the range in δ^2H (approximate resource breadth) was greatest at Semi-Arid (58) compared to Transition (43) and the Sub-Humid sites (41). The greatest niche width observed at the Semi-Arid site could be attributed to the herbivore, P. latipinna, which comprised 42% of the fish abundance and extended the niche width of the community by 57%. Similarly, at the Transition site, *C. lutrensis*, an opportunistic herbivore, comprised 35% of the fish abundance and extended the niche width of the community by 126%. The Sub-Humid fish community contained species capable of herbivory, such as P. latipinna, but lacked herbivorous H signatures.

Isotopic Community Niche

In fish, the δ^2H x δ^{15}N standard ellipse area, reflecting niche space, progressively expanded from Sub-Humid (43; 32-55) to Transition (57; 42-78) to Semi-Arid (88; 60-133) sites (Figure 3.5). Variations in standard ellipse area were more effectively accounted for by differences in δ^2H isotope ranges, indicative of resource breadth, rather than variations in δ^{15}N range, representing food chain length (Table 3.4).

Within fish, the range in δ^2H (approximate resource breadth) was greatest at Semi-Arid (58; 51-73) compared to Transition (43; 38-57) and the Sub-Humid sites (41; 33-60). The greatest niche width observed at the Semi-Arid site could be attributed to the herbivore, *P. latipinna*, which comprised 42% of the fish abundance (fish/m^2) and extended the niche width of the community by 57%. Similarly, at the Transition site, *C. lutrensis*, an opportunistic herbivore, comprised 35% of the fish abundance and extended the niche width of the community by 126%. The Sub-Humid fish community contained species capable of herbivory such as *P. latipinna* but lacked herbivorous δ^2H signatures. Unlike the drier sites, the Sub-Humid niche width was influenced by *L. macrochirus*, which extended the niche width 50% towards allochthonous resource signatures and comprised 15% of the total fish abundance. The influence of *L. macrochirus* at the Sub-Humid site was modest in comparison to the effects of *P. latipinna* or *C. lutrensis* on niche widths at the Transition and Semi-Arid sites.

δ^{15}N range (approximate food-chain length) decreased incrementally from wetter to drier sites but exerted little influence on δ^2H x δ^{15}N standard ellipse area among fish communities. Credible intervals overlapped among sites; δ^{15}N range was highest at the Sub-Humid site (11; 8-16), moderate at the Transition site (8; 8-10), and least at the Semi-Arid site (7; 6-9). A few piscivores, *Lepisosteus oculatus* (Spotted Gar) and *M. salmoides*, extended δ^{15}N ranges at the Semi-Arid (26%) and Transition (15%) sites, while abundant and omnivorous *L. macrochirus* were most influential at the Sub-Humid site (49%). High resource breadth at the Semi-Arid site and high food-chain length at the Sub-Humid helped sustain higher nearest-neighbor distances (5 and 4, respectively) compared to the Transition site (1).

Invertebrate δ^2H x $\delta^{15}N$ standard ellipse areas exhibited a slight increase, but the presence of large and overlapping confidence intervals suggests consistent community niche space across sites in the study region (Figure 3.5). While δ^2H and $\delta^{15}N$ ranges indicated higher resource breadth and lower food-chain length at the Sub-Humid site, it's important to note that the confidence intervals overlapped. Specifically, δ^2H range (approximate resource breadth) was greatest at the Sub-Humid site (70; 59-108) compared to Transition (61; 52-88) and Semi-Arid (54; 41-88) sites (Figure 3.5C). Additionally, Sub-Humid invertebrates exhibited the relatively low $\delta^{15}N$ range (5; 4-7) compared to Transition (10; 9-12) and Semi-Arid (12; 10-17) sites.

At the Semi-Arid site, Belostomatidae (a predator of herbivorous snails) extended the niche width 41% towards the autochthonous source signature and comprised less than 1% of kick-net invertebrates. At the Transition site, Thiaridae (an obligate grazer) extended the niche width 20% and comprised 3% of the kick-net invertebrates. Obligate grazers were rare at the Sub-Humid site, but Dytiscidae (a predacious diving beetle) and Corduliidae extended the niche width 24% and 17%, respectively, at the Sub-Humid site. Corduliidae (dragonfly midge) and Corydalidae (dobson fly midge) δ^2H signatures resembled allochthonous sources at all three sites. For each taxonomic group of fish and invertebrates, autochthonous assimilation estimates, isotopic trophic level, relative abundance, as well as range extension for δ^2H and $\delta^{15}N$ are reported in the appendices 3.08-3.09.

3.5 Discussion

As we explore the ramifications of aridity on trophic interactions, our study takes a detailed look at how climatic aridification fundamentally reshapes the structure and functioning of riverine food webs. The observed patterns in our exclosure experiment and community assessments provide valuable insights into the dynamics of riparian ecosystems along a rainfall gradient. Our findings suggest that aridity-induced changes in nutrient concentrations and hydrology contribute to enhanced autochthonous production, resulting in increased standing algal stocks, particularly in drier climates. Secondly, we note a shift in the impact of fish on algal standing stocks across the rainfall gradient. In arid sites, fish exert a positive influence by grazing on algae, while in more humid environments, their role transitions to controlling invertebrate grazers, reflecting a nuanced interaction shaped by precipitation levels. Thirdly, our stable isotope analysis indicates that in arid climates, both fish and invertebrates assimilate higher amounts of carbon ($\delta^{13}C$) and hydrogen (δ^2H) from autochthonous sources, underscoring the nutritional importance of algae in these conditions compared to detritus. Finally, our data supports the hypothesis that isotopic niche width (δ^2H range) and height ($\delta^{15}N$ range) positively correlate with aridity, suggesting that abundant algal sources in drier conditions support more generalized foraging habits across trophic levels. Subsequently, we delve into a detailed discussion of these results, placing them in the context of scientific literature, and elucidating their broader implications.

Beyond Canopy Influence: Unveiling Variables Driving Benthic Algae Standing Stocks

Our data suggests that enhanced algal production in arid climate is more likely related to nutrient concentrations and flow variability than canopy-driven variation in insolation. While increased precipitation leads to increased productivity and herbivory in terrestrial grassland systems (Chase *et al.* 2000, Ahlborn *et al.* 2021), we observed the opposite in perennial, sub-tropical streams. We expected arid-adapted riparian vegetation would have incomplete canopy coverage which would permit greater insolation driving increased algal productivity. During the summer experiment, minimal differences in canopy coverage were measured using spherical densiometers, suggesting consistent full canopies in arid riparian areas. However, limitations in mid-day visits and potential solar insolation variation throughout the diurnal cycle warrant integrated light meters for accuracy. The observed negligible effects in summer may not apply to other seasons or sites, necessitating consideration of semi-deciduous and arid-adapted trees' potential denser canopies, especially in winter. To improve measurements of incidental light reaching stream benthos, deploying light sensors above and within streams is recommended, providing a more rigorous assessment of insolation effects and addressing potential turbidity impacts.

Other variables besides riparian vegetation seem to be driving the differences in standing stocks of benthic algae. For instance, total algae coincided with high conductivity, NO_3^- and PO_4^- concentrations at the Semi-Arid and Transition sites compared to the Sub-Humid site. Nutrient concentrations and conductivity related negatively with annual precipitation and also best explained site separation in constrained ordinations. We reason that arid climate facilitates salinization and elevated nutrients by decreasing dilution of point sources of pollution (e.g. treated wastewaters) (Brooks *et al.* 2006), and disconnecting streams from catchment geochemistry (denitrification) during drought conditions (Mosley 2015). Nutrient loading promotes algal production, but it also might reduce grazing pressure by excluding herbivores (Ephemeroptera and Trichoptera) which are known to be sensitive to adverse water quality conditions such as hypoxia and salinization (Bonada and Resh 2013).

Consistent base flows and low variability at drier sites could promote higher total algae. During the experiment, flow variability was highest at the Sub-Humid site with major flooding in the first two weeks declining to imperceptible flows in the last week of deployment. In contrast, base flows remained stable at the Transition and Semi-Arid sites, likely due in part to consistent wastewater discharge in those watersheds. Additionally, no flooding occurred at the Semi-Arid site throughout deployment in contrast to the other sites. Periods of infrequent flooding at the Semi-Arid site reduce risk of scour and may contribute to stable, benthic algae growth (Biggs and Hickey 1994, Biggs *et al.* 1999). With only three sites to compare, our inferences connecting annual rainfall with observed algal patterns remain general. These results typify a hot and dry season and patterns in base flows or variability should change in wetter seasons. Thus, a more thorough evaluation of flow-algae effects should incorporate monthly assessments in each season.

Shift in Fish Diets: Unveiling Insectivory to Herbivory in Arid Climates

The exclosure effects and stable isotope data unveil a significant transition in fish diets from insectivory to herbivory in arid climates. This departure from established ecological norms challenges assumptions about the predominant insectivorous feeding behaviors of fish in response to changing environmental conditions. The chlorophyll concentrations within exclosures at the Sub-Humid site indicate a trophic cascade, suggesting the release of invertebrate grazers from predatory controls exerted by fish (Figure 3.4) (Blanchette *et al.* 2014). Surprisingly, autochthonous assimilation within invertebrates shows minimal changes, whereas arid fish communities, notably *P. latipinna* and *L. macrochirus*, display pronounced dietary shifts.

The decrease in isotopic trophic level ($\delta^{15}N$) suggests a simplification in the food web structure, indicating a potential reduction in the number of trophic levels between primary producers and fish. This reduction supports the hypothesis of increased fish grazing activity. The evidence is further emphasized by the divergent impacts of fish exclosures observed at the Sub-Humid and Semi-Arid sites, indicating the role of fish in shaping trophic interactions. The identified dietary shift towards herbivory aligns with comparable observations in intermittent rivers of northern Australia, where fish populations demonstrated an inclination towards herbivorous feeding strategies, predominantly relying on autochthonous resources (Blanchette *et al.* 2014).

As we transition from wetter to drier sites, the shift in community dominance from mostly carnivorous centrarchids to primarily herbivorous poeciliids is influenced by various factors, including adaptation to drought, variations in algal production, and reduced predatory controls. Despite the harsh physical conditions imposed by droughts, such as low dissolved oxygen, certain species like *P. latipinna* and *L. oculatus* demonstrate adaptive behaviors, such as air surface respiration and ingesting air into their swim bladder during hypoxic periods (Doudoroff and Shumway 1970). In arid streams, enhanced primary production, particularly by algae and biofilm, provides a valuable source of nutrition, supporting remarkable secondary production (Mantel *et al.* 2004, Kieckbusch *et al.* 2004, Lau *et al.* 2009). While harsh environments may offer poeciliids refuge from many predators, significant predatory controls can persist even in challenging conditions. The availability of highly digestible and nutritious algae and biofilm, in contrast to detritus, may contribute to the ability of poeciliids to establish sizable populations, ensuring safety in numbers through schooling (Seghers 1974). Additional reductions in top-down predatory controls may result from the spatial restriction of gar to deeper pools during low flows (Schiller *et al.* 2011). In presenting evidence for aridity-facilitated fish herbivory, our study underscores the need for further analysis, particularly in estimating biomass and production, as well as conducting gut-content analyses (Doudoroff and Shumway 1970), to better understand the intricate dynamics of predatory controls in these ecosystems.

Opportunistic Grazing and Niche Space: Insights into Fish Community Dynamics in Arid Streams

The broader resource breadth observed in less diverse fish communities at drier sites challenges conventional theories of inter-species co-existence, particularly in the context of arid environments. Traditionally, prevailing assumptions suggested that greater resource variety and availability would promote higher species richness, with a broader utilization of resources by different species (Sánchez González *et al.* 2023). Contrary to these expectations, we anticipated a negative relationship between resource breadth and aridity, considering the perceived loss of allochthonous inputs and the historically observed low species richness in arid streams (Mosley 2015, Kinard *et al.* 2021).

Surprisingly, our findings in fish communities suggest that species with more generalist diets can adapt to changes in resource availability, leading to an expansion of community niche space. For instance, the exceptional opportunistic grazing behavior of *P. latipinna* played a pivotal role in broadening resource breadth at the Semi-Arid site. In small streams, where body size may limit herbivory, small-bodied fish like *P. latipinna* can access additional algal resources in shallow stream edges. This adaptive opportunistic grazing strategy was superior to that of other species, significantly influencing the expansion of isotopic niche space in a more arid climate. These results align with findings from other studies, emphasizing that omnivory provides adaptive advantages in coping with the boom-and-bust production cycles typical of arid lotic systems (Pusey *et al.* 2010, Blanchette *et al.* 2014).

Unfortunately, our data were insufficient to follow up on this unexpected result with intra-species ellipse or convex hull area comparisons (e.g., Sánchez González *et al.* (2023)). Ideally, we would weight community isotopic metrics with abundance surveys, but mixing models necessitated aggregating fish and invertebrate species into functional groups. So future sampling efforts are advised to intensify within-site stable isotope collections (n=10 per species) (Jackson *et al.* 2011). Also, stable isotope collections from sandy streams should supplement kick-nets with benthic cores to include invertebrates living in sediments, such as herbivorous chironomids (non-biting midges) which constitute a large proportion secondary production in sandy-bottom coastal plain streams (Benke *et al.* 1985).

Ongoing Research and Implications of Climate-Induced Changes in Freshwater Ecosystems

Climate-induced shifts in precipitation patterns profoundly impact flowing waters, altering the structure and function of freshwater food webs. Our study reveals that aridity enhances autochthonous production, increases herbivory, shortens food chain length, and prompts adaptation to boom-and-bust production cycles. This insight holds significance for ecologists, unraveling the complex environmental mechanisms governing food web dynamics. Species well-adapted to arid climates exhibit resilience in harsh conditions and exploit variable resources (Bonada *et al.*, 2007; Díaz *et al.*, 2008). Unlike detrital food webs, our observations suggest that algal resources quickly reappear after scouring floods, supporting rapid recolonization by arid-adapted taxa. Dominant species in arid communities display specialization, characterized by traits such as hypoxia tolerance, enhanced dispersal, and rapid reproduction, facilitating quick responses to the feast or famine conditions induced by droughts and flash floods (Bonada *et al.*, 2007; Díaz *et al.*, 2008; Fisher *et al.*, 1982).

Comparatively, our study highlights heightened allochthonous dependency in wetter climates, reflecting more consistent but less nutritious catchment inputs. This might render these systems slower to recover from catastrophic floods, as detrital food webs and secondary production integrate more gradually (Flecker *et al.*, 2002; Lau *et al.*, 2009; Neres-Lima *et al.*, 2016). Importantly, our findings suggest that future aridification is likely to drive comparable changes in stream food web structure and function. Moreover, the strength and dynamics of predation and herbivory, particularly in response to changing precipitation patterns, represent intriguing areas for further exploration. These predictions shed light on the seasonal nuances of ecological shifts, contemplating how humid communities might adapt to arid-like conditions after prolonged dry spells. Our inferences, though, are constrained to the hot and dry season, emphasizing the need for ongoing research to comprehend the full spectrum of seasonal variations and the broader implications of climate-induced alterations on freshwater ecosystems.

Concluding Remarks

In deciphering the intricate impacts of aridity on trophic interactions within riverine ecosystems, our study not only unveils the underlying dynamics but also highlights the adaptability of freshwater communities in the face of changing climates. The shift in predator-prey dynamics—from insectivory to herbivory among fish in drier climates—challenges established ecological norms. The revelation that fish communities in less diverse, drier sites exhibit a greater resource breadth adds complexity to our understanding, defying traditional expectations and emphasizing the nuanced nature of ecological responses.

Moving beyond immediate implications, our findings suggest a narrative of opportunistic grazing by fish, challenging the conventional understanding of bottom-up cascades through invertebrates in arid conditions. The isotopic trophic levels, indicating shorter food chains in drier climates, provide a glimpse into altered community dynamics influenced by aridity. As we contemplate these intricate shifts, our study becomes a poignant snapshot of ecosystems adapting to the relentless forces of climate change. Nature's adaptive intricacies defy conventional expectations, highlighting the resilience of species well-adapted to arid conditions.

In a broader context, this study stands as a testament to the adaptability of freshwater ecosystems amidst changing climates. As Aldo Leopold stated, 'A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community.' The processes unveiled in this study exemplify nature’s resilient response to aridity, reflecting the intricate interplay between species and their environments in the face of climate change. Understanding and appreciating these 'right' processes observed in natural systems offer valuable insights into the resilience of ecosystems, inspiring a deeper connection with the wisdom ingrained in the natural world.

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3.7 Tables

E.Variable	Units	Semi-Arid	Transition	Sub-Humid
Site Name	NA	San Fernando Creek	Aransas River	Garcitas Creek
Latitude	DD	27.773	28.283	28.891
Longitude	DD	-98.034	-97.621	-96.819
Rainfall	cm/yr	56.67	68.53	84.25
Temperature	°C	22.22	21.55	21.21
Elevation	m	62	47	20
Discharge	cfs	144. ± 83.1	89.2 ± 50.2	30.9 ± 17.8
Measurements	NA	9	9	9
Canopy	%	0.87 ± 0.03	0.89 ± 0.01	0.94 ± 0.01
Algae	µg/cm^2	0.60 ± 0.10	2.23 ± 0.39	1.44 ± 0.49
Channel Width	m	2.83 ± 0.13	3.28 ± 0.22	6.33 ± 0.60
Depth Max	m	0.32 ± 0.05	0.17 ± 0.01	0.27 ± 0.03
Conductivity	µcm/S	1165 ± 91.7	1546 ± 40.0	517. ± 41.3
Nitrate	mg/L	11.9 ± 0.63	4.51 ± 0.34	0.20 ± 0.06
Phosphate	mg/L	2.20 ± 0.05	2.12 ± 0.14	0.18 ± 0.04

Table 3.1 Site Characteristics

Sampling location environmental characteristics (E.variables). Annual rainfall, annual average temperature and elevation were obtained from the USGS Gages-ii database. In-situ measurements represent the seasonal mean ± the standard error; three measurements were taken every 25 meters within each stream, May-July of 2018, for a total of nine samples.

Group	Semi-Arid	Transition	Sub-Humid
Fish	75 (65:87)**	36 (32:40)**	5 (1:10)**
F-Herbivore	80 (60:96)*	39 (8:77)	18 (3:51)*
P.latipinna	80 (61:96)*	39 (8:76)	18 (3:49)*
F-Invertivore	61 (44:77)**	36 (30:42)**	5 (1:11)**
L.macrochirus	61 (25:91)*	36 (16:52)	8 (1:19)*
F-Piscivore	70 (42:92)*	34 (22:42)*	10 (2:21)**
L.cyanellus	62 (22:92)	33 (8:52)	18 (3:45)
L.gulosus	62 (28:92)	35 (8:67)	12 (2:33)
Invertebrate	57 (38:73)*	28 (20:35)*	32 (10:55)
I-Filterer	42 (13:73)	31 (10:50)	20 (4:51)
Corbiculidae	41 (13:73)	30 (6:57)	20 (4:48)
I-Gatherer	46 (6:92)	27 (11:42)	46 (10:85)
I-Predator	62 (30:86)	22 (8:32)	41 (7:85)
Coenagrionidae	47 (6:91)	25 (6:50)	30 (4:74)
I-Herbivore	55 (17:91)	60 (33:91)	NA

Table 3.2: Autochthonous Assimilation

Autochthonous Source assimilation (%) in fish and invertebrate communities, functional feeding groups, and common taxa at Semi-Arid, Transition, and Sub-Humid sites. Values reflect the high density mode and associated 95% credible interval with asterisks indicating the number of non-overlapping intervals between sites. Autochthonous source assimilation is estimated using $\delta^{13}\mathrm{C}$ and $\delta^{2}\mathrm{H}$ in Bayesian mixing models for each level of comparison (community, feeding group, species/family), calibrated to local aquatic and terrestrial source signatures.

Group	Semi-Arid	Transition	Sub-Humid
Fish	0.7 (0.5, 0.9)**	1.8 (1.6, 2.0)**	2.1 (2.0, 2.3)**
F-Herbivore	0.4 (0.2, 0.6)**	1.6 (1.1, 2.1)*	2.2 (1.8, 2.7)*
P.latipinna	0.4 (0.2, 0.6)**	1.6 (1.1, 2.1)*	2.2 (1.9, 2.7)*
F-Invertivore	0.7 (0.5, 1.0)**	1.7 (1.5, 1.9)*	2.1 (1.9, 2.3)*
L.macrochirus	0.7 (0.2, 1.1)**	1.3 (1.1, 1.6)**	2.6 (2.0, 3.2)**
F-Piscivore	1.1 (0.5, 1.6)*	1.9 (1.5, 2.3)	2.1 (1.9, 2.3)*
L.cyanellus	0.7 (0.2, 1.2)*	1.1 (1.0, 1.3)*	2.2 (2.0, 2.4)**
L.gulosus	0.7 (0.1, 1.3)**	1.8 (1.7, 1.9)*	1.9 (1.9, 2.0)*
Invertebrate	0.2 (0.0, 0.4)**	1.2 (0.9, 1.4)*	0.9 (0.6, 1.2)*
I-Filterer	0.0 (0.0, 0.0)*	0.4 (0.0, 0.9)	0.8 (0.7, 0.9)*
Corbiculidae	0.0 (0.0, 0.0)*	0.2 (-0.1, 0.6)*	0.8 (0.7, 0.9)**
I-Predator	0.3 (0.1, 0.6)*	1.4 (1.0, 1.8)*	0.9 (0.5, 1.3)

Table 3.3: Isotopic Trophic Level

Isotopic trophic levels for fish and invertebrate communities as well as functional feeding groups. Each row contains the group of comparison, the mean $\pm$ the standard deviation, the sample size (in parentheses) as well as the statistical significance denoted by asterisks (whether 95% credible intervals overlap between sites). Sample $\delta^{15}\mathrm{N}$ values were calibrated to the local resources, so isotopic trophic levels represent the distance from local resources in steps of 3.4‰ $\delta^{15}\mathrm{N}$.

Guild	Estimate	Unit	Semi-Arid	Transition	Sub-Humid
Fish	C-Range	‰	4 (4, 5)	4 (4, 5)	6 (5, 7)
Fish	Ellipse Area	‰²	88 (60, 133)*	57 (42, 78)	43 (32, 55)*
Fish	H-Range	‰	58 (51, 73)	43 (38, 57)	41 (33, 60)
Fish	N-Range	‰	7 (6, 9)	8 (8, 10)	11 (8, 16)
Fish	Neighbor Distance	‰	5 (4, 6)**	1 (0, 2)**	4 (3, 4)*
Invertebrate	C-Range	‰	6 (5, 7)*	6 (5, 8)*	13 (10, 20)**
Invertebrate	Ellipse Area	‰²	101 (57, 165)	97 (61, 146)	92 (44, 173)
Invertebrate	H-Range	‰	54 (41, 88)	61 (52, 88)	70 (59, 108)
Invertebrate	N-Range	‰	12 (10, 17)*	10 (9, 12)*	5 (4, 7)**
Invertebrate	Neighbor Distance	‰	4 (3, 5)*	1 (0, 2)**	19 (17, 20)**

Table 3.4: Niche Estimates

Bayesian estimates for the $\delta^{2}\mathrm{H}$ x $\delta^{15}\mathrm{N}$ standard ellipse area and nearest-neighbor distance, as well as boostrapped estimates of $\delta^{2}\mathrm{H}$ range and $\delta^{15}\mathrm{N}$ range for fish and invertebrate communities. Summary statistics represent the mean and the associated 95% credible interval. Asterisks represent whether one or more pairs of sites have non-overlapping credible intervals.

3.8 Figures

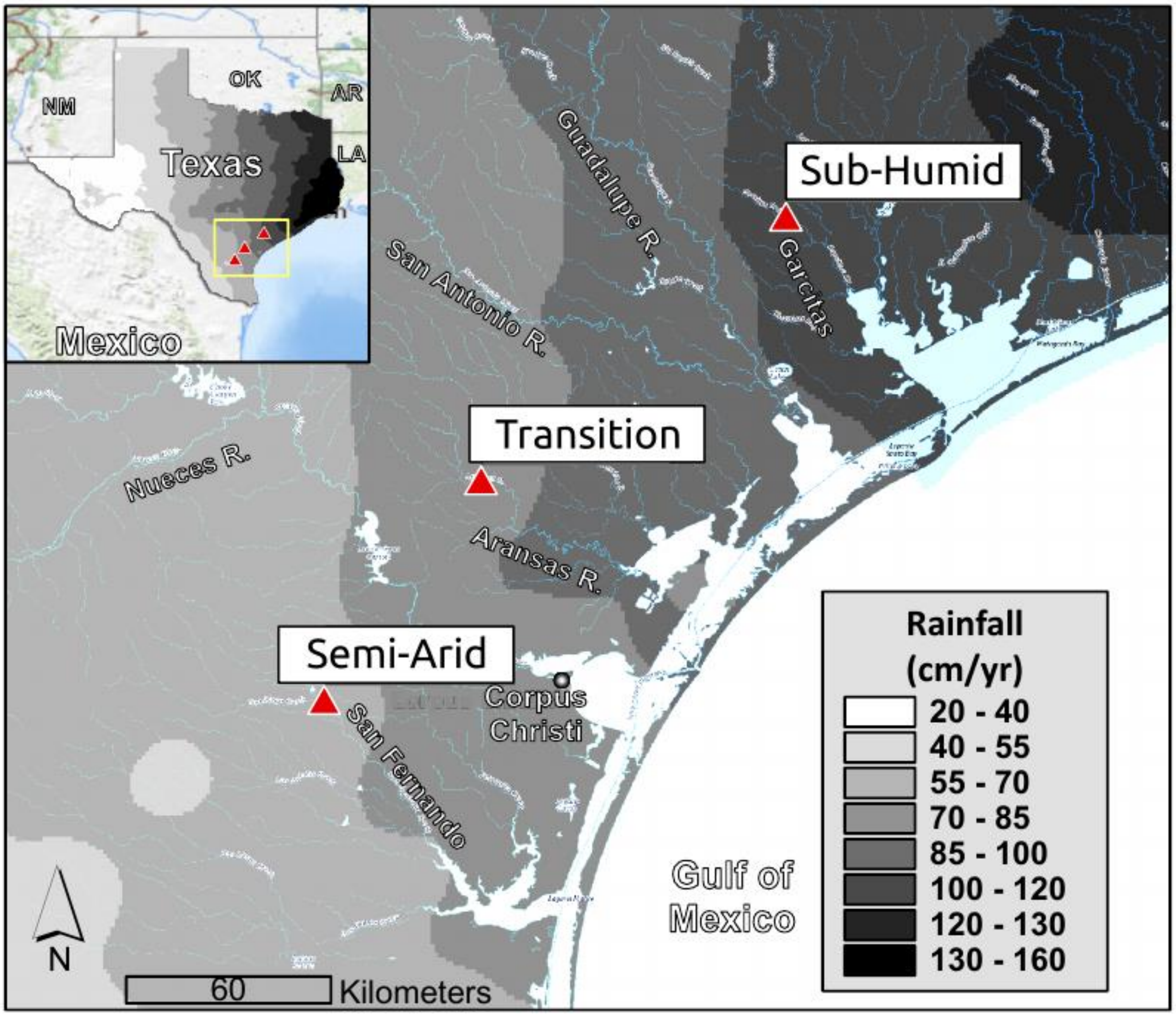


Figure 3.1: Site Map

Locations (red triangles) where stable isotope samples were collected and algal exclosure experiments were conducted. These wadeable USGS gauged streams span a natural precipitation gradient (shading overlay indicates increasing precipitation) in coastal plain of South-Central Texas, USA. Sites include San Fernando, Aransas River and Garcitas Creek and are labeled according to their precipitation regime (Semi-Arid, Transition, and Sub-Humid respectively).

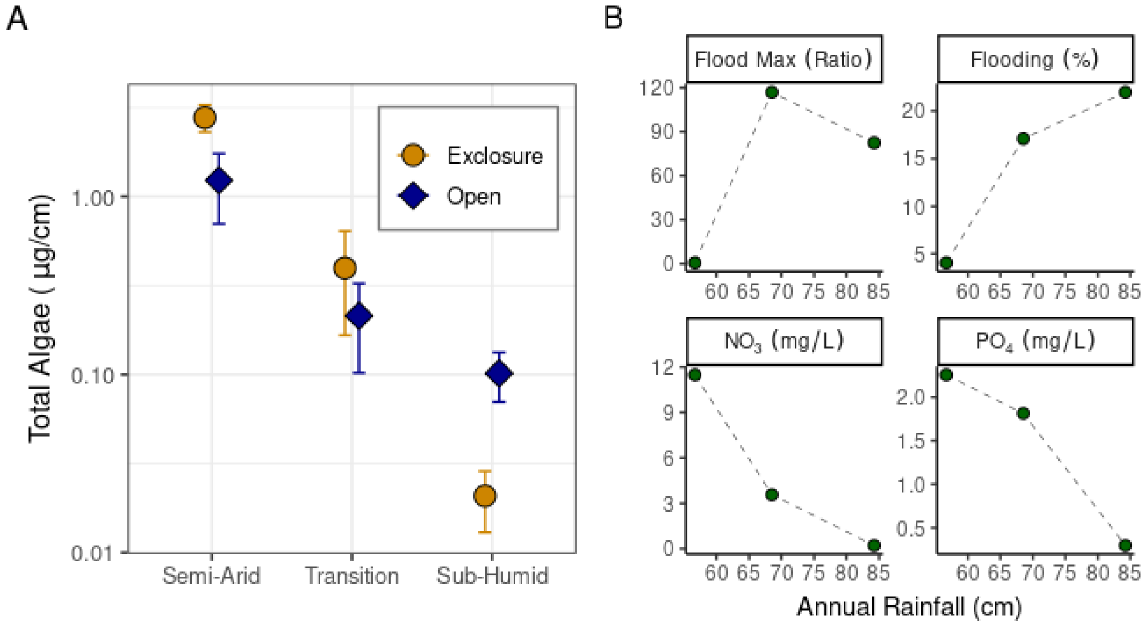


Figure 3.2: Exclosure

(A) Total algae abundance on ceramic growth plates at 3 sites differentiated by annual rainfall (vertical axis is logarithmic). Experimental groups are separated by color (light = fish excluded, dark = fish accessible). Points represent bootstrap mean estimates with 95% confidence intervals. The vertical axis is log transformed to enhance visual comparisons. **(B)** Predictors of total algae include maximum flood strength ((max-base)/base), proportion of flows over three times median average daily discharge, NO_3^-, and PO_4^- concentration at Semi-Arid (55 cm/yr), Transition (70 cm/yr), and Sub-Humid (85 cm/yr) sites.

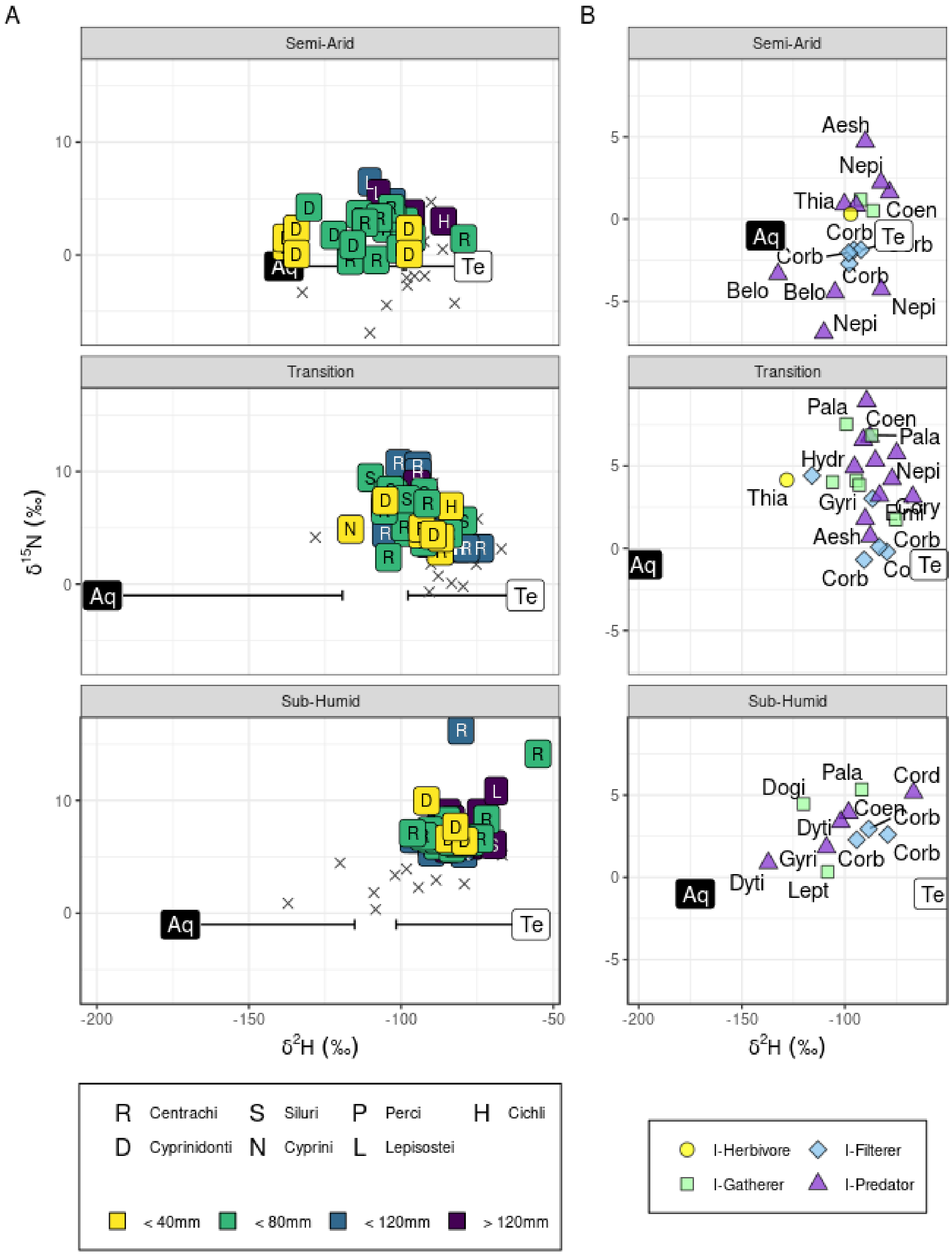

A
B
Semi-Arid
Transition
Sub-Humid
δ15N (‰)
δ2H (‰)
-200
-150
-100
-50
10
0
5
-5
Aq
Te
Aesh
Nepi
Thia
Coen
Corb
Belo
Pala
Hydr
Gyri
Cory
Dogi
Dyti
Lept
Cord
R Centrachi
S Siluri
P Perci
H Cichli
D Cyprinidonti
N Cyprini
L Lepisostei
< 40mm
< 80mm
< 120mm
> 120mm
I-Herbivore
I-Filterer
I-Gatherer
I-Predator

Figure 3.3: Isotope Scatterplot

σ^{15}N versus σ^{2}H of **(A)** Fish, darkening with size and labeled by taxonomic order with invertebrates (grey x) and **(B)** invertebrates, shaped/colored by functional feeding group and labeled by abbreviated taxonomic family. σ^{15}N values are relative to local resource σ^{15}N values and σ^{2}H values are corrected for environmental water contribution. Aquatic (Aq) and terrestrial (Te) source σ^{2}H ranges are plotted at σ^{15}N=0. Semi-Arid fish signatures separate by size group and are spread across a wide range of σ^{2}H which contrasts with highly overlapping signatures within other fish communities within narrow σ^{2}H but stretch vertically in σ^{15}N signatures. Low numbers of recovered samples at the Sub-Humid site (11 compared to 16 and 23) may contribute to low nearest neighbor distances as well as underestimates of σ^{15}N and σ^{2}H ranges. Despite the low sample count, Sub-Humid invertebrates spread widely across σ^{2}H values. Invertebrates at the Semi-Arid site have the lowest σ^{15}N average but variability within predators also produces a high range in σ^{15}N signatures. Corbiculidae cluster tightly and paralellel shifts in σ^{15}N and σ^{2}H signatures from Sub-Humid to Semi-Arid consistent with increases autochthonous assimilation. Predators (including Coenagrionaidae) show similar shifts, albeit with fewer samples., Unexpectedly, only one obligate grazer (Thiaridae) was collected from Semi-Arid and Transition sites, hindering total food-web reconstruction and subsequent community analyses.

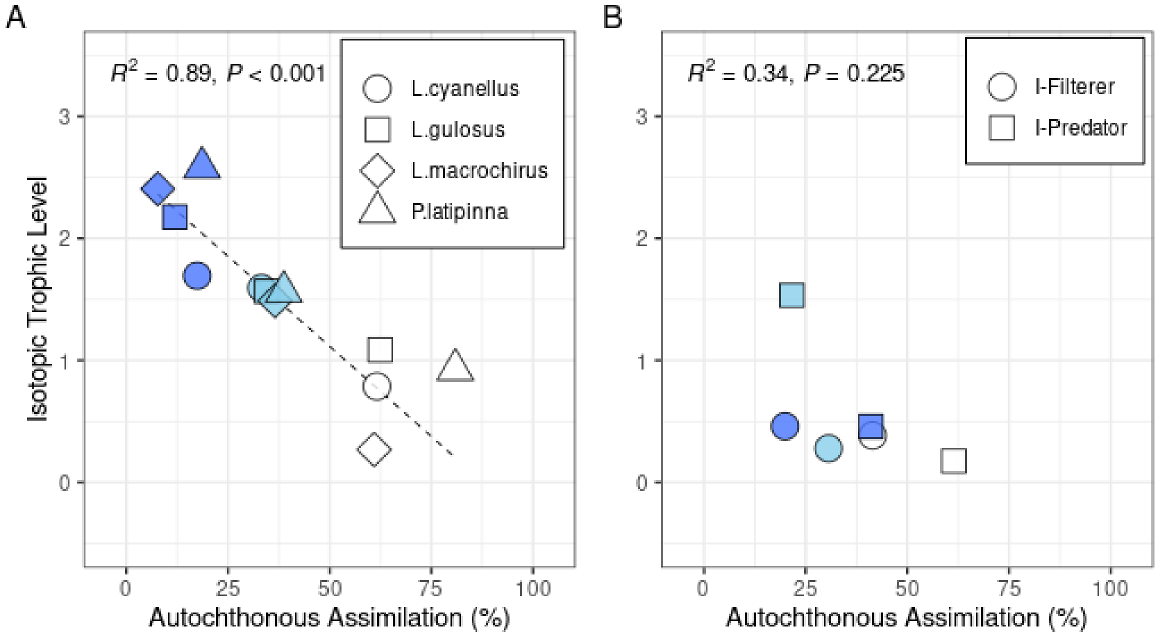


Figure 3.4: Autochthonous Assimilation & Isotopic Trophic Level

Isotopic trophic level (estimated using δ^{15}N) plotted against aquatic assimilation (estimated using δ^{13}C and δ^{2}H) for common **(A)** fish species and **(B)** invertebrate feeding groups. Scatter plot points are shaped according to their taxonomic group and colored by site (darkening with annual rainfall). Comparisons within fish display a strong negative relationship between isotopic trophic level and autochthonous resource assimilation which coincides with increasing aridity.

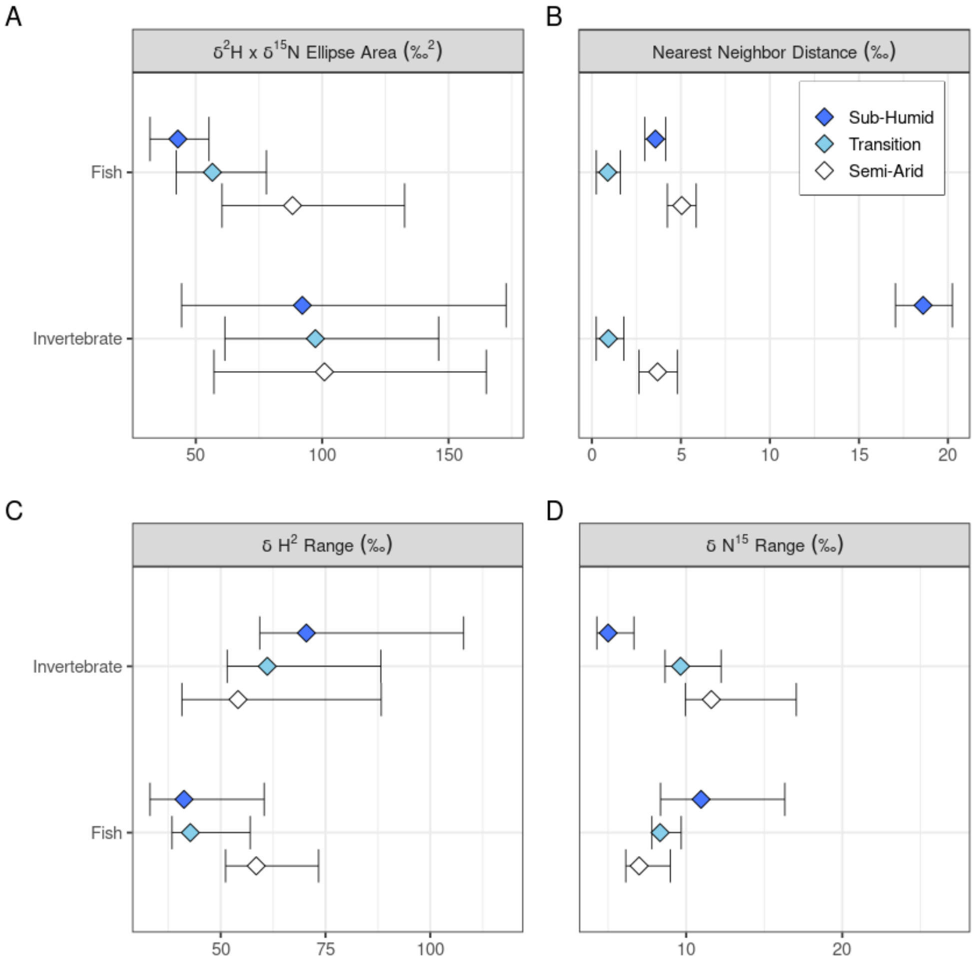


Figure 3.5: Niche Estimates

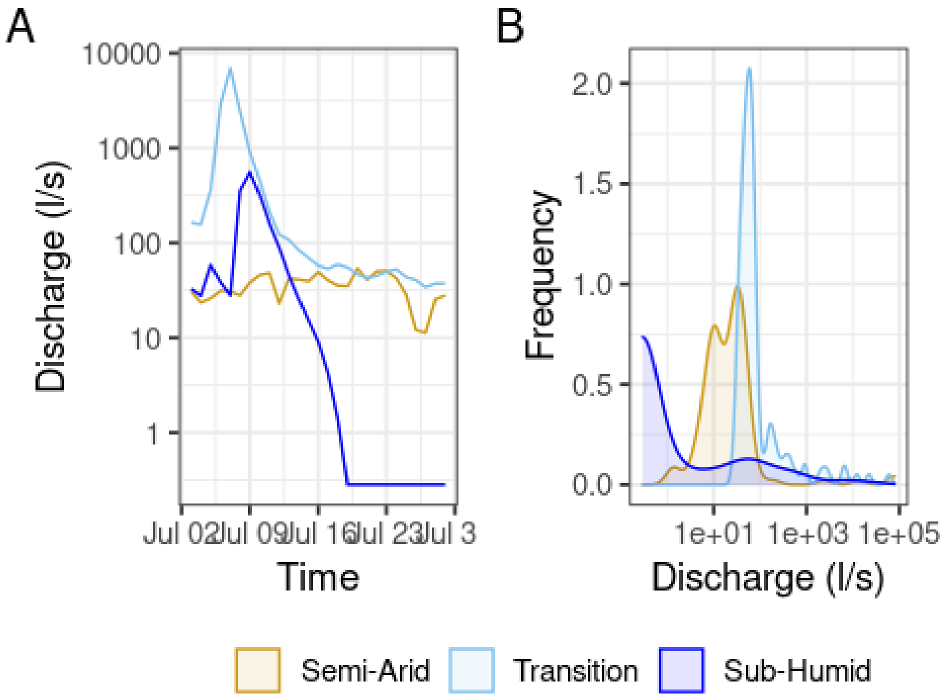
(A) Bayesian estimates δ^{15}N x δ^2H standard ellipse area (community niche space) and **(B)** nearest neighbor distances (niche separation). Bootstrapped estimates of **(C)** δ^2H range (resource breadth) and **(D)** δ^{15}N range (food-chain length) within fish and invertebrate communities. Diamonds represent mean values, colored by site (darkening with annual rainfall), and the bars extend to the associated 95% confidence interval. fish community niche space increases with aridity because increases in resource breadth are larger than reductions in food chain length. Niche spacing is least among fish at the Transition site despite a moderate available niche space. For invertebrates, community niche spaces are indistinguishable because decreases in resource breadth oppose increases in food-chain length.

3.9 Appendix

Site	Treatment	Algae	CI.95	Site.Sig	Treatment.Sig
Semi-Arid	Exclosure	2.78	(2.30, 3.26)	**	*
Transition	Exclosure	0.40	(0.17, 0.64)	**	
Sub-Humid	Exclosure	0.02	(0.01, 0.03)	**	*
Semi-Arid	Open	1.23	(0.70, 1.74)	**	*
Transition	Open	0.21	(0.10, 0.32)	*	
Sub-Humid	Open	0.10	(0.07, 0.13)	*	*

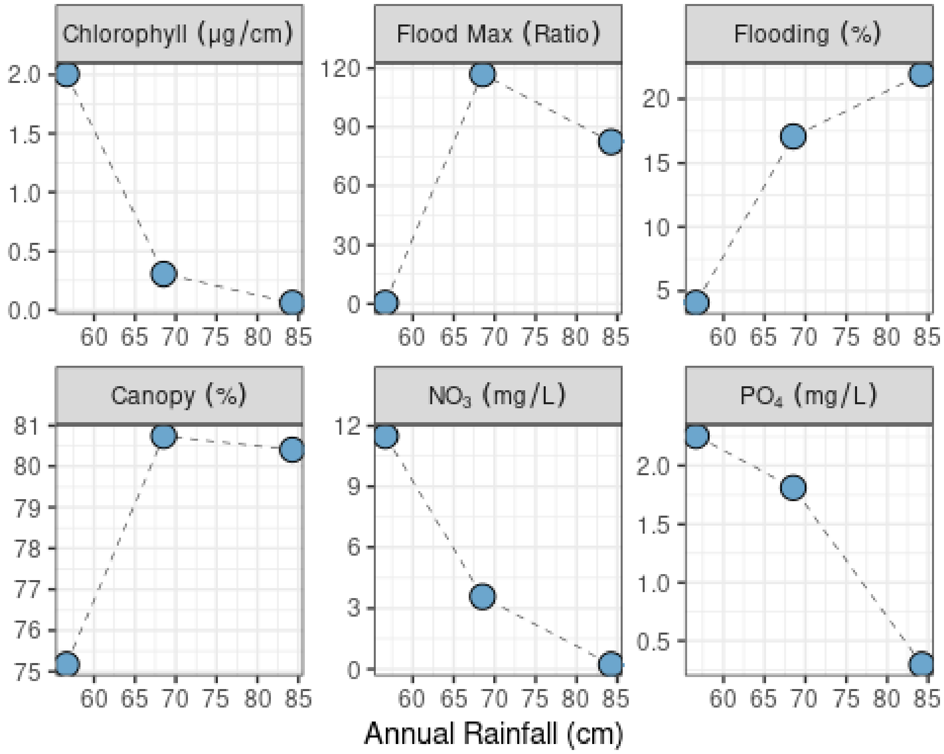
Appendix 3.01: Exclosure Algae Comparison Table

Bootstrap mean and 95% confidence intervals of site and exclosure effects on total algae abundance on ceramic plates measured by irradiance. Stars denote significant differences between a pair of sites (Sit.Sig) or treatments (Tre.Sig).



Appendix 3.02: Exclosure Discharge Summary

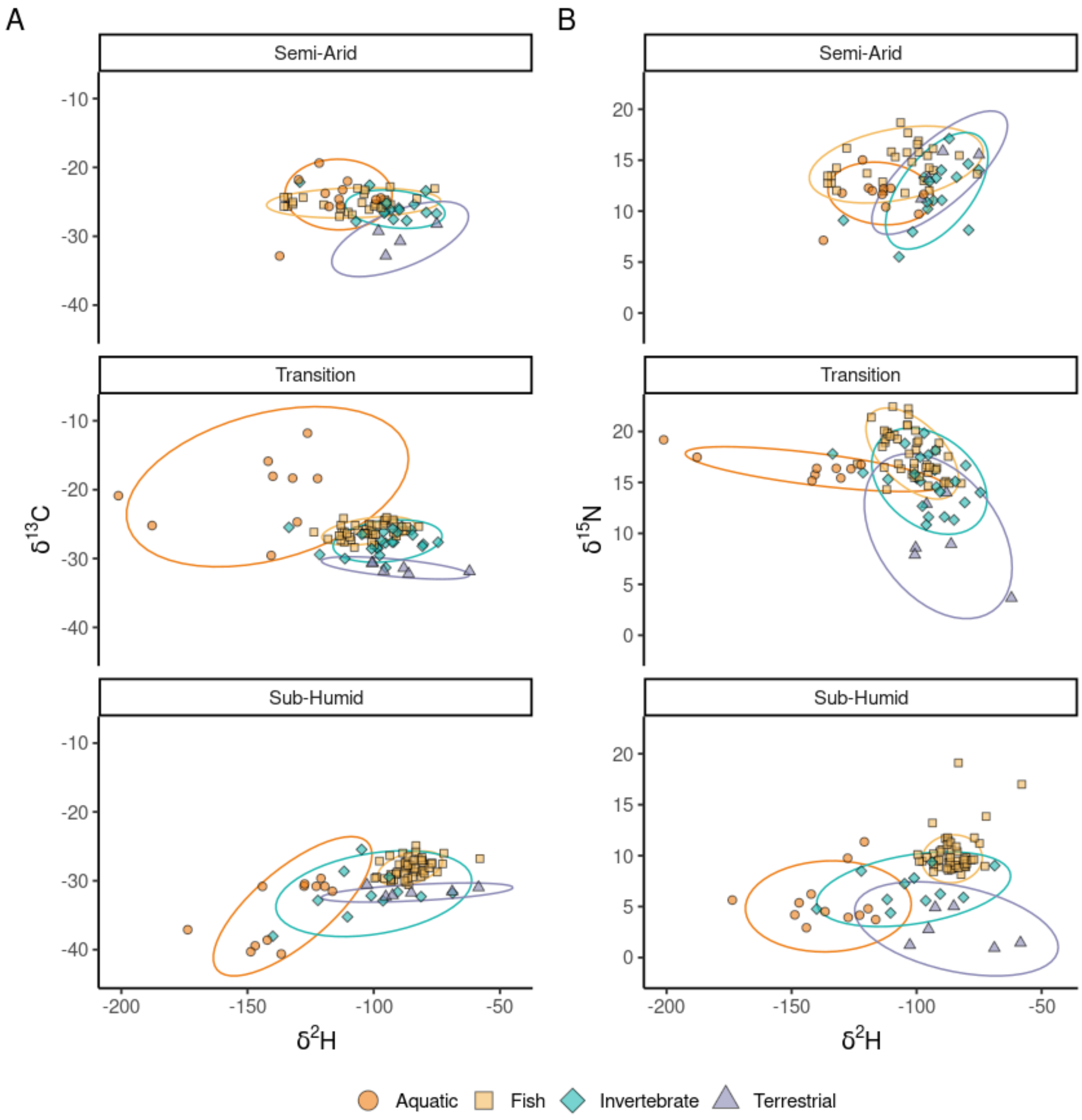
(A) Time series and (B) histogram of average daily discharge (l/s) during 2018 exclosure deployment at Semi-Arid (gold), Transition (light blue), and Sub-Humid sites (dark blue). Flows were stable at the Semi-Arid site. The Transition site experienced a large flood in the first week of deployment, but flows were stable thereafter. The Sub-Humid site experienced a small flood in the second week of deployment and then flows stagnated at ~0 l/s for the last 2 weeks of deployment.



Appendix 3.03: Exclosure Predictor Summary

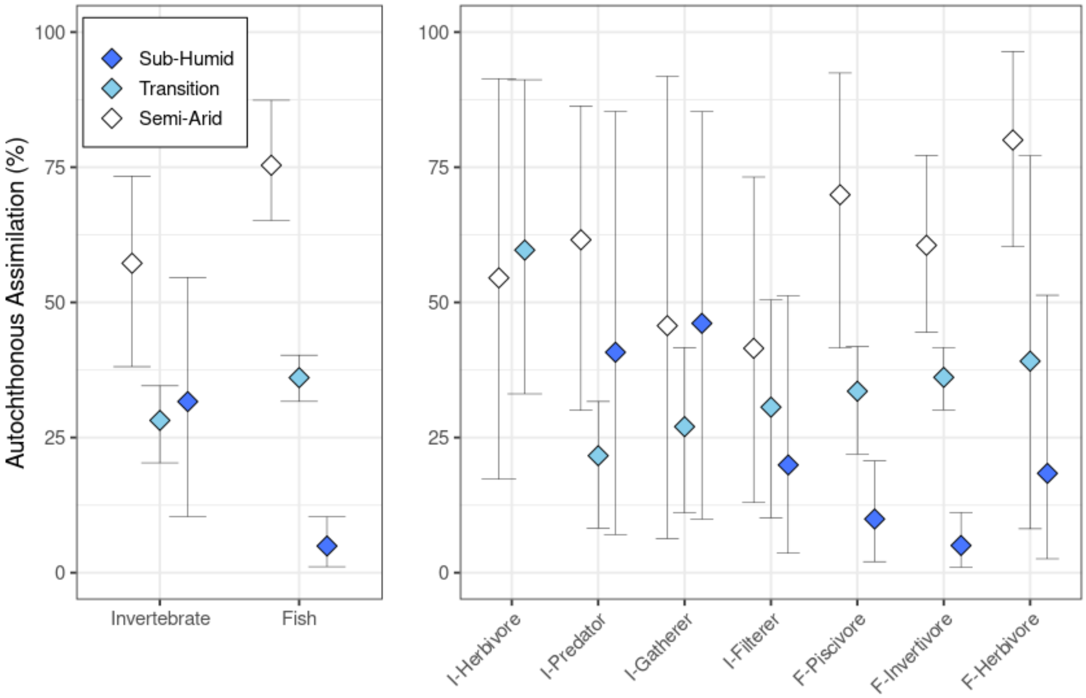
Total Chlorophyll on tiles after 30-day deployment, maximum flood strength ((max-base)/base), proportion of flows over three times median average daily discharge, canopy coverage, nitrate concentration, and ortho-phosphate concentration at Semi-Arid (55 cm/yr), Transition (70 cm/yr), and Sub-Humid (85 cm/yr) sites.

Variable	Units	Semi-Arid	Transition	Sub-Humid
Chl α	µg/cm	2.0	0.3	0.1
Rain	cm/yr	56.7	68.5	84.3
Canopy	%	75.2	80.7	80.4
NO3-	mg/l	11.5	3.6	0.2
PO4-	mg/l	2.3	1.8	0.3
Q Median	l/s	35.4	58.6	6.7
Q SD	l/s	11.1	1426.2	131.9
Q Max	l/s	0.5	116.9	82.4
Flood	%	4.1	17.1	22.0



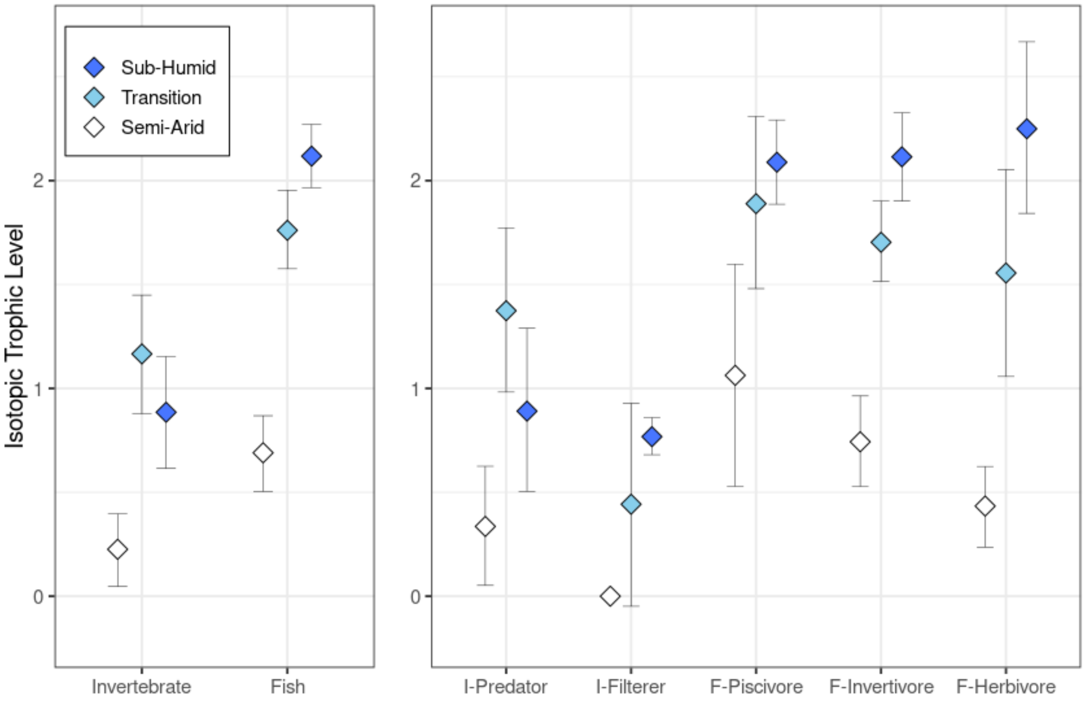
Appendix 3.04: Isotope Scatterplots

(A) δ^{13}C () or (B) δ^{15}N () versus δ^{2}H () scatter plots of aquatic (grey circles) and terrestrial (white squares) sources, as well as invertebrates (blue diamonds) and fish (pink triangles). Samples were collected from Semi-Arid, Transition, and Sub-Humid sites. Dotted lines encompass the area as an ellipse, containing 95% of the estimated t-distribution for each group.



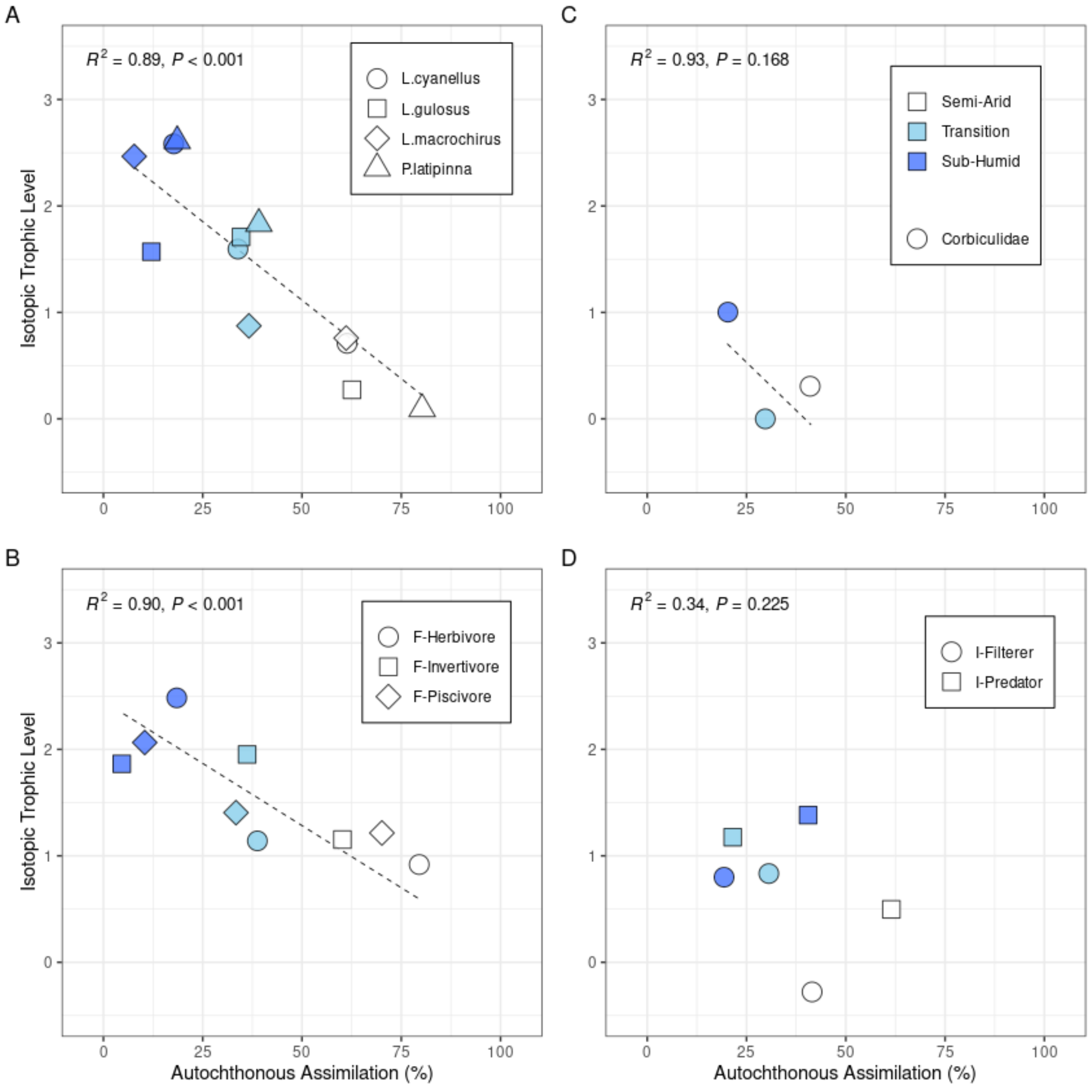
Appendix 3.05: Autochthonous Assmiliation Figure

Estimated assimilation of autochthonous (aquatic source) in fish and Invertebrate communities as well as functional feeding groups within Semi-Arid, Transition, and Sub-Humid streams. Diamonds represent mean values and are colored according to sample site (darkening with increased precipitation) with bars extending to the 95% credible interval. Autochthonous assimilation is estimated using δ^{13}C and δ^{2}H in a Bayesian mixing model for each group of comparison and calibrated to local source signatures.



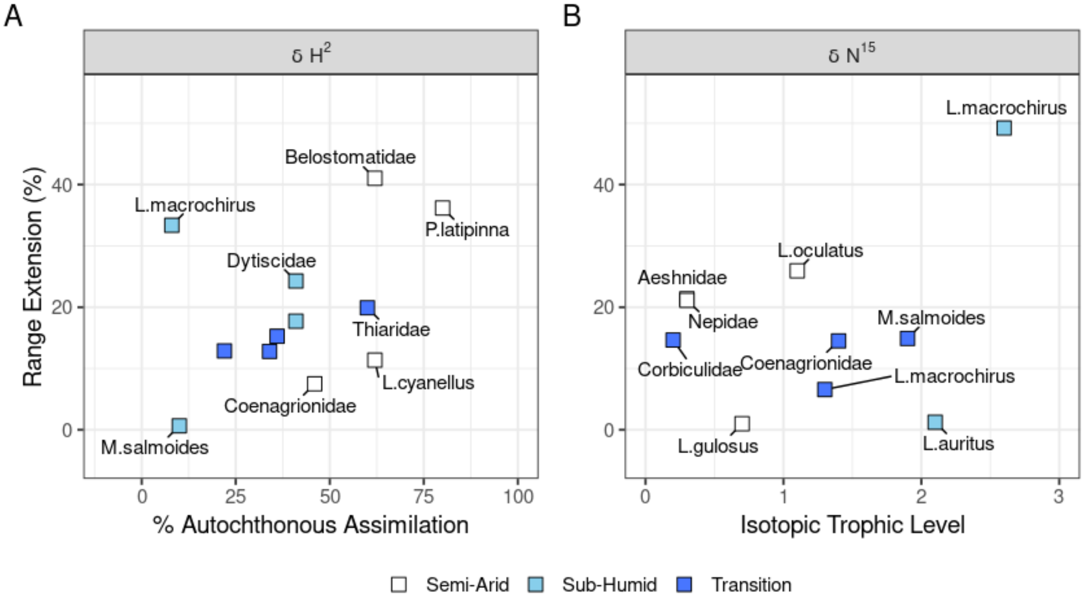
Appendix 3.06: Isotopic Trophic Level Figure

Isotopic trophic levels for fish and invertebrate communities as well as functional feeding groups. Diamonds represent mean values and are colored according to sample site (darkening with increased precipitation) with bars extending to the 95% credible interval. Isotopic trophic levels are estimated using δ^{15}N signatures, calibrated to local source signatures and use a trophic discrimination factor of 3.4‰.



Appendix 3.07: Isotope Autochthony vs Torphic Level

Isotopic trophic level (estimated using δ^{15}N) plotted against aquatic assimilation (estimated using δ^{13}C and δ^{2}H) for **(A)** common fish species, **(B)** fish feeding groups, **(C)** common invertebrate species, and **(D)** invertebrate feeding groups. Scatter plot points are shaped according to their taxonomic group and colored by site (darkening with annual rainfall). Comparisons within fish display a strong negative relationship between isotopic trophic level and autochthonous resource assimilation which coincides with increasing aridity. Invertebrate comparisons reveal a weak negative relationship between isotopic trophic level and aquatic resource assimilation that weakly coincides with site precipitation patterns.



Appendix 3.08: Isotope Range Influence Figure

Fish and invertebrates influence **(A)** resource breadth σ^2H range) and **(B)** food-chain length (σ^{15}N range) at Semi-Arid (white), Transiiton (light), and Sub-Humid (dark) sites. Range extension reflects the difference between the bootstrapped range estimate with and without each taxa. Semi-Arid resource breadth was largely influenced by Belostomatidae (62% autochthonous) and *P.latipinna* (80% autochthonous) and food-chain length was driven by invertebrate predators (Aeshnidae and Nepidae) as well as piscivorous *L.oculatus*. Excepting Thiaridae (60% autochthonous), no taxa at the Transition extend σ^{15}N or σ^2H ranges more than 20%, which may reflect greater dietary overlap among taxa. At the Sub-Humid site, resource breadth and food-chain length are highly influenced by *L.macrochirus* (8% autochthonous).

Element	Taxa	Range Ext.	Site	R.Abundance	% Autoch.	I.T.L	T.Group
H	Thiaridae	19.9	Transition	3	60 †	†	I-Herbivore
H	Belostomatidae	41.0	Semi-Arid	1	62 †	0.3 †	I-Predator
H	Dytiscidae	24.3	Sub-Humid	1	41 †	0.9 †	I-Predator
H	Corduliidae	17.7	Sub-Humid	1	41 †	0.9 †	I-Predator
H	Corydalidae	12.9	Transition		22 †	1.4 †	I-Predator
H	Coenagrionidae	7.5	Semi-Arid	3	46	0.3 †	I-Predator
H	P.latipinna	36.2	Semi-Arid	42	80	0.4	F-Herbivore
H	L.macrochirus	33.4	Sub-Humid	15	8	2.6	F-Invertivore
H	C.lutrensis	15.3	Transition	35	36 †	1.7 †	F-Invertivore
H	L.cyanellus	12.8	Transition	10	34	1.1	F-Piscivore
H	L.cyanellus	11.4	Semi-Arid	2	62	0.7	F-Piscivore
H	M.salmoides	0.6	Sub-Humid	3	10 †	2.1 †	F-Piscivore
N	Leptophlebiidae	10.7	Sub-Humid	4	46 †	†	I-Gatherer
N	Palaemonidae	3.9	Sub-Humid	4	46 †	†	I-Gatherer
N	Corbiculidae	14.6	Transition	2	31	0.2	I-Filterer
N	Aeshnidae	21.4	Semi-Arid	1	62 †	0.3 †	I-Predator
N	Nepidae	21.1	Semi-Arid	2	62 †	0.3 †	I-Predator
N	Coenagrionidae	14.5	Transition	4	25	1.4 †	I-Predator
N	L.macrochirus	49.2	Sub-Humid	15	8	2.6	F-Invertivore
N	L.macrochirus	6.6	Transition	19	36	1.3	F-Invertivore
N	L.auritus	1.2	Sub-Humid	9	5 †	2.1 †	F-Invertivore
N	L.gulosus	1.0	Semi-Arid	2	63	0.7	F-Invertivore
N	L.oculatus	25.9	Semi-Arid	2	70 †	1.1 †	F-Piscivore
N	M.salmoides	14.9	Transition	5	34 †	1.9 †	F-Piscivore

Appendix 3.09: Isotope Range Influence Table

Influential fish and invertebrate taxa on σ^{2}H (resource breadth) and σ^{15}N (food-chain length) range extension (Range Ext.) with relative abundance (R.Abundance) and mixing model estimates of autochthonous assimilation (% Autochthonous) and isotopic trophic level (I.T.L). † indicates values are taken from the trophic category.

Species	Site	d2H	d13C	d15N
Filamentous Algae	Semi-Arid	-129.6 ± 7.8 (3)	-24.7 ± 7.2 (3)	11.3 ± 4.0 (3)
Filamentous Algae	Transition	-176.5 ± 31.8 (3)	-25.2 ± 6.1 (3)	17.5 ± 2.4 (3)
Filamentous Algae	Sub-Humid	-148.7 ± 14.5 (6)	-37.8 ± 3.7 (6)	4.8 ± 1.2 (6)
Periphyton	Semi-Arid	-110.4 ± 8.7 (8)	-24.2 ± 1.2 (8)	11.5 ± 1.0 (8)
Periphyton	Transition	-132.1 ± 8.5 (6)	-17.9 ± 4.2 (6)	16.1 ± 0.6 (6)
Periphyton	Sub-Humid	-122.4 ± 4.5 (6)	-30.7 ± 0.6 (6)	6.3 ± 3.4 (6)
C3 Grass	Semi-Arid	-75.2 ± 0.3 (2)	-21.6 ± 9.3 (2)	14.4 ± 1.7 (2)
C3 Grass	Transition	-94.8 ± 6.2 (3)	-31.3 ± 0.6 (3)	11.8 ± 2.9 (3)
C3 Grass	Sub-Humid	-85.6 ± 16.9 (3)	-31.3 ± 0.6 (3)	2.4 ± 2.3 (3)
Green Leaves	Semi-Arid	-94.3 ± 4.4 (3)	-30.9 ± 1.8 (3)	13.4 ± 2.3 (3)
Green Leaves	Transition	-83.0 ± 19.5 (3)	-31.6 ± 0.8 (3)	6.8 ± 2.8 (3)
Green Leaves	Sub-Humid	-82.1 ± 20.5 (3)	-31.8 ± 0.7 (3)	3.0 ± 1.8 (3)

Appendix 3.10: Source Stable Isotope Summary Table

δ^{2}H, δ^{13}C, and δ^{15}N mean ± standard deviation (number of samples) for aquatic and terrestrial resources at three sample sites (Transition, Semi-Arid, and Sub-Humid).

Taxon	Site	d2H	d13C	d15N
A.natalis	Transition	-102.0 ± 15.4 (3)	-26.5 ± 0.6 (3)	19.7 ± 2.0 (3)
A.natalis	Sub-Humid	-85.7 ± 6.8 (12)	-27.9 ± 0.5 (12)	9.2 ± 0.7 (12)
C.lutrensis	Semi-Arid	-93.3 (1)	-25.4 (1)	14.0 (1)
C.lutrensis	Transition	-133.0 ± 26.3 (3)	-27.0 ± 1.5 (3)	18.4 ± 1.5 (3)
E.gracile	Sub-Humid	-86.2 (1)	-30.6 (1)	8.6 (1)
H.cyanoguttatus	Semi-Arid	-93.5 ± 9.6 (4)	-24.5 ± 1.7 (4)	15.5 ± 0.6 (4)
H.cyanoguttatus	Transition	-101.8 ± 9.7 (8)	-26.6 ± 1.0 (8)	18.2 ± 1.9 (8)
I.punctatus	Transition	-110.8 ± 2.8 (3)	-27.8 ± 0.6 (3)	19.7 ± 0.4 (3)
L.auritus	Sub-Humid	-87.2 ± 7.7 (8)	-28.2 ± 1.6 (8)	9.8 ± 1.2 (8)
L.cyanellus	Semi-Arid	-97.5 ± 15.1 (4)	-25.0 ± 1.4 (4)	14.5 ± 2.3 (4)
L.cyanellus	Transition	-95.4 ± 10.7 (9)	-25.4 ± 1.3 (9)	14.9 ± 2.4 (9)
L.cyanellus	Sub-Humid	-87.2 ± 5 (4)	-28.7 ± 2.1 (4)	10.4 ± 1.5 (4)
L.gulosus	Semi-Arid	-104.1 ± 7.9 (3)	-25.6 ± 0.3 (3)	14.8 ± 2.5 (3)
L.gulosus	Transition	-103.0 ± 15.2 (3)	-26.2 ± 0.6 (3)	18.2 ± 0.5 (3)
L.gulosus	Sub-Humid	-82.1 ± 2 (5)	-28.8 ± 0.6 (5)	9.5 ± 0.3 (5)
L.macrochirus	Semi-Arid	-103.2 ± 5.7 (3)	-25.5 ± 1.5 (3)	14.7 ± 1.5 (3)
L.macrochirus	Transition	-101.0 ± 8.2 (9)	-25.2 ± 0.8 (9)	16.5 ± 1.4 (9)
L.macrochirus	Sub-Humid	-80.9 ± 10.1 (10)	-27.4 ± 1.6 (10)	11.8 ± 4.0 (10)
L.megalotis	Sub-Humid	-87.6 ± 8 (4)	-28.9 ± 1.0 (4)	9.6 ± 0.2 (4)
L.microlophus	Sub-Humid	-91.4 ± 3.1 (3)	-29.9 ± 0.2 (3)	8.7 ± 0.5 (3)
L.oculatus	Semi-Arid	-104.9 ± 2.1 (2)	-23.2 ± 0.2 (2)	18.2 ± 0.7 (2)
L.oculatus	Sub-Humid	-79.3 ± 10 (2)	-26.2 ± 0.4 (2)	12.6 ± 1.8 (2)
M.salmoides	Transition	-105.4 ± 3.6 (3)	-26.5 ± 0.3 (3)	22.1 ± 0.4 (3)
M.salmoides	Sub-Humid	-99.6 (1)	-29.6 (1)	10.1 (1)
P.latipinna	Semi-Arid	-123.2 ± 15.5 (11)	-25.2 ± 0.8 (11)	13.4 ± 1.2 (11)
P.latipinna	Transition	-99.3 ± 9.9 (3)	-24.9 ± 1.3 (3)	17.4 ± 1.8 (3)
P.latipinna	Sub-Humid	-86.3 ± 5.4 (4)	-27.0 ± 0.7 (4)	10.9 ± 2.0 (4)
P.olivaris	Transition	-103.7 (2)	-26.4 (2)	20.6 (2)

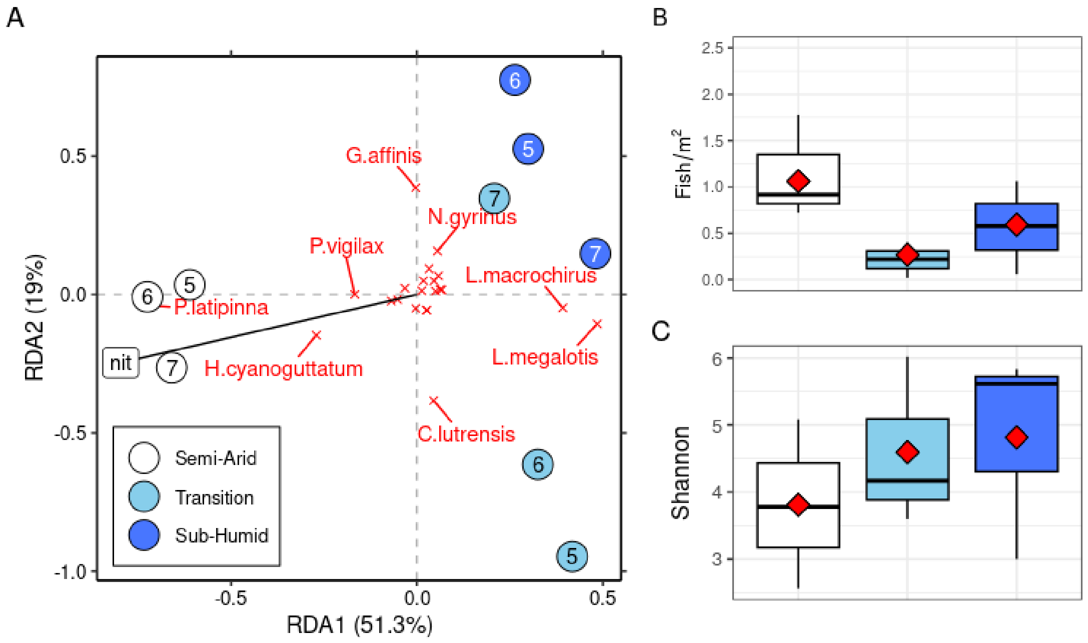
Appendix 3.11: Fish Stable Isotope Summary Table

δ^{2}H, δ^{12}C, and δ^{15}N mean ± standard deviation (number of samples) for fish at three sample sites (Transition, Semi-Arid, and Sub-Humid).

Taxon	Site	d2H	d13C	d15N
Aeshnidae	Semi-Arid	-87.0 (1)	-27.7 (1)	17.1 (1)
Aeshnidae	Transition	-95.3 (1)	-31.3 (1)	11.6 (1)
Annelidae	Semi-Arid	-84.0 (1)	-25.4 (1)	13.3 (1)
Belastomatidae	Semi-Arid	-115.4 ± 19.5 (2)	-22.4 ± 0.3 (2)	8.5 ± 0.8 (2)
Chironomidae	Semi-Arid	-90.1 (1)	-25.9 (1)	14.0 (1)
Coenagrionidae	Semi-Arid	-86.1 ± 15.5 (2)	-26.2 ± 0.7 (2)	13.7 ± 0.5 (2)
Coenagrionidae	Transition	-97.0 ± 2.3 (3)	-27.9 ± 0.5 (3)	18.3 ± 1.3 (3)
Coenagrionidae	Sub-Humid	-101.0 (1)	-32.2 (1)	7.8 (1)
Corbiculidae	Semi-Arid	-93.7 ± 2.7 (4)	-26.3 ± 0.2 (4)	10.8 ± 0.4 (4)
Corbiculidae	Transition	-90.5 ± 4.7 (4)	-26.2 ± 1.0 (4)	12.1 ± 1.7 (4)
Corbiculidae	Sub-Humid	-89.4 ± 7.6 (3)	-32.3 ± 0.6 (3)	5.9 ± 0.3 (3)
Corduliidae	Semi-Arid	-92.2 (1)	-27.5 (1)	13.2 (1)
Corduliidae	Transition	-80.4 (1)	-27.9 (1)	16.7 (1)
Corduliidae	Sub-Humid	-68.8 (1)	-31.8 (1)	9.0 (1)
Corydalidae	Transition	-74.5 (1)	-27.6 (1)	14.0 (1)
Dogielinotidae	Transition	-100.0 (1)	-26.0 (1)	15.4 (1)
Dogielinotidae	Sub-Humid	-122.1 (1)	-32.9 (1)	8.5 (1)
Dystiscidae	Sub-Humid	-122.4 ± 24.9 (2)	-31.8 ± 8.9 (2)	6.0 ± 1.8 (2)
Elmidae	Transition	-89.6 ± 12.5 (2)	-28.4 ± 0.2 (2)	14.1 ± 1.5 (2)
Gomphidae	Transition	-92.7 (1)	-27.6 (1)	16.2 (1)
Gyrinidae	Transition	-97.7 (1)	-29.5 (1)	12.7 (1)
Gyrinidae	Sub-Humid	-111.8 (1)	-28.6 (1)	5.7 (1)
Hydropsychidae	Transition	-121.4 (1)	-29.4 (1)	16.0 (1)
Leptophlebiidae	Transition	-111.4 (1)	-30.0 (1)	15.3 (1)
Leptophlebiidae	Sub-Humid	-110.4 (1)	-35.2 (1)	4.4 (1)
Nepidae	Semi-Arid	-88.5 ± 16 (3)	-25.9 ± 2.3 (3)	9.4 ± 4.7 (3)
Nepidae	Transition	-87.6 ± 4.3 (2)	-26.4 ± 0.3 (2)	14.6 ± 0.7 (2)
Palaemonidae	Transition	-98.6 ± 8.6 (2)	-26.1 ± 0.6 (2)	18.5 ± 0.5 (2)
Palaemonidae	Sub-Humid	-93.9 (1)	-29.4 (1)	9.4 (1)
Thiaridae	Semi-Arid	-94.9 (1)	-25.2 (1)	12.9 (1)
Thiaridae	Transition	-133.6 (1)	-25.5 (1)	17.8 (1)
Veliidae	Transition	-100.8 (1)	-28.6 (1)	15.8 (1)

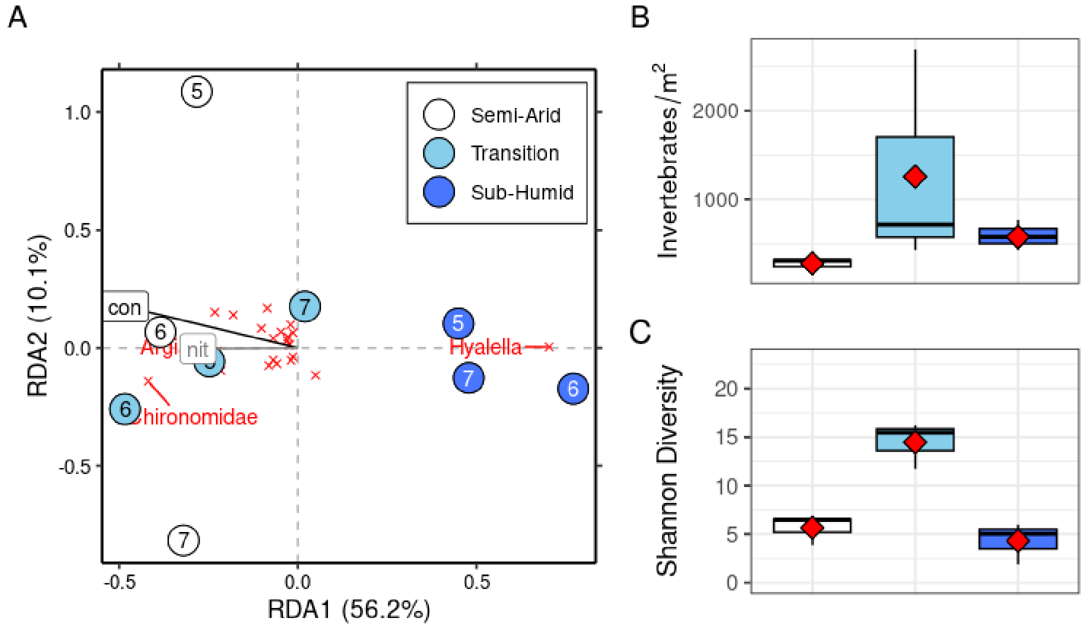
Appendix 3.12: Invertebrate Stable Isotope Summary Table

δ^{2}H, δ^{12}C, and δ^{15}N mean ± standard deviation (number of samples) for Inverterbates at three sample sites (Transition, Semi-Arid, and Sub-Humid).



Appendix 3.13: Fish Community Overview

(A) Ordination of fish communities at Semi-Arid, Transition, and Sub-Humid sites collected in May-July of 2018. Redundancy Analysis axes are labeled with the proportion of variation within the community matrix is explained. The ordination is constrained by 6 environmental variables represented by labeled, arrows (only those with $p<0.1$ are plotted). Circles represent communities with numeric labels for the month sampled and shaded by annual precipitation. Red crosses with spread-out labels represent species; rare and region-wide species ordinate in the center while site-specific and populous species ordinate next to their community. The Semi-Arid site is characterized by *P.latipinna*. The other sites contain more sunfish (*L.macrochirus* and *L.megalotis*) with the Transition site uniquely containing *C.lutrensis* (2/3 months) and the Sub-Humid site containing more *G.affinis*. (B) Boxplot of fish densities at semi-arid, transition, and sub-humid sites. (C) Boxplot of Shannon-Wiener diversity for fish communities at Semi-Arid, Transition, and Sub-Humid sites. Boxplot colors darken with increasing precipitation and red diamonds represent mean values.



Appendix 3.14: Invertebrate Community Overview

(A) Ordination of invertebrate kicknet communities at Semi-Arid, Transition, and Sub-Humid sites collected in May-July of 2018. Redundancy Analysis axes are labeled with the proportion of variation within the community matrix is explained. The ordination is constrained by 6 environmental variables represented by labeled, arrows (only those with $p<0.1$ are plotted). Circles represent communities with numeric labels for the month sampled and shaded by annual precipitation. Red crosses with spread-out labels represent taxonomic families; rare and region-wide species ordinate in the center while site-specific and populous species ordinate next to their community. The Sub-Humid site is distinguished from Transition and Semi-Arid site communities by the presence of abundant amphipods (*Hyalella*) (B) Boxplot of invertebrate densities at semi-arid, transition, and sub-humid sites surveyed with kicknets May-July in 2018. Box colors darken with rising annual precipitation and red diamonds represent site mean values. Visually, invertebrate densities appear greatest at the transition site, although Tukey comparisons between site means lack statistical significance. (C) Boxplot of Shannon-Wiener diversity for invertebrate communities at Semi-Arid, Transition, and Sub-Humid sites surveyed May-July of 2018. Boxplot colors darken with increasing precipitation and red diamonds represent mean values. Invertebrate diversity is highest at the Transition site.

Vector	Axis 1	Axis 2	R^2	*p*
Algae	0.83	-0.56	0.49	0.12
Canopy	0.87	-0.49	0.17	0.58
Conductivity	-0.35	-0.94	0.29	0.35
Flow	-1.00	-0.03	0.09	0.82
Max Depth	0.89	0.46	0.04	0.93
Nitrate	-0.96	-0.30	0.91	0.00**
A.melas	0.03	-0.06	0.24	0.56
A.natalis	0.03	-0.06	0.24	0.56
C.carpio	-0.05	-0.02	0.27	0.44
C.lutrensis	0.05	-0.38	0.77	0.01*
C.variegatus	-0.07	-0.02	0.27	0.44
F.grandis	0.05	0.05	0.18	0.78
G.affinis	0.00	0.39	0.83	0.00**
H.cyanoguttatum	-0.27	-0.15	0.97	0.00**
L.auritus	0.03	0.09	0.32	0.23
L.cyanellus	0.06	0.02	0.26	0.46
L.gulosus	0.00	-0.05	0.01	0.93
L.macrochirus	0.39	-0.05	0.66	0.03*
L.megalotis	0.49	-0.11	0.95	0.00**
L.microlophus	0.02	0.05	0.32	0.23
L.miniatus	0.01	0.01	0.18	0.78
L.oculatus	0.07	0.02	0.27	0.43
M.salmoides	0.05	0.01	0.14	0.72
N.gyrinus	0.06	0.16	0.32	0.23
N.texanus	0.06	0.07	0.23	0.47
O.aureus	-0.03	0.02	0.21	0.64
P.latipinna	-0.72	-0.04	0.98	0.01*
P.vigilax	-0.17	0.00	0.88	0.01*

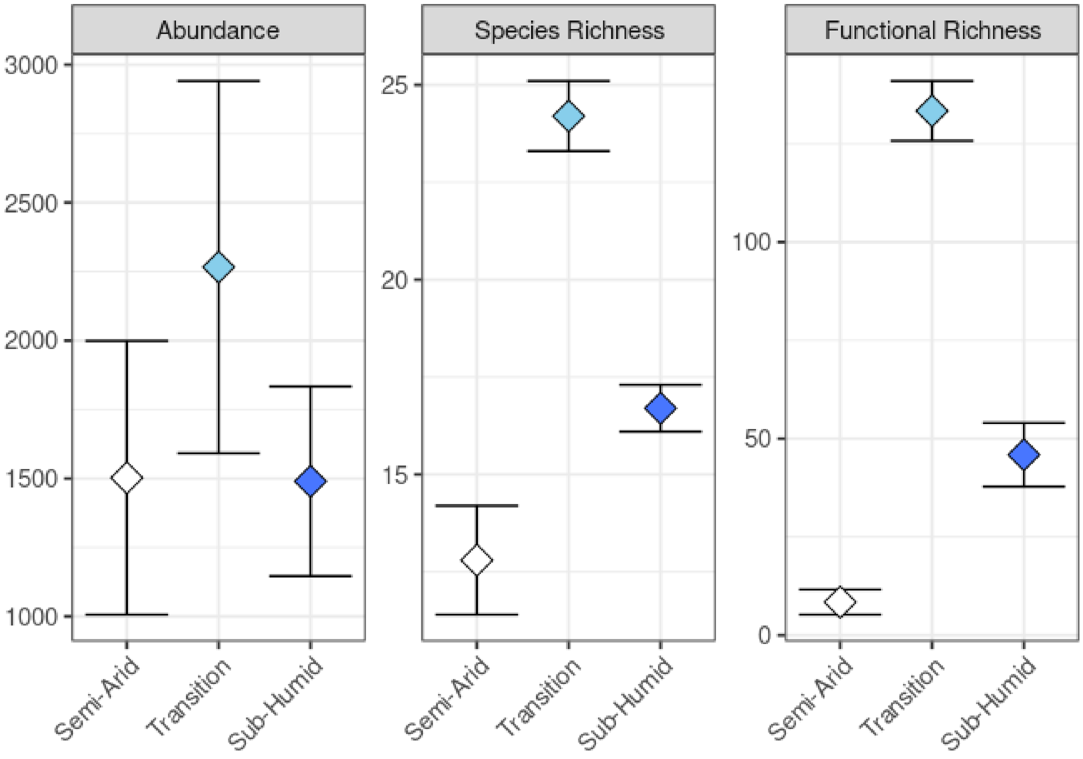
Appendix 3.15: Fish Redundancy Analysis (RDA) Table

Axes values (in radians), correlation coefficients and *p*-values for fitted vectors of environmental variables and influential taxa in the Redundancy Analysis of fish communities.

Vector	Axis 1	Axis 2	R^2	*p*
Algae	-0.28	-0.96	0.07	0.79
Canopy	-0.91	-0.41	0.02	0.96
Conductivity	-0.94	0.34	0.72	0.02*
Flow	-0.36	-0.93	0.29	0.35
Max Depth	0.88	-0.47	0.11	0.68
Nitrate	-1.00	-0.01	0.53	0.10
Anax	-0.02	0.01	0.10	0.80
Aphididae	-0.03	0.03	0.05	0.82
Argia	-0.23	-0.01	0.53	0.10
Caenis	-0.18	0.14	0.62	0.05
Carabidae	-0.01	-0.04	0.46	0.23
Ceratopogon	-0.01	0.06	0.70	0.09
Chironomidae	-0.42	-0.14	0.78	0.01*
Chrysomelidae	-0.02	-0.05	0.46	0.23
Corbicula	-0.09	0.17	0.59	0.07
Enallagma	-0.06	-0.07	0.37	0.26
Erpetogomphus	-0.08	-0.07	0.55	0.07
Hyalella	0.70	0.00	0.99	0.00**
Hydropsyche	-0.02	0.10	0.70	0.09
Libellulidae	-0.02	0.01	0.10	0.80
Melanoides	-0.22	-0.10	0.78	0.02*
Microcylloepus	-0.10	0.08	0.62	0.05
Odontomyia	-0.07	-0.05	0.57	0.10
Probezzia	-0.03	0.05	0.01	0.99
Protoneura	-0.07	0.04	0.10	0.80
Ranatra	-0.05	0.07	0.48	0.16
Rhagovelia	-0.23	0.15	0.67	0.03*
Scirtidae	0.05	-0.12	0.16	0.58

Appendix 3.16: Invertebrate Redundancy Analysis (RDA) Table

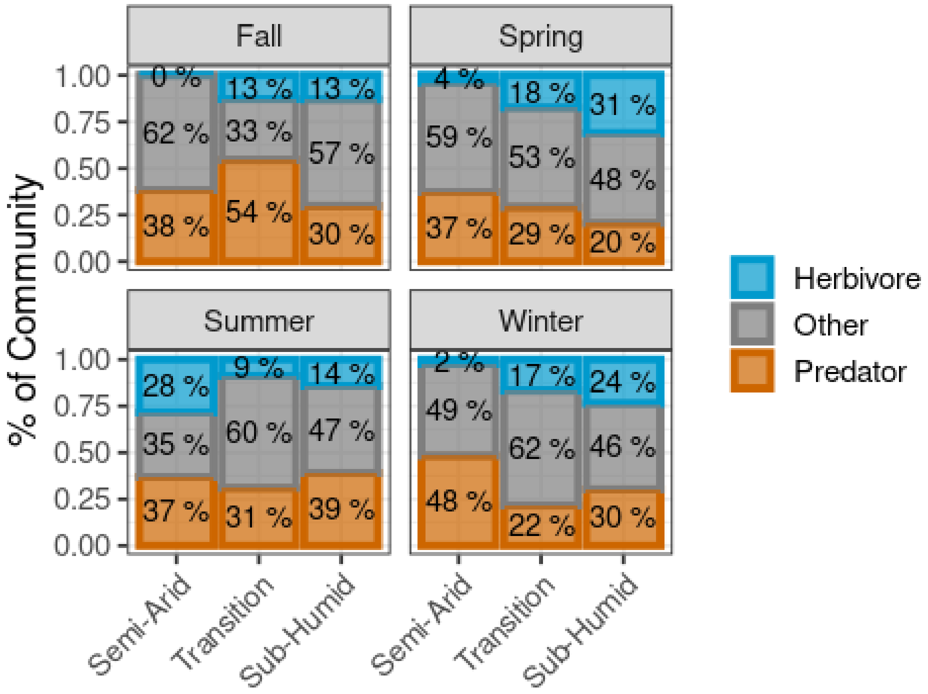
Axes values (in radians), correlation coefficients and *p*-values for fitted vectors of environmental variables and influential taxa in the Redundancy Analysis of invertebrate communities.



Appendix 3.17: Community *Carvallo et al. 2021* Summary

Annual Mean and standard errors for sediment-core invertebrate abundance (individuals/m^2), species richness, and functional richness at Fernando Creek (Semi-Arid), Aransas River (Transition), and Garcitas Creek (Sub-Humid) (Cavallo *et al.* 2022).

Site	Functional Richness	Species Richness	Abundance
Semi-Arid	8 ± 3	13 ± 1	1502 ± 497
Transition	133 ± 8	24 ± 1	2266 ± 675
Sub-Humid	46 ± 8	17 ± 1	1490 ± 344



Appendix 3.18: Community *Carvallo et al. 2021* Feeding Groups Summary

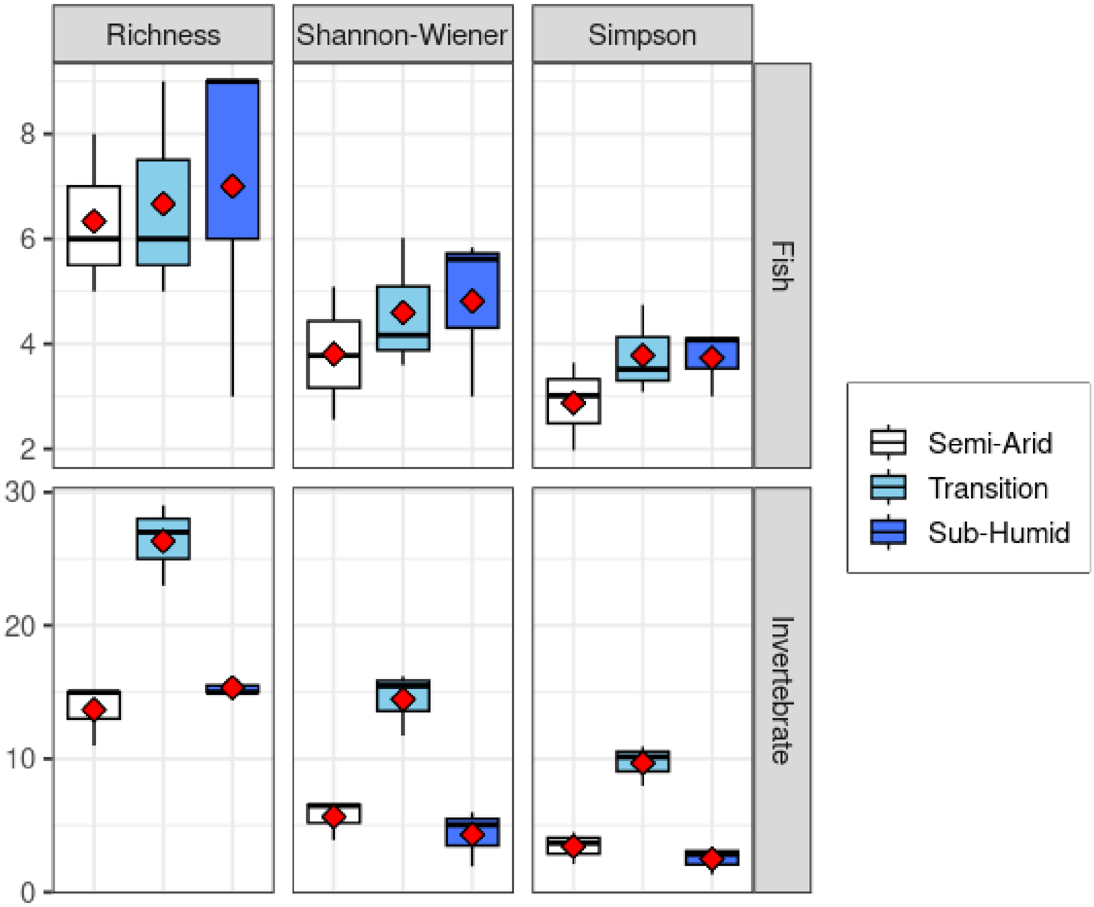
Proportions of herbivore, predator, and other invertebrate functional feeding groups in each season of 2018. Data extracted from supplemental table 6 in Carvallo *et al.* 2022.

Site	Filterer	Gatherer	Herbivore	Predator	Shredder
Semi-Arid	0.06	0.29	0.28	0.37	0
Transition	0.27	0.33	0.09	0.31	0
Sub-Humid	0.24	0.23	0.14	0.39	0

Guild	Semi-Arid	Sub-Humid	Transition	TukeyHSD Comparison	Difference	*p*-value
Fish	1.1 ± 0.4	0.3 ± 0.1	0.6 ± 0.4	Transition-Semi-Arid	-5.7e-01	0.33
Fish	1.1 ± 0.4	0.3 ± 0.1	0.6 ± 0.4	Sub-Humid-Semi-Arid	-9.3e-01	0.10
Fish	1.1 ± 0.4	0.3 ± 0.1	0.6 ± 0.4	Sub-Humid-Transition	-3.5e-01	0.62
Invertebrate	278 ± 66	1257 ± 1002	577 ± 137	Transition-Semi-Arid	3.2e+02	0.85
Invertebrate	278 ± 66	1257 ± 1002	577 ± 137	Sub-Humid-Semi-Arid	1.0e+03	0.27
Invertebrate	278 ± 66	1257 ± 1002	577 ± 137	Sub-Humid-Transition	6.9e+02	0.51

Appendix 3.19: Community Abundance Comparisons Table

Density statistics and mean comparisons for fish or invertebrates densities. Summary statistics for each site include the mean ± the standard deviation for collections during May-July of 2018. Tukey 'Honest Significant Difference' comparisons are described in terms of the differences between means and the associated *p*-value. The semi-arid site had greater fish densities than the transition or the sub-humid sites.



Appendix 3.20: Community Diversity Comparisons Figure

Species richness, Shannon-Wiener, and Simpson diversity estimates for fish and invertebrate communities at Semi-Arid, Transition, and Sub-Humid sites surveyed May-July of 2018. Boxplot colors darken with increasing precipitation and red diamonds represent mean values. Fish species richness and evenness were lowest at the Semi-Arid site and highest at the Sub-humid site. Invertebrate species richness and evenness were greatest at the Transition site.

Guild	TukeyHSD Comparison	Difference	Lower	Upper	p-value
Invertebrate	Transition-Semi-Arid	9.0	3.6	14.4	5.1e-03
Invertebrate	Sub-Humid-Semi-Arid	-1.4	-6.8	3.9	0.71
Invertebrate	Sub-Humid-Transition	-10.5	-15.8	-5.1	2.4e-03
Fish	Transition-Semi-Arid	1.7	-1.6	5.0	0.32
Fish	Sub-Humid-Semi-Arid	3.0	-0.3	6.3	0.07
Fish	Sub-Humid-Transition	1.3	-2.0	4.6	0.50

Appendix 3.21: Community Diversity Comparisons Table

Comparisons of mean Shannon-Wiener indices of fish or invertebrates across sites using Tukey's 'Honest Significant Difference' method. Comparisons are described in terms of the differences between means, the lower interval limit, upper interval limit, and associated *p*-value. Invertebrate diversity is greater at the Transition site compared to Semi-Arid and Sub-Humid sites.

Chapter 4: Proximity and Dams Restrict Upstream Nutrient-Transport in Sub-Tropical, Coastal Rivers

4.1 Abstract:

Coastal plain ecosystems in North America, despite their known diversity, have received relatively little ecological attention. This research sheds light on the substantial upstream material movement in coastal rivers, challenging traditional perspectives and highlighting the presence of diverse species, including those that were historically abundant and are now in decline. We leveraged stable isotope analysis ($\delta^{34}S$ and $\delta^{13}C$) of primary producers, fish, and invertebrates from ten rivers across a climate gradient, to investigate the cumulative influence of diadromous and euryhaline species observed during a four-year monitoring program. We had two primary objectives: first, to quantify the connectivity between estuaries and streams, driven by the combination of diadromous and euryhaline species, and second, to assess the impact of natural factors like rainfall, proximity to the sea, elevation, and the presence of dams on estuary-stream connections.

Our findings reveal substantial estuarine assimilation (EA) by diadromous and euryhaline species (73%), particularly those from the Fundulidae, Cyprinidontidae, and Palaemonidae families. The proximity of sites to estuaries primarily influences estuary-stream connectivity. However, the presence of dams within 25 kilometers of an estuary disrupts this connectivity, with above-dam EA deviating by -39% from model predictions and -40% from below-dam EA. This underscores the vital role of ecological connectivity

and its significance in environmental impact assessments for coastal dams. While precipitation was not identified as the primary predictor of estuarine assimilation, our findings highlight the dominance of euryhaline taxa in arid stream ecosystems.

These findings highlight the cumulative ecosystem services conferred by inconspicuous diadromous and euryhaline fish and invertebrates, with particular significance in xeric systems. These coastal linkages induce alterations in community compositions, predatory-prey dynamics, and have the potential to sustain remarkable productivity. The study unveils pervasive ecological connections that likely influence coastal rivers worldwide, emphasizing their susceptibility to interruption by coastal urbanization and climate change. This highlights the imperative need for a more profound understanding of these influential yet frequently overlooked species, challenging the predominant focus on charismatic migrations and island ecosystems in research on marine derived nutrient transport into freshwater ecosystems.

4.2 Introduction

Reviewing the Significance of Freshwater Rivers for Marine and Estuarine Organisms

Coastal plain ecosystems are some of the most biologically diverse ecological systems in North America and yet they remain relatively under-studied (Noss *et al.* 2015). Within the coastal plain, coastal rivers feeding the estuaries play a crucial role by supplying vital resources to estuaries and coastal environments (Montagna, Palmer, and Pollack 2023) and they are a mixing zone of fauna that providing key habitat for some marine and estuarine organisms. However, the overall significance of the connections between freshwater rivers and downstream estuaries for marine and estuarine organisms remains uncertain. While the importance of marine nutrients for upstream rivers has been examined in systems with charismatic migrations of marine fauna such as salmon, the extent of material and energy transfer upstream delivered by mobile fauna from the estuary into riverine ecosystems worldwide, and the subsequent impact of migrating species and lotic food webs, has not been quantified.

Well known instances of marine substances traveling upstream are associated with the migrations of anadromous species, such as salmon (Helfield and Naiman 2002; Lessard, Merritt, and Berg 2009), and river herring (MacAvoy *et al.* 2000; Walters, Barnes, and Post 2009). However, the movement of materials upstream in coastal rivers may be much more widespread and significant than just those systems that are home to massive visible migrations (Doughty *et al.* 2016). For instance, a variety of species, including red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), southern flounder (*Paralichthys lethostigma*), and blue crab (*Callinectes sapidus*), have been documented in coastal rivers along the Gulf Coast (Lowe *et al.* 2011; Woodcock and Walther 2014). Moreover, smaller species, such as gobies and prawns, were once abundant in coastal rivers but have quietly disappeared from much of their ranges over the past century (Bowles, Aziz, and Knight 2000). River prawns in the Macrobrachium genus were once a significant gulf coast fishery in the 1800s and were distributed across much of the Mississippi River ecosystem, reaching as far inland as Ohio and Illinois (Hedgpeth 1949; Bowles, Aziz, and Knight 2000). These species have vanished from 90% of their original habitat (Horne and Beisser 1977; Bauer and

Delahoussaye 2008). The American eel (*Anguilla rostrata*), another migratory (catadromous) species, has experienced a 64% reduction in its overall population in recent years, with some river systems suffering losses of up to 99% of their historical populations (Arai 2016). These losses, many of which are rooted in historical factors, can be attributed to human-induced stressors such as decreased freshwater inflow, dam construction, and changes in land use. However, due to the scarcity of historical data on coastal rivers, it remains unclear exactly what has been forfeited.

The urgency of these inquiries is underscored by the substantial modifications occurring in coastal regions. Human population expansion is notably accelerated in coastal areas, surpassing growth rates observed in other global sectors (Steven *et al.* 2020). Projections indicate positive growth trends persisting across all regions throughout the 21st century, with certain estimates reaching as high as 228% (Merkens *et al.* 2016). This development brings changes to watershed land-use, impacting water quality and hydrology (Bilgiç and Baba 2023; Gold, Thompson, and Piehler 2019; Freeman *et al.* 2019), and breaks in riverine connectivity in the form of dams and road crossing culverts or riprap revetments (Waldman and Quinn 2022). In addition to these regional impacts, global climate forcing is projected to alter the hydrology of coastal systems worldwide through changes to rainfall regimes (Sung *et al.* 2021), altering the magnitude and timing of freshwater flows critical for river corridor to estuary connectivity (Abbas, Zhao, and Wang 2022). It is critically important that we understand the relationships between coastal rivers and estuaries so that we can gain a deeper understanding of the life cycle of coastal species and provide essential insights for coastal management and conservation efforts.

Tracers of Habitat Usage: δ^{13}C, δ^{34}S, and δ^{15}N Isotopes in Freshwater and Marine Systems

Stable isotope analysis can provide insights into the relative contributions of freshwater and marine sources, shedding light on food web structure, energy flow, and ecological interactions. The most useful stable isotopes for differentiating freshwater and marine sources are δ^{13}C and δ^{34}S, but δ^{15}N has been a useful tracer in some instances (Connolly *et al.* 2004; Childress, Allan, and McIntyre 2014). Due to differences in photosynthetic pathways and carbon enrichment within marine environments, terrestrial and freshwater plants tend to have lower δ^{13}C values (-30‰) compared to around -15‰ in marine phytoplankton and algae. Likewise, marine environments have higher δ^{34}S than terrestrial sources because of enrichment of heavier sulfur isotopes in seawater. Baseline δ^{15}N values in marine environments tend to be higher in marine (3‰) compared to terrestrial (-2.5‰) environments. However, marine and freshwater baseline N values also vary based on the presence of nitrogen-fixing plants or the influence of human activities like agricultural runoff (which elevate δ^{15}N in freshwater systems).

The relative abundance of freshwater and terrestrial sources in migratory marine species is indicative of the level freshwater habitat usage (Lowe *et al.* 2011; Nims and Walther 2014). Similarly, the presence and abundance of marine derived nutrients in freshwater taxa in the rivers provides a measure of the relative importance of marine resources carried upstream to resident freshwater fauna. However, temporal variability in marine organism movement across seasons and life history stages, as well as the potential for migrant and non-migrant individuals (partial migration) in the estuarine populations (Gillanders *et al.* 2011; Deurs *et al.* 2016) may obscure some of these patterns in marine organisms at the population level. While synoptic surveys of isotopic signatures of estuarine organisms in freshwater rivers provides one measure of the importance of freshwater habitat usage, the signature of marine nutrients in resident freshwater fauna and primary producers also represents the aggregate signature of the marine migrants and this signature is likely to be more stable and persistent in the rivers long after the amphidromous species have moved back downstream (Naiman and Decamps 1997; Ben-David, Hanley, and Schell 1998; Helfield and Naiman 2002). However, given the potential for anthropogenic impacts to alter these patterns, the challenge with establishing baseline expectations is evaluating these isotopic patterns in places where connections between the freshwater and estuarine habitats remain relatively intact. Fortunately, the Southwest gulf coastline of the United States is such a region.

Texas Coastal Plain: A Natural Laboratory for Investigating Climate Impact on Estuary-Stream Connectivity

The Gulf Coastline of the United States of America is relatively undeveloped (U. S. C. 2013), providing an opportunity to look at coastal–riverine connections in the absence of strong anthropogenic forcing present in other areas of the coterminous United States. The central and southern Texas coastline is particularly attractive in this regard, with many areas that are both under-developed and home to abundant populations of amphidromous taxa (Kinard, Patrick, and Carvallo 2021). This region also sets the stage for a natural experiment on the role of climate on estuarine to riverine connectivity. The region features a naturally sharp precipitation gradient with mean annual precipitation changing from 55 $cm.yr^{-1}$(semi-arid) to 135 $cm.yr^{-1}$ (sub-humid) over a 300km distance (Δ 0.27$cm.yr^{-1}$ rainfall per km). Freshwater inflow varies naturally along the precipitation gradient providing a natural laboratory for investigating the importance of inflow on the strength of the estuary-stream connectivity.

Moreover, the Texas coastal plain, ecoregion 34 (Gulf Prairies and Marshes), suffers from a significant lack of data, even in comparison to understudied coastal plain systems worldwide, making any data collected in this region highly valuable for local management purposes. There have been limited comprehensive surveys conducted in both tidal and non-tidal rivers within ecoregion 34. The Texas Parks and Wildlife Department (TPWD) and the Texas Commission on Environmental Quality (TCEQ) have both identified a notable data deficiency in the coastal plain, especially in the central and southern sections of the Texas coastline, which they consider a priority data gap that requires attention. This region exhibits distinctive climate characteristics, including the aforementioned unique precipitation and hydrology patterns, as well as a sub-tropical mixing zone of flora and fauna. As a result, there is a substantial demand for additional data regarding the aquatic habitat in the Gulf Prairies and Marshes ecoregion in central-southern Texas.

Recent surveys were undertaken over a 14-month duration, with additional samplings at wider intervals spanning three years in freshwater coastal rivers along the precipitation gradient in South Texas (Kinard, Patrick, and Carvallo 2021; Carvallo *et al.* 2022). These surveys involved the thorough examination of diverse aquatic species, including fish, crustaceans, and invertebrates. Among the species frequently encountered in these surveys were euryhaline wanderers including blue crab (*Callinectes sapidus*), naked gobie (*Gobiosom bosci*), sheepshead minnow (*Cyprinodon variegatus*), and gulf killifish (*Fundulus grandis*). Diadromous species were also encountered including three anadromous species (*Menidia menidia*, *Anchoa mitchilli*, and *Mugil cephalus*), one catadromous species (*Anguilla rostrata*), and three amphidromous species (*Macrobrachium ohione*, *Ctenogobius shufeldti*, and *Agonostomus monticola*). For clarity and consistency throughout this paper, the terms 'euryhaline wanderers' and 'diadromous taxa' will collectively be referred to as 'transients.' Conversely, permanent residents in these rivers included species such as dragonfly larvae (Odonata), fly larvae (Diptera), snails (Gastropoda), sunfish (*Lepomis spp.*), largemouth bass (*Micropterus salmoides*), red shiner (*Cyprinella lutrensis*), catfish (*Ameiurus natalis*, *Ameiurus melas*, *Pylodictis olivaris*), and live bearers (*Gambusia affinis*, *Poecilia latipinna*). Although the observational data demonstrates that a diversity of marine species utilize coastal rivers in this region, the influence of these transients on freshwater ecosystems and, consequently, the importance of freshwater habitat to these transient species, remains uncertain.

Study Goals and Hypotheses: Investigating the Role of Climate and Precipitation in Estuarine Nutrient Dynamics along Coastal Rivers

Here we use coastal rivers along a rainfall gradient in central and south coastal Texas as a case study region to assess the spatial distribution of marine-derived nutrients (MDN) in the coastal freshwater rivers and the role that climate, specifically precipitation regime, plays in moderating the strength of connectivity. Using $\delta^{34}S$ and $\delta^{13}C$ stable isotopes derived from fish, invertebrates, and foundational resources collected from rivers and estuaries within the study region, we test the following hypotheses:

(1) Freshwater communities in coastal rivers will display a significant estuarine isotopic signature, indicating the importance of marine nutrients carried by marine migrants to freshwater productivity.

(2) Transient species will have higher estuarine assimilation signatures than obligate freshwater fauna due to their use of estuarine and marine habitat (Sorensen and Hobson 2005; Augspurger, Warburton, and Closs 2017).

(3) The degree of estuarine assimilation observed in freshwater species will correlate with the frequency of transient species, as these migratory species provide essential subsidies to local food webs (Novak *et al.* 2016; Samways, Soto, and Cunjak 2018; Benbow, Receveur, and Lamberti 2020).

(4) Distance to the estuary and elevation are negatively correlated with community estuarine assimilation since these factors impose greater physiological demands on upstream movement.

(5) Annual rainfall will positively correlate with community estuarine assimilation, as regular floods enhance connectivity and support upstream migrations (Covich *et al.* 1996; Blanco and Scatena 2005).

(6) Migration obstructions such as coastal salt-dams and road crossings reduce the movement of marine nutrients to upstream coastal rivers.

4.3 Methods:

Study Region

The study was conducted in ecoregion 34, gulf coasts and prairies region, of central and southern Texas (Figure 4.1). Study sites included sites in ten coastal rivers co-located with USGS gauging stations and the five downstream receiving estuaries (Table 1). Nine of the rivers were part of a multi-year (2016 – 2020) electrofishing and macroinvertebrate monitoring program (Kinard, Patrick, and Carvallo 2021; Carvallo *et al.* 2022). The tenth river, the Nueces, featured two study sites, one directly below and the other directly above, the Calallen salt dam, a 1.5m high rock-fill dam that serves as a barrier to saltwater intrusion from Nueces Bay. Distributed along a southwest to northeast gradient, average annual rainfall increases from 67 to 113 cm/yr^{-1}. All of these sites are ≤ 50 meters of sea level (Table 4.01) and have similar underlying geology. The sampled rivers drain into one of five estuaries: Baffin Bay, Nueces Bay, Copano Bay, Hynes Bay, and Lavaca Bay and ranged from 16-93 river kilometers upstream of the receiving bays. Aside from the site on the Nueces River, three out of the nine remaining river sites were located upstream of dams. Specifically, Perdido Creek was situated above the Coleto Dam, while the West and East Mustang Creek locations were upstream of the Palmetto Bend Dam, which form Lake Texana. One to three road crossing bridges were present between most sample sites and their nearest estuary, but there were no culverts. Environmental data for sampling locations was obtained from the USGS gauges ii database (Falcone 2011) and USGS National Map Streamer (https://txpub.usgs.gov/DSS/streamer/web/).

Sample Collection:

In January 2020, we gathered samples of sources (detritus & primary producers) from all study sites and collected fish, and invertebrate samples from each river site for stable isotope analysis. All samples were placed in coolers with ice and transported back to the lab to be frozen until laboratory processing. Primary producer samples include filamentous algae, periphyton, and terrestrial leaves. Filamentous algae were manually collected from substrates in all sample locations and cleaned of debris in the laboratory prior to further processing. Periphyton samples were obtained with a Loeb Sampler on hard substrate (Lamberti *et al.* 2007). Submerged debris/detritus were manually collected from the substrate. Green leaves were collected from dominant tree species (*Quercus*, *Prospis*, *Carya,* and *Vachellia*) along the stream banks.

For fish sampling, block nets (3mm mesh) were placed both at the upper and lower ends of a 75-meter sample reach. Fish communities were sampled using a three-pass depletion method, employing a Smith-Root LR-24 Backpack Electrofisher (Hauer and Lamberti 2017). All fish specimens were meticulously identified to the species level in accordance with a field guide and dichotomous key, and each species was counted

(Bonner, Whiteside, and Gelwick 2007; Hubbs, Edwards, and Garrett 2008). The first ten individuals of each species were humanely euthanized using an ice slurry and preserved in 95% ethanol. Once the sampling process was concluded, the remaining fish were returned to the stream, ensuring their continued survival. The collection of vertebrate samples was carried out in compliance with the regulations and approvals of the Institutional Animal Care and Use Committee at Texas A&M University Corpus Christi (AUP#05-17) and TPWD permit (SPR-0716-170).

Invertebrates were collected using a 0.3m wide D-frame net, fitted with 500µm mesh. A total of twenty samples, each covering an area of approximately 0.1 m^2, were gathered through a combination of kick and sweep techniques, each lasting 15 seconds. These samples were collected from various types of suitable habitats, including riffles, areas with large woody debris, and locations with overhanging vegetation (Southerland *et al.* 2007). The collected samples were combined, and any debris present was removed at the collection site. Subsequently, the samples were transported to the laboratory on ice and submerged in 95% ethanol. The processing of these samples followed the guidelines outlined in the Texas Commission for Environmental Quality Surface Water Quality Monitoring Protocol (https://www.tceq.texas.gov/downloads/publications/rg/chapter-5-rg-416.pdf). Samples were gridded/sub-divided, randomized, and then picked to completion in sequence until the total invertebrate count was ≥ 175 individuals. All invertebrates were enumerated and identified to family (Thorp and Rogers 2016).

Sample Processing:

All samples were dried in an oven at 55°C for 48 hours. Large invertebrates that could comprise single samples, like Palaemonidae, were dried individually, whereas smaller taxa such as Hyallelidae (amphipods) were grouped and dried together in aggregate samples. The fins, heads, internal organs, and skin of fish were removed before drying. After drying, we extracted the skeletal muscle from fish with fork lengths exceeding 30mm, whereas fish with fork lengths less than 30mm were ground whole, including both skeletal muscle and bone. Following drying all samples were ground into a uniform powder using a mortar and pestle, weighed (using a microbalance with a readability of up to 0.001mg), and packed into two 5x9mm tin capsules, one of which was designated for $\delta^{34}S$ analysis, while the other was simultaneously analyzed for $\delta^{13}C$ and $\delta^{15}N$.

For $\delta^{34}S$ samples, the following target weights (±0.050mg) were used: fish (0.45mg), invertebrates (0.55mg), and primary producers and detritus (4.00mg). The packed tin capsules were arranged in 96-well plates and shipped to the Washington State University Stable Isotope Core Laboratory where they underwent combustion using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and separation by a continuous flow isotope ratio mass spectrometer (delta PlusXP, Thermofinnigan, Bremen). Various standards (e.g. Costech analytical BBOT, Alpha Aesar $BaSO_4$, Salt Lake Medals Ag_2S, Acros elemental, and local grizzly hair) were run between sample runs. WSU standards were calibrated against seven international references: IAEA-S-1, IAEA-S-2, IAEA-S-3, IAEA-S-4, IAEA-SO5, IAEA-SO5, and NBS127. $\delta^{34}S$ values are reported in per mille (‰) relative to VCDT (Vienna Canyon Diablo Troilite).

For $\delta^{13}C$ and $\delta^{15}N$ samples, the following target weights (±0.05mg) were used: fish (0.35mg), invertebrates (0.45 mg), aquatic vegetation (1.25mg), filamentous algae (1.55mg), periphyton (4.45mg), and leaves (1.85mg). $\delta^{13}C$ and $\delta^{15}N$ samples were analyzed at the University of Florida using a Thermo DeltaV Advantage isotope ratio mass spectrometer with a ConFlo-II interface attached to a Carlo Erba elemental analyzer. UF standards included USGS40, USGS41a, as well as wheat and sorghum flour for vegetative samples, bovine liver for fish samples, and crab chitin for invertebrate samples. The results were reported in terms of C_{VPDB} and N_{air}.

Sample Overview:

A total of 407 samples were examined for their $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ content. 33 primary producer samples were collected from five estuaries, including filamentous algae, detritus, and aquatic macrophytes. In addition to these resource types, riparian leaves and periphyton were gathered from twelve stream locations, resulting in a total of 96 samples. From the streams, a combined total of 172 fish and 72 invertebrate samples were collected and processed.

The dataset included 28 transient fish samples, such as bay anchovie, (*Anchoa mitchilli*), alligator gar (*Atractosteus spatula*), sheepshead minnow (*Cyprinidon variegatus*), gulf killifish (*Fundulus grandis*), sleeper goby (*Gobiomorus dormitor*), inland silverside (*Menida beryllina*), fat sleeper (*Dormitator maculatus*), and sailfin molly (*Poecilia latipinna*). 18 transient invertebrate samples included blue crab (*Callinectes sapidus*), grass shrimp (Palaemonetes pugio) and Ohio shrimp (*Macrobrachium ohione*). The dataset had 144 freshwater fish samples, covering seven Centrarchid taxa (sunfishes and basses), two Cichlid taxa, two Ictalurid taxa (catfishes), and single species within Fundulid (topminnows), Percid (perches), and Poeciliid (livebearers) families. Furthermore, 54 freshwater invertebrates were analyzed, including representatives from four Odonata families (dragonflies, damselflies, etc.), three Hemiptera (water-bugs), three Gastropoda (snails), two Decapoda (crabs, prawns, etc.), and singular families within Amphipoda, Coleoptera (beetles), Diptera (flies), and Ephemeroptera (mayflies). $\delta^{13}C$ and $\delta^{34}S$ summary statistics for each taxonomic group and sample location are reported in appendices 4.09-4.13.

Mixing Models

Reported mixing models incorporated $\delta^{34}S$ and $\delta^{13}C$ but not $\delta^{15}N$ because after initial data exploration we identified an inability to differentiate $\delta^{15}N$ source signatures between estuaries and streams (df = 325, $p = 0.76$). We visually examined scatterplots of $\delta^{34}S$ and $\delta^{13}C$ to assess the assumptions of Bayesian mixing models and found that less than 2% of the mixtures exceeded the source ranges (Figure 4.2 and Figure 4.3). We used a two-source mixing model, which incorporated the mean and standard deviation of primary producers collected from streams and those collected from estuaries. The 95% confidence intervals for bootstrapped distributions of $\delta^{13}C$ and $\delta^{34}S$ values did not overlap among source systems for either element, with the exception of periphyton which was excluded from the end-member determination process because some of their $\delta^{13}C$ and $\delta^{34}S$ values fell in between the signatures of streams and estuaries.

Amphidromous Detection Models

Stream community data was acquired from stream monitoring surveys conducted between 2017 and 2020, as detailed in the references by Kinard (2021) and Carvallo (2022). Fish and invertebrate species were categorized into three transient types: (1) Euryhaline species that regularly frequent both estuaries and streams, (2) diadromous animals that make predictably timed migrations to/from marine environments for reproduction, and (3) potamodromous or freshwater species remain exclusively in freshwater habitats.

To assess the distribution of these transient species across the study area, we employed an Transient Presence Proportion (TPP), which is calculated as the proportion of sampling events at a site where one or more transient species were identified. We utilized linear regression analysis to investigate the influence of annual rainfall and the distance to estuaries on the APP of each transient type.

Estimating Estuarine Assimilation (EA)

The study employed “Stable Isotope Mixing Models in R (simmr)” to assess the diet composition of stream-dwelling animals, focusing on estuarine and freshwater contributions (Govan and Parnell 2019). We used regional averages and standard deviations for streams or estuaries to establish end-member sources for all mixing models. Prior to aggregating site sources, we used Kruskal-Wallis tests to ascertain significant differences between site resource signatures. We found no differences between site resource C ($p = 0.23$), but resource S signatures were comparatively unique at Tranquitas Creek and Garcitas Creek ($p < 0.001$)).

To avoid confounding effects within mixing models, we did not include periphyton or coarse detritus in end-member source signature calculations. Despite representing key food-web components with values comparable to those previously reported in the literature (Ishikawa, Hyodo, and Tayasu 2013) and significantly different between estuaries and streams ($\delta^{34}S$: p <0.0001, $\delta^{13}C$: $p < 0.001$ respectively), the values for each fell in between other primary resource signatures from streams and estuaries indicating they were the product of mixed sources and their inclusion would have confounded the mixing models.

Using the remaining resource types, we combined filamentous algae and aquatic macrophytes to define 'Estuary Sources.' In addition to these two aquatic resource types, 'Stream Sources' include green leaves from riparian vegetation which should embody the most 'terrestrial' signature. A total of six mixing model frameworks were executed using three site groupings (individual site, estuary distance category, or dam category) with two taxonomic groupings (entire community or amphidromous category).

The simmr function 'simmr_mcmc' was used to derive individual source proportions for each group being compared within the model. The model itself underwent 10,000 iterations, discarding the initial 1,000 iterations from the burn in period. The outcome consisted of probability density function distributions that revealed the most likely source solutions for each group of comparisons. Statistical significance was assessed by examining the 95% credible intervals between different sites.

Estuarine Assimilation Model

We created linear regression models to predict estuarine assimilation, taking into account variables such as annual rainfall, estuary distance, elevation, and their interactions with annual rainfall. The Nueces River sites above and below Calallen Dam were excluded from the model fitting process. Models were compared using the Akaike Information Criterion (AIC).

To evaluate the impact of the Calallen Dam on the movement of marine nutrients in the Nueces River, we compared the estuarine assimilation estimates from our models (expected values) with observations we made above and below the dam. The calculations for linear regression and AIC statistics were performed using the R software, utilizing the ‘stats’ and ‘MASS’ packages (Venables and Ripley 2002).

4.4 Results

Source C and S signatures

Estuarine sources exhibited mean δ^{13}C and δ^{34}S values of +9.8 and +6.2, respectively, compared to freshwater and terrestrial sources (Figure 4.2 and Figure 4.3). All the δ^{13}C and δ^{34}S values for the sources fell within the previously reported expected ranges (MacAvoy *et al.* 2000; Fry 2006; Hicks *et al.* 2005). Ninety eight percent of the measured isotopic values from the animal samples fell within the range of the source values (Figure 4.3).

Estuarine Assimilation Versus Rainfall or Estuary Distance

The top-performing model, as determined by the Akaike Information Criterion (AIC), predicted mean Estuarine Assimilation (EA) of the community using additive predictors: annual rainfall, estuary distance, and elevation ($R^2 = 0.68$, $p < 0.001$). EA exhibited an inverse relationship with average annual rainfall (-1.6% per cm), estuary distance (-0.6% per km), and elevation (-0.69% per m). The second-ranked model ($R^2 = 0.64$, $p < 0.001$) excluded elevation as a predictor while maintaining consistent coefficients for annual rainfall (-1.21% per cm) and estuary distance (-0.85% per km). In the third-ranked model ($R^2 = 0.62$, $p < 0.001$), an interaction term between annual rainfall and estuary distance was introduced (+0.02% per cm.km), indicating a nuanced relationship. The slightly more negative coefficients for annual rainfall (-1.74% per cm) and estuary distance (-2.16% per km) reflect the joint influence of these variables. Multiple regression and coefficient statistics, including the interaction term, are reported in Table 4.02.

Dam Effects

The stream community below the Calallen Dam had a significantly higher EA (62%) than the community directly above the dam (20%) (Figure 4.5). *Palaemonetes pugio (*Daggerblade grass shrimp) was the only species caught both above and below the dam. *P. pugio* below the dam had an average of +5.4 for $\delta^{13}C$ and +4 for $\delta^{34}S$ compared to *P. pugio* specimens collected above the dam, as illustrated in the Dam Scatterplot (Figure 4.3). Similarly, *P. pugio* below the dam exhibited an average of +7.7 for $\delta^{13}C$ and +4 for $\delta^{34}S$ in comparison to *P. pugio* collected from other stream locations. Model predicted EA values closely aligned with the observations below the dam, showing only a slight difference of +3%. In contrast, the average community EA above the Calallen Dam was 39% lower than the expected value based on annual rainfall, estuary distance, and elevation.

Transient Species

Estuarine sources constituted 73% (64-82%) of the tissue of euryhaline species in our streams (Figure 4.4). The transient Presence Probability (APP) is negatively correlated with the amount of annual rainfall ($R^2 = 0.59$, *p*-value of 0.016; Figure 4.6). In contrast, EA was 9% (2-22%) in diadromous taxa and 13% (8-17%) in freshwater taxa. Additionally, catadromous species were only observed in streams with an annual rainfall exceeding 72cm. APP did not vary predictably with distance to estuaries. However, APP was positively correlated with the EA of freshwater taxa ($R^2 = 0.34$, $p = 0.099$).

4.5 Discussion

Investigating the intricate dynamics of downstream to upstream connectivity, our study centered on the movement of transient (euryhaline and diadromous) taxa within estuaries and coastal rivers. Our dual objectives encompassed the quantification of this connectivity and the assessment of its dependence on key environmental factors, including mean annual precipitation, distance to the sea, elevation, and the presence of dams. We identified significant levels of estuarine assimilation in all of our study sites, with Fundulidae, Cyprinidontidae, and Palaemonidae families playing a central role in facilitating the transfer of estuarine resources into these lotic ecosystems. We found evidence for the strength of that connection being controlled by climate, distance from the estuary, and presence of dams. These results fit within the existing narrative that marine-derived nutrients may subsidize upstream freshwater ecosystems, but expands the concept beyond a focus on mass synchronized migrations of charismatic anadromous species in temperate climates, to consider the role of more inconspicuous euryhaline and diadromous migrants. Lastly, these results underscore the importance of ecological connectivity, which should be a focal point in environmental impact assessments for the management of coastal dams. Below, we relate our findings to our initial expectations and position them within the current body of scientific literature.

Amphidromous Species Modify Coastal Stream Dynamics

Elucidating the combined impact of the community of transient taxa is challenging due to the diversity of species with varying movement patterns. However, the net effect of these connections can have far-reaching ecological consequences within coastal rivers. Our findings indicate that the estuarine contributes to freshwater ecosystems connections observed in coastal plain streams are quantitatively comparable to the impact of salmonid migrations. The logarithmic response ratio of estuarine assimilation above and below Calallen Dam yielded an effect size of 1.9, falling within the range of significant nutrient contributions observed in salmon experiments (ranging from 1.1 to 3.1) (Janetski *et al.* 2009). In temperate ecosystems, nutrient delivery through direct consumption is more evident but contributes less to nutrient uptake than less visible processes such as excretion, carcass decomposition, and subsequent absorption and primary production by autotrophic organisms (Cederholm *et al.* 1999). Likewise, we propose that primary production serves as the main pathway through which marine-derived nutrients enter tropical and subtropical stream food webs. This hypothesis provides a plausible explanation for the intermediary isotopic signatures observed in periphyton, suggesting its potential significance as a key pathway for estuarine nutrient subsidies. This perspective also aligns with the ecological understanding that these nutrients, though less conspicuous in their delivery, play a substantial role in influencing the dynamics of these ecosystems (Twining *et al.* 2017; Benbow, Receveur, and Lamberti 2020). However, additional pathways, including predation, may also be important.

A key difference between seasonal synchronized mass migrations of large organisms and continuous upstream/downstream movement of small migrants is that smaller migrants can act as a subsidy to upstream predator populations. We observed that dryland coastal rivers were dominated by euryhaline fish like sailfin molly (*Poecilia latipinna*), accompanied by gulf killifish (*Fundulus grandis*) and occasional mass aggregations of sheepshead minnow (*Cyprinodon variegatus*) (Kinard, Patrick, and Carvallo 2021). Further up the coast, aggregations of amphidromous *Macrobrachium ohione*, were observed in both fall and spring seasons and this species was present in at least low levels year-round (Carvallo *et al.* 2022). Apart from influencing community composition (Scheuerell *et al.* 2007; Honea and Gara 2009), we hypothesize that the movements of small species like killifish, livebearers, pupfish, and prawn are shaping the dynamics of predator-prey interactions in coastal streams. As amphidromous taxa move back and forth between freshwater and marine environments, they may serve as a reliable prey subsidy for various aquatic predators. This dynamic interaction could fundamentally alter the foraging behaviors and distribution patterns of resident predators. For example, predatory species such as gar (*Lepisosteus spp.*) and largemouth bass (*Micropterus salmoides*) in coastal streams have been observed to actively target migrants during their reproductive migrations (Hunt 1953; Wheeler and Allen 2003; Fletcher *et al.* 2015). This predation pressure can have a substantial impact on the distribution and abundance of predators, creating a complex and dynamic web of ecological relationships within these ecosystems. These intricate interactions underscore the profound influence of euryhaline and diadromous species on the trophic dynamics of coastal stream communities.

Additionally, euryhaline and diadromous taxa in these systems may be playing important functional roles, much like the ecosystem engineering and disturbance effects of salmon spawning (Moore, Schindler, and Scheuerell 2004). For example, species in the genus *Macrobrachium*, which are very common in some of our study sites, occasionally reaching densities greater than 2.5 prawns per m^2, can act as ecosystem engineers, contributing to the breakdown of coarse detritus and sediment displacement (Covich *et al.* 1996; Bauer and Delahoussaye 2008). As a result, migratory prawns play a pivotal role in initiating detrital food web pathways and maintaining a bio-mechanical disturbance regime within the stream's benthic environment. Furthermore, these migratory species not only alter community structures but also influence nutrient cycling (Uno *et al.* 2022). These initial investigations underscore the significance of downstream connectivity to oceans, as well as the impact of watershed and upstream conditions, in comprehending and managing coastal rivers.

Dams Threaten Coastal Stream Linkages

The importance of marine connections to coastal river productivity renders them susceptible to breaks in those connections created by dams, culverts, and other obstructions. Dams are known to pose significant ecological challenges, especially for anadromous fish like salmon, by impeding their upstream spawning migrations (Thorstad *et al.* 2008; Limburg and Waldman 2009; Ferguson *et al.* 2011). This impediment can result in reduced salmon populations and disturbances in ecosystem functioning. Additionally, dams can perturb river flow patterns, impacting sediment transport, habitat availability, and species' life cycles. For example, streams influenced by dams in Puerto Rico displayed a decrease in species diversity, with invasive species frequently taking over the ecosystem (Greathouse *et al.* 2006). Furthermore, these modified streams showed lower productivity and a reduced ability to retain nutrients.

Our results, which indicate that the construction of a 1.5m tall dam on the Nueces River reduced upstream nutrient movement by 65%, serves as an example of this phenomenon in action and fits with the broader literature. Importantly, our findings demonstrate that even relatively small impoundments can serve as significant barriers to migration. Given their potential to negatively impact ecosystems, it is essential to consider their removal when they no longer serve a vital function or when their ecological costs outweigh their benefits. In cases where dams have outlived their intended purpose or where their environmental costs outweigh their benefits, removal can help restore natural river ecosystems (Bednarek 2001). For instance, the removal of the Edwards Dam on the Kennebec River in Maine not only restored migratory fish populations but also improved water quality, making it an exemplar of the positive ecological impacts associated with dam removal (Crane 2009).

Euryhaline Wanderers May Sustain Arid Streams

While precipitation did not emerge as the primary predictor of estuarine assimilation in our study, we did observe that climate plays an important modifying role on the dominance of euryhaline taxa within coastal rivers, with euryhaline taxa being most dominant in more xeric systems in our study. Arid coastal streams are characterized by variable flow patterns, often punctuated by drought periods and low base flows (Bernal *et al.* 2013). These intermittent drying events serve as a natural selective force, favoring species capable of survival or long-distance migration during arid spells (Arthington and Balcombe 2011). Euryhaline species, with their adaptations for moving between freshwater and marine habitats, thrive in such conditions. Their specialized behaviors and life history traits enable them to persist in arid coastal streams, even when these streams become isolated during dry seasons (Warfe *et al.* 2011). In contrast, humid precipitation regimes typically maintain more stable and continuous flow conditions. This consistency allows for a broader array of resident species to establish themselves. These resident species have evolved specific adaptations and life history strategies suited to the predictable and relatively stable environmental conditions found in humid coastal streams (Lytle and Poff 2004; Clarke *et al.* 2010).

The relative importance of these taxa may be more important in arid systems not only because of their relative dominance, but also because these systems may be more nutrient limited. Arid watersheds are characterized by limited terrestrial productivity due to the scarcity of water and nutrients in the soil as well as a lack of lush vegetation (Scholes 2020). In such environments, coastal streams may face challenges in sustaining aquatic life and productivity. However, the input of marine-derived nutrients can play a pivotal role in significantly enhancing the productivity of these coastal streams (Young and Zilz 2021). For example, in arid regions like the Atacama Desert in Chile, where terrestrial nutrient input to streams is minimal due to the harsh, dry conditions and infertile soils (Navarro-González *et al.* 2003), making it difficult for these streams to maintain robust ecosystems (Alvial *et al.* 2013), the presence of diadromous connections due to their proximity to the Pacific Ocean plays a crucial role in subsidizing communities (Bakun and Weeks 2008). Similar effects have been observed in Patagonia, where the introduction of non-native Chinook salmon subsidizes otherwise nutrient limited arid systems (Becker, Pascual, and Basso 2007). These nutrients, including nitrogen and phosphorus, which are essential for supporting aquatic life (Soto *et al.* 2006; Twining *et al.* 2017), compensate for low terrestrial productivity by supporting algal production, which, in turn, supports various invertebrates and fish (Childress, Allan, and McIntyre 2014; Samways, Soto, and Cunjak 2018). This ecological phenomenon highlights the crucial role that marine-derived nutrients play in bolstering coastal stream productivity in arid watersheds, where terrestrial nutrient sources are limited.

Climate Change Implications

The predominance of euryhaline species in arid coastal streams and their contribution of estuarine-derived nutrient subsidies has substantial ecological implications within the context of climate change. Predicted shifts in global precipitation patterns are expected to increase aridity or, alternatively, intensify rainfall in specific regions (Dai, Zhao, and Chen 2018). Arid coastal streams, which typically experience irregular flow patterns and periodic drying episodes, are particularly susceptible to alterations in precipitation. Diminished rainfall can worsen drought conditions, posing challenges for diadromous species in terms of migration and completing their life cycles. Conversely, augmented rainfall can result in more frequent flooding, potentially affecting the timing and success of reproductive migrations.

Changes in the abundance and behaviors of euryhaline and diadromous species can set off a cascade of effects throughout the ecosystem. Modifications in nutrient subsidies, stemming from shifts in the distribution or population sizes of transient species, can influence primary production and the composition of local communities in arid coastal streams. Acknowledging the vulnerability of transient species in the face of climate change underscores the significance of conservation initiatives. For example, one implication of this work is that the negative effects of coastal dams may be exacerbated in areas that become drier in the future. Effective conservation strategies may involve the preservation of habitats, the maintenance of connections between freshwater and marine environments, and the mitigation of additional stressors that could compound challenges linked to climate change.

In summary, climate change can exert significant impacts on euryhaline and diadromous species in arid coastal streams and the ecosystems they inhabit. Adapting to these changes and ensuring the long-term resilience of these species and their associated nutrient contributions necessitates a multifaceted comprehension of their ecological requisites and the formulation of adaptive conservation and management measures.

Inconspicuous Migrant Ecosystem Services Are Cumulative

In tropical regions, migratory fish, invertebrates, and birds rely on the connections between freshwater and marine environments for various aspects of their life cycle, including breeding and feeding (McConnell and Lowe-McConnell 1987; Barthem and Goulding 1997; Smith, Covich, and Brasher 2003). This interdependence has profound implications, as the natural maintenance of connectivity between coastal streams and estuaries not only enhances the resilience of ecosystems but also elevates terrestrial productivity. Typically, diadromous species or euryhaline wanderers have been studied individually or in small groups, with limited attention given to their interactions at the community level. However, there is now a growing recognition of the potential importance of these taxa, particularly in island ecosystems.

For instance, in the tropical streams of Hawaii, the presence of amphidromous species, such as gobies and prawns, significantly enhances nutrient cycling by transferring marine-derived nutrients to the stream ecosystem (Sorensen and Hobson 2005). Similarly, migrations of amphidromous crustaceans have been identified as a critically important part of stream food webs in Puerto Rico and Japan (Kikkert, Crowl, and Covich 2009; Uno *et al.* 2022). However, these island examples may not be unique, as many of the same types of taxa are present in coastal plain regions worldwide. For example, some of same taxa we identify as important in our systems have also been documented in coastal streams of Florida, where the presence of estuarine subsidies leads to increased primary production and supports a diverse community of fish, including species like sailfin molly, gulf killifish, and sheepshead minnow (McBride and Matheson 2011).

Despite the unassuming nature of these species, their ecological significance cannot be overstated. Prominent euryhaline species from our study such as the daggerblade grass shrimp (*Palaemonetes pugio*) and sheepshead minnow (*Cyprinodon variegatus*) exhibit extensive distributions along the Atlantic and Gulf coastlines of North America, spanning from Massachusetts to Mexico. Despite more limited distributions in other observed species like the Gulf killifish (*Fundulus grandis*), these taxa have functionally equivalent counterparts in other regions, such as the mummichog (*Fundulus heteroclitus*). Their widespread distributions highlight the potential interconnectedness of seemingly distinct coastal ecosystems, reinforcing the importance of considering these less conspicuous species. Our results underscore the cumulative contributions of a myriad of species to coastal stream nutrition, supplying information necessary to develop ecosystem- rather than species- conservation models as suggested in the Diadromous Watersheds Ocean Continuum framework (Ouellet *et al.* 2022).

Future Research Directions

Elucidating the cumulative role of euryhaline and diadromouscommunities and evaluating the effects anthropogenic stressors like dam construction on coastal rivers worldwide presents a critical research frontier. Three fundamental research questions stand out as central to advancing our understanding of these complex systems. Firstly, investigations should focus on the specific ecological functions of migratory species within these ecosystems, with a particular emphasis on their roles as ecosystem engineers and their impacts on detrital food web pathways, sediment dynamics, and interactions with resident species. Secondly, understanding the spatial and temporal variability of migratory species' contributions to nutrient cycling is essential. This includes an exploration of how changes in precipitation patterns and the presence of dams affect the consistency of nutrient subsidies in these streams. Thirdly, the influences of dam construction on estuarine-stream connectivity need to be examined comprehensively. This entails a deep dive into the specific characteristics of dams and their implications for the flow of estuarine-derived nutrients and the well-being of coastal stream communities. These research questions collectively offer a pathway toward unraveling the ecological intricacies of euryhaline and diadromous species in coastal subtropical and tropical systems and guiding effective conservation and management strategies.

Conclusions

In summary, our study has shed light on the intricate dynamics of estuary-stream connectivity, with a specific focus on the often under-appreciated euryhaline and diadromous species that thrive in coastal subtropical and tropical systems. Through our research, we unveiled a significant level of estuarine assimilation by these transients, emphasizing their pivotal role in transferring estuarine-derived resources to lotic ecosystems. Our findings challenge the predominant focus on charismatic migrations and island ecosystems, revealing the prevalence of these mixed food webs in coastal rivers worldwide. Moreover, our work underscores a critical knowledge gap in these systems, accentuating the need for a deeper understanding of these less conspicuous, yet highly influential, species.

The division between marine and freshwater scientists, which has sometimes caused coastal systems to fall through the cracks, becomes increasingly evident in this context. Our research emphasizes the importance of bridging these disciplinary boundaries to unravel the complexities of coastal ecosystems comprehensively. The dearth of data on these systems, as highlighted by our findings, beckons for a collective effort to expand the knowledge base in this critical ecological realm.

As we position our results within the current body of scientific literature, it becomes apparent that coastal rivers and their mixed food webs deserve more attention. This awareness opens new avenues for research, prompting scientists to explore and conserve these systems with greater diligence. The ecological resilience and vitality of these coastal ecosystems may hinge on the appreciation and protection of the often-overlooked euryhaline and diadromous species and their integral role in maintaining their delicate balance.

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4.7 Tables

Code	Site Name	USGS ID	Lat	Lon	Rain, cm/yr	Nearest Bay	Bay Dist, km	Elevation, m
No Dam								
SF	San Fernando Creek	8211900	27.773	-98.035	56.7	BB	57.9	50
TR	Tranquitas Creek	8212300	27.517	-97.838	54.2	BB	14.8	18
AR	Aransas River	8189700	28.284	-97.620	68.5	CB	93.3	24
MR	Mission River	8189500	28.292	-97.277	72.9	CB	36.0	6
GC	Garcitas Creek	8164600	28.892	-96.815	84.3	LB	33.2	13
PL	Placedo Creek	8164800	28.724	-96.769	82.1	LB	16.1	8
LN	Lower Nueces River	8211500	27.890	-97.629	62.6	NB	19.8	8
Dam								
PD	Perdido Creek	8177300	28.750	-97.316	78.7	CB	91.1	45
WM	West Mustang Creek	8164503	29.071	-96.467	94.2	LB	61.2	17
EM	East Mustang Creek	8164504	29.071	-96.417	95.0	LB	61.5	19
UN	Upper Nueces River	8211500	27.876	-97.626	62.6	NB	26.4	6
Estuary								
BB	Baffin Bay		27.356	-97.695				
NB	Nueces Bay		27.825	-97.470				
CB	Copano Bay		28.120	-97.022				
HB	Hynes Bay		28.393	-96.838				
LB	Lavaca Bay		28.691	-96.661				

Table 4.01: Sample Characteristics

Sampling location climate and geographic details. Annual rainfall and site elevation were obtained from the USGS Gages-ii database. Bay distance is the distance within the waterway, assessed using a path distance tool in ArcMap.

Formula	Adj.R^2^	AIC	Rain	Distance	Rain:Distance	Elevation	*p*
EA ~ Rain + Elevation + Distance	0.68	129	-1.60				2.8e-03
EA ~ Rain + Elevation + Distance	0.68	129				-0.69	1.2e-01
EA ~ Rain + Elevation + Distance	0.68	129		-0.60			2.7e-02
EA ~ Rain + Distance	0.64	130	-1.21				6.9e-03
EA ~ Rain + Distance	0.64	130		-0.85			9.1e-04
EA ~ Rain * Distance	0.62	132	-1.74				5.7e-02
EA ~ Rain * Distance	0.62	132		-2.16			2.6e-01
EA ~ Rain * Distance	0.62	132			0.02		4.8e-01

EA = Estuarine Assimilation (%)

Rain (cm/yr), Estuary Distance (km), Elevation (m)

Table 4.02 Multiple Regression: Predicting Estuarine Assimilation

Regression and coefficient statistics for the top three AIC ranked models predicting average community estuarine assimilation. Predictors include annual rainfall (cm/yr), estuary distance (km), and elevation (m). Within formulas, asterisks indicate the inclusion of an interaction component.

4.8 Figures

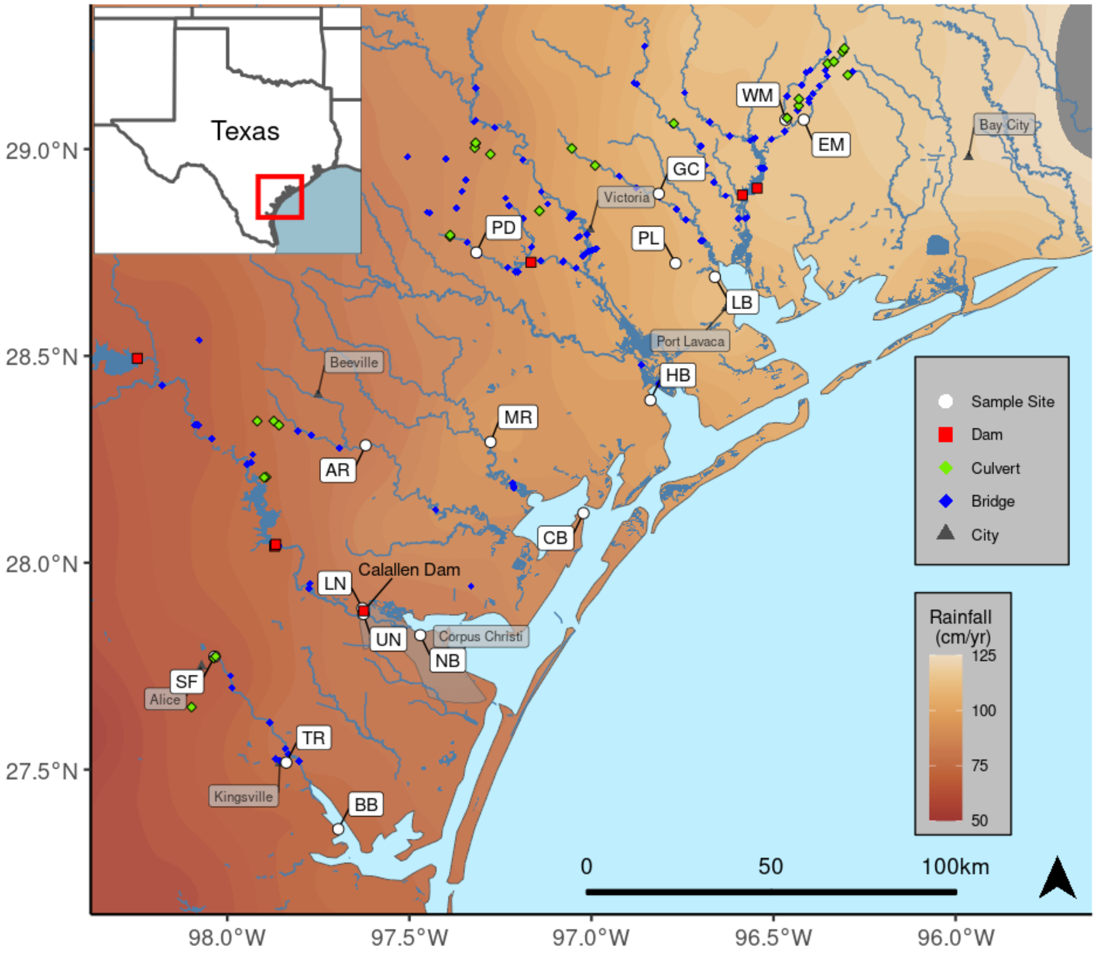


Figure 4.1: Study Region Map

Stable Isotope collection sites (labeled in white), where primary producers, fish, invertebrates, and environmental data were collected in January 2020. An overlay indicates the average annual precipitation (white-tan-green) from USGS PRISM data (1981-2010). Point features crossing streams of interest include dams (red), culverts (green), and bridges (blue). Cities and urban areas (labeled in grey) were included for geographic reference. This map was made with the National Hydrography Dataset and Natural Earth.

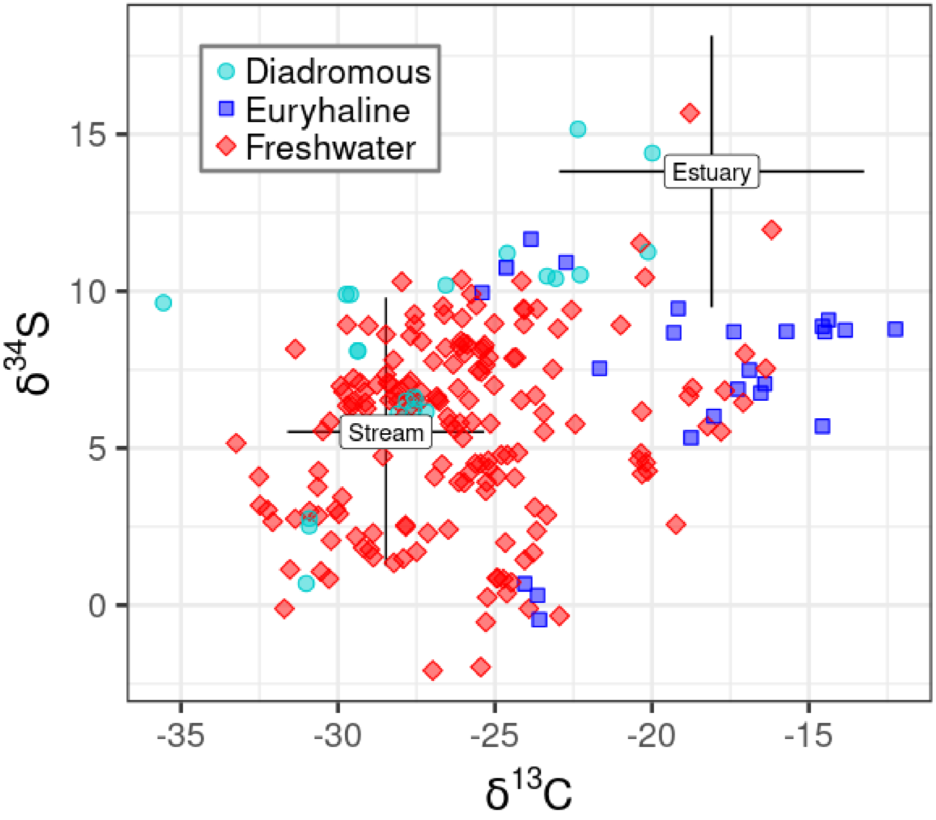


Figure 4.2: Fish and Invertebrate Signatures at Coastal Rivers: δ^{34}S versus δ^{13}C

$\delta\delta^{34}$S versus δ^{13}C values for fish and invertebrates, shaped and colored according to their migratory habits. Labels mark mean source signatures from streams and estuaries with cross-hairs extending to the 95% confidence interval.

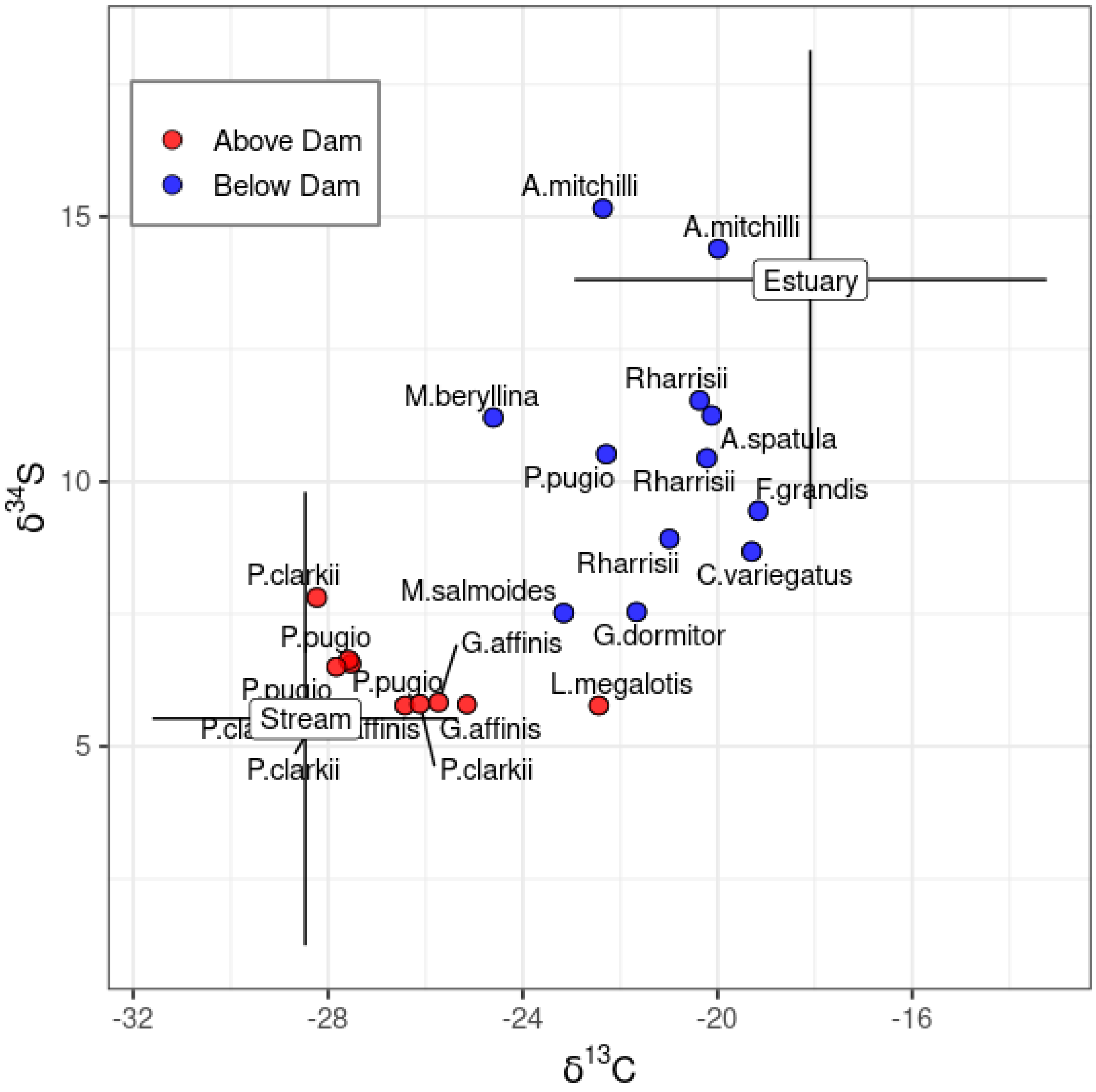


Figure 4.3: Fish and Invertebrate Signatures at Calallen Dam: $\delta^{34}S$ versus $\delta^{13}C$

$\delta^{34}S$ versus $\delta^{13}C$ values for fish and invertebrates, shaped and colored according to their migratory habits. Labels mark mean source signatures from streams and estuaries with cross-hairs extending to the 95% confidence interval.

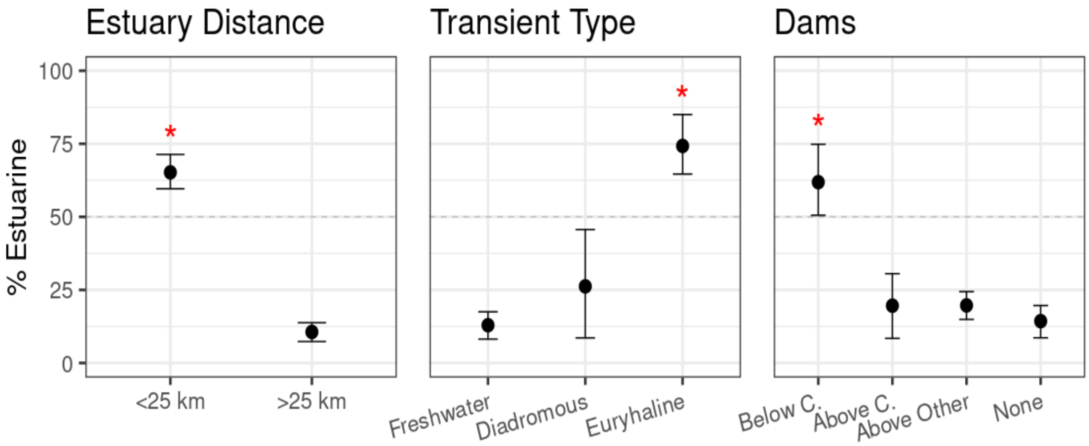


Figure 4.4: Estuarine Assimilation Comparisons: Distance, Transient-Type, Dams

Estimated estuarine assimilation for fish and invertebrates categorized by estuary distance (left), transient type (middle), and Impediment by Calallen Dam (right). Red stars indicate mean-comparisons with non-overlapping credible intervals. Estimates and 95% credible intervals were obtained from Bayesian mixing models using $\delta^{13}C$ and $\delta^{34}S$.

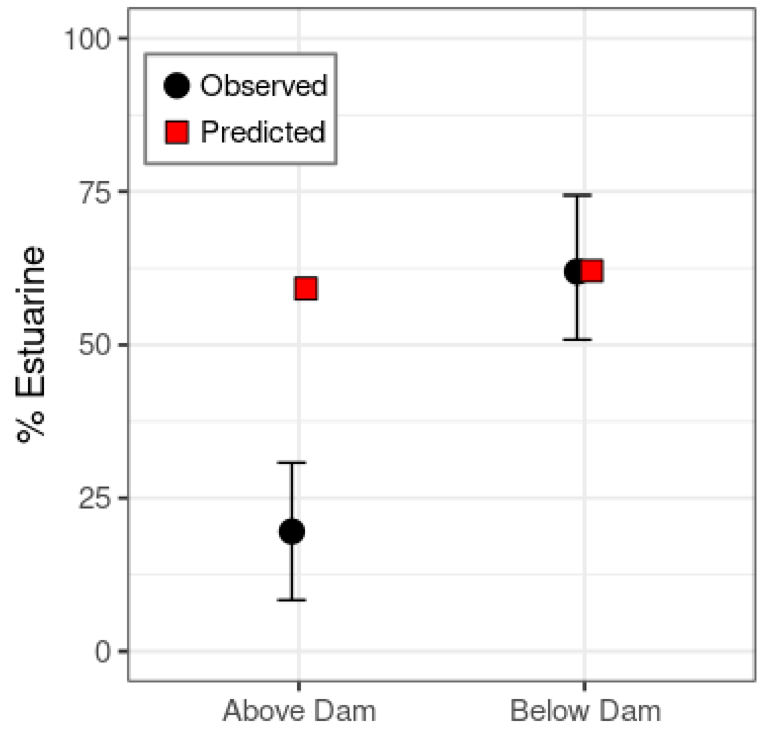


Figure 4.5: Estuarine Assimilation at Calallen Dam

Observed vs predicted estuarine assimilation for fish and invertebrates collected above and below Calallen Dam on the Nueces River. Observations with 95% credible intervals were obtained from Bayesian mixing models using $\delta^{13}C$ and $\delta^{34}S$. Predicted values came from fitted regression using estuary distance and annual rainfall at sites without dams.

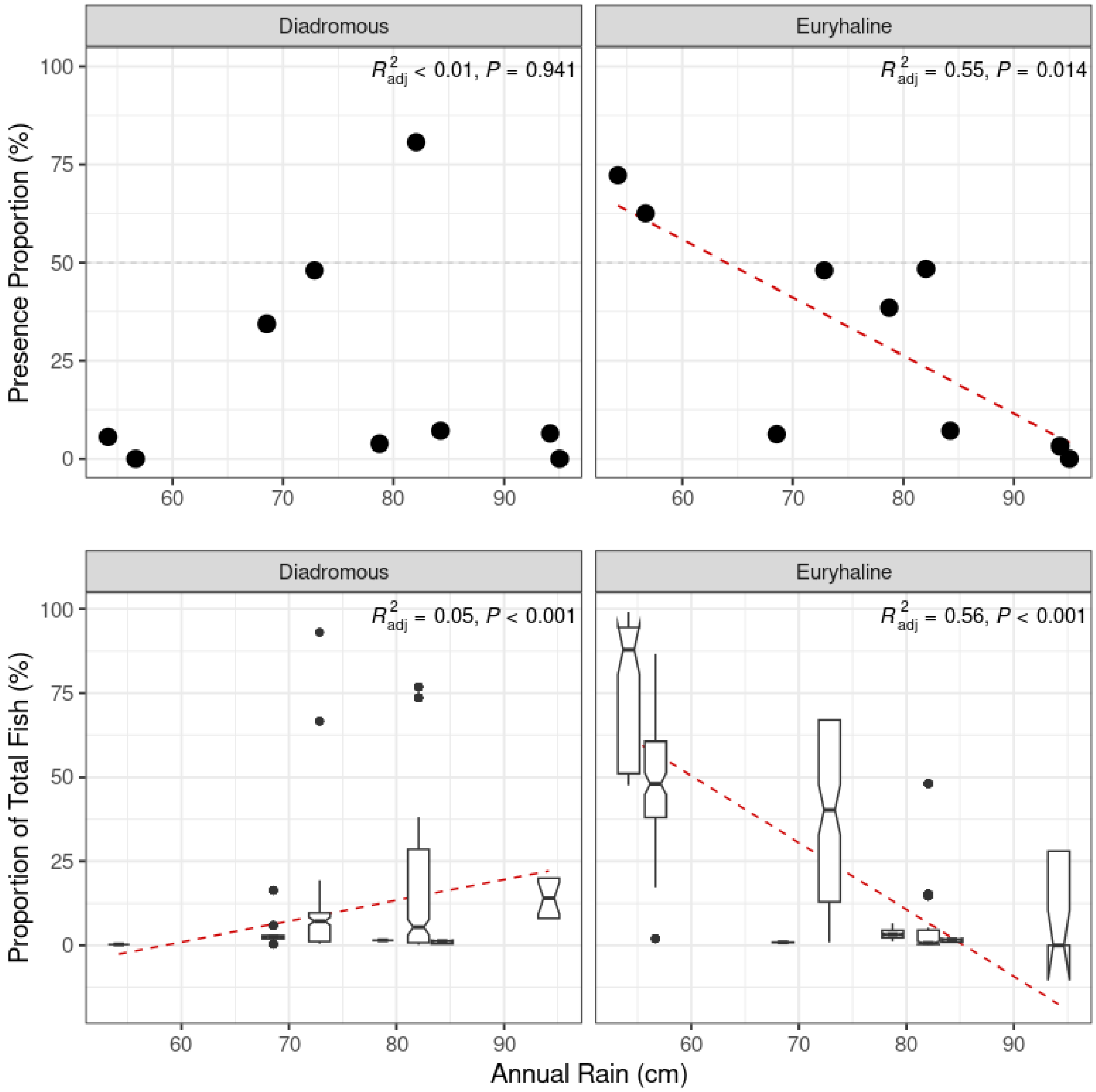
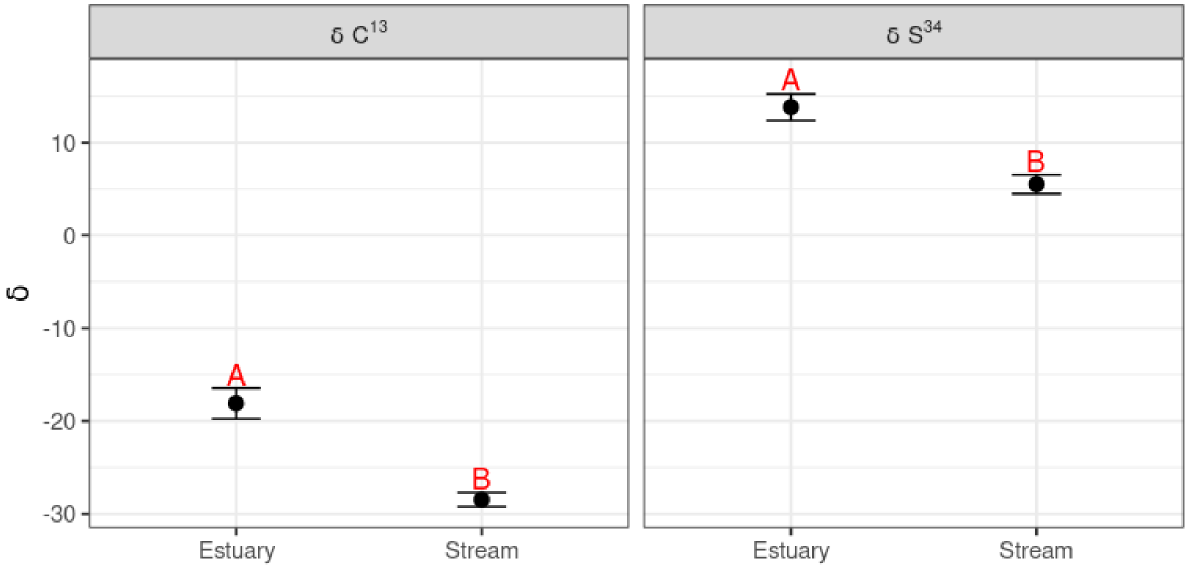


Figure 4.6: Transient Frequencies and Community Proportions vs Annual Rainfall

The top two panels display Presence Probability (PP) for Diadromous (left) and Euryhaline (right) fish and invertebrates versus annual rainfall. PP is the percentage of events (within each site) containing at least one transient from monitoring surveys (2017-2020). The lower panels display the proportion of the total fish community constituted by diadromous (left) or euryhaline (right) species for sampling events in which they were present.4.9 Appendix



Appendix 4.1: Stream vs Estuary Signatures Figure

Bootstrapped mean and 95% confidence intervals for primary producer $\delta^{13}C$ and $\delta^{34}S$ signatures for streams and estuaries. Red stars indicate confidence intervals do not overlap.

Isotope	Mean (δ)	2.5% (δ)	97.5% (δ)
Estuary			
Carbon-13	-18.1	-19.8	-16.5
Sulfur-34	13.8	12.4	15.2
Stream			
Carbon-13	-28.5	-29.2	-27.7
Sulfur-34	5.5	4.5	6.5

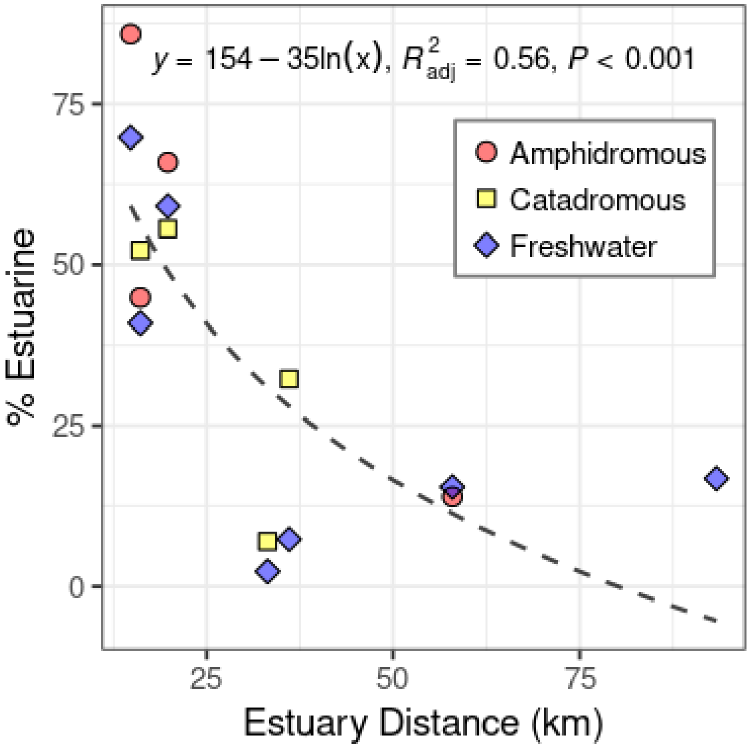
Appendix 4.02: Stream vs Estuary Signatures Table

Bootstrapped mean and 95% confidence intervals for primary producer $\delta^{13}C$ and $\delta^{34}S$ signatures for streams and estuaries.

Transient Type	Estimate (δ)	2.5% (δ)	97.5% (δ)
Site			
AR	16.8	9.6	23.7
EM	25.6	16.2	34.8
GC	2.1	0.4	5.0
LN	61.9	50.2	74.3
MR	5.4	1.0	13.2
PD	31.0	21.2	40.5
PL	42.8	33.8	52.0
SF	14.1	5.2	22.8
TR	80.9	71.3	91.8
UN	19.4	8.2	30.3
WM	12.7	6.2	19.1
Distance			
<25 km	65.2	59.6	71.3
>25 km	10.7	7.5	13.9
Transient			
Euryhaline	72.5	63.6	82.0
Diadromous	9.4	1.7	21.8
Freshwater	12.9	8.3	17.3
Dam			
Above C.D.	19.6	8.3	30.7
Below C.D.	61.9	50.9	74.4
Above Other	19.7	15.2	24.4
None	14.3	8.4	19.7

Appendix 4.03: Estuarine Assimilation vs Transient Type

Estimated estuarine assimilation for fish and invertebrates categorized by site, estuary-distance, transient type, and dam. Estimates and 95% credible intervals were obtained from Bayesian mixing models using $\delta^{13}C$ and $\delta^{34}S$.



Appendix 4.04: Modeling Estuarine Assimilation

Estimated estuarine assimilation plotted against the distance to the nearest estuary. Points representing site averages are shaped and colored according to migratory habit. The dotted curve depicts a fitted linear regression with log-transformed estuary distance. Estimates were obtained from Bayesian mixing models using δ^{13}C and δ^{34}S.

Predictors	R^2	Adj R^2	*p*-value	AIC	n
Rain + Elevation + Distance	0.75	0.68	1.20e-03	129	15
Rain + Distance	0.69	0.64	9.36e-04	130	15
Rain * Distance	0.70	0.62	3.14e-03	132	15
Rain + Elevation	0.60	0.54	3.84e-03	134	15
Rain * Elevation	0.64	0.54	9.12e-03	135	15
Distance	0.41	0.37	9.92e-03	138	15
Rain	0.19	0.13	1.06e-01	143	15
Rain^2	0.19	0.13	1.06e-01	143	15
Rain^2	0.19	0.13	1.06e-01	143	15
Elevation	0.11	0.04	2.33e-01	144	15
Elevation	0.11	0.04	2.33e-01	144	15

Appendix 4.05: Multiple Regression: AIC Ranking

Regression statistics, ordered by AIC, for first and second order equations predicting average community estuarine assimilation. Predictors include annual rainfall (cm/yr), estuary distance (km), and elevation (m). Asterisks indicate equations with an interaction component.

Location	Rain (cm/yr)	Distance (km)	Predicted	observed	Difference
Below Dam	62.600	19.795	57.298	60.197	2.899
Above Dam	62.600	26.393	51.284	19.929	-31.355

Appendix 4.06: Multiple Regression: Calallen Dam Predictions

Predicted versus observed average estuarine assimilation above and below Calallen Dam. Predictions were obtained using the “best” fit equation from multiple regression analysis. Observed estimates were obtained from Bayesian mixing models using $\delta^{13}C$ and $\delta^{34}S$.

Euryhaline	Amphidromous	Catadromous
Adinia xenica	Anchoa mitchilli	Anguilla rostrata
Brevoortia patronus	Agonostomus monticola	Atractosteus spatula
Cyprinodon variegatus	Rhonciscus crocro	Dormitator maculatus
Dorosoma cepedianum	Trinectes maculatus	Mugil cephalus
Fundulus grandis	Macrobrachium ohione	
Gobiomorus dormitor	Palaemonetes pugio	
Menidia beryllina		
Menidia menidia		
Poecilia latipinna		
Callinectes sapidus		
Minuca longisignalis		

Appendix 4.07: List of Transient Species

Transient fish and invertebrate species categorized as euryhaline or diadromous (catadromous, and amphidromous).

Order	Species
Fish	
Centrarchiformes	L. auritus
Centrarchiformes	L. cyanellus
Centrarchiformes	L. gulosus
Centrarchiformes	L. humilis
Centrarchiformes	L. macrochirus
Centrarchiformes	L. megalotis
Centrarchiformes	M. salmoides
Cichliformes	H. cyanoguttatus
Cichliformes	O. aureus
Cyprinodontiformes	F. notatus
Cyprinodontiformes	G. affinis
Perciformes	E. gracile
Siluriformes	I. punctatus
Siluriformes	N. gyrinus
Invertebrate	
Decapoda	P. clarkii
Decapoda	Rharrisii
Gastropoda	Melanoides

Appendix 4.08: List of Freshwater Species

Freshwater (Potamodromous) fish and invertebrate species and their respective taxonomic order.

Location	δ Carbon-13	δ Sulfur-34
Estuary - Algae		
BB	-17.5, 3.1 (2)	17.1, 0.8 (2)
CB	-23.2, (1)	19.9, (1)
HB	-16.7, 4.3 (2)	18.7, 1.8 (2)
LB	-17.5, (1)	17.2, (1)
NB	-23.6, 0.2 (2)	19.0, 0.6 (2)
Estuary - Detritus		
BB	-14.5, 0.9 (2)	7.52, 4.0 (2)
CB	-13.1, 0.2 (2)	11.0, 2.6 (2)
HB	-17.0, 2.6 (4)	14.6, 0.6 (4)
LB	-20.5, 7.1 (2)	9.81, 0.3 (2)
NB	-15.4, 0.8 (2)	9.68, 4.5 (2)
Estuary - Macrophyte		
BB	-16.1, 5.1 (3)	16.5, 2.9 (3)
CB	-19.5, 6.4 (4)	15.2, 2.6 (4)
HB	-13.4, (1)	13.6, (1)
LB	-20.2, 10.1 (2)	13.9, 5.7 (2)
NB	-21.9, 6.4 (3)	7.78, 1.9 (3)
Stream - Algae		
AR	-29.0, 0.7 (3)	2.33, 0.09 (3)
GC	-31.2, 0.3 (2)	4.66, 0.3 (2)
MR	-29.7, 2.7 (2)	11.2, 1.6 (2)
PD	-23.4, (1)	10.1, (1)
PL	-25.6, 0.2 (2)	12.5, 0.04 (2)
TR	-18.7, (1)	9.06, (1)
Stream - Detritus		
AR	-27.8, 3.3 (6)	4.04, 0.7 (6)
EM	-29.1, 1.0 (3)	5.5, 0.9 (3)
GC	-29.2, 1.4 (7)	0.697, 4.0 (7)
MR	-27.4, 1.9 (3)	4.26, 2.9 (3)
PL	-28.4, 1.4 (2)	5.46, 0.5 (2)
SF	-26.8, 3.0 (2)	1.62, 0.007 (2)
TR	-29.9, 1.7 (3)	9.01, 1.1 (3)
WM	-27.9, 0.4 (2)	2.61, 2.3 (2)
Stream - Macrophyte		

Location	δ Carbon-13	δ Sulfur-34
AR	-30.3, 1.3 (3)	3.81, 0.7 (3)
EM	-27.9, 0.07 (2)	8.2, 0.0 (2)
GC	-30.4, 1.9 (4)	4.63, 1.2 (4)
MR	-30.2, 1.6 (3)	9.12, 0.5 (3)
PD	-28.7, 1.2 (2)	9.64, 1.7 (2)
SF	-30.1, (1)	-1.54, (1)
WM	-29.2, 2.6 (3)	7.23, 1.8 (3)
Stream - Periphyton		
AR	-23.0, (1)	4.25, (1)
EM	-21.2, 0.5 (2)	9.13, 0.3 (2)
GC	-23.4, (1)	11.3, (1)
MR	-23.8, (1)	14.5, (1)
PD	-27.3, (1)	9.1, (1)
PL	-20.5, (1)	4.11, (1)
SF	-15.2, (1)	12.9, (1)
TR	-25.6, (1)	11.9, (1)
Stream - Riparian Leaves		
GC	-30.4, 1.7 (5)	1.03, 2.0 (5)
PD	-29.2, (1)	16.9, (1)
TR	-23.4, 7.3 (4)	11.8, 1.8 (4)

Appendix 4.09: Basal Resource δ^{13}C and δ^{34}S

Basal resource δ^{13}C and δ^{34}S summary statistics at estuary and stream sites. Cell contents contain “mean, standard deviation (n)”.

Location	δ Carbon-13	δ Sulfur-34
Centrarchidae		
AR	-25.6, 1.3 (21)	3.83, 1.3 (21)
EM	-26.3, 1.4 (10)	8.08, 0.7 (10)
GC	-30.3, 1.4 (16)	2.53, 1.1 (16)
MR	-30.1, 4.4 (2)	1.54, 5.1 (2)
PD	-25.3, 1.0 (7)	7.36, 0.8 (7)
PL	-23.7, 0.6 (8)	9.21, 0.7 (8)
SF	-21.6, 1.8 (8)	3.13, 2.5 (8)
TR	-18.4, 0.5 (4)	6.53, 0.6 (4)
WM	-27.9, 1.0 (23)	6.56, 0.6 (23)
Cichlidae		
AR	-26.4, 1.3 (3)	3.46, 0.8 (3)
MR	-31.4, (1)	8.16, (1)
PD	-27.2, 1.0 (3)	9.98, 0.6 (3)
SF	-24.8, 0.8 (4)	0.368, 2.2 (4)
TR	-18.2, 1.5 (2)	4.51, 2.7 (2)
Cyprinodontidae		
TR	-14.1, 1.3 (5)	8.81, 0.2 (5)
Eleotridae		
PL	-26.6, (1)	10.2, (1)
Fundulidae		
PD	-25.8, (1)	9.91, (1)
TR	-17.2, 0.9 (6)	7.04, 1.1 (6)
Ictaluridae		
AR	-26.7, (1)	4.48, (1)
EM	-25.7, 0.5 (3)	7.6, 0.1 (3)
GC	-30.4, 0.2 (2)	0.955, 0.2 (2)
PD	-27.0, 2.8 (2)	8.94, 0.05 (2)
Pecidae		
WM	-29.6, 0.3 (3)	7.1, 0.1 (3)
Poeciliidae		
GC	-30.5, 0.2 (4)	3.56, 1.5 (4)
MR	-29.7, (1)	8.93, (1)
PL	-23.7, 1.0 (3)	11.1, 0.5 (3)
SF	-23.7, 0.2 (6)	1.24, 1.3 (6)

Location	δ Carbon-13	δ Sulfur-34
TR	-16.9, 2.0 (7)	6.6, 1.6 (7)
WM	-28.7, 1.4 (3)	6.22, 0.3 (3)

Appendix 4.10: Fish δ^{13}C and δ^{34}S at Stream Sites

Invertebrate δ^{13}C and δ^{34}S summary statistics grouped by taxonomic family at stream sites. Cell contents contain “mean, standard deviation (n)”.

Location	δ Carbon-13	δ Sulfur-34
Aeshnidae		
AR	-28.6, (1)	4.02, (1)
Baetidae		
GC	-35.4, (1)	3.71, (1)
Belastomatidae		
EM	-31.3, (1)	11.0, (1)
Cambaridae		
AR	-26.0, (1)	5.33, (1)
EM	-26.4, 0.8 (3)	8.35, 0.05 (3)
GC	-31.8, 0.4 (2)	1.9, 1.1 (2)
PD	-26.4, 0.5 (3)	8.38, 0.7 (3)
PL	-26.3, 0.6 (3)	9.44, 0.2 (3)
SF	-24.8, 0.3 (5)	0.61, 0.3 (5)
WM	-29.6, 0.1 (3)	6.38, 0.07 (3)
Coenagrionidae		
AR	-26.1, (1)	4.41, (1)
EM	-31.8, (1)	8.59, (1)
GC	-31.2, (1)	1.4, (1)
MR	-32.7, (1)	8.66, (1)
Corduliidae		
GC	-31.3, (1)	-0.57, (1)
Gomphidae		
EM	-29.0, (1)	7.13, (1)
GC	-29.6, (1)	0.11, (1)
Gyrinidae		
MR	-32.1, (1)	8.99, (1)
Hyalellidae		
EM	-30.9, (1)	8.05, (1)
GC	-33.9, (1)	2.13, (1)
Naucoridae		
MR	-21.8, (1)	10.7, (1)
Nepidae		
EM	-21.0, (1)	8.8, (1)
Palaemonidae		

Location	δ Carbon-13	δ Sulfur-34
EM	-29.4, 0.02 (2)	8.1, 0.0 (2)
GC	-30.9, 0.06 (3)	1.99, 1.1 (3)
MR	-35.6, (1)	9.63, (1)
PD	-29.7, 0.09 (2)	9.9, 0.0 (2)
PL	-23.2, 0.2 (2)	10.4, 0.06 (2)
WM	-27.6, 0.5 (3)	6.17, 0.08 (3)
Panopeidae		
CB	-18.8, (1)	15.7, (1)
Physidae		
EM	-28.9, (1)	9.82, (1)
Planorbidae		
EM	-33.5, (1)	9.11, (1)
Portunidae		
PL	-25.4, (1)	9.95, (1)
Thiaridae		
PD	-16.2, (1)	12.0, (1)

Appendix 4.11: Invertebrate δ^{13}C and δ^{34}S at Stream Sites

Invertebrate δ^{13}C and δ^{34}S summary statistics grouped by taxonomic family at stream sites. Cell contents contain “mean, standard deviation (n)”.

Location	δ Carbon-13	δ Sulfur-34
Stream - Fish - Atherinopsidae		
Below Dam	-24.6, (1)	11.2, (1)
Stream - Fish - Centrarchidae		
Above Dam	-22.4, (1)	5.77, (1)
Below Dam	-23.2, (1)	7.52, (1)
Stream - Fish - Cyprinodontidae		
Below Dam	-19.3, (1)	8.68, (1)
Stream - Fish - Eleotridae		
Below Dam	-21.7, (1)	7.54, (1)
Stream - Fish - Engraulidae		
Below Dam	-21.2, 1.7 (2)	14.8, 0.5 (2)
Stream - Fish - Fundulidae		
Below Dam	-19.2, (1)	9.45, (1)
Stream - Fish - Lepisosteidae		
Below Dam	-20.1, (1)	11.2, (1)
Stream - Fish - Poeciliidae		
Above Dam	-25.8, 0.6 (3)	5.8, 0.03 (3)

Appendix 4.12: Callen Dam Fish δ^{13}C and δ^{34}S

Fish δ^{13}C and δ^{34}S summary statistics grouped by taxonomic family sampled above and below Calallen Dam. Cells contain “mean, standard deviation (n)”.

Location	δ Carbon-13	δ Sulfur-34
Stream - Invertebrate - Belastomatidae		
Above Dam	-27.5, (1)	6.92, (1)
Stream - Invertebrate - Cambaridae		
Above Dam	-27.8, 1.1 (4)	6.14, 1.1 (4)
Stream - Invertebrate - Chironomidae		
Below Dam	-25.6, (1)	3.45, (1)
Stream - Invertebrate - Coenagrionidae		
Above Dam	-29.1, 0.2 (2)	5.8, 0.2 (2)
Stream - Invertebrate - Gomphidae		
Above Dam	-26.5, (1)	6.18, (1)
Stream - Invertebrate - Hyalellidae		
Above Dam	-26.2, (1)	5.82, (1)
Stream - Invertebrate - Naucoridae		
Above Dam	-26.2, (1)	8.17, (1)
Stream - Invertebrate - Palaemonidae		
Above Dam	-27.6, 0.2 (3)	6.56, 0.07 (3)
Below Dam	-22.3, (1)	10.5, (1)
Stream - Invertebrate - Panopeidae		
Below Dam	-20.5, 0.4 (3)	10.3, 1.3 (3)
Stream - Invertebrate - Physidae		
Above Dam	-26.3, (1)	6.11, (1)

Appendix 4.13: Callen Dam Invertebrate δ^{13}C and δ^{34}S

Invertebrate δ^{13}C and δ^{34}S summary statistics grouped by taxonomic family at Calallen Dam. Cells contain “mean, standard deviation (n)”.

Chapter 5: The Interplay of Precipitation Patterns, Hydrological Extremes, and Season on Fish Community Structure

5.1 Abstract:

In this study, we investigated the ecological impacts of hydrological disturbances on stream fish communities, considering the interplay among floods, droughts, seasonality, and long-term precipitation patterns. Conducted at nine wadeable streams in South-Central Texas over irregular intervals from 2017 to 2020, our research integrated fish collection and comprehensive environmental assessments, utilizing USGS gauges. Employing linear regression, mixed-effects models, and structural equation models, we explored the effects of extreme hydrological events and seasonality on fish community abundance, diversity, and composition.

Our results highlight the nuanced relationship between antecedent maximum flows and fish abundance or diversity, contingent on the long-term precipitation regime. Semi-arid sites exhibited reduced abundances and increased diversity following higher antecedent flows, while mesic sites showed higher densities and lower diversity with rising antecedent maximum flows. The impacts of drought events were also influenced by the long-term precipitation regime, with increased annual rainfall correlating with heightened species diversity and compositional shifts after droughts. Hydrological droughts during hot and arid summers disrupted regional abundance and diversity patterns, revealing a reduction in centrarchid abundances and the resilience of poeciliids.

Notably, our findings challenge prevailing precepts regarding the uniform positive or negative effects of floods on ecosystems. Instead, we highlight that these effects are intricately linked to the historic climate of the region, providing a more nuanced perspective on the ecological consequences of hydrological disturbances. Such insights into the region-specific nature of flood effects contribute to a more refined understanding of the interplay between climate, hydrology, and fish communities, paving the way for more context-sensitive conservation and management strategies.

5.2 Introduction

Hydrologic Disturbances Shape Stream Ecosystems and Resilience

Floods and droughts actively impose physical stresses on stream fish communities, playing a pivotal role in shaping the dynamics of these aquatic ecosystems. The overarching importance of hydrologic disturbance on stream structure and function cannot be overstated (Resh et al. 1988, Stanley et al. 2010, Mirus et al. 2017). These disturbances create a mosaic of habitat types within streams, fostering habitat heterogeneity that supports a diverse array of species with varying ecological requirements (Lake 2000). Floods and high-flow events transport essential nutrients and organic matter downstream, influencing primary productivity and nutrient cycling (Bernal et al. 2013, Chen et al. 2022). These fluctuations in flow also impact the composition of stream communities, with some species adapted to high-flow conditions and others to droughts (Lytle and Poff 2004, Magalhães et al. 2007). Hydrologic disturbances drive shifts in competitive interactions, predation patterns, and overall community structure

(Dorn and Cook 2015, Marino et al. 2017). Moreover, they provide a pulse of food resources, contributing to the functioning of these ecosystems (Junk et al. 1989, Harms and Grimm 2010). Understanding how stream organisms adapt and respond to these disturbances is essential to deciphering the resilience of stream ecosystems in the face of changing climate conditions. Furthermore, the ecosystem services provided by streams, such as water purification, flood regulation, and support for fisheries, are intricately tied to the disturbance regime, underscoring the critical importance of managing and conserving these freshwater resources (Krauze and Wagner 2008).

Unraveling the Interplay Between Long-Term Precipitation and Hydrological Disturbances

While considerable progress has been made in understanding the ecological effects of hydrological disturbances on fish communities, limited knowledge exists regarding the influence of long-term precipitation patterns on the resilience of stream communities to such disturbances. Existing research has primarily focused on the immediate impacts of events such as floods and droughts, elucidating their effects on fish populations and ecosystem dynamics. However, the long-term implications of historical precipitation patterns and their role in shaping the ability of stream communities to withstand and recover from hydrological disturbances have received comparatively less attention.

Recent studies in semi-arid and mesic regions have emphasized the significance of long-term precipitation patterns as a crucial factor in shaping the resilience of stream ecosystems. The Colorado and Rio Grande river basins provide case studies of how changes in precipitation patterns and human interventions, such as dam construction and water diversions, have disrupted the natural flow regimes (Propst et al. 2008, Gido et al. 2013, Ruhí et al. 2016). Native fish species, adapted to historical hydrology including floods and droughts, now face challenges due to altered flow patterns. Reduced floods impact spawning habitats, while artificial releases from dams can disturb ecological balance. This illustrates the need for sustainable water management and conservation efforts in semi-arid regions to preserve the resilience of native fish communities. These studies emphasize the intricate connection between precipitation patterns and hydrological disturbances, suggesting that alterations in historical precipitation patterns can drive adaptation in fish communities.

Despite this emerging understanding, a comprehensive assessment of the intricate relationships between long-term precipitation patterns and hydrological disturbances, and their cumulative effects on stream communities, remains an essential research frontier. Bridging this knowledge gap is fundamental for developing effective strategies to mitigate the impacts of climate change on freshwater ecosystems and to enhance our ability to conserve and manage these critical environments (Leigh et al. 2012, Yang et al. 2018).

Long-term Precipitation Influences Resilience

Semi-arid and mesic regions differ in their sensitivity to intra-annual variation in rainfall. Semi-arid regions, marked by their inherent water limitations, are particularly sensitive to slight fluctuations in precipitation. In these areas, hydrologic flashiness, characterized by prolonged drought interspersed with sudden, intense flash floods, amplifies the consequences of even minor changes in rainfall patterns (Arthington and Balcombe 2011). The southwestern United States, a typical semi-arid region, faces severe water scarcity and ecosystem stress during extended dry periods. These periods impact not only fish communities but also riparian vegetation and wildlife (Stromberg et al. 2007, 2013). Importantly, fish communities in semi-arid regions have often adapted to their historical precipitation regimes and may struggle to cope with the rapid changes induced by climate change, which can disrupt the familiar hydrological patterns to which they are acclimated (Pool and Olden 2015, Magoulick et al. 2021).

In contrast, mesic regions, characterized by higher average rainfall and greater water availability, tend to exhibit a comparatively high resilience to extreme disturbances (Newbery et al. 1999) and lower sensitivity to rainfall fluctuations (Ciemer et al. 2019). Drought-effects in tropical rainforests are not explicitly negative (Gutiérrez-Fonseca et al. 2020), implying that even during periods of reduced rainfall, these regions maintain a consistent water supply compared to more arid areas. Systems with more abundant rainfall should be less likely to experience acute ecological disruptions due to short-term variations in precipitation. Understanding these differences in sensitivity and the potential challenges faced by fish communities in adapting to changing precipitation regimes is crucial for managing and conserving freshwater ecosystems in the face of evolving climate patterns. These insights also aid in prioritizing conservation efforts in regions most susceptible to drought-related impacts.

Integrating Hydrological Disturbances into Climate Change Perspectives for Lotic Ecosystems

Incorporating the effects of hydrological disturbances on stream communities into a climate change framework expands our understanding of lotic systems and equips us to predict the outcomes of climate change (Filipe et al. 2013, Hotaling et al. 2017). This approach enables a more comprehensive assessment of the interplay between these two drivers, shedding light on their combined impacts on freshwater ecosystems. By discerning how climate change influences precipitation patterns and how subsequent hydrological disturbances shape aquatic communities (Chalise *et al.* 2021), we gain a more holistic view of ecosystem dynamics. This integrated perspective allows for the anticipation of shifts in lotic system structure and function and improves our ability to engineer desirable flow regimes (Tonkin et al. 2021). It also aids in predicting responses in aquatic communities, identifying at-risk species and habitats (Jarić et al. 2019, Lintermans et al. 2020, Barbarossa et al. 2021), and guiding effective conservation efforts to safeguard these crucial ecosystems amid ongoing climate change challenges.

Exploring Lotic Communities Along a Natural Precipitation Gradient in South-Central Texas

The spatial distribution of lotic communities along a natural precipitation gradient in South-Central Texas provides a singular opportunity for the application of a space-for-time substitution approach, especially with respect to studying the impacts of precipitation (Kinard et al. 2021, Carvallo et al. 2022). This region stands out due to its wind-driven precipitation gradient occurring over a relatively short geographic span, while maintaining consistent geological and altitude conditions. Furthermore, the notably steep rainfall gradient ensures equitable regional access to the species pool, distinguishing it from other space-for-time substitution studies often conducted on larger continental scales (Damgaard 2019). By investigating how fish communities respond to hydrological disturbances within this unique context of short geographic range, we can leverage these spatial trends to predict the temporal effects of climate change-induced hydrological events. This method empowers us to forecast the potential evolutionary trajectories of lotic ecosystems under evolving climate scenarios, facilitating proactive ecological conservation and management strategies to address the challenges posed by climate change.

Linking Fish Community Resilience to Precipitation Patterns and Flow Conditions

We propose that the local adaptation of fish communities to flood or drought disturbances is intrinsically tied to their long-term precipitation regime. In arid regions with frequent and severe low-flow periods, we expect that local fish communities have developed specific adaptations to survive and persist through drought events (Lytle and Poff 2004, Hershkovitz and Gasith 2013, Carvallo et al. 2022). These adaptations are likely to encompass a range of physiological and behavioral traits that enhance their resilience in the face of water scarcity. Conversely, in mesic and humid environments where stormy and flood-prone conditions are more prevalent, fish communities are anticipated to exhibit distinct sets of adaptations that enable them to thrive amidst flood events (Ortega et al. 1991, Suren and Jowett 2006, Díaz et al. 2008, Bonada and Resh 2013). These overarching concepts will guide our forthcoming predictions and empirical investigations, offering valuable insights into the intricate relationships between long-term precipitation patterns and the responses of fish communities to hydrological disturbances in lotic ecosystems.

We hypothesize that the relationship between fish community resilience and antecedent flow conditions (both minimum and maximum) is contingent upon the long-term precipitation regime. To test this hypothesis, we will employ linear regression, using the slope parameter extracted from linear mixed effects models predicting fish abundance or diversity based on antecedent minimum and maximum flows. The null hypothesis assumes similar relationships across the precipitation gradient, while our alternative hypothesis posits that fish communities in semi-arid sites will exhibit positive responses to drought events and negative responses to floods. Conversely, we expect mesic sites to respond positively to floods and negatively to droughts. These predictions are founded on the premise that long-term adaptation to specific precipitation patterns influences the sensitivity of fish communities to antecedent flow conditions (Propst et al. 2008, Pool and Olden 2015, Verdonschot and Verdonschot 2023). Through this analysis, we aim to elucidate the intricate relationships between long-term precipitation regimes, antecedent flow conditions, and fish community dynamics along a natural gradient.

Precipitation Gradients and Seasonal Dynamics in South Texas Fish Communities

Across the precipitation gradient in South Texas, we anticipate that the influence of precipitation on fish abundance, composition, and diversity is most evident during seasons when monthly rainfall closely resembles the long-term averages (Jiang and Yang 2012). However, the situation differs during the summer months, characterized by widespread arid and hot conditions leading to a region-wide decrease in water levels across our study sites. We predict that these hot and dry summers trigger the most significant responses in fish communities in more humid environments. In contrast, we expect that extreme rainfall events during the spring and fall lead to more pronounced changes in fish communities in arid regions.

To investigate the influence of annual rainfall on fish communities across South Texas, we conducted seasonal regression analyses, aiming to uncover the intricate relationship between precipitation patterns and community response variables (density, biomass, species richness, and diversity) during different seasons. We expect the influence of precipitation on fish abundance, composition, and diversity will be most noticeable in winter, when monthly rainfall closely resembled the long-term averages. Subtropical regions undergo reduced climatic variability during winter because of milder temperatures and diminished drought stress, resulting in more predictable and consistent flow conditions. This predictability enables us to align observed ecological patterns closely with the typical precipitation patterns in the study area.

Conversely, during arid and hot summer months, characterized by widespread water level reductions across our study sites, we expected the most significant responses in fish communities, particularly in more humid environments where drought-induced stress might prevail. In contrast, we anticipated that extreme rainfall events during the spring and fall would lead to more pronounced changes in fish communities, particularly in arid regions where short-term deluge events could significantly alter aquatic habitats.

These findings serve to contextualize the effects of hydrological disturbances on stream fish communities within the context of climate. This knowledge is invaluable for informing conservation efforts, resource management, and adaptation strategies, particularly as we grapple with the challenges of a changing climate.

5.3 Methods

Study Region

Distinct geological, vegetative, and climatic patterns exist across the approximately 350 km stretch of the Texas coast encompassing our nine study streams, from Kingsville in the southwest to Ganado in the northeast (Table 5.1 and Figure 5.1). From Kingsville to Ganado average annual precipitation transitions from semi-arid conditions (55 cm/yr) in the west to a sub-humid climate (135 cm/yr) in the east, with an average precipitation change of about 0.25 cm per kilometer. Despite this precipitation gradient, the region maintains consistent elevation levels (18 to 61.6 meters), shares common geological characteristics (predominantly quaternary or sedimentary), and sustains uniform air temperatures (ranging from 20.8 to 22.2°C). In essence, this transect showcases not only the climatic variability but also the geological and topographical coherence, providing a comprehensive understanding of the environmental dynamics shaping aquatic ecosystems in this coastal stretch. Our selection process for stream sites within this area involved choosing nine locations with similar mixed upstream land-cover characteristics, ensuring they were wadeable, and verifying their proximity to a U.S. Geological Survey (USGS) flow gauge with multi-year daily flow records (Falcone, 2011).

Sampling events were carried out at irregular intervals throughout the four-year dataset used in this study. Monthly samples were gathered from August 2017 to November 2018, while in 2019, we reduced our sampling efforts to only include both Spring and Fall collections. In 2020, we increased to quarterly sampling. This comprehensive sampling approach provided us with valuable insights into the dynamic responses of stream ecosystems to shifting environmental conditions along the coastal stretch, characterized by significant variations in precipitation patterns. Tabular and written summaries of watershed characteristics, discharge, water chemistry, stream geomorphology, and benthic algae are reported in the appendices 5.01-5.04.

Environmental Measurements

During each site visit, we conducted a comprehensive array of environmental assessments at four designated sampling stations within 75 meter reaches of each stream. At each of these stations, we employed a YSI ProDSS multiparameter meter from YSI Incorporated (Yellow Springs, OH, USA) to measure critical parameters, including oxygen levels (mg/L), temperature (°C), conductivity (µcm), turbidity (NTU), and pH. In addition to these measurements, we assessed the abundance of diatoms (ug/cm^2), green algae (ug/cm^2), and blue-green algae/cyanobacteria (ug/cm2) using a bbe BenthoTorch from bbe (Moldaenke, Germany). We measured wetted channel width (m) with a tape measure and left bank, right bank, and thalweg depth (m) with a meter stick, as well as the proportion of sediment within specific grain size categories at each station according to Wentworth’s classification (1922). Furthermore, bank slope measurements were conducted on both sides of the stream at each station using a digital angle gauge.

To characterize dissolved nutrients in the water, we collected two 60 mL water samples during each visit. These samples were field-filtered through 0.7 µm membrane filters, immediately stored in a cooler, and subsequently transported to the laboratory. In the lab, one of the bottles was analyzed for NO_3^-, NH_4^+, and soluble reactive phosphate (SRP) using a Lachat Flow Injection Auto-Analyzer at the Oklahoma Soil Water Forage Testing Lab. The other bottle was analyzed for total nitrogen ions (TN) and dissolved organic carbon (DOC) on a Shimadzu TOC Analyzer at the Ulseth Lab, Sam Houston State University. This comprehensive suite of measurements allowed us to gain a detailed understanding of the ecological conditions and dynamics of the stream ecosystem.

Community Sampling

Before commencing the sampling process, we positioned block nets with a mesh size of 3/8 inches at both the upper and lower ends of the study reach to ensure that fish remained within the sampling area. Following the collection of environmental data, we quantified the composition and abundance of the fish community using a systematic 3-pass depletion method, employing a Smith-Root LR-24 electro-fisher backpack (Hauer and Lamberti 2017).

During this process, we identified fish species directly in the field with the assistance of field guides (Bonner et al. 2007). For each pass we recorded the total length (mm) of the first 20 individuals within each species using a measuring board. For verification and confirmation of species identification, several specimens of each species were humanely euthanized using tricaine mesylate (MS-222) and then preserved in >70% denatured ethanol, serving as voucher specimens for subsequent lab analysis. The identified fish voucher specimens underwent a thorough species identification process utilizing the Texas Academy of Science’s dichotomous key (Hubbs et al. 2008) and were carefully stored in >70% denatured ethanol. Any discrepancies between field identifications and laboratory identifications were reconciled by making necessary corrections to the field data.

Hydrological Predictors

We obtained 30 years of daily discharge data corresponding to the date of each sample event from the USGS hydrological gauge located within 75 meters of each site, using the “waterData” package in R (version 4.1.2). We used the daily discharge data in the four weeks preceding each sampling event to calculate minimum and maximum flows preceding sampling (standardized for each location). To determine whether a flood or drought occurred, we first calculated the 30-year average daily discharge for each 4-week period. We defined major flooding events as a daily discharge exceeding 10 times the 30-year average for that 4-week period. We defined droughts as events where 7 consecutive days were below the annual 25th percentile daily discharge.

Community Response Variables

We used five key metrics to assess fish community abundance, diversity, and composition. In terms of abundance, we quantified fish density and biomass per square meter. Using length-weight relationships (LWR), we predicted weight W in wet g from length L in cm.

$$W = aL^b$$

where parameter b describes isometric growth in body proportions if b ~ 3 and parameter a defines body shape and condition (Froese 2006). Species-specific parameters a and b were estimated using a Bayesian hierarchical approach (Froese et al. 2014) and gathered from the online resource, FishBase (Froese et al. 2010). For mass conversions, we used global estimates for freshwater Osteichthyes provided in Brey, Müller-Wiegmann et al. (Brey et al. 2010).

Diversity was characterized through two parameters: the total number of species captured (species richness) and the Shannon-Weiner Index, which provides a simultaneous assessment of species richness and evenness within the community. To satisfy the assumptions of normality, both density and biomass were natural log-transformed prior to fitting models.

To delve into community composition anomalies, we measured the Euclidean distance of each sampling event to a site's centroid, a metric hereafter referred to as centroid-distance (CD) (Yeager et al. 2020). This measurement was based on the first two axes derived from a Redundancy Analysis (RDA) of Hellinger-transformed community data, constrained by twelve environmental variables (Legendre and Legendre 2012). These constrained variables included monthly median daily discharge (log-transformed), monthly relative standard deviation of discharge (log-transformed), the proportion of high flow pulses (representing monthly flows over three times the median discharge), conductivity, NO_3^- concentrations, PO_4^- concentrations, oxygen saturation (%), substrate composition (% gravel and % silt), water temperature (°C), monthly rainfall (log-transformed), and total benthic algae. Centroid distances were square-root transformed prior to model fitting to satisfy assumptions of normality. This approach allowed us to comprehensively characterize compositional deviations from the long-term average.

Extreme Flow Responses Vs Annual Rainfall

To discern whether biological responses to extreme hydrological conditions depend on precipitation regime, we analyzed the biological responses using linear mixed effects (LME) models. We fit two sets of five for a total of ten LMEs; we used either minimum or maximum antecedent flows to predict each of the five biological responses. We incorporated random slopes for each site using the following equation: (a)

$$R_x \sim q_y + \left(1 + q_y \vee site\right)$$

The variable x in R_x represents the specific biological response, encompassing parameters like biomass, density, richness, Shannon-Weiner Index, or centroid distance, while y in q_y corresponds to either maximum or minimum antecedent (4 weeks prior) discharge.

We conducted linear mixed effects modeling using the ‘nlme’ package in R and assessed model fits using ANOVA with adjusted *p*-values obtained via the ‘car’ package (Fox et al. 2007, Pinheiro et al. 2007). Furthermore, we ensured the normality of residuals by subjecting them to a Shapiro-Wilkes test. To gain insights into the relationship between biological responses and antecedent flow extremes and its potential variability in response to long-term precipitation patterns, we extracted and plotted the fitted slopes for each site versus average annual precipitation. This allowed us to explore how the relationship between biological responses and antecedent flow conditions may change in accordance with the prevailing long-term precipitation regime.

Structural Equation Models

To unravel the mechanistic connections between rainfall patterns, flood events, drought occurrences, and biological responses, we fit Structural Equation Models (SEM) using the R package 'lavaan' (Rosseel 2012). Our approach involved the development of a total of ten models, each linking one of the five biological response variables (as a log-response ratio) with either flood or drought characteristics. In our model construction, we defined flood events as instances where flow rates exceeded ten times the annual median flows within the four weeks preceding the sampling and identified 38 flood events. Droughts were characterized by the presence of seven or more consecutive days with discharge values falling below the 25th percentile of annual discharges and identified 26 drought events. We also quantified the duration of hydrological events, delineating them as periods of either flooding (exceeding 10 times the median flow) or drought (falling below the 25th percentile). Event magnitudes were evaluated as the maximum or minimum discharge relative to the annual median. To assess the quality of our models, we established well-fitting criteria, considering models with chi-square (x^2) values less than 0.05, a comparative fit index greater than 0.90, and a RMSE of approximation less than 0.05 as indicative of robust and accurate representations of the relationships under investigation.

Season Classification

We employed data spanning from 2017 to 2021, encompassing monthly rainfall and water temperatures (appendices 5.06-5.07). We standardized values within each site and used the average across the region to delineate the seasonal transitions. When solely considering temperature, the distinction could be simplified to two seasons, comprising a prolonged, hot summer and a cooler winter period. However, the persistent high levels of rainfall typically occurring in May and September justify segmenting the warm season into three distinct phases. The winter season extends from November through March, characterized by below-average temperatures and limited precipitation. Spring commences in April and extends through June, marked by elevated temperatures and copious rainfall. Summer encompasses July and August, featuring high temperatures and reduced rainfall. Finally, fall initiates in September and extends through October, with warm temperatures and substantial precipitation.

Spatial trends vs Season

We employed heatmap visualizations to examine abundance and diversity patterns on a monthly basis, while also assessing the occurrence of drought and flood events within each season (appendices 5.08-5.09). In response to observed patterns, we conducted linear regression analyses to investigate the relationship between biological responses and annual rainfall for individual seasons, aiming to identify seasonal variations in precipitation-driven community trends.

To elucidate species-driven mechanisms, we investigated the seasonal effects on community composition by employing linear regression analyses. Specifically, we focused on the relative abundance (expressed as a percentage of the total fish community) of two dominant fish families across the study area: Centrarchidae and Poeciliidae. For each season, we plotted the relative abundance of these families against the annual precipitation and quantified the strength of trends using Pearson's correlation coefficient, accompanied by the associated *p*-value. We substantiated the seasonal variation in the distribution of centrarchid fish during the summer months across different regions. This was achieved by conducting an analysis of variance (ANOVA) on centrarchid density data, which had been log-transformed and standardized to account for site-specific factors, in relation to season. This analytical approach allowed us to explore how these dominant fish families responded to changing seasonal conditions in relation to annual precipitation patterns.

5.4 Results

Extreme Discharge Effects vs Precipitation

Antecedent floods exhibited predictable effects on fish abundance and diversity, with the nature of this relationship depending on the long-term precipitation patterns within the watershed (Figure 5.2, Table 5.2). Regression of slope coefficients versus annual rainfall were not statistically significant. However, the ANOVA comparison revealed significant differences between sites for density, biomass, and richness (each ANOVA $p < 0.001$), and when plotted against annual rainfall, it was visually apparent that there are rainfall dependent relationships between density and richness versus antecedent maximum discharge. In semi-arid watersheds, antecedent floods were associated with a decrease in fish abundance but an increase in fish diversity. Conversely, in mesic watersheds (receiving more than 75cm/yr of rainfall), the pattern reversed: antecedent floods positively influenced fish abundance but had a negative impact on fish diversity. Minimum antecedent flows did not consistently induce changes in fish communities.

Drought and Flood Models

Structural Equation Models (SEMs) revealed that annual rainfall and flood characteristics are drivers of fish biomass and diversity (Figure 5.3, Table 5.3). The total effects of monthly rainfall on fish community biomass and diversity were relatively small compared to other effects (both are approximately -0.05). But intermediate flood characteristics provided mechanistic insights. Monthly rain had a positive impact on flood magnitude (+0.21) and duration (+0.15), with flood magnitude, positively influencing (+0.53) flood duration. Flood duration was the primary determinant of fish community characteristics, acting to reduce biomass (-0.25) and diversity (-0.52). In contrast, flood magnitude had weakly positive total effects on biomass and diversity (+0.05 and +0.13). Annual rainfall had a moderate positive effect (+0.12) on fish biomass which contrasted regional trends observed when including flood and non-flood sampling events. In contrast to regional trends using all of the sampling data, the SEM indicated that fish community diversity after flood events decreased with annual rainfall (-0.06). This result was consistent with the rainfall-dependent slopes discovered in the linear mixed effects models discussed previously.

SEMs indicated that in the context of drought events, monthly rainfall and annual rainfall influenced compositional deviation (CD) and diversity. The total effects of monthly rain on CD and diversity were +0.03 and -0.13 respectively. As expected, monthly rainfall negatively effected both drought magnitude (-0.19) and duration (-0.42). Also, drought magnitude (i.e. minimum discharge) had a positive effect (+0.37) on drought duration. Drought magnitude had a reducing effect on CD, meaning that community compositions resembled long-term community compositions more as minimum flows become more extreme. While the effect of drought duration was minor (+0.04) on CD, it had a substantial effect (+0.25) on diversity. Annual rainfall promoted diversity (+0.30) and reduced CD (-0.21) and, meaning that diversity was lower in more xeric streams and their compositions deviated less after drought events. These results were also consistent with observed trends in Kinard *et al.* 2020, and our data exploration of long-term trends in these fish communities. The sample event distribution is reported in appendix 5.05.

Rainfall-Driven Trends vs Season

We found marked seasonal fish biomass dynamics evidenced by a substantial increase in biomass during the spring at most sites and a consistent trend of higher fish densities and increased biomass compared to spring and summer. Our exploration of log-response ratios for mean community attributed across sites and months identified a recurring pattern of seasonal fluctuations in population density and biomass (appendix 5.08). Nevertheless, understanding the intricate aspects of diversity patterns remained a challenge. Notably, sites with intermediate annual precipitation levels, ranging from 69 to 84cm/yr, experienced pronounced reductions in fish biomass during the summer months and exhibited declines in species diversity compared to winter.

Linear relationships of annual precipitation with density and diversity exhibited their most distinct characteristics during the winter and fall seasons (Figure 5.4). Within these periods, we observed a positive relationship between annual rainfall and fish diversity ($R^2 = 0.12$, $p = 0.04$), along with a negative association between annual rainfall and fish density ($R^2 = 0.14$, $p = 0.03$). In the context of absent patterns of biomass, these regressions signified that fish communities in drier climates typically consisted of smaller but more numerous fish species, resulting in a reduced overall species count compared to their counterparts in more humid stream ecosystems. Throughout the seasons, fish biomass demonstrated considerable variation across the region, devoid of any discernible consistent pattern. Lastly, regional patterns in fish community abundance and diversity were weak in spring and were entirely absent in summer. Linear regressions for each biological response versus annual rainfall in each season are reported in the appendices 5.10-5.13.

To explore the reasons behind these disruptions in fish community patterns, particularly during summer, we examined the proportion of fish communities consisting of the two most prevalent fish families across the region, centrarchids and poeciliids (Figure 5.5). Our findings indicated that during wetter seasons, annual rainfall correlated positively with centrarchid densities ($R^2 = 0.29$, $p < 0.001$), and conversely, it was inversely related to poeciliid densities ($R^2 = 0.44$, $p < 0.001$). This finding aligned with community metrics pointing to higher fish densities in arid stream environments, accompanied by relatively stable biomass levels across the region. Nevertheless, a region-wide decline in centrarchid densities was evident during the summer (ANOVA $p = 0.04$), while poeciliid densities remained relatively consistent throughout the seasons.

5.5 Discussion

Our study sought to place the impacts of hydrological disturbances on stream fish communities within a broader ecological context, emphasizing the interactions among floods, droughts, season, and long-term precipitation patterns in shaping aquatic ecosystems. Over irregular intervals between 2017 and 2020, we collected fish and conducted extensive environmental assessments at nine wadeable streams along a natural precipitation gradient in South-Central Texas, each equipped with USGS gauges. Using a combination of linear regression, mixed-effects models, and structural equations models, we examined the effects of extreme hydrological events and seasonality on fish community abundance, diversity, and composition.

Our findings reveal that the association between antecedent maximum flows and fish abundance or diversity is contingent upon the long-term precipitation regime. Semi-arid sites exhibit reduced abundances and increased diversity following higher antecedent flows, whereas mesic sites show higher densities and lower diversity with rising antecedent maximum flows. The effects of drought events are also influenced by long-term precipitation regime. More precisely, increased annual rainfall correlates with heightened species diversity and more pronounced compositional shifts in the aftermath of droughts. Finally, hydrological droughts occurring in hot and arid summers (July-August) disturb regional abundance and diversity patterns influenced by the long-term precipitation gradient. In this timeframe, we observed a reduction in regional abundances of centrarchids, whereas poeciliids demonstrated resilience, possibly indicating their superior adaptation to seasonal drought conditions compared to centrarchids.

These findings hold broader implications for freshwater ecosystem management, particularly in regions susceptible to changing precipitation patterns and increasing drought events. In the ensuing discussion, we will contextualize our results within the existing body of scientific literature, addressing the gaps in current understanding and elucidating how our findings contribute to the evolving discourse on the ecological consequences of hydrological disturbances. By integrating our results with established knowledge, we aim to provide a comprehensive understanding of the interconnected factors shaping stream fish communities, thereby contributing valuable insights for both ecological research and conservation practices.

Rainfall Regime as a Modulator of Extreme Flow Events

The dependence of the flood-fish abundance and diversity relationship on long-term precipitation patterns challenges previous broad assumptions (Junk et al. 1989). The observed reversal in the effects of antecedent floods between semi-arid and more humid regions contradicts a uniform perspective (Lake et al. 2006), emphasizing the need for nuanced approaches in conservation and research endeavors (Stanley et al. 2010). This discovery underscores the importance of considering region-specific climatic factors when predicting ecological responses to floods, recognizing that long-term climate considerations play a pivotal role in shaping the dynamics of fish communities.

The observed pattern in semi-arid watersheds, marked by a decrease in fish abundance but an increase in diversity following antecedent floods, finds its explanation in the complex dynamics of habitat redistribution among various fish species. In our study region, semi-arid streams are primarily inhabited by poeciliids, such as the sailfin molly (*Poecilia latipinna*), and cyprinidonts, exemplified by the sheepshead minnow (*Cyprinodon variegatus*). These resident species exhibit adaptations conducive to surviving drought conditions, characterized by their euryhaline nature and hypoxia tolerance. However, their relatively small size, limited defenses against predation, and weak swimming abilities render them vulnerable to the impacts of scouring floods.

Following flood events, there is a discernible shift in community composition in semi-arid streams, occasionally introducing various centrarchids. This alteration in species makeup implies nuanced changes in habitat utilization and access. The transient surge in flow during floods facilitates the connectivity of lotic systems, enabling the entry of higher trophic level predators from adjacent reservoirs, such as spotted gar (*Lepisosteus oculatus*), green sunfish (*Lepomis cyanellus*), warmouth sunfish (*Lepomis gulosus*), and largemouth bass (*Micropterus salmoides*).

The observed post-flood community dynamics in semi-arid regions, resembling more mesic ecosystems, align with the notion that stream communities adapt to flood regimes, exhibiting increased inherent resiliency with greater flood frequencies (Robinson et al. 2004). The impact of swimming abilities becomes evident in these dynamics, as smaller species like poeciliids and cyprinodonts potentially being carried downstream (Chapman and Kramer 1991), while more proficient swimmers like flood-quiescent centrarchids thrive in the inundated conditions (Ross and Baker 1983). However, an alternative factor contributing to the decline in overall fish abundance post-flood could be the influx of predators preying upon or displacing typical residents (Luz-Agostinho et al. 2009). The findings are consistent with the broader implications highlighted in experimental flooding studies, which suggest that floods drive stream community resilience (Robinson and Uehlinger 2008, Magdaleno 2017).

Drought Dynamics and Biodiversity: Insights from Structural Equation Models

Structural equation models (SEMs) effectively quantify relationships between monthly rainfall with flood and drought characteristics which subsequently drive community dynamics that vary depending on long-term rainfall patterns. The total effects of monthly rainfall on CD and diversity (+0.03 and -0.13, respectively) underscore the importance of precipitation patterns in shaping fish community dynamics during droughts. As expected, the negative effects of monthly rainfall on drought magnitude (-0.19) and duration (-0.42) highlight the role of reduced rainfall in intensifying drought conditions. Additionally, the positive effect of drought magnitude on drought duration (+0.37) indicates that more extreme minimum flows are associated with prolonged drought periods.

The trend of compositional convergence towards the site mean reveals the influential role of drought conditions in shaping the core taxa of fish communities. In a manner reminiscent of the Everglades ecosystem in Florida, where prolonged drought has demonstrated a significant impact on fish community composition, periods of water scarcity favor species like the Florida gar (*Lepisosteus platyrhincus*) and the eastern mosquitofish (*Gambusia holbrooki*), leading to their dominance in aquatic habitats (Parkos et al. 2015). Conversely, during episodes of heavy rainfall and subsequent flooding, species such as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) take advantage of increased water availability and habitat structure changes (Giles 1999). This ecological analogy underscores the pivotal role of drought in defining the core structure of fish communities, while variations in composition depend on the intricate interplay between hydrological disturbances and water availability.

Furthermore, the substantial impact of drought duration on diversity (+0.25) underscores the pivotal role of prolonged drought events in concentrating species into smaller remaining aquatic habitats (Magoulick and Kobza 2003). Studies in Australian streams have reported that droughts, which reduce water levels and isolate pools, create unique ecological niches. This isolation can lead to increased fish diversity in the remaining pools as different species exhibit varying levels of resilience to drought conditions. The positive relationship between annual rainfall and diversity (+0.30) suggests that increased rainfall enhances diversity, aligning with species patterns observed during monsoonal rainfall in the Mekong River basin (Chea et al. 2020) and wetland communities following floods in the Southeast United States (Baker and Killgore 1994). The results highlight the greater baseline diversity in mesic communities and how drought events coerce cohabitation by more species in channels via habitat constriction.

Rainfall Resilience: Insights and Implications for Fish Communities in Humid Environments

The finding that higher annual rainfall reduces compositional deviation (CD) (-0.21) implies that fish community compositions in regions with elevated annual rainfall are more stable and exhibit less deviation after drought events. This observation has significant implications for the overall resilience of fish communities in more humid environments. In regions with abundant annual rainfall, the fish communities seem to possess a greater capacity to maintain consistent species compositions even after experiencing drought conditions. This resilience suggests that these communities may be better equipped to recover and adapt to disturbances, contributing to their overall stability and persistence in the face of hydrological fluctuations.

While specific examples pertinent to this study may be limited, drawing parallels from broader ecological research and theoretical frameworks illuminates the intricate interplay between environmental stability, rainfall patterns, and community resilience. For instance, insights from studies in tropical rainforests, where increased and consistent rainfall is correlated with heightened stability and biodiversity (Rosser 1998, Thompson et al. 2009), provide a foundational framework for comprehending the potential resilience of fish communities in regions characterized by higher annual rainfall.

Exploring long-term ecological research sites in humid environments, such as those found in the Congo Basin or specific regions of Southeast Asia (Anthony *et al.* 2015, Kim *et al*. 2018), holds promise for gaining insights into how fish communities respond to and recover from disturbances, including drought events, within the context of predictable annual rainfall. Leveraging overarching ecological principles and findings supports the interpretation of the observed patterns in fish community dynamics in more humid environments. The parallels drawn from diverse ecosystems underscore the robustness of the identified relationship between rainfall, compositional stability, and the resilience of fish communities. This multifaceted perspective enhances the credibility and broader applicability of the study's implications for comprehending and managing fish communities amidst climate variability. Future research endeavors should delve into the specific mechanisms underpinning mesic compositional resilience and explore how climate change may influence these dynamics, guiding conservation and management strategies in the face of environmental uncertainties.

Decoding Seasonal Precipitation Patterns: Insights from Cooler Seasons

Our study uncovers distinct ecological patterns during winter and fall, revealing a positive correlation between annual rainfall and fish diversity ($R^2 = 0.12$, $p = 0.047$) and a negative association with fish density ($R^2 = 0.14$, $p = 0.03$). This implies that fish communities in drier climates consist of smaller but more numerous species, reducing overall species count compared to more humid stream ecosystems.

Enhanced differentiation in fall and winter fish assemblages is partly attributed to precipitation-driven variations in leaf litter and woody inputs. Lower productivity and scarcity of these inputs in semi-arid watersheds impact the nutritional foundation for invertebrates and shape habitat complexity dynamics (Tonin et al. 2017). Other considerations in semi-arid watersheds during fall and winter include reproductive timing, modes, and predatory habitat availability. Prevailing base flow conditions in these regions may be insufficient for nest-building centrarchids (Lukas and Orth 1993, Clark et al. 2008), and larger predators sensitive to salinity or hypoxic conditions might be excluded (Williams 1999, Kieffer and Cooke 2009). Thus, fall and winter may amplify aridity-driven mechanisms of fish assembly through reduced allochthonous resources, diminished habitat availability, and the absence of top-down trophic cascades.

Seasonal Dynamics of Dominant Fish Families

Our detailed analysis of fish community disruptions, particularly in summer, focused on two key fish families: centrarchids and poeciliids. The positive correlation between annual rainfall and centrarchid densities ($R^2 = 0.29$, $p = 0.002$) during wetter seasons reveals the impact of precipitation on centrarchid concentrations. Conversely, the inverse relationship between annual rainfall and poeciliid densities ($R^2 = 0.44$, $p < 0.001$) underscores stable biomass levels in arid stream environments.

The notable decline in centrarchid densities during summer (ANOVA $p = 0.041$) indicates a substantial seasonal shift, likely driven by physiological stress in hot and dry conditions. This shift, coupled with the consistent poeciliid densities, underscores the intricate dynamics influencing these fish families. Exploring the physiological and behavioral adaptations of centrarchids to extreme weather conditions during hot and dry summers could provide insights into the evolutionary strategies employed by these species to navigate environmental variability (Larimore et al. 1959, Crans 2014). Concurrently, the stability of poeciliid biomass in arid environments suggests a robust and resilient ecological strategy, potentially influencing the biogeography of poeciliid populations in response to climate-driven disturbances (Kerezsy et al. 2017, García-Andrade et al. 2021). These observations highlight the need for nuanced investigations into the seasonal responses of fish families to better comprehend their adaptive mechanisms in the face of changing environmental conditions.

Study Constraints and Future Research Directions

Several limitations in our study design warrant consideration when interpreting the findings. Our study focused exclusively on fish communities, neglecting the dynamics of macroinvertebrates. Integrating macroinvertebrate data would offer a more integrated perspective on stream ecosystem dynamics, considering the inter-connectedness between these taxa and fish populations. Future studies should aim to bridge this gap, providing a more comprehensive understanding of community interactions and responses to environmental variations.

Our discussion of the explanations outside of our models of fish community dynamics is speculative. To enhance mechanistic insights, future research endeavors should prioritize linking primary and secondary production dynamics to observed fish community patterns. Incorporating data on key ecological processes such as nutrient cycling, primary productivity, and energy transfer within the ecosystem would contribute to a more robust understanding of the underlying mechanisms governing fish community responses to floods, droughts, and season. Overcoming these limitations by implementing more precise study designs and incorporating interdisciplinary methodologies will not only enhance the reliability of our results but also open avenues for a more detailed understanding of the specific ecological mechanisms shaping aquatic ecosystems in response to environmental fluctuations.

Concluding Remarks

This study extends upon spatial trends observed in Kinard et al. 2021, by analyzing the temporal dynamics of fish communities across distinct precipitation regimes. Our findings underscore the importance of contextualizing community responses to disturbance within the specific rainfall regime of the region. The association between antecedent maximum flows and fish abundance or diversity is intricately tied to the long-term precipitation patterns, revealing divergent trends between semi-arid and mesic sites.

A key highlight of our study is the recognition of heightened resilience in mesic fish communities compared to their semi-arid counterparts. The distinct responses to increased antecedent flows and the aftermath of drought events emphasize the need for tailored conservation and management strategies that consider the local precipitation regime. These findings have broader implications for understanding and predicting the impacts of hydrological disturbances on fish communities, particularly in the context of climate change.

The intensified trend strength in Fall and Winter, driven by the interplay between annual rainfall and fish community responses, holds ecological significance. These seasonal patterns, with reduced species count in drier climates and increased diversity with higher rainfall, illuminate nuanced dynamics in shaping fish communities. These findings have broad implications for predicting and managing climate-driven disturbances on fish communities. Future research should focus on uncovering specific ecological processes, including leaf litter, reproductive timing, and habitat availability, contributing to observed trends.

Moreover, our observations during hot and arid summers provide a crucial temporal dimension to the ecological dynamics. The reduction in regional abundances of centrarchids, contrasted with the resilience of poeciliids, hints at differential adaptation strategies to drought conditions. This prompts further exploration into the physiological and behavioral adaptations of these fish families to extreme weather conditions, contributing to our understanding of evolutionary strategies employed in the face of environmental variability.

In essence, this study not only advances our understanding of the hydrological drivers shaping fish communities but also highlights the importance of considering the broader climatic context for effective conservation and management practices. Future research endeavors could delve deeper into the mechanisms underlying these observed patterns, linking primary and secondary production dynamics to fish community responses, and refining study designs to address the limitations identified. These efforts will undoubtedly contribute to a more multifaceted comprehension of the complex interactions within aquatic ecosystems.

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5.7 Tables

Site	Lat	Lon	Temp°C	Raincm/yr	Developed %	Forest%	Crop%	USGS ID
SF	27.773	-98.034	22.2	56.7	4.7	1.5	28.0	8211900
TR	27.521	-97.840	22.2	54.2	15.8	1.4	26.3	8212300
AR	28.283	-97.621	21.5	68.5	8.3	3.6	52.4	8189700
PD	28.752	-97.317	21.5	78.7	2.5	34.9	27.4	8177300
MR	28.292	-97.279	21.5	72.9	3.7	8.4	35.1	8189500
GC	28.891	-96.819	21.2	84.3	4.3	17.5	50.3	8164600
PL	28.725	-96.769	21.4	82.1	5.3	26.2	48.3	8164800
WM	29.072	-96.468	20.8	94.2	3.6	4.2	82.5	8164503
EM	29.071	-96.417	20.9	95.0	6.8	1.6	85.9	8164504

Data from USGS Gauges ii (1990-2009)

Table 5.01: Watershed Summary

As we move from the western to the eastern part of the region, there is a gradual increase in annual rainfall, while temperature and urban development remain relatively stable (Figure 5.1). The study area maintains a uniform range of annual average temperatures, exhibiting minimal fluctuations, ranging from 20.8°C to 22.4°C. It's important to note that agricultural land-use introduces a potential confounding factor. The extent of cropland positively correlates with annual precipitation ($R^2 = 0.67$, $p =$ .001), encompassing a range from 26% to 85%. However, when examining urban development and forested watersheds, no discernible linear relationships emerged along the gradient of precipitation.

LME		Slope ~ Annual Rainfall				
Response	Predictor	ANOVA-*p*	SW-*p*	Estimate	R^2	*p*
sqrt(centroid. dist)	q_min	5.1e-01	1.6e-01	8.3e-13	0.06	0.54
ln(density)	q_min	4.4e-01	2.7e-01	1.1e-03	0.03	0.67
ln(biomass)	q_min	2.2e-01	1.7e-02	1.4e-10	0.25	0.17
shannon	q_min	3.1e-01	1.4e-02	1.2e-10	0.05	0.56
richness	q_min	9.6e-02	4.0e-01	2.3e-12	0.02	0.69
sqrt(centroid. dist)	q_max	2.8e-01	1.8e-01	-2.0e-12	0.00	0.93
shannon	q_max	2.8e-01	4.6e-03	-2.0e-03	0.14	0.31
Significant						
ln(density)	q_max	2.1e-05	6.8e-01	5.4e-12	0.11	0.38
ln(biomass)	q_max	3.5e-06	4.5e-02	2.9e-12	0.00	0.96
richness	q_max	9.5e-04	2.9e-01	-1.9e-03	0.22	0.21

Table 5.02: Linear Mixed Effects (LME) model outputs

Output statistics for linear mixed effects models (LME) with random slope for each site using minimum or maximum antecedent discharges to predict biological responses. Significant LME models were determined by ANOVA with adjusted *p*-values. Residual normality was checked using a Shapiro-Wilkes test. Additionally, summary statistics for linear regression of the estimated slopes for each site were related to annual rainfall using linear regression. Responses include square root transformed centroid distance (approximate compositional deviation), natural log transformed density (fish/m^2), natural log transformed biomass (g/m^2), and species richness. Predictors include minimum (q_min) and maximum (q_max) daily discharges in the four weeks preceding sampling events.

		Flood		Drought	
Response	Predictor	Estimate	SE	Estimate	SE
Magnitude	Rain.Month	373.671	0.212	-0.098	-0.189
Duration	Rain.Month	0.815	0.150	-3.012	-0.351
Duration	Magnitude	0.002	0.534	6.232	0.375
Sp.Richness	Magnitude	0.000	0.123	-0.133	-0.154
Sp.Richness	Duration	-0.036	-0.354	0.022	0.416
Sp.Richness	Rain.30yr	-0.003	-0.099	0.001	0.026
SW.Index	Magnitude	0.000	0.407	0.086	0.136
SW.Index	Duration	-0.049	-0.518	0.010	0.250
SW.Index	Rain.30yr	-0.002	-0.058	0.008	0.295
Biomass	Magnitude	0.000	0.047		
Biomass	Duration	-0.094	-0.252		
Biomass	Rain.30yr	0.013	0.118		

Estimates are standardized, SE = Standardized Estimate

Table 5.03: Structural Equation Model (SEM) Parameter Estimates

Output statistics for two sets of structural equation models (flood or drought events) predicting event magnitude, duration, and community metrics including species richness (Sp.Richness), Shannon-Weiner Index (S.W. Index) and Biomass (g.m^{-2}). Predictors included monthly rainfall (Rain.Month), annual average rainfall (Rain.30yr), as well as event duration and magnitude.

5.8 Figures

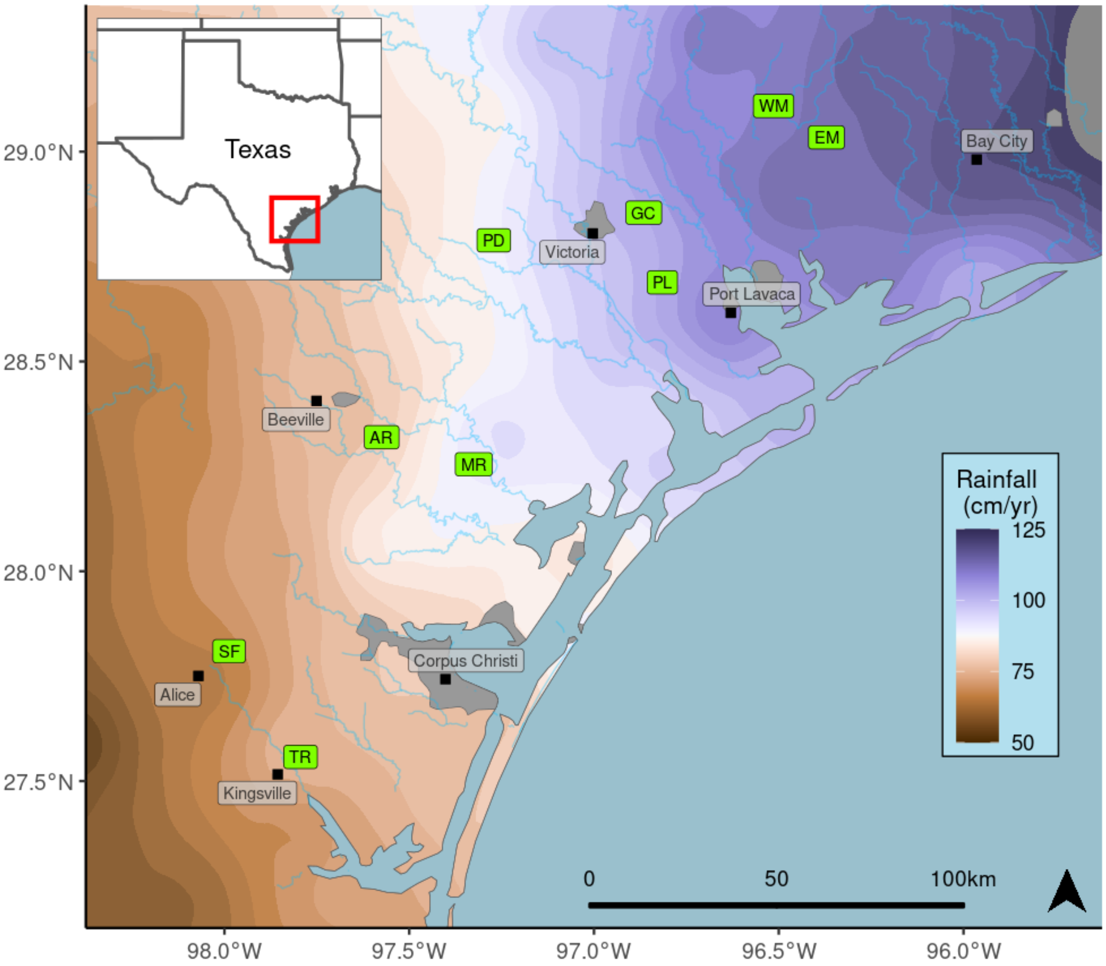


Figure 5.01: Study Region: Coastal Streams Along A Natural Precipitation Gradient

Study sites (in green) where fish and environmental data were collected from 2017-2020. An overlay indicates the average annual precipitation (brown-purple) from USGS PRISM data (1981-2010). Cities (black squares) and urban areas (grey) were included for geographic reference. This map was made with Natural Earth.

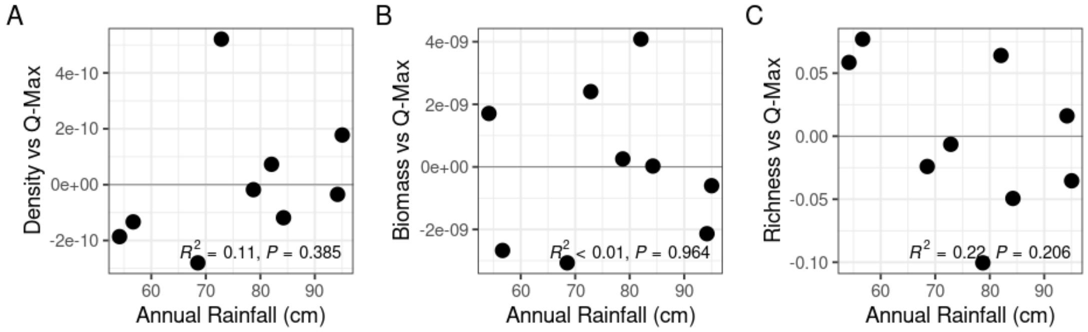


Figure 5.02: Modeling (Community Responses to Extreme Antecedent Flows) vs Annual Rainfall

Relationships between (A) density, (B) biomass, and (C) species richness versus maximum antecedent discharge plotted against annual rainfall. Relationships are estimated slopes obtained from linear mixed effects models with random slopes for each site. Community response variables are log response ratios to the long term average within each site. Q-max and Q-min are absolute ratios of the maximum or minimum discharge to the annual median discharge within each site.

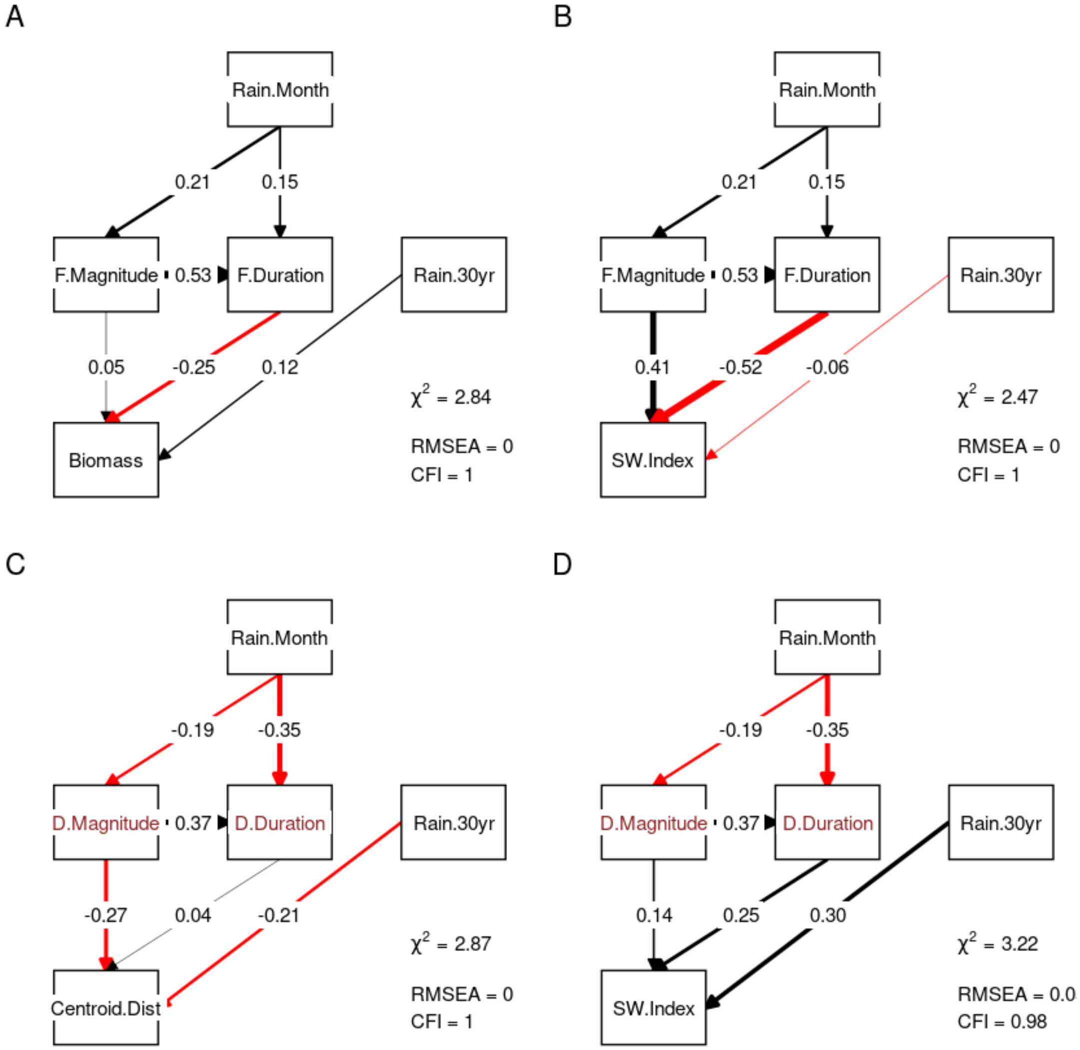


Figure 5.03: Mechanistic Model Linking Rainfall and Flood/Drought Events to Community Responses

Structural Equation Model (SEM) for Flood (A and B) and Drought (C and D) events. Arrow Thickness denotes relationship strength. Numbers on arrows are standardized correlation coefficients. Red arrows indicate negative relationships, while black arrows indicate positive relationships. Well-fitting models have $\chi^2 > 0.05$, Comparative Fit Index (CFI) > 0.90, and a Root Mean Square Error of Approximation (RMSEA) < 0.05.

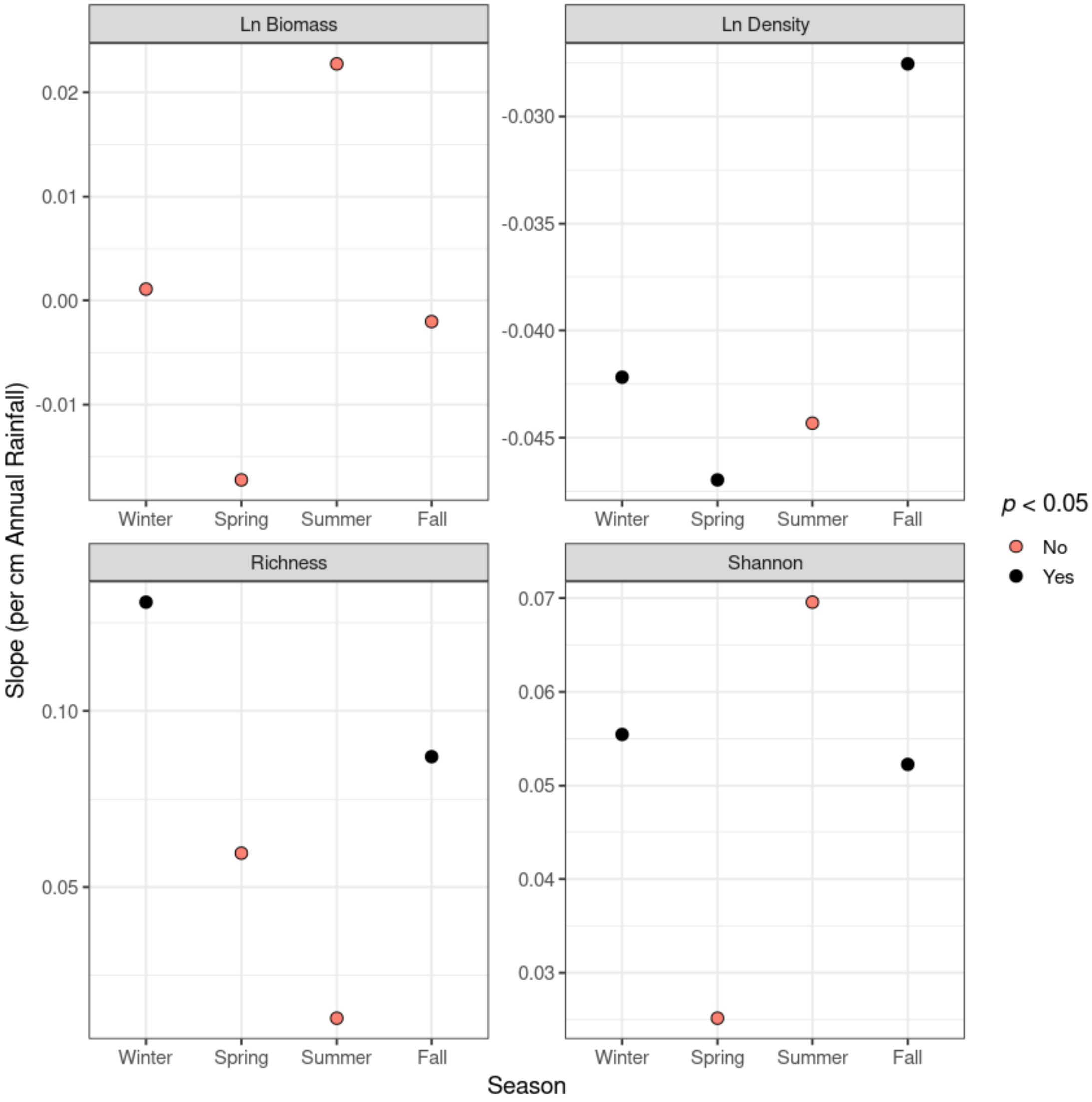


Figure 5.04: Detecting Seasonal Shifts in Regional, Precipitation-driven Patterns

Seasonal trend strength between Community Metrics and Annual Rainfall. Each facet contains a scatterplot illustrating the estimated slopes obtained from linear regressions of four community response variables as they relate to the four seasons (winter, spring, summer, fall). Community response variables include natural log-transformed biomass, natural log-transformed density, species richness, and Shannon-Weiner diversity. Data points are shaded pink for statistically spurious correlation coefficients ($p > 0.05$).

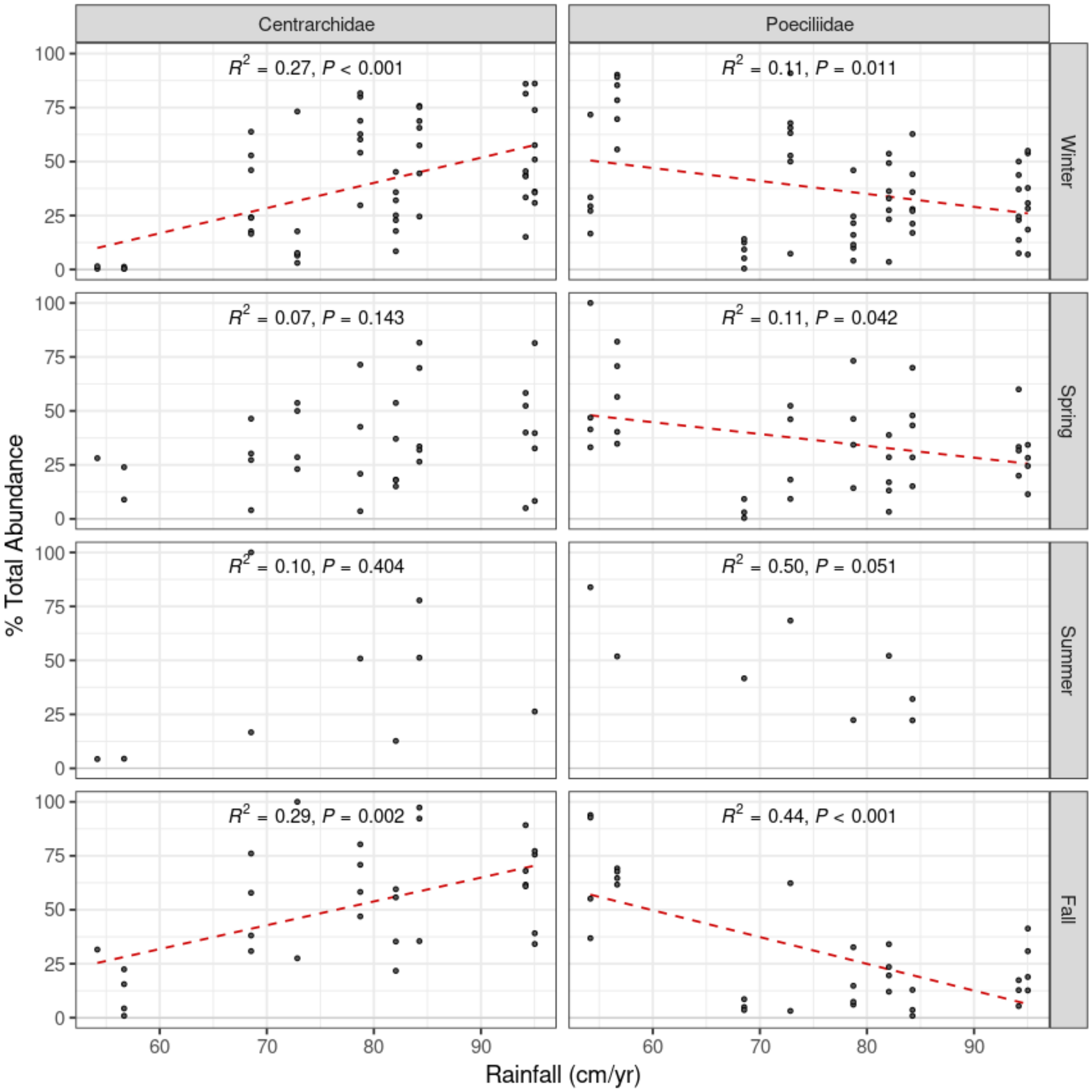


Figure 5.05: Seasonal patterns in fish community composition

A comparative analysis of Centrarchidae and Poeciliidae responses to annual precipitation variability across four seasons. Each facet showcases a scatterplot depicting the proportion of the fish community as a percentage against annual precipitation (cm/year). Linear regression trends, represented by red dotted lines, and their corresponding R^2 and p values are annotated at the top middle of each facet. Data from Winter, Spring, Summer, and Fall seasons provide insights into the ecological dynamics of these fish families in response to changing precipitation regimes.

5.9 Appendices

Site	Median l/s	Maximum l/s	Relative Standard Deviation	Cumulative Daily Changes	Flood Index	Drought Index	High Flow Proportion %
SF	3.7e01	3.0e05	138.8	9.5	69.8	0.7	7.8
TR	5.9e00	3.5e03	25.9	7.4	44.9	1.0	20.1
AR	1.4e02	8.3e05	73.0	7.0	38.5	0.7	6.7
PD	2.3e00	1.6e05	953.4	85.0	409.9	0.9	14.9
MR	3.7e02	9.1e05	61.8	6.4	61.3	1.0	11.3
GC	5.8e01	3.7e05	168.7	22.1	162.3	1.0	18.4
PL	3.2e01	2.9e05	298.4	45.3	287.6	1.0	18.4
WM	4.8e02	5.3e05	38.1	5.9	54.6	1.0	16.4
EM	2.4e01	1.5e05	251.9	40.6	323.9	1.0	25.3

Relative Standard Deviation = relative standard deviation = standard deviation / median,
Cumulative Daily Changes = cumulative daily changes relative to annual median,
Flood Index = flood strength = abs(average(over_75th_percentile) - annual_median) / annual_median,
Drought Index = drought strength = abs(average(under_25th_percentile) - annual_median) / annual_median,
High Flow Proportion = high flow proportion = % of days over 7x annual_median
Data from USGS Gauges ii (1990-2009)

Appendix 5.01: Discharge Summary

30-year mean annual statistics (1990-2020) obtained from of mean daily discharge (l/s). Median base flows remain relatively consistent across most sites, differing by no more than a single order of magnitude. However, Perdido Creek stands out as an exception, displaying the lowest base flow, albeit still within two orders of magnitude in comparison to the other sites. Furthermore, Perdido Creek exhibits notably high flow variability, as evident in both the relative standard deviation and cumulative daily changes. On average, streams located in regions with more abundant precipitation tend to showcase broader variations in daily discharge values (as indicated by relative standard deviation, cumulative daily changes, flood index, and drought index). Additionally, they have a higher likelihood of entering a flooding state (high flow proportion).

Site	W.Temp °C	pH	Cond. uS/cm	Turbidity NTU	O_2 %	NO_3^- mL/L	NH_4^+ mL/L	PO_4^- mL/L	DOC ppm
SF	24.0	7.4	1.0e03	88.1	69.3	11.3	0.2	2.4	6.8
TR	22.4	8.2	4.8e03	101.7	56.3	0.5	0.2	0.2	13.7
AR	22.4	8.0	1.1e03	77.7	78.0	6.3	0.2	1.9	7.2
PD	22.9	7.9	9.0e02	78.8	76.1	0.1	0.5	0.1	6.5
MR	23.4	7.9	2.1e03	68.9	70.6	0.1	0.1	0.1	7.4
GC	21.4	7.5	4.5e02	163.2	54.4	0.2	0.2	0.4	9.2
PL	22.6	8.0	1.4e03	115.4	90.1	1.5	0.1	0.1	4.2
WM	21.7	7.9	5.0e02	131.7	71.1	0.3	0.2	0.2	11.2
EM	22.2	7.7	5.6e02	126.0	68.9	0.6	0.1	0.3	5.3

Site averages from in-situ sampling (2017-2020)

Appendix 5.02: Water Chemistry Summary

Site mean values (2017-2020) for water temperature, pH, conductivity, turbidity, dissolved oxygen, NO3-, NH4+, PO4-, and dissolved organic carbon. Most of the water quality parameters did not exhibit a linear relationship with annual precipitation. However, one variable did display such a correlation: Linear regression analysis revealed that stream conductivity decreases as annual rainfall increases ($R^2 = 0.46$, $p = 0.046$). pH values at the various sites were slightly basic, falling within the range of 7.4 to 8.2. Oxygen saturation ranged from 54 to 90% across the sites. Notably, San Fernando Creek showed exceptionally high levels of nitrates and phosphates ($NO_3^- =$ 11.3 mL/L, $PO_4^- =$ 2.4 mL/L) in contrast to the lower averages observed at the other sites ($NO_3^- =$ 1.2 mL/L, $PO_4^- =$ 0.4 mL/L). Ammonia levels spanned from 0.1 to 0.2 mL/L at most sites, with Perdido exhibiting a relatively high value of 0.5 mL/L. Dissolved organic carbon (DOC) levels showed a range from 4.2 to 13.7 ppm, with elevated values observed at Tranquitas Creek and West Mustang Creek.

Site	Gravel (%)	Sand (%)	Silt (%)	Canopy (%)	Depth^a (m)	Width (m)
SF	26	21	42	67	0.24	3.04
TR	16	17	63	69	0.33	4.40
AR	40	31	8	65	0.27	4.16
PD	9	42	28	8	0.41	4.24
MR	7	63	26	47	0.51	6.92
GC	8	76	16	63	0.33	6.33
PL	6	48	31	42	0.30	3.60
WM	1	80	17	65	0.59	8.78
EM	9	46	42	7	0.59	5.48

Site averages from in-situ sampling (2017-2020)

^{a}Depth = Maximum Depth

Appendix 5.03: Geomorphology Summary

Site mean values (2017-2020) for substrate proportions, canopy coverage, maximum transect depth, and stream width. Canopy coverage does not vary predictably with rainfall. However coverage is exceptionally low at Perdido Creek and East Mustang (8% and 7%, respectively) in comparison to the other sites, which exhibit an average canopy coverage of around 60%. Substrates also exhibited nonlinear variation across the region, but substrate gravel content is notably elevated (approximately 27%) at the three driest sites. Linear regression analyses reveal a positive correlation between stream depth and annual rainfall ($R^2 = 0.5$, $p = 0.03$), indicating that deeper streams are associated with higher annual precipitation. Nevertheless, despite the tendency for arid streams to be narrower than mesic streams, a statistically significant regression was not observed in this regard.

Site	Total	BGC[a]	Green	Diatom
SF	1.06	0.28	0.08	0.70
TR	0.99	0.37	0.07	0.55
AR	1.67	0.88	0.08	0.71
PD	1.05	0.59	0.14	0.32
MR	0.79	0.23	0.16	0.40
GC	1.07	0.35	0.22	0.50
PL	1.55	0.43	0.10	1.02
WM	0.51	0.16	0.09	0.27
EM	0.67	0.29	0.13	0.26

Units = chlorophyll α (μg/cm)

[a] BGC = Blue-Green Cyanobacteria

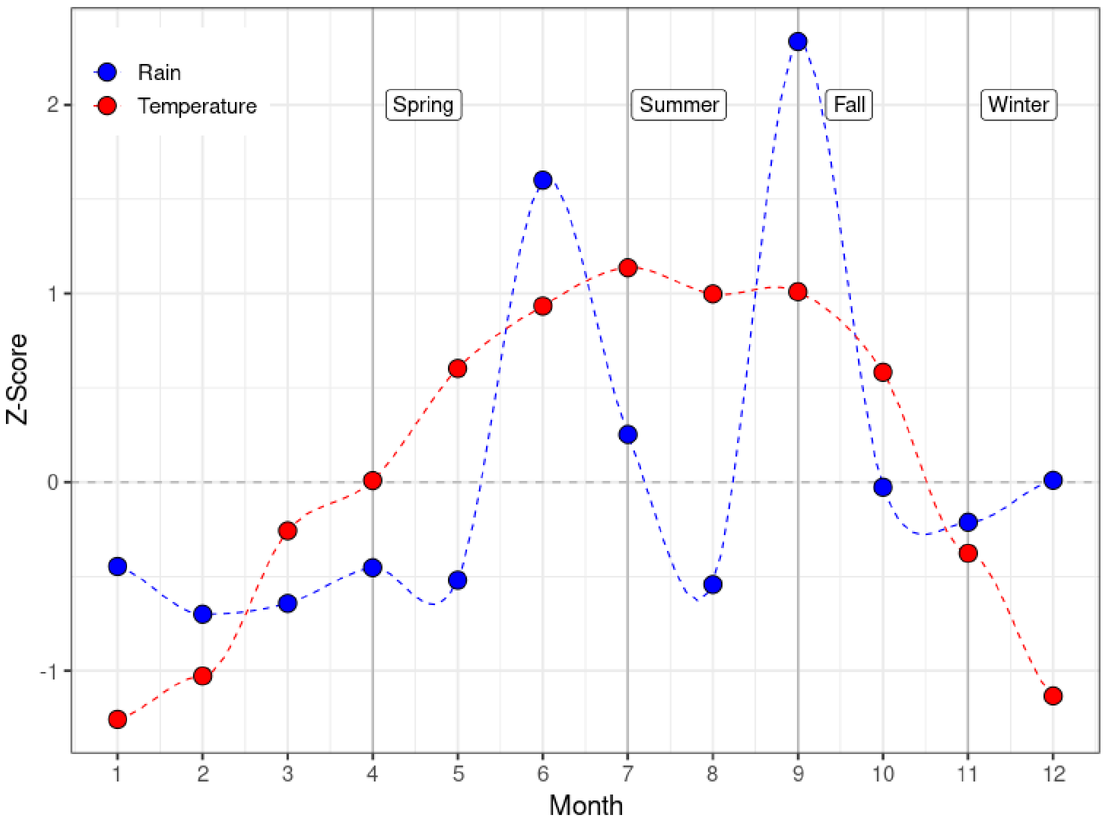
Appendix 5.04: Benthic Algae Summary

Site mean values (2017-2020) for total algae (μg/cm) which is the sum of blue-green cyanobacteria, green algae, and diatoms. Standing stocks of benthic algae, as assessed using the Benthotorch, demonstrate non-linear fluctuations throughout the area. Diatoms were the predominant type of algae in the region, with blue-green cyanobacteria and green algae following as the secondary categories in terms of abundance.

Site	Rain (cm.yr^{-1})	Floods	Droughts
SF	57	2	
TR	54	5	4
AR	69	4	
PD	79	2	12
MR	73	3	
GC	84	5	8
PL	82	7	
WM	94	3	
EM	95	7	2
total	—	38	26

Appendix 5.05: Flood and Drought Event Distribution Table

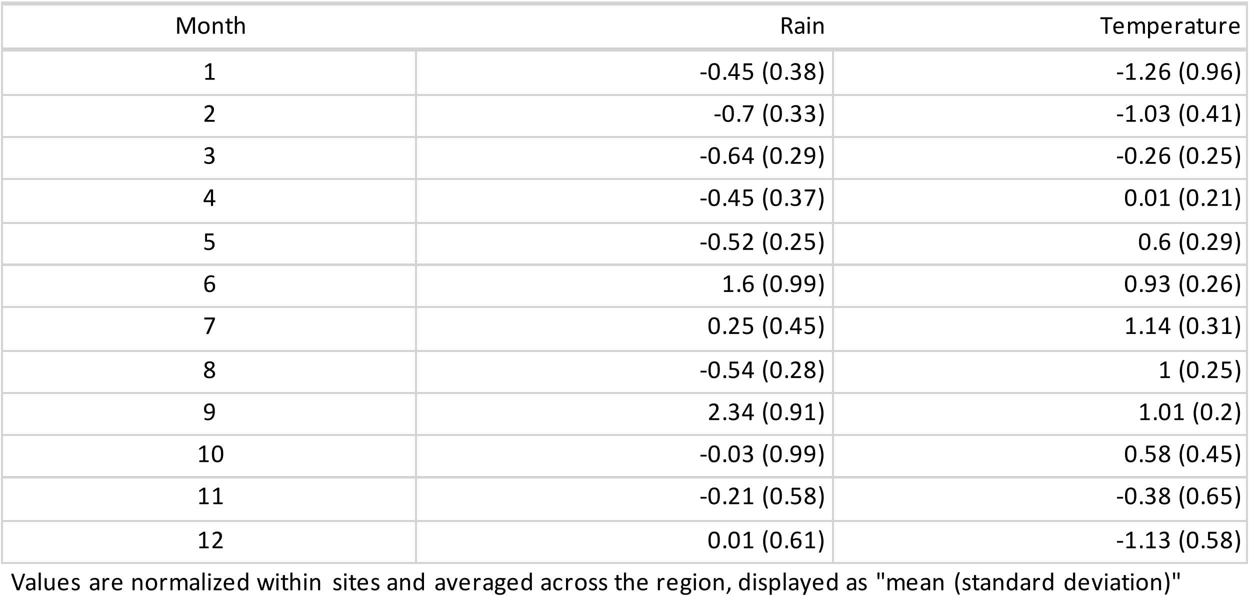
Summary table for sample events following classified flood or drought events used in the structural equation models. Using daily discharges, we defined floods as flows exceeding ten times the annual median and droughts as seven or more contiguous days below the annual 25th percentile.



Appendix 5.06: Identifying Seasons: Monthly Rain and Temperature

Figure

Regional average monthly rainfall (blue) and water temperature (red). Vertical grey lines indicate the start of the labeled season. Winter (November-March) is cool and dry, Spring (April-June) is warm and wet, Summer (July-August) is warm and dry, and Fall (September-October) is warm and wet.

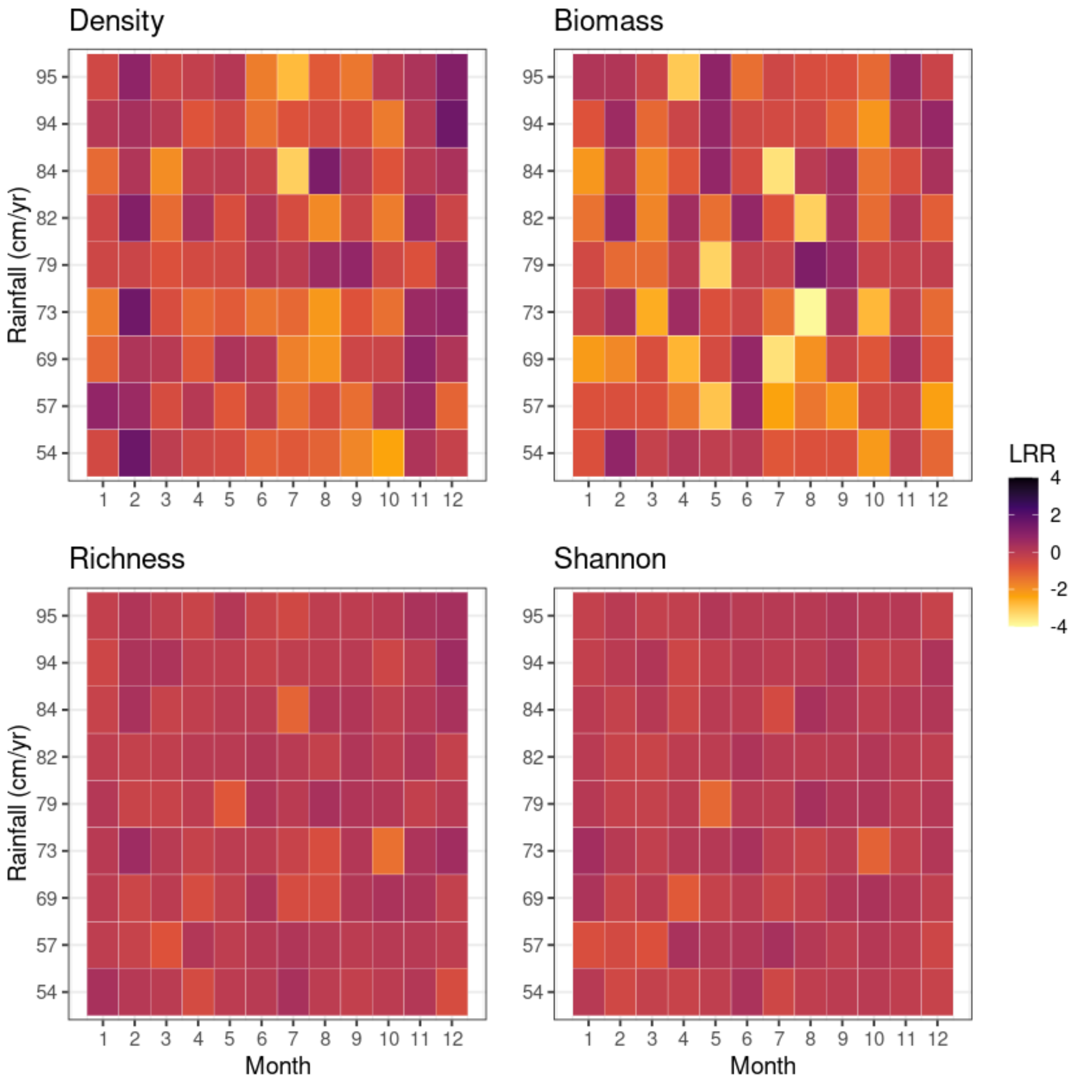


Month	Rain	Temperature
1	-0.45 (0.38)	-1.26 (0.96)
2	-0.7 (0.33)	-1.03 (0.41)
3	-0.64 (0.29)	-0.26 (0.25)
4	-0.45 (0.37)	0.01 (0.21)
5	-0.52 (0.25)	0.6 (0.29)
6	1.6 (0.99)	0.93 (0.26)
7	0.25 (0.45)	1.14 (0.31)
8	-0.54 (0.28)	1 (0.25)
9	2.34 (0.91)	1.01 (0.2)
10	-0.03 (0.99)	0.58 (0.45)
11	-0.21 (0.58)	-0.38 (0.65)
12	0.01 (0.61)	-1.13 (0.58)

Values are normalized within sites and averaged across the region, displayed as "mean (standard deviation)"

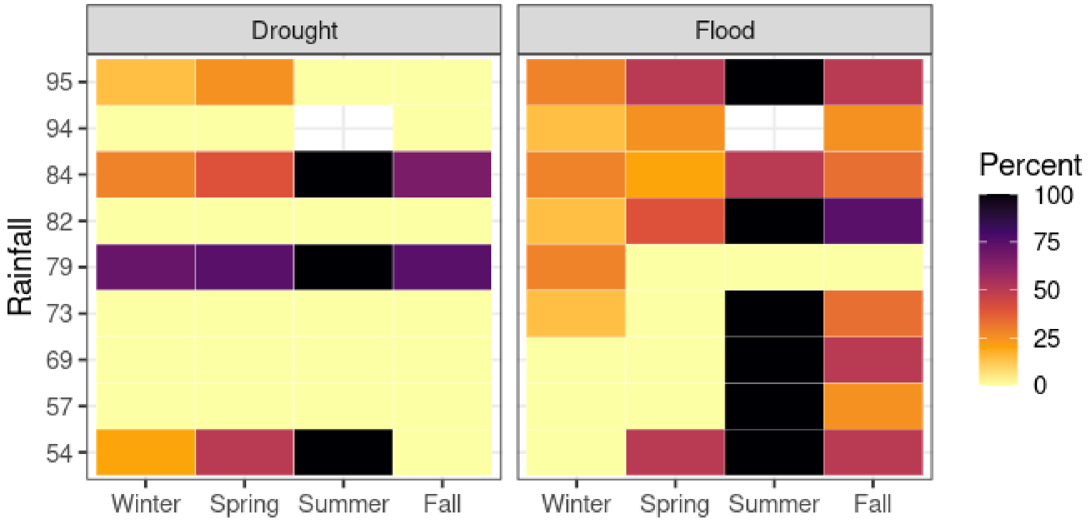
Appendix 5.07: Identifying Seasons: Monthly Rain and Temperature Table

Monthly rainfall and water temperature, reported as the average z-score from nine streams spanning the study region. Values are reported as “mean (standard deviation)”.



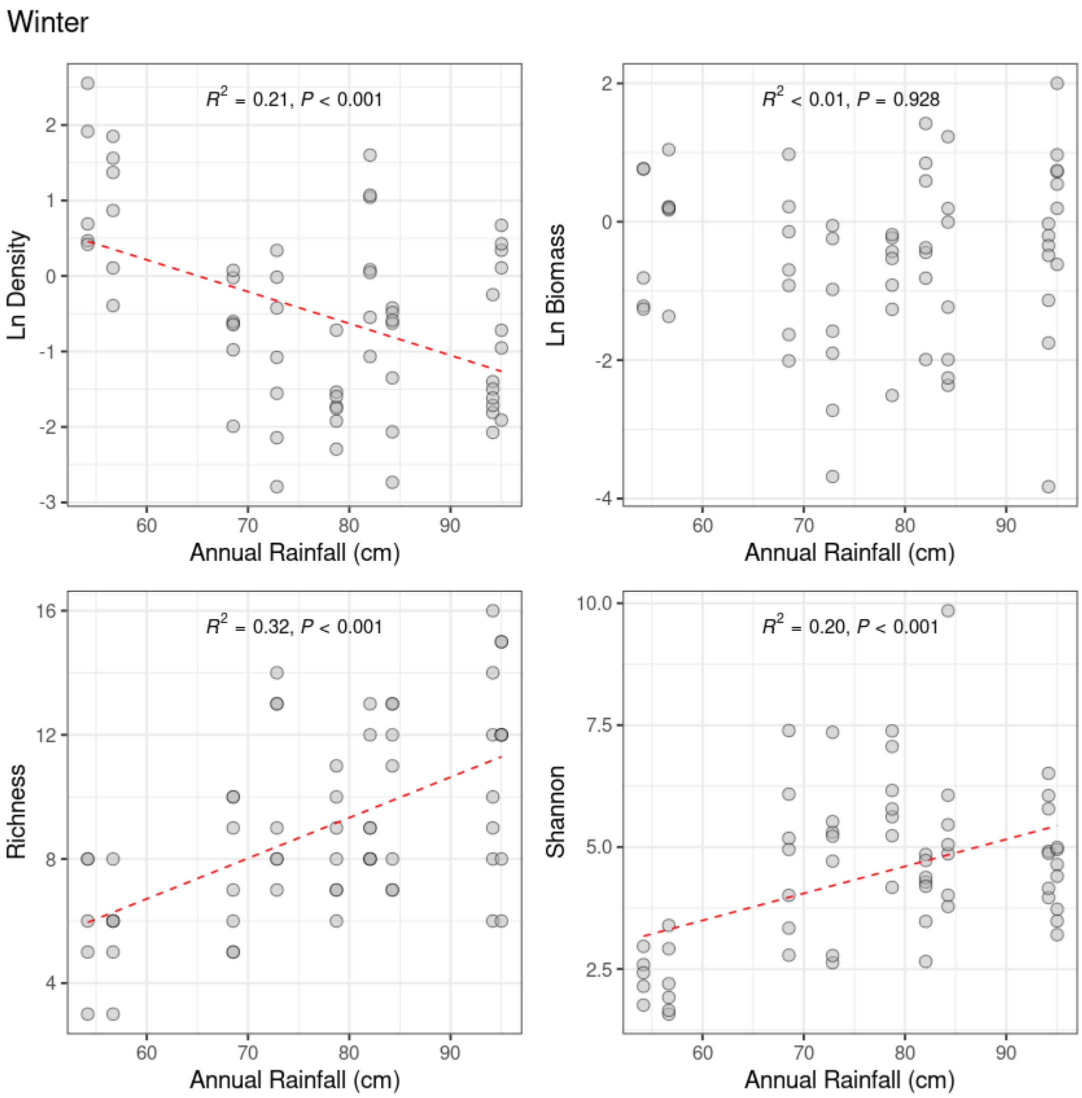
Appendix 5.08: Community Metric Log Response Ratios vs Season

Heat map of average log-response ratios (LRR) for fish communities for each site and month (2017-2020). Colors of cells transition from light negative values to dark positive values. Log response ratios were calculated against the long-term average.



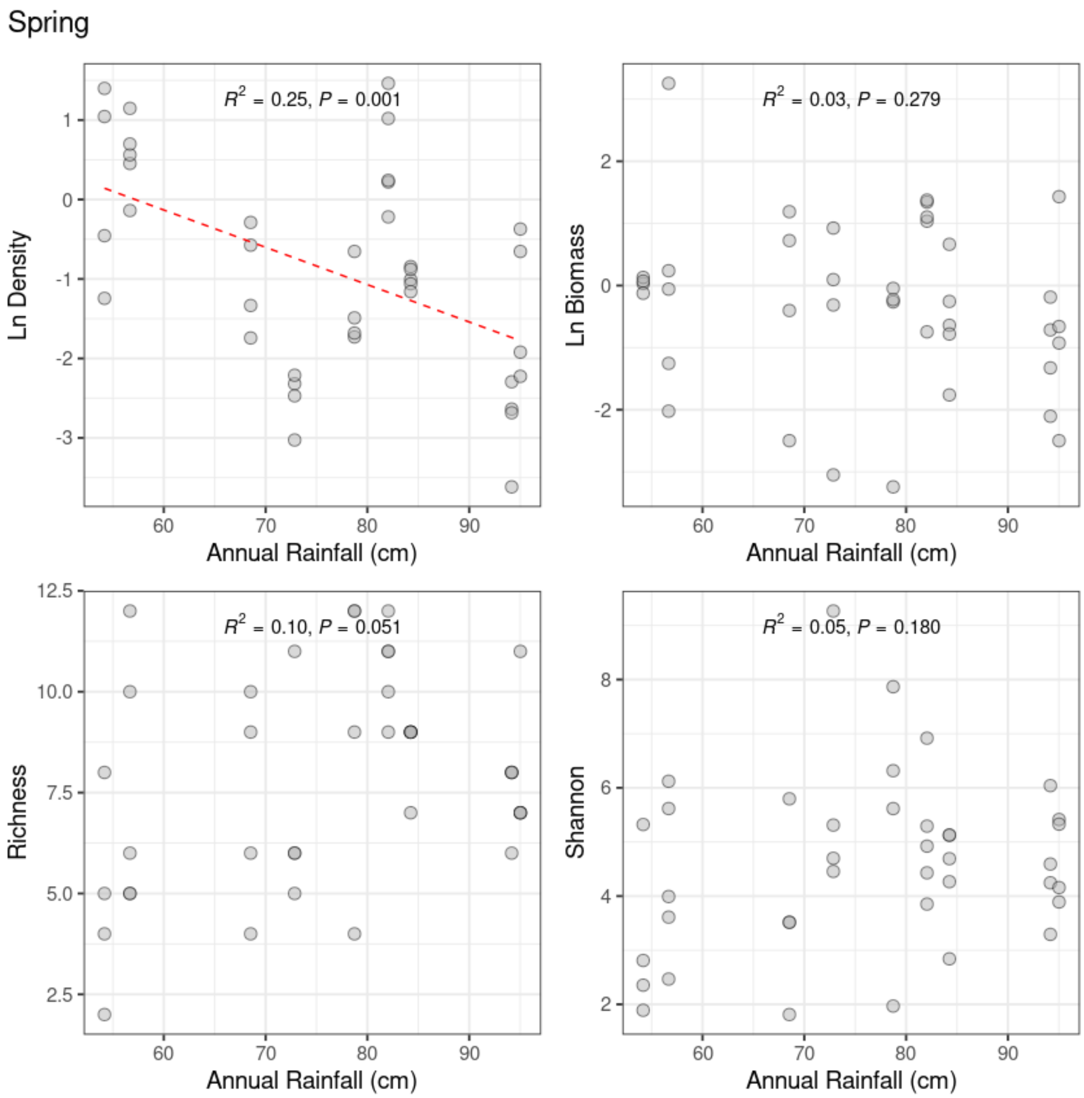
Appendix 5.09: Drought and Flood Occurance vs Season

Heat map of the proportion of months containing droughts or floods (2017-2020). Cell colors darken with increased proportion. Droughts were seven or more contiguous days under the annual 25% percentile. Flood were flows exceeding 10 times the annual median.



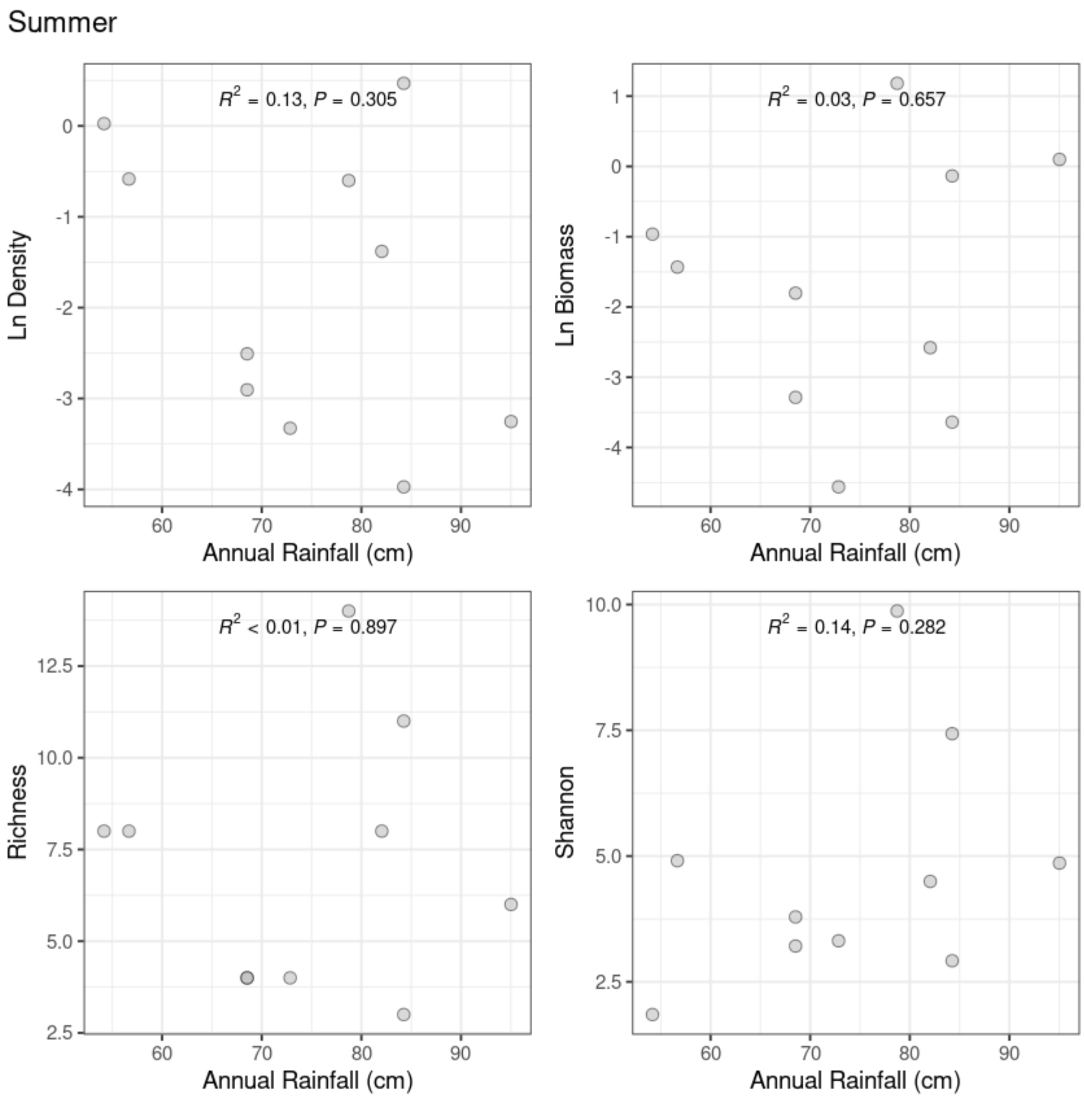
Appendix 5.10: Winter Fish Community Regressions

Linear regressions of fish community characteristics versus annual rainfall during Winter (2017-2020). Community descriptors include density (fish per m^2), biomass (g/m^2), species richness, and Shannon-Wiener diversity.



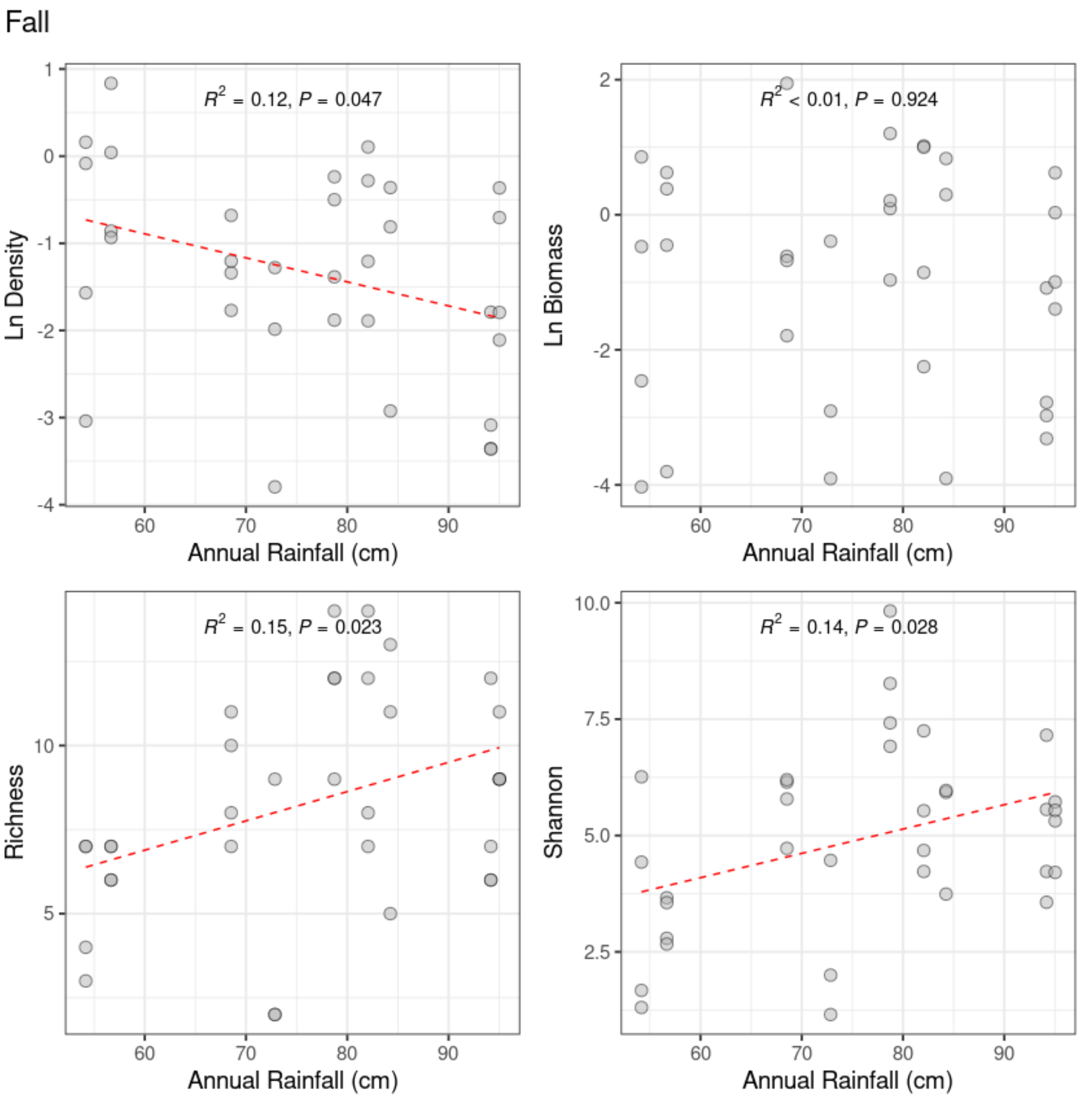
Appendix 5.11: Spring Fish Community Regressions

Linear regressions of fish community characteristics versus annual rainfall during Spring (2017-2020). Community descriptors include density (fish per m^2), biomass (g/m^2), species richness, and Shannon-Wiener diversity.



Appendix 5.12: Summer Fish Community Regressions

Linear regressions of fish community characteristics versus annual rainfall during Summer (2017-2020). Community descriptors include density (fish per m^2), biomass (g/m^2), species richness, and Shannon-Wiener diversity.



Appendix 5.13: Fall Fish Community Regressions

Linear regressions of fish community characteristics versus annual rainfall during Fall (2017-2020). Community descriptors include density (fish per m^2), biomass (g/m^2), species richness, and Shannon-Wiener diversity.

Chapter 6: Conclusions

Impetus for Research:

This research was motivated by the necessity to comprehend the implications of aridification on streams within the context of escalating climate warming and shifting precipitation patterns worldwide. With drylands expanding and precipitation cycles transforming, concerns about water scarcity have heightened, particularly in vulnerable regions such as the Southwestern USA. Focusing on the semi-arid to sub-humid coastal rivers of South Texas, I aimed to address the intricate dynamics of climate-induced shifts in precipitation patterns and their effects on ecosystems. Employing a space-for-time approach, the research established connections between climate drivers, local environmental conditions, and animal population abundances, offering insights applicable to analogous ecosystems globally. The urgency of this investigation was underscored by global climate models predicting increased aridity, emphasizing the need to enhance our understanding of the mechanistic links between precipitation, flow regimes, and aquatic biota.

Study Design Overview:

This dissertation features comprehensive study design encompassing multiple key elements across its chapters. The focal point was the semi-arid to sub-humid coastal rivers of South Texas, identified as an ideal study system that was both at risk due to climate change and yet severely undersampled, emphasizing the imperative to understand the consequences of aridification on stream ecosystems. By employing a space-for-time substitution approach, the research leveraged the natural spatial precipitation gradient in South Texas to unravel the intricate dynamics of climate-induced shifts in precipitation patterns and their impact on ecosystems. The studies integrated fish, invertebrate, and environmental surveys conducted from 2017 to 2020, as well as USGS gage data, long-term climate data, experimental work, and targeted sampling for stable isotopes. Using these data I evaluate phenomenological patterns in stream communities in relation to annual rainfall and then attempt to characterize mechanistic drivers of the observed patterns including resource availability, type, and acquisition strategies, connectivity to downstream marine environments, and differential responses to various hydrologic disturbance events. This multifaceted approach aimed not only to fill critical data gaps in ecoregion 34 but also to provide essential insights into the life cycle of coastal species, offering valuable information for proactive conservation and management strategies amid ongoing environmental changes.

Key Findings Summary:

In Chapter 2, our investigation of fish and invertebrate communities along the precipitation gradient uncovered compositional shifts and nuanced responses, revealing positive correlations between fish diversity and rainfall. This chapter emphasized the role of water quality in shaping fish assemblages, showcasing the impact of drier conditions through abiotic filters, which reduced diversity and favored taxa with specialized adaptations, particularly in semi-arid systems dominated by euryhaline and live-bearing species. In Chapter 3, a comprehensive exploration of allochthonous and autochthonous dependency, alongside overall food-web structure, highlighted shifts from insect predation to herbivory in drier climates. Stable isotope data indicated increased autochthonous assimilation, wider resource use, and reduced food-chain length, with Chapter 4 extending the ecological narrative to consider estuarine connectivity. This chapter elucidated inconspicuous amphidromous species' significant downstream-to-upstream connectivity, emphasizing vulnerability to disruptions by dams, urbanization, and climate change. Lastly, Chapter 5 challenged prevailing notions about flood effects, offering insights into the nuanced relationships influenced by long-term precipitation patterns and varied impacts of drought events based on precipitation regimes. These results collectively refine our understanding of climate, hydrology, and fish communities, providing valuable insights into how different precipitation regimes shape responses to hydrological disturbances, with a specific focus on Poeciliid resilience and reduced centrarchid abundances during hydrological droughts in hot and arid summers.

Specialized Taxa and Reduced Diversity in Semi-Arid Stream Systems

Employing hierarchical community assembly models and a space-for-time substitution, the research explored the relationships between precipitation gradients, environmental variables, and organismal responses. This study contributes to our understanding of the impact of precipitation on community composition and diversity in streams. The findings reveal that local environmental conditions plays a crucial role, acting as an abiotic filter under drier conditions, resulting in reduced diversity and favoring specialized taxa, particularly in semi-arid systems. This insight provides a nuanced perspective on the role of precipitation in shaping aquatic communities. Beyond its immediate implications, this knowledge is essential for predicting and managing the consequences of changing precipitation patterns, emphasizing the need for tailored conservation strategies based on local precipitation regimes. The findings challenge traditional assumptions about how communities respond to hydrological disturbances, offering a foundation for more effective freshwater ecosystem management in the context of climate change. While Chapter 2 demonstrated that rainfall plays a pivotal role in shaping community composition, Chapter 3 shows how aridity changes basal resource availability and consumption within stream ecosystems.

Autochthonous Assimilation and Trophic Shifts in Arid Streams

The investigation centered on unraveling the impacts of aridity on basal resource availability and consumption within stream ecosystems along a natural precipitation gradient. From mesic to semi-arid climate, there is a shift from insect predation to herbivory, and a simplification of stream food webs. Stable isotope data highlight increased autochthonous assimilation, wider resource use, and reduced trophic levels in semi-arid streams, contributing to a more comprehensive understanding of how aridification influences energy flow in aquatic ecosystems. This knowledge extends beyond the immediate study sites, providing insights into the general principles governing trophic interactions in arid regions. My synthesis offers a theoretical framework for understanding how changes in precipitation regimes can cascade through food webs, with potential implications for ecosystem stability and resilience. By revealing the mechanisms underlying these trophic shifts, the results enhance our ability to predict and manage the ecological consequences of aridification on aquatic ecosystems globally.

Amphidromous Nutrient Pathways and Vulnerabilities in Coastal Waters

This exploration sheds light on the ecological connectivity in coastal rivers, particularly emphasizing the significance of inconspicuous amphidromous species. The downstream-to-upstream connectivity driven by these species highlights the vulnerability of estuarine nutrient subsidies to disruptions, offering insights into the intricate relationships between river and coastal ecosystems. The findings carry significant implications for conservation and management practices, especially in regions where coastal ecosystems depend on nutrient subsidies from rivers. The study underscores the importance of considering the ecological role of less conspicuous species in maintaining overall ecosystem health and resilience. This understanding is crucial for developing conservation strategies that effectively account for the intricate connectivity between freshwater and coastal environments, thereby contributing to more holistic and impactful ecosystem management.

Long-Term Precipitation, Floods, Droughts, and Seasonal Dynamics in Fish Communities

This investigation delved into the intricate interplay between long-term precipitation patterns and hydrological disturbances, shedding light on their cumulative effects on stream communities. Departing from studies primarily focused on immediate impacts, this research extended its scope to encompass the enduring implications of historical precipitation patterns on the resilience and recovery of stream communities in the face of hydrological disturbances. Utilizing linear mixed effects models, the study unveiled that community responses to antecedent floods were contingent upon long-term precipitation patterns. In semi-arid watersheds, floods correlated with decreased fish abundance but increased diversity, contrasting with the opposite trend observed in mesic watersheds. Structural Equation Models elucidated that both annual rainfall and flood characteristics played pivotal roles in driving fish biomass and diversity. The influence of monthly rainfall on fish community metrics was relatively modest, highlighting the predominant role of flood characteristics, especially duration. This study challenges prevailing notions about the impacts of floods, enriching our understanding of climate, hydrology, and fish communities. The nuanced relationships, influenced by long-term precipitation patterns, unveil diverse impacts of drought events contingent upon regional precipitation regimes. These insights offer valuable guidance for managing aquatic ecosystems in the context of climate change, particularly in crafting adaptive management strategies that account for finer-scale differences in regional climate. Emphasizing the significance of long-term climate considerations, my conclusions challenge traditional assumptions about the uniform effects of hydrological disturbances, providing a foundation for more nuanced, context-specific conservation and management approaches amidst the dynamic landscape of climate-induced alterations to aquatic ecosystems.

Foundations in Mesic and Semi-Arid Stream Ecology:

This research serves as a foundational cornerstone for the development of a comprehensive model encompassing mesic and semi-arid stream communities, resilience dynamics, and intricate food-web interactions. While each region harbors unique intrinsic processes, ecological studies of this nature aim to uncover common threads and processes that exhibit similarities across diverse ecosystems. The amalgamation of observational insights, experimental data, and stable isotope analyses presented in this dissertation lays the groundwork for understanding rainfall as the fundamental driver of stream community dynamics. Furthermore, the intermediate mechanisms linking these rainfall effects are elucidated, providing essential principles that contribute to a broader comprehension of ecological processes in streams. This holistic approach not only enhances our understanding of regional intricacies but also facilitates the identification of universal ecological principles that can be applied across different ecosystems, fostering a more comprehensive understanding of the broader ecological landscape.

Conclusion:

In conclusion, this dissertation contributes to ecological knowledge by addressing the urgent need to understand the implications of aridification on streams in the face of global climate change. The research, driven by the escalating challenges of climate warming and shifting precipitation patterns, focused on the semi-arid to sub-humid coastal rivers of South Texas. By adopting a comprehensive study design and employing a space-for-time substitution approach, I successfully unraveled the intricate dynamics of climate-induced shifts in precipitation patterns and their impact on ecosystems. The key findings across chapters provide valuable insights into the stratification of fish and invertebrate communities along the precipitation gradient, the nuanced impacts of aridity on trophic dynamics, and the vulnerability of amphidromous nutrient pathways in coastal waters. The implications extend beyond the Texas Coastal Plain, serving as a foundational cornerstone for a comprehensive model that contributes to a broader understanding of ecological processes in streams. By challenging assumptions, offering region-specific considerations, and emphasizing the need for tailored conservation strategies based on local precipitation regimes, my work sets the stage for future investigations and management practices in the context of aridification and climate change.