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CONNECTING DIVERSITY INDICES, ECOSYSTEM PROCESSES, AND LANGUAGE USE TO BETTER UNDERSTAND AND MANAGE FRESHWATER SYSTEMS

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DEPARTMENT OF BIOLOGY

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

LIST OF FIGURES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

ABSTRACT

Rivers and streams are among the world’s most threatened ecosystems despite the importance of freshwater to human society. Rivers have been dammed, dried, and moved for human needs and consumption. They have experienced a dramatic loss of biodiversity, particularly in response to human population growth and climate change. Understanding the drivers of ecological community change is vital to mitigate threats to water scarcity and biodiversity. In my dissertation, I explore how elements of climate change, river drying, and dam management alter river biodiversity. By quantifying how aquatic assemblages change in response to multiple stressors, my work highlights ways to better manage river ecosystems in a future that will be increasingly defined by changes in climate and water use. Further, the development of effective management strategies depends on effective communication of research findings. Therefore, I also analyze language use describing dry river systems, and provide universal definitions. Combined, my research addresses multiple threats to freshwater diversity across space and over time in complementary ways to allow for better river management and protection.

Rivers and streams that sometimes cease to flow (non-perennial streams) are the most common form of flowing waterways on the planet. In the past 20 years, research on these systems has increased exponentially across multiple disciplines. Despite the need to connect research across scientific fields to better understand these dynamic systems, a consensus on terminology has not been reached, making meta-analyses, syntheses, management, and policy difficult. Published in 2020, my first chapter quantitatively explored 12 frequently used names for non-perennial streams over time and suggest universal terms and definitions. I found no consensus for a single name in any scientific field, but found substantial research overlap when exploring research topics across terms. I also found significant thematic overlap in definitions across papers from various fields of study, indicating redundancy across many terms. Finally, I suggest universal definitions for three specific terms to better facilitate effective communication across research fields, the public, and policy makers.

As climate change alters physical environments, understanding changes in community structure is essential for effective management and species conservation. While species diversity has historically been the focus of community studies, research demonstrates the value of using functional and phylogenetic diversity. Functional traits describe differences in ecological roles

among species and phylogenetic diversity captures the evolutionary relatedness among species. For my second chapter, published in 2023, I explored changes in fish community composition in streams across Oklahoma over a 42-year time frame to see how shifts in the physical environment alter functional and phylogenetic diversity. I found that historical diversity influenced how communities changed over time. That is, historically less diverse communities changed in a different way than historically more diverse communities did. Changes in functional richness demonstrated the importance of environmental conditions while phylogenetic diversity trends showed no clear trend of community structure. Both types of diversity, however, were significantly correlated to annual changes in maximum temperature. Overall, I found that community assembly has changed over time, although specific changes were related to the historical diversity of the community.

Though aquatic ecologists have long recognized the importance of flow variation in flowing rivers, these variations do not represent the full conditions biological communities may experience in streams that seasonally dry, known as non-perennial streams. For non-perennial stream communities, equally important to flow variation are the drying and wetting regimes, or the characteristics of drying and wetting events. Drying and wetting can act as disturbances on these systems, and the timing, duration, frequency, magnitude, and rate of drying and wetting could have varying effects on riverine communities. My third chapter connected drying and wetting characteristics with patterns of macroinvertebrate, soft-bodied algal, and diatom assemblages. I found the amount of flow duration prior to sampling was correlated with macroinvertebrate and soft-bodied algal assemblage structures, though I found no drying or wetting characteristics predicted richness of these two assemblages. Diatom richness and structure, however, were heavily influenced by the date of drying. Thus, I found no single characteristic that explained structure or richness across every assemblage, highlighting the need for multiple ecological and hydrological benchmarks to meet management goals. Given the increasing prevalence of non-perennial freshwater ecosystems, understanding how various drying events influence stream communities is important to understanding these dynamic systems.

Humans have a long history of controlling water flow, particularly through the construction of dams. Dams vary in size, purpose, and management strategy, which combined can significantly change the temperature, flow, and physical structure of downstream waters.

Southeastern Oklahoma provides a unique opportunity to compare management strategies across rivers of similar ecological and evolutionary histories. Three out of four major rivers in southeastern Oklahoma are dammed; each dam is managed for a different purpose and the presence of a fourth, un-impounded river provides a unique opportunity to understand how management alters ecological communities. In my last chapter, I used field surveys to sample sites above and below dams, as well as sites along a fourth un-impounded river. I found significant biological differences among the four rivers, but smaller differences among site types across the rivers, regardless of dam presence or management type. While biologic metrics did not show differences among site types, ordinations with full assemblage data did indicate some effect of dams on assemblage composition. We found biological metric and assemblage differences in this study were correlated to both local and watershed environmental variables. The higher elevation regions between these four watersheds may lead to biogeographic barriers, isolating the assemblages within each river. In addition, the strong aerial dispersal ability of many of the common taxa we found may allow for dispersal longitudinally along the rivers, damping the influence of dams on differences between communities upstream and downstream of the impoundment. The nuances within the results of our data highlight the importance of site-specific studies to fully understand how anthropogenic activities alter riverine ecosystems. As demands for freshwater continue to grow, clearly understanding how dam management strategies alter river communities will allow for clearer policies to protect these ecosystems.

Taken together, my dissertation broadly examines the impacts humans have on freshwater systems. Understanding the effects of multiple stressors on these diverse ecosystems and sharing common language is crucial to understanding how to properly manage them. My research highlights how rivers have responded to environmental alterations, which, via climate change, are only expected to continue and increase in magnitude and will provide novel ways to manage these diverse, dynamic, and threatened systems.

CHAPTER ONE

WHAT'S IN A NAME? PATTERNS, TRENDS, AND SUGGESTIONS FOR DEFINING NON-PERENNIAL RIVERS AND STREAMS

Keywords:

non-perennial, intermittent, ephemeral, temporary, stream, river, literature review, latent Dirichlet allocation, text mining, synthesis

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ABSTRACT

Rivers that cease to flow are globally prevalent. Although many epithets have been used for these rivers, a consensus on terminology has not yet been reached. Doing so would facilitate a marked increase in interdisciplinary interest as well as the critical need for clear regulations. Here we reviewed literature from Web of Science database searches of 12 epithets to learn (Objective 1—O1) if epithet topics are consistent across Web of Science categories using latent Dirichlet allocation topic modeling. We also analyzed publication rates and topics over time to (O2) assess changes in epithet use. We compiled literature definitions to (O3) identify how epithets have been delineated and, lastly, suggest universal terms and definitions. We found a lack of consensus in epithet use between and among various fields. We also found that epithet usage has changed over time, as research focus has shifted from description to modeling. We conclude that multiple epithets are redundant. We offer specific definitions for three epithets (non-perennial, intermittent, and ephemeral) to guide consensus on epithet use. Limiting the number of epithets used in non-perennial river research can facilitate more effective communication among research fields and provide clear guidelines for writing regulatory documents.

INTRODUCTION

Rivers and streams that cease to flow at some point in time or space—hereafter referred to as non-perennial—are hydrologically diverse and globally prevalent. Their defining characteristic is a temporary lack of surface flow, which leads to isolated pools or dry channels (Uys & O'Keeffe, 1997; Steward *et al.*, 2012; Leigh *et al.*, 2015). By some estimates, these watercourses comprise at least 30% of the global river network (Tooth, 2000), reaching up to 44% of the river network in South Africa (Uys & O'Keeffe, 1997), 59% in the United States (Goodrich *et al.*, 2018), and about 70% of river channels in Australia (Datry, Larned & Tockner, 2014). The occurrence of non-perennial rivers is expected to increase in the future due to shifts in global climate, construction of dams and impoundments, and increased water abstractions to meet human demands (Postel, 2000; Gleick, 2003; Larned *et al.*, 2010; Datry *et al.*, 2014; Jaeger, Olden & Pelland, 2014). Despite their prevalence worldwide, our understanding of the hydrology and ecology of non-perennial rivers is minimal when compared to perennial systems (Datry *et al.*, 2014; Leigh *et al.*, 2015). While non-perennial river systems have recently become the focus for researchers across many fields, the terminology used to describe them is incredibly diverse (Shanafield *et al.*, 2020).

A number of terms currently exist to describe the temporal and spatial characterization of surface flow cessation or the partial or complete drying of rivers and streams (hereafter referred to as epithets, e.g., intermittent, ephemeral, temporary, dry, etc.; Uys & O'Keeffe, 1997; Steward *et al.*, 2012; Leigh *et al.*, 2015). The issue of using multiple terms to describe the same concept has plagued ecology for years and is prevalent in some of the most frequently used terms in ecology (Peters, 1978; Fauth *et al.*, 1996; Stroud *et al.*, 2015) and hydrology (Venhuizen *et al.*, 2019). A recent survey found substantial differences in how laypeople and experts consider words like river, dam, and river basin (Fauth *et al.*, 1996). These examples demonstrate the confusion and misunderstanding that surround word use and scientific concepts, preventing clear and effective communication and potentially hindering scientific progress and effective management (Venhuizen *et al.*, 2019).

Standardized terminology is required to unify the rapidly growing literature on non-perennial streams and rivers (Leigh *et al.*, 2015) because effective science communication is "dependent on careful definition" (Poff, 1992). Previous attempts to define non-perennial rivers exist, though their definitions have not been widely accepted (Uys & O'Keeffe, 1997; Williams, 2006; Gallart *et al.*, 2012). Uys and O'Keeffe (1997), for example, provide detailed terms and definitions based on various hydrologic stages and yearly timing of intermittency, though their paper is primarily focused on rivers and streams in South Africa. A more recent attempt focused on the timing and location of aquatic habitats, such as riffles and pools (Gallart *et al.*, 2012). Despite these efforts, there is no global consensus on terminology (Leigh *et al.*, 2015). It has been theorized that this could be in part because a single river may fit into various categories depending on the section of the channel requiring a definition (Datry, Bonada & Boulton, 2017). Previous attempts to define non-perennial terminology also rely on specific details about the timing and magnitude of flows of the river in question (Uys & O'Keeffe, 1997; Gallart *et al.*, 2012). These details may not always be available, however, as hydrologic data on non-perennial rivers and streams are scarce due to the lack of river gages on them and the historical research focus on perennial rivers (Leigh *et al.*, 2015; Datry *et al.*, 2017; Zimmer *et al.*, 2020).

Despite the lack of current consensus, using common terms and definitions ensures continued opportunities for multidisciplinary research (Shanafield *et al.*, 2020), supports research synthesis such as comprehensive reviews and meta-analyses (Ward, 2016), and ensures that assumptions behind the definition of non-perennial waters are explicit (Shanafield *et al.*, 2020). Taken together, clarifications on terminology should further aid progress in connecting research and management (Shanafield *et al.*, 2020). For example, in the United States, the Clean Water Act allows states to adopt individual definitions and water quality standards after approval from the Environmental Protection Agency. These state-by-state definitions of non-perennial rivers, along with a lack of consistent epithets, allow for a wide variety of policy and enforcement. Out of 56 states and territories, only 17 define "ephemeral" and 20 define "intermittent" waterways. This lack of consistency allows for protections of these valuable resources to vary widely, placing non-perennial systems further at risk and complicating management efforts (Fritz, Cid & Autrey, 2017; Sullivan, Rains & Rodewald, 2019). Common nomenclature will allow for easier comparisons across fields, lead to more inter- and multidisciplinary research, (Ward, 2016) and be inclusive of the wide hydrologic range of non-perennial systems (Leigh *et al.*, 2015; Costigan *et al.*, 2016). More open and connected research will also help refine and build conceptual models and meta-analyses (Ward, 2016), allowing for clearer research synthesis and better protection for non-perennial river systems.

Our aim in this review was to identify, define, and synthesize the diversity of epithets used to describe non-perennial streams in research (Uys & O'Keeffe, 1997; Steward *et al.*, 2012; Leigh *et al.*, 2015) across various fields and to provide common terminology (Leigh *et al.*, 2015). Here we address the nomenclature surrounding non-perennial river systems and review how their various epithets are used. Our objectives are to: (Objective 1, hereafter O1) synthesize the large and growing literature to evaluate how epithets are used across Web of Science categories; (O2) assess how epithet use has changed over time; and (O3) identify how epithets have been defined throughout the literature. We use bibliometric techniques including topic modeling to explore how epithets for non-perennial river systems vary across research fields (e.g., hydrology, ecology) and over time to allow for a consensus in epithet use. In this way, we provide an overview of non-perennial river research trends to allow for more consistent terminology to further inter- and multidisciplinary non-perennial river research and protections. Finally, we suggest universal terms and definitions to provide common epithets across research fields.

METHODS

Data Sources

We performed a comprehensive literature review using the search engine in Clarivate Web of Science (WoS; Core Collection) for papers published between 1 January 1900 and 30 May, 2019. Our searches were not limited to the English language, though all analyses assumed that text was written in English. WoS has indexed scholarly books, peer-reviewed journals, reviews, editorials, chronologies, and reports within multiple research fields since 1900. We created two-word search phrases that included (1) an epithet (a common descriptor used to describe a non-perennial system) and (2) a waterbody term, a noun for a flowing (i.e., lotic) freshwater system. We first generated a list of epithets of non-flowing conditions by selecting terms found in previous reviews of non-perennial literature (Uys & O'Keeffe, 1997; Steward *et al.*, 2012; Leigh *et al.*, 2015; Costigan *et al.*, 2016) and those resulting from discussions among authors for a total of 12 epithets (**Table 1**). We completed separate searches for "semi-perennial" and "non-perennial" systems due to the large number of papers that refer to perennial systems (i.e., those with uninterrupted surface flow). After conducting the semi-perennial and non-perennial searches separately, we combined the results to create the final "non-perennial" corpus (a corpus is defined as a set of text documents which are analyzed together). We used the same approach to create the “non-permanent” corpus, again to exclude papers that focus on perennial or permanent streams.

Next, we paired each epithet (**Table 1**) with an adjacent waterbody term (Campbell, 1991; Steward *et al.*, 2012; Leigh *et al.*, 2015). Similar to the epithets, waterbody terms were those commonly used to describe lotic systems and selected based on a series of discussions among authors. We included papers using both singular and plural terms (e.g., “river” and “rivers”). While we included 41 lotic waterbody terms, closer examination of search results indicated that some lentic (still or non-flowing water) focused papers were included in our results. Lastly, we limited the search results according to 37 WoS research field categories that include journals publishing natural science research (see S1 for example search), resulting in 11,696 papers to be analyzed (**Table 1**).

We downloaded full search results for each epithet separately (includes author list, year published, WoS categories, abstracts) and combined text from the abstracts to create a unique, epithet specific final corpus (**Table 1**). Abstracts were decomposed into a list of individual words (tokenized) without punctuation or numbers. Each word was then reduced to its base form (stemmed, e.g., “rivers” and “riverine” both became “river”) and common English words (stop words, e.g., “the”, “and”, “or”) were removed. All analyses were run in R as described in the following sections (R Core Team, 2019). A methodological flow chart was created to provide additional clarity (**Figure S1**).

O1: Topical Differences among Epithets

We compared the proportion of search results across categories as defined by WoS to quantify epithet use across fields (**Figure 1**). We then used a Fisher’s exact test to determine if there were any significant differences between WoS categories and the number of papers per epithet. Due to the size of the matrix, we had to use a simulated p value based on over a million replicates. We then deployed topic modeling with Bayesian latent Dirichlet allocation (LDA) models in the R package “textmineR” (Jones & Doane, 2019). This model assumes that each document in a corpus is made up of multiple topics, and each topic is made up of multiple words. The model finds common clusters of words within documents, grouping them together and forming topics. For example, the topic “agriculture” is created due to the common occurrence of the following words found together throughout documents: soil *, water *, irrig *, yield *, us *, season *, crop *, and so on (* indicates the result of stemming). Using these clusters, the model calculates the prevalence of each topic within individual documents within the corpus and estimates the probability of finding each topic within an individual document (theta matrix). This analysis requires the number of topics to be decided a priori. We calculated and averaged the probabilistic coherence, which tests how understandable each topic is, for 1–50 topics to determine the number of topics for modeling (Jones, 2019). We tested 1–50 topics to determine the trends of increasing the number of topics while keeping a smaller number of topics that would be manageable to explore. We chose six topics for topic modeling based on a plot of coherence versus the number of topics (**Table A1**; **Figure S2**).

We combined all 12 abstract corpora into a complete corpus for topic modeling. We calculated the probability of finding a topic in each document in the corpus with the theta matrix using the package "textmineR" (Jones & Doane, 2019). After designating the six topics, we extracted the top 20 words used to define each topic for comparison across epithets, and named each topic based on the 20 words associated with it. We averaged the theta matrix for each epithet and performed an unconstrained ordination using non-metric multidimensional scaling (nMDS; using the R package "vegan" (Oksanen *et al.*, 2011) to assess similarities in topical overlap among papers categorized according to the epithets (**Figure 2**).

O2: Epithet Uses over Time

We conducted WoS searches based on ten-time frames and explored how publishing rates of the epithets have changed over time. Prior to 1990, very few papers were published (or cataloged by WoS) on non-perennial systems (Leigh *et al.*, 2015). We therefore used three 25-year and one 15-year timeframes between 1900 and 1990. After 1990, publications on non-perennial systems became more frequent. Thus, we created timeframes for periods of five years. We used a Fisher's exact test to test the differences between the number of papers for each epithet across the time frames.

We used the same topic modeling approach described above (Jones & Doane, 2019) on the combined time series corpus to investigate changes in topics over time in the literature. We selected nine topics based on coherence calculations (**Figure S3**) and visualized their prevalence over time.

O3: Epithet Definitions

We first selected papers where epithets paired with “river” or “stream” were most important to compare epithet definitions. To select these papers, we calculated the “term frequency—inverse document frequency” (*tf_idf*) across the abstracts found in each corpus (Jones & Doane, 2019; Equation (1)).

$$\text{tf\_idf}=(f_a) / (n)+\log(N_d / N_a) \qquad (1)$$

where f_a is the frequency that word “*a*” appears in a document, n is the total number of words in a document, N_d is the number of documents in the corpus, and N_a is the number of documents within the corpus containing word “*a*”. The *tf_idf* describes the relative importance of a word in each document within a larger corpus. This value increases proportionally to how frequently the word appears in a document but is offset by how frequently the word is found within the full corpus (Equation (1)). We limited waterbody terms to either “river” or “stream” for definition analysis to ensure search results would be limited to lotic freshwater systems (for example, TS = (* arid * NEAR/0 (river * OR stream *) and WC = (listed S2)), where TS stands for search term, * indicates any prefix or suffix, NEAR/0 forces adjacency for the two search terms, and WC refers to Web of Science Category).

We selected a maximum of 50 papers for each epithet (25 using river and 25 using stream), totaling 374 papers used to collect definitions (**Table S1**). We manually searched each paper selected to record definitions of the epithets used. If other epithets were used in a paper, they were noted along with any definitions for analysis. Not every paper with a high tf_idf value included a definition, thus, we randomly selected an additional 25 papers from each corpus (not limited by waterbody term) to increase sample sizes. This led to a maximum of 75 and a minimum of 28 papers selected for definition mining (total of 672 papers used for definition analysis; **Table S1**). Before analysis, definitions were carefully reviewed to ensure proper spelling and to remove openings (e.g., “ephemeral streams are characterized by low flow during summer months” became “low flow during summer months”).

Definition corpora were too small to allow for LDA topic modeling. Therefore, we developed a set of important themes common across non-perennial river literature related to water sources, predictability, time frame, climate, and various phases of drying to assess how epithet definitions overlapped (**Table S2**). We reviewed each definition to assess its match to each theme. The number of themes that fit each epithet definition was totaled and divided by the total number of definitions per epithet term available. In this way, we assessed the degree of overlap among themes to see which epithets had the most similar definitions. We visualized epithet similarities using nMDS ordination with Euclidean distance. We used the R package ‘vegan’ (Oksanen *et al.*, 2011) with the proportions of each theme in epithet definitions for the nMDS. After running the initial nMDS, we excluded two themes that lacked a large proportion of any definitions (water scarcity and phases of drying: no subsurface flow) and “irregular,” which only had one definition.

We then compared how various research fields use the same epithet. Using our results from definition mining, we selected five epithets whose definition analysis papers were over 80% covering non-perennial river systems (non-perennial, 100%; ephemeral, 98%; temporary, 89%; intermittent, 88%; arid, 83%; **Table 2**). We chose to assign WoS defined categories by broader research fields (ecology, hydrology, and eco-hydrology; **Table 3**) to simplify comparisons. We reviewed definitions in each field to create a summary definition.

RESULTS

O1: Topical Differences among Epithets

A wide range of research fields use highly varied terms to describe non-perennial systems. While most WoS categories contained papers that used each of the 12 epithets, there were some epithets that were more associated with specific categories (Fisher’s Exact Test, simulated *p*-value > 0.001 with $1e^{05}$ replicates; **Figure 1**). Categories that were least likely to be about non-perennial rivers (biochemistry, physical/multidisciplinary/applied chemistry, computer science, materials science) had the greatest proportions of the epithets “arid,” “dry,” and “discontinuous”. Categories that are likely related to lotic non-perennial systems (water resources, marine and freshwater biology, multidisciplinary geosciences, environmental sciences, ecology) each contained over 1000 papers. These categories mostly used “seasonal” and “ephemeral,” though “seasonal” was the epithet which dominated most categories. Seven of the twelve epithets dominated across the 40 categories which were made up of at least 50 papers. Despite these differences, no single category was limited to the use of one epithet. Each category includes papers from at least six epithets (**Figure 1**).

Topic modeling from the complete corpus identified only six topics that we labeled based on the top 20 words associated with each topic (**Appendix A**). When exploring the similarities between epithets and topics, we found four main groups of epithets, each related to at least one topic (**Figure 2**). We calculated the stress of the nMDS to demonstrate how well the ordination works on a two-dimensional plane, with a stress below 0.2 demonstrating a good representation (Legendre & Legendre, 2012). The largest cluster contains “arid,” “dry,” “intermittent,” “non-permanent,” “seasonal,” and “temporary” and is associated with topics focused on agriculture, hydrology, and vegetation. The second largest cluster includes “discontinuous,” “interrupted,” and “irregular,” though “discontinuous” is farther removed from the other epithets. The topic most associated with this cluster is temperature. “Non-perennial” was the smallest cluster, with a close association to ecohydrology.

O2: Epithet Uses over Time

The rate of publications on non-perennial rivers increased drastically after 1990 (from 16.1 papers published per year to 154.2; **Figure 3A**). Publishing rates continued to increase quickly over time until the last time frame, 2016 to 2019. However, this time frame was much smaller than previous ones due to the search date of May 2019 as opposed to December 2020, which would have made it a full 5-year interval.

We found a difference in the proportion of the most common epithet per year (Fisher’s Exact Test, simulated *p*-value > 0.001 with $1e^{05}$ replicates). After 1950, 11 epithets are found throughout literature (excluding “non-perennial”; **Figure 3B**). “Non-perennial” appears between 1990 and 1995, disappears between 2001 and 2005, and appears again after 2006 with less frequency than the other terms. “Seasonal,” “ephemeral,” and “arid” appear frequently in all time frames after 1950. “Intermittent” is prominent in all time frames and has been used at approximately the same rate since 2000. Up until 1975, “discontinuous” was used frequently (33% between 1900 and 1925 and between 1926 and 1950), however its use decreased after 1950 (1% between 2016 and 2019). “Episodic” appears after 1975, though it also does not make a large proportion of results. “Interrupted,” “irregular,” “non-perennial,” and “non-permanent” are similarly used infrequently over time.

“Seasonal” has been used most frequently over time, followed by “dry” and “arid” (**Figure 4**). These three terms can also be related to the description of a study site, are broad, and are common in language and therefore may not require a specific definition. “Irregular,” “episodic,” “discontinuous,” “interrupted,” and “non-permanent” are used by the fewest papers over time.

Nine topics were identified using the LDA topic modeling from the combined Time Series Corpus. While some topics from the time frame sampling have the same names as those from epithet corpora, note they are from separate analyses (**Table A2**; **Figure S4**). Generally, the topics that have decreased in proportion over time are agriculture (9% decrease from 1991–1995 to 2016–2018) and geomorphology (6% decrease from 1991–1995 to 2016–2018). Topics that show the greatest increase over time are hydrology (14% increase from 1991–1995 to 2016–2018), community ecology (6% increase from 1996–2000 to 2016–2018), and modeling (5% increase from 1991–1995 to 2016–2018; **Figure S3**).

O3: Epithet Definitions

In total, 672 papers were reviewed for definition analysis. Although we limited our WoS searches, some search results included papers about topics other than non-perennial rivers or streams. For example, “dry stream” could be found in a chemistry paper testing adsorption ability of various volatile organic compounds under humid and dry streams of gas (Long *et al.*, 2011). “Non-perennial” and “ephemeral” had the largest proportion of papers that were about non-perennial river systems (100% and 98.7%, respectively) while “episodic” and “irregular” had the smallest proportion of papers on non-perennial systems (19.1% and 11.1%, respectively; **Table 3**). Roughly 22% of “episodic” papers focused on episodic acidification in streams as opposed to drying flow regimes (e.g., Sharpe & Demchik, 1998; Long *et al.*, 2011). “Non-perennial” was the smallest corpora with only 28 papers, though 100% of these papers were related to our topic (note that our WoS search for “non-perennial” and “non-permanent” excluded papers covering systems that flow continuously over time).

Out of the 672 papers analyzed for this study, 54% lacked any definition of its epithet. Out of the 452 papers classified to be about non-perennial river systems (67% of total papers explored), 39% did not include any definition (**Table 2**).

In total, we compiled 315 definitions from the original 672 papers. “Irregular” was the only epithet that had one paper providing a definition, while “discontinuous” had four.

The themes identified for definition analysis were chosen to represent the broader ideas that characterize non-perennial river systems (**Figure 5**). “Intermittent,” “temporary,” and “non-perennial” overlap with one another. These epithets are strongly related to the topic “Phases of Drying: No Flow” (see **Table S2** for full theme list). These three epithets are also related to “non-permanent” and “seasonal” and the themes “Phases of Drying: No Surface Water” and “Predictability/Seasonality.” Conversely, “discontinuous” (with four definitions) was strongly related to the ideas of disconnections (“Phases of Drying: Low Flow” and Phases of Drying: Isolated Pools”). “Interrupted” was surrounded by various themes and yet not closely related to any (“Phases of Drying: Not Specific”, “Source: Groundwater”, and “Tied to Specific Landscape or Climate”). Based on the nMDS, “interrupted” and “discontinuous” are the least related to other epithets, yet also lack strong correlations with most themes. Generally, overlap exists among definitions found for all 12 epithets.

We explored the five epithets that had the highest number of definitions to broadly examine how different fields use the same epithet (**Table 3**). The epithets we analyzed further were “non-perennial” (28 definitions), “ephemeral” (65 definitions), “temporary” (51 definitions), “intermittent” (59 definitions), and “arid” (72 definitions). Summary definitions were created for ecology, hydrology, and eco-hydrology fields (**Table S3**). These definitions also demonstrated overlap between epithets and among fields and many definitions were similar to one another.

DISCUSSION

Consistent terminology remains fundamental to advance science and communicate its broader implications (Leigh *et al.*, 2015; Stroud *et al.*, 2015; Ward, 2016). Here we highlight this issue with the diverse terminology used to describe non-perennial rivers systems over the past century (Uys & O’Keeffe, 1997; Steward *et al.*, 2012; Leigh *et al.*, 2015). As non-perennial river systems are both widespread and increasing numerically in response to climate change and increasing human demands (Postel, 2000; Gleick, 2003; Larned *et al.*, 2010; Datry *et al.*, 2017), research on these systems continues to grow. By conducting a bibliometric review of the published literature, we assessed whether epithet use is consistent across WoS categories using topic analysis; examined how epithet use to describe non-perennial rivers has changed over time; and identified how epithets have been defined. We conclude with recommendations for universal terms and definitions moving forward.

O1: Topical Differences among Epithets: Lack of Consensus

Our findings demonstrate the lack of consensus on epithet use within specific categories—each one included at least six epithets within their search results. While some epithets are more prevalent in certain categories than others (Fisher's Exact Test, simulated p-value > 0.001), many epithets are common across multiple categories. For example, "seasonal," "temporary," and "dry" can be found in each WoS category we explored (**Figure 1**). These epithets may simply be too broad, enabling their use across multiple categories.

We found widespread epithet use within and among WoS categories, with many of them using multiple epithets to describe non-perennial river systems. Despite limiting our searches to categories closely related to non-perennial river systems, some papers in our search results were in different WoS categories (e.g., computer science). Generally, these categories contained fewer papers than those likely related to freshwater lotic systems (e.g., water resources, environmental sciences, ecology, marine and freshwater biology). However, computer science, applied chemistry, and applied physics were all categories that had at least 50 papers across the 12 corpora. Epithets that made up the largest proportion in these categories were "arid," "dry," "discontinuous," and "irregular." For example, "arid" makes up a large proportion of both the applied chemistry and biochemistry and molecular biology fields (e.g., Sullivan *et al.*, 2019). Therefore, some epithets used in research surrounding non-perennial systems are also used for different fields beyond describing water flow in lotic ecosystems. While these papers could be related to non-perennial systems, the number of papers in our search results was too many to thoroughly examine as has been done in other LDA analyses (Luiz *et al.* 2019). This highlights the need for specific titles and keywords to ensure related papers appear in WoS searches.

While hydrology was not a distinct category included in the WoS searches, it did appear as a topic in LDA topic modeling. This topic was closely related to agriculture and vegetation themes and was related to the largest cluster of epithets ("non-permanent," "seasonal," "arid," "dry," "intermittent," and "temporary"). The relationship between these topics demonstrates similar research themes within hydrology and ecology, as we also relate topics of agriculture and vegetation broadly to ecology. The six topics that came out of LDA topic modeling further demonstrate the overlap between epithets in general, suggesting that the use of twelve epithets in non-perennial research is excessive.

O2: Epithet Uses over Time: Shift towards Syntheses

Epithet usage has been dynamic during the past 120 years (Fisher's Exact Test, simulated *p*-value > 0.001). "Seasonal" was the most common epithet of non-perennial rivers used in the literature across the entire time period (**Figure 3**) and was consistently used across WoS categories (**Figure 1**). Over time, the epithets that appear the most frequently tend to be more broad ("seasonal," "temporary," "dry") as well as more likely to be found in WoS categories other than those most likely to be about non-perennial systems (**Figure 1** and **Figure 4**). These epithets are likely most often used in WoS categories that focus on topics other than non-perennial systems. This observation was supported by our definition analyses. Based on the papers used for definition mining, less than 70% of papers that used "dry" and "seasonal" were about topics involving non-perennial river ecosystems (66% and 60%, respectively). Some papers used "interrupted stream" to describe airflow over chemicals (Long *et al.*, 2011) or "episodic river" to discuss infrequent river acidification (Lepori *et al.*, 2006; Neff *et al.*, 2009; Long *et al.*, 2011). Moving forward, it may be beneficial to avoid the use of general epithets of non-perennial systems and instead be more specific in terminology, so publications become more accessible and more likely to be included in future searches of non-perennial rivers.

Our analysis of how topics have changed over time offers further insight into temporal trends in epithet use (**Figure 5**). Topics that have decreased in use over time appear to be more descriptive and less about the river systems themselves. Conversely, topics related to hydrology, community ecology, and modeling have increased in prevalence (**Figure 5**). This shift is logical—observations and descriptions about systems are needed before hypotheses can be made and tested. The shift found in our results reflects this and demonstrates an increase in syntheses. This trend has been reported in other non-perennial river research, where historical papers tend to be descriptive while contemporary research is focused on, for example, the impacts of climate change (modeling) or how human interactions will impact communities (community ecology) (Leigh *et al.*, 2015; McCallen *et al.*, 2019).

We found a large shift in publication rates in our time frame analysis after 1990, which may be due to historical events that increased societal and environmental awareness of non-perennial rivers. The North American Benthological Society (NABS) held a Stream Solute Workshop in 1990 (Stream Solute Workshop Concepts and Methods, 1990) which led to multiple papers, including some which were the first to explore the biogeochemistry of non-perennial rivers (e.g., (Stream Solute Workshop Concepts and Methods, 1990; Holmes, Fisher & Grimm, 1994; Leigh *et al.*, 2015). The 2000 Water Framework Directive (WFD) in Europe encouraged research to include river condition assessments, as the classification of "waterbodies" determines river protection status including non-perennial streams (Leigh *et al.*, 2015). Similarly, in 2007 Australia established the Commonwealth Water Act to ensure proper management of the Murray–Darling Basin to protect intermittent rivers (Fritz *et al.*, 2017). The story of non-perennial rivers is complex in the United States. In 2001, the court case of Solid Waste Agency of Northern Cook County v. U.S., the U.S. Army Corps of Engineers focused on the definition of "jurisdictional waters" within the Clean Water Act. Lawyers for the Solid Waste Agency argued that the Army Corps of Engineers did not have jurisdiction over waterways not adjacent to open water, which often include non-perennial rivers (Legal Information Institute, 2001). In 2006, Rapanos v. United States case highlighted the need for clear definitions of non-perennial rivers and led to a large increase in non-perennial river research as scientists worked to demonstrate the importance of non-perennial rivers to navigable waters (Leigh *et al.*, 2015; Fritz *et al.*, 2017). The definition of jurisdictional waters further evolved in 2015 with the Clean Water Act (Fritz *et al.*, 2017) and again in 2020 when the Navigable Waters Protection Rule was completed, which included definitions for non-perennial rivers. Changes in policies and regulations within the past two decades surrounding non-perennial river systems have brought these systems further into the public eye, encouraging scientific research. With additional policies and water governance decisions regarding the definition and classification of non-perennial rivers, such as the 2020 U.S. Navigable Water Protection Rule, research on these systems will continue to grow.

O3: Epithet Definitions: The Issue of Overlap

Over one third (38.5%) of all papers did not offer a clear definition for the epithet of non-perennial rivers. Missing or vague definitions could be due in part to the increase in research and familiarity around these systems (Ward, 2016) or because resources on technical definitions are not well known (Osterkamp, 2008). The limitations of our WoS searches were also demonstrated while attempting to mine definitions. Out of the 672 papers selected, only two-thirds focused on non-perennial river systems. Only "arid," "ephemeral," "intermittent," "non-perennial," and "temporary" had over 80% of papers report an epithet definition.

Topics chosen for our definition analysis demonstrate the overlap between our multiple epithets. There was direct overlap between "intermittent," "temporary," and "non-perennial." "Non-permanent" and "seasonal" were also closely related to this cluster. This broad overlap demonstrates that using 12 epithets across non-perennial river research is redundant and could lead to confusion when attempting to synthesize papers for further research.

The summary definitions by broad fields demonstrate overlaps as well as unique characteristics of specific epithets. "Intermittent" and "temporary" demonstrate overlap in their broad definitions. Across all three fields, seasonal or predictable cycles are mentioned as well as a lack of surface water leading to isolated pools. Thus, we conclude that despite the range of fields which use various epithets, there is large overlap in their definitions. We also found that descriptive rather than quantitative definitions (e.g., how many weeks or months a river was without water) were more common throughout our definition analysis. While descriptive definitions have merit, we argue that a lack of quantitative definitions make classifying rivers and streams more difficult. While previous attempts at offering definitions included quantitative definitions (Uys & O'Keeffe, 1997; Gallart *et al.*, 2012), their attempts at offering universal definitions were unsuccessful. As previously stated, these quantitative definitions were extremely specific, requiring hydrological data that is often unavailable for non-perennial systems. Therefore, we argue that while quantitative definitions are useful in stream classification, they must be broad enough to allow for a lack of hydrological data. We further conclude that the use of so many epithets for non-perennial river systems is more confusing than helpful, highlighting the need for common epithets and definitions.

The results from our study must be interpreted with the following limitations in mind. First, our literature search was designed to be as specific as possible (limited epithets, waterbody terms, and categories), yet papers reporting on research other than non-perennial systems made it into our analyses. Examining each paper individually was outside the scope of this study. While the papers on other topics may skew our results, they are also indicative of the papers a researcher would identify when conducting a WoS search for a meta-analysis. Second, our review is based solely on the WoS search engine. Following similar methods with Google Scholar searches may have resulted in a different set of papers. However, the number of papers returned by our WoS search provided us with a large corpus that we believe represented the body of literature on non-perennial systems. We therefore chose to limit overlap by focusing on WoS search results. These methods may have excluded some papers on non-perennial river systems (Leigh *et al.*, 2015), however the aim of the paper was to capture overall trends in non-perennial river research. We felt that the logic behind our methods was sound and maintaining these methods prevented any biases in data collection.

RECOMMENDATIONS AND CONCLUSIONS

We find the use of multiple epithets of non-perennial river research to be redundant and confounding, likely challenging literature syntheses and meta-analyses in the future, and potentially limiting communication and knowledge exchange among researchers. Of the twelve epithets we analyzed, we suggest the continued use of the following three:

1. Non-perennial: this epithet typically had the broadest, but also the fewest, definitions. We speculate the lack of definitions is in part due to the broad nature of the epithet and that there is an implicit assumption that readers understand what the term means. We suggest the following definition: Any lotic, freshwater system that periodically ceases to flow and/or is dry at some point in time and/or space.
2. Intermittent: this epithet frequently overlapped with "temporary" (**Figure 2** and **Figure 5**). We chose "intermittent" as opposed to "temporary" because "temporary river" could imply that the river channel is not always present, as opposed to the surface flow within the riverbed being temporary. We argue that because the riverbed is always present, even if there is no water flowing, use of the word temporary is misleading. Intermittent rivers are those which do not only depend solely on precipitation for surface flow, and interface with groundwater that allows for prolonged flow. We suggest the following definition: A non-perennial river or stream with a considerable connection to the groundwater table, having variable cycles of wetting and flow cessation, and with flow that is sustained longer than a single storm event. These waterways are hydrologically gaining the majority of the time when considering long term flow patterns.
3. Ephemeral: "ephemeral" was not included in the same clusters as "intermittent" (**Figure 2** and **Figure 5**), implying that the two epithets lack overlap among their topics. Definitions for ephemeral were often related to precipitation patterns or extreme events, such as flooding and droughts, although not all definitions included these extremes and

> not every river that dries during a severe drought is ephemeral. However, the general focus on precipitation events implies that ephemeral streams lack a connection with groundwater and depend solely on precipitation for flow. We suggest the following definition: A type of non-perennial river or stream without a considerable groundwater connection that flows for a short period of time, typically only after precipitation events. These waterways are hydrologically losing the majority of the time when considering long term flow patterns.

These definitions were designed to be flexible enough to encompass existing definitions and enable their use across space and time (Ward, 2016). We also avoid broader epithets to be more specific for non-perennial systems as well as avoiding epithets that seem to reference perennial flow ("seasonal," "dry," "discontinuous.") In addition, these three epithets are used and defined in the 2020 Navigable Waters Protection Rule by the U.S. EPA. We acknowledge that the wide range of epithets currently used to describe these systems reflects the range of non-perennial systems in space and time as well as various disciplinary and cultural perspectives. We also acknowledge that many scientists may be accustomed to using epithets not listed here and may have their reasons to resist changing their epithet use. We strongly suggest that clear definitions be provided regardless of which epithets researchers use, or that authors cite a reference that provides a clear definition. Ideally, this definition would be located early in the introduction, or by clearly identifying a study site as non-perennial with a quantitative analysis or measurement that underlies its classification. By offering a clear definition, authors will ensure that their work will be included in research surrounding non-perennial river systems, ensuring that it will be included in future syntheses.

The use of consistent epithets for non-perennial research is imperative not only for future research, but also for policies surrounding these river systems (Leigh *et al.*, 2015). Non-perennial systems are dynamic, variable, and abundant (Uys & O'Keeffe, 1997; Steward *et al.*, 2012; Datry *et al.*, 2014; Leigh *et al.*, 2015). They play an important role in ecosystems, and their protection and management are vital to biodiversity and human health. Effectively communicating research using consistent language and providing clear definitions for key terms will enable scientific research to effectively bridge research fields (Ward, 2016), enhance communication with the public (Fauth *et al.*, 1996; Stroud *et al.*, 2015; Venhuizen *et al.*, 2019), and influence protections surrounding these systems (Fritz *et al.*, 2017).

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TABLES

Table 1. Table of search results from Web of Science. Epithets used to define non-perennial systems in the present study, paired with the source it was pulled from in brackets. We limited our search results by WoS categories to narrow our results to papers specifically related to natural river systems.

Adjective (and Reference)	**Number of Papers**
Arid (Tooth, 2000)	837
Discontinuous (Goodrich et al., 2018)	223
Dry (Goodrich et al., 2018)	1,580
Ephemeral (Goodrich et al., 2018)	1,652
Episodic (Datry et al., 2014)	201
Intermittent (Goodrich et al., 2018)	1,582
Interrupted (Goodrich et al., 2018)	103
Irregular (Ewart, 2018)	347
Non-Perennial (Goodrich et al., 2018)	59
Non-Permanent (Goodrich et al., 2018)	40
Seasonal (Goodrich et al., 2018)	4,358
Temporary (Goodrich et al., 2018)	1,404
Total	11,696

Table 2. Content of papers by epithet (NP refers to non-perennial). We examined 672 papers to mine definitions. However, many of these papers were not about non-perennial systems or lacked definitions. “Non-perennial” had the lowest number of papers included in the analysis, the largest percentage of papers that were about non-perennial systems, and one of the smallest proportions of papers without definitions (only “episodic” was lower).

Epithet	Number of Papers	% About NP Systems	% of NP Papers Without Definitions	NP Papers Without Definitions	Final Definition Counts
Arid	72	83.30	36.70	22	36
Discontinuous	36	33.30	66.70	8	4
Dry	75	66.70	52.00	26	24
Ephemeral	75	98.70	32.40	24	65
Episodic	63	19.10	16.70	2	13
Intermittent	75	88.00	33.30	22	59
Interrupted	33	33.30	54.60	6	5
Irregular	36	11.10	75.00	3	1
Non-perennial	28	100.00	17.90	5	23
Non-permanent	29	79.30	52.20	12	11
Seasonal	75	60.00	51.10	23	23
Temporary	75	89.30	31.30	21	51
Total	672		38.50	174	315

Table 3. Summary definitions for arid, ephemeral, intermittent, non-perennial, and temporary by broad research fields. Each one of these five epithets had over 80% of their papers provide a definition.

Adjective	Field	Summary Definition
Arid	Ecology	natural drying and wetting phases following seasonal fluctuations, leads to natural expansion (connected stream) and contractions (isolated pools)
Arid	Hydrology	may not flow every year depending on precipitation, minimal groundwater recharge
Arid	Eco-Hydrology	variable flows between or within years, sensitive to changes in climate
Ephemeral	Ecology	streams that only flow variably for a short period of time, after precipitation events during certain times of the year
Ephemeral	Hydrology	flow is scarce and sporadic in streams with high drainage, flow typically as a result of an extreme precipitation event
Ephemeral	Eco-Hydrology	rivers without flow for most of the year, yet which have high intensity flooding periods in response to precipitation events
Intermittent	Ecology	seasonal flowing and drying conditions that may result in isolated pools
Intermittent	Hydrology	regular wet and dry cycles with extreme floods and droughts, resulting in disconnected pools during the dry season
Intermittent	Eco-Hydrology	naturally dynamic and variable cycles of wetting and drying that can change from year to year in response to precipitation patterns
Non-Perennial	Ecology	lose surface water in drying and rewetting cycles for a period of time in most years
Non-Perennial	Hydrology	variable low and no flow periods
Non-Perennial	Eco-Hydrology	loss of flow and connectivity, reducing a stream to isolated pools during dry season
Temporary	Ecology	rivers that cease to flow for a period of time during cycle of drying and rewetting
Temporary	Hydrology	recurrent dry phase with no flow for variable time periods

Temporary	Eco-Hydrology	rivers that experience wetting after precipitation events and drying in drier seasons leading to isolated pools

FIGURE CAPTIONS

Figure 1. Proportion of epithets by Web of Science (WoS) category. Displayed are the 40 categories (out of 148 unique WoS categories) that contained at least 50 papers across all 12 epithet corpora on the *y*-axis. The proportion of each category made up of epithets is on the *x*-axis. Each color represents a different epithet, with the most dominate epithet per category highlighted in black. The total number of papers appearing in each category is displayed as the sample size along each column for reference (environmental sciences had the largest number with 2398 while multidisciplinary chemistry had the smallest with 55 papers).

Figure 2. A non-metric multidimensional scaling (nMDS) ordination (stress = 0.1029) representing similarities among the six topics found from latent Dirichlet allocation (LDA) topic modeling (blue words) and how they relate to papers about each epithet (black words). The large sample size made plotting each paper too cluttered, so average probabilities of the topic appearing in papers across all twelve corpora were used to understand broad, topical terms between epithets.

Figure 3. Number of total papers published (**A**) and proportion of papers published under different epithets (**B**) over time frames. Note the large jump in publication rates after 1990, and the steady increase until 2016. Papers from all 12 epithets are published between 1996 and 2000, though “non-perennial” does not appear in 2001–2005, all 12 are again represented in results from 2006 onward.

Figure 4. Publications of each epithet over time. Abstracts from 1990 to 2017 were compiled to see how epithet use has changed over time. Each epithet was counted once per abstract. Broader terms such as “seasonal,” “dry,” and “temporary” have been used the most frequently. “Temporary,” “non-perennial,” and “intermittent” are the three terms with the largest rate of increase over time.

Figure 5. An nMDS representing the Euclidean distance among epithets and definition themes (stress = 0.0962). Epithets in blue text, definition themes in larger, black text. The section of the nMDS with overlap includes epithets “intermittent”, “temporary”, and “non-perennial” as well as the theme *Phases of Drying: No Flow.* Full theme list: predictability = predictability/seasonality; variability = variability/unpredictability; time frame = specific time frame mentioned;

landform/climate = related to specific landform/climate; extremes = related to extremes (droughts and floods); pod = phases of drying: (**Table S2**).

FIGURES

Figure 1.

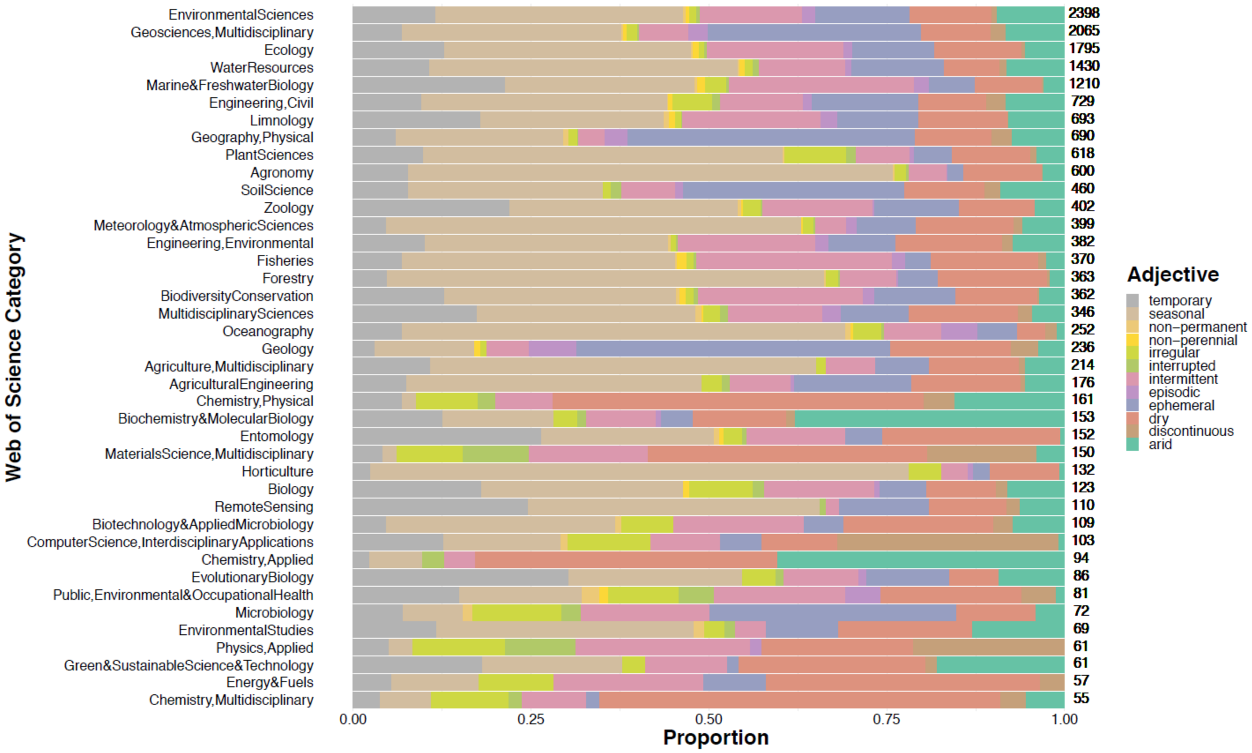

Figure 2.

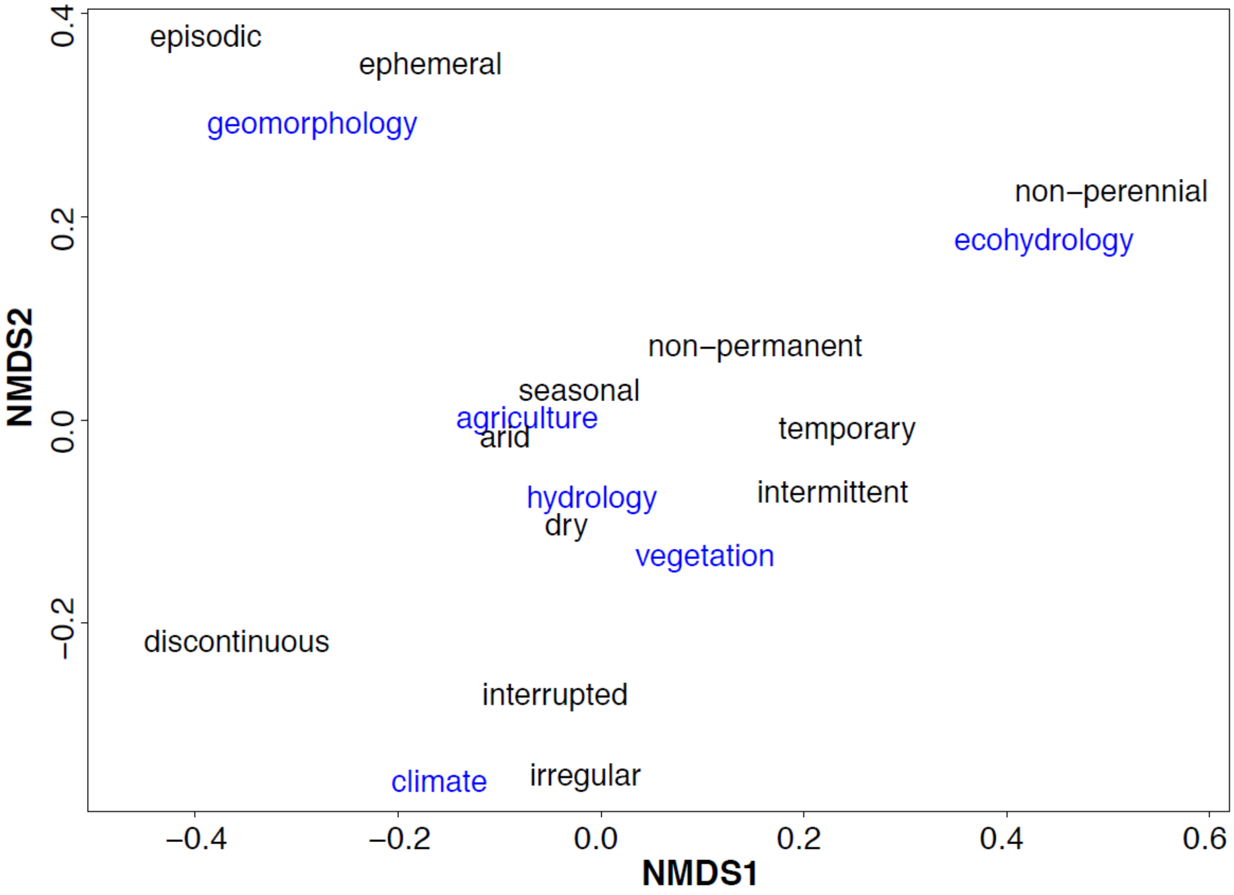
episodic
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Figure 3.

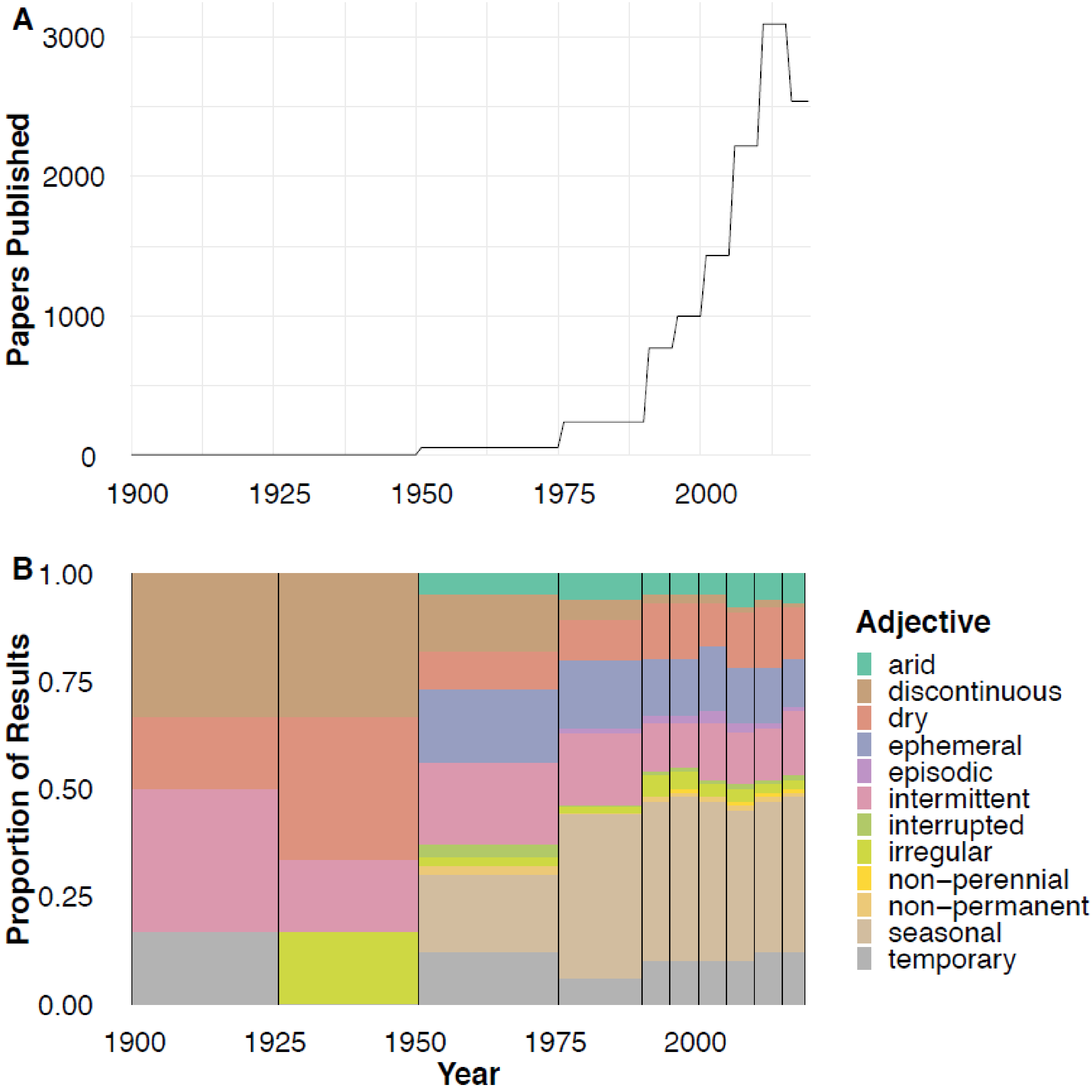
A
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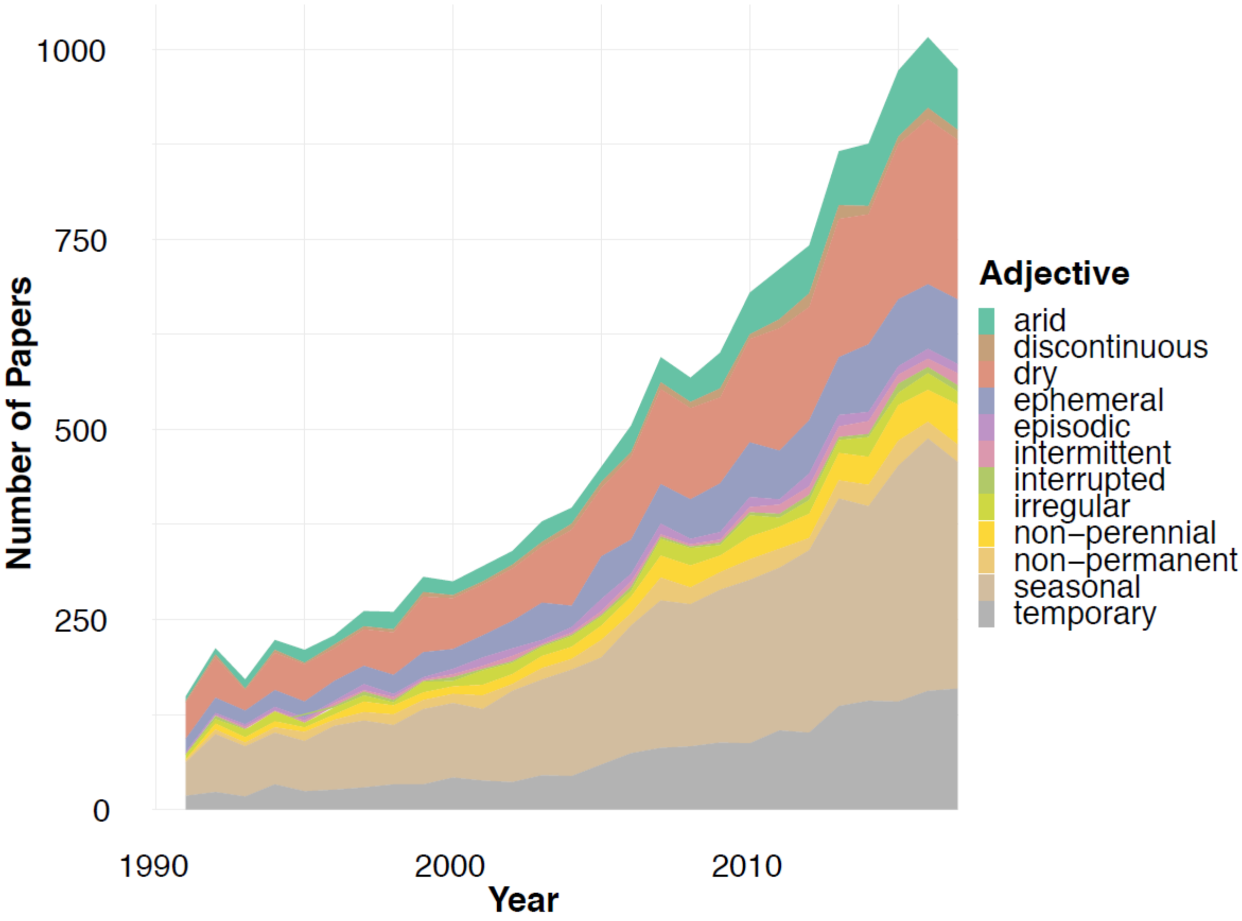
Figure 4.



Number of Papers
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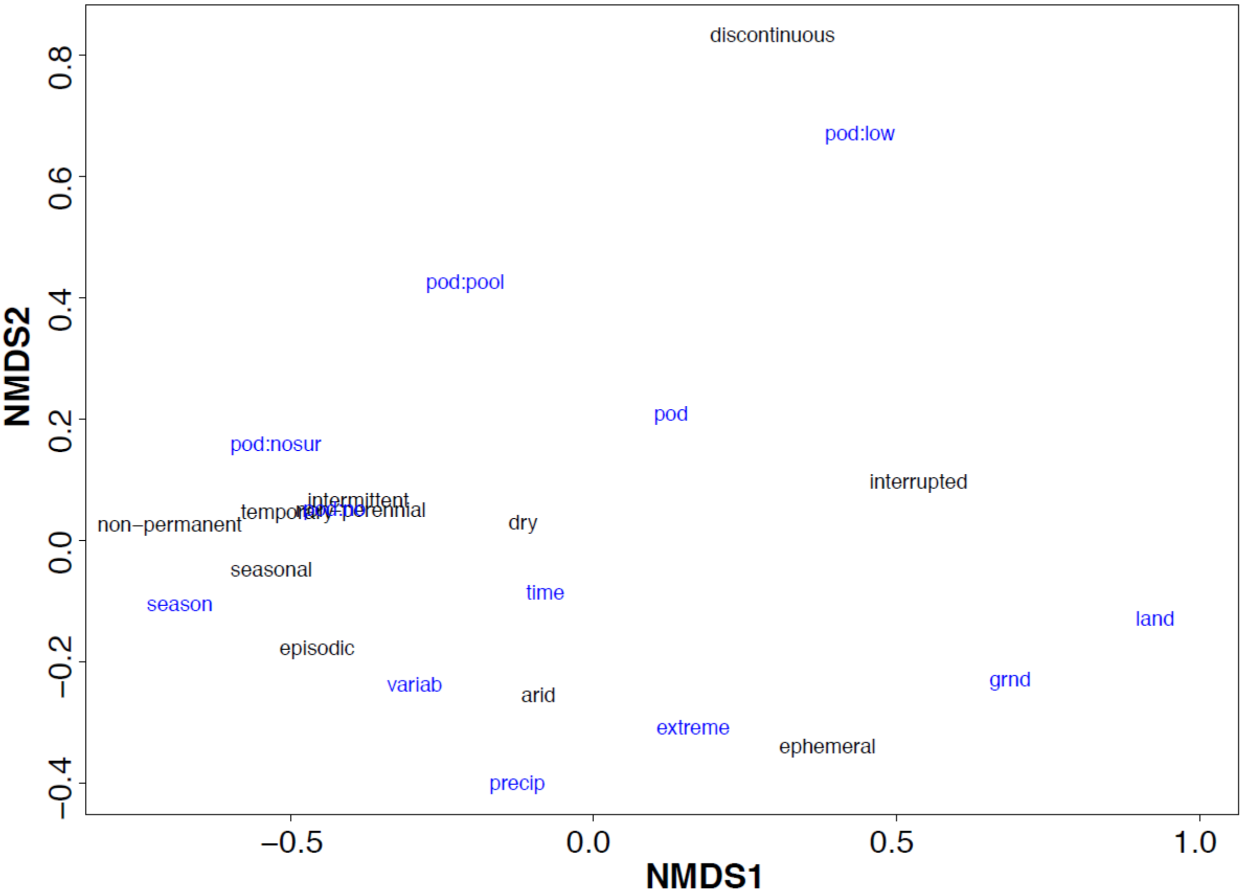
Figure 5.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CHAPTER TWO

THE ONLY LASTING TRUTH IS CHANGE: MULTIPLE DIMENSIONS OF BIODIVERSITY SHOW HISTORICAL LEGACY EFFECTS IN COMMUNITY ASSEMBLY PROCESSES OF FRESHWATER FISH

Keywords:

climate change, freshwater fish, functional traits, niche dimensions, phylogenetic diversity, temporal trends

Published in *Oikos*

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ABSTRACT

How communities are structured is a fundamental ecological question. Community structure, while constrained by the regional species pool, may be altered by changes in climate and other environmental stressors. Changes in patterns of functional and phylogenetic dispersion over time can illuminate the temporal dynamics of the processes structuring communities. We quantified temporal changes in taxonomic, functional, and phylogenetic diversity of stream fish assemblages in the southern plains of the U.S. across four decades to assess how climatic change has influenced community patterns. We also explored how the use of three different functional trait categories (life history, environmental tolerance and trophic level) and all traits combined affected the response of functional diversity to environmental drivers. We found, for all diversity indices, that assemblages with low historical richness had high contemporary diversity, while assemblages with high historical richness had low contemporary diversity. Functional richness based on life history traits, trophic traits, and all traits combined decreased in diversity over time, while functional richness based on environmental tolerance traits showed the opposite pattern. Phylogenetic dispersion of both over- and under-dispersed communities shifted toward randomness. Changes in fish diversity patterns were influenced by changes in temperature over time, though impacts were metric dependent. Overall, we found that while community structure has changed, specific changes were more strongly predicted by the historical richness of the community than by regional climate change.

INTRODUCTION

Linking diversity patterns to community structure is central to understanding how communities are assembled (Weiher and Keddy 1995). Several mechanisms can shape the phylogenetic and functional diversity of communities, including historical priority effects (Fukami 2015), interspecific interactions, and environmental constraints (Weiher and Keddy 1995). While phylogenetic and functional diversity have been shown to vary across spatial scales and environmental gradients (Giam and Olden 2018, Li et al. 2019, Jia et al. 2021), changes to the same communities over time can offer new insights into how climate change may influence diversity patterns. As changing climates impact species' environments, altering ranges (Moritz and Agudo 2013) and likely increasing the stress many species experience (Kuczynski and Grenouillet 2018), the processes by which communities assemble may also change.

The stress dominance hypothesis relates community structure with environmental conditions, where increased environmental harshness results in low diversity (Weiher and Keddy 1995). Under environmental filtering, only species able to tolerate specific abiotic conditions persist, resulting in communities in which species exhibit greater trait similarity or are more closely related than expected by random chance (resulting in patterns of under-dispersion; Webb et al. 2002, Swenson and Enquist 2007). Conversely, in benign habitats many species can co-exist, resulting in higher diversity than expected by chance (resulting in patterns of over-dispersion). As species are limited by the niches available, competitive exclusion results in a single species occupying each niche (i.e. limiting similarity; Webb et al. 2002). Under climate change, as environments become more stressful (van Vliet et al. 2013), communities may lose diversity through time. Although other processes, such as mutualism and facilitation can also influence community structure, they typically act at smaller spatial and temporal scales, making their impacts difficult to distinguish at larger-scales (Ågren and Fagerström 1984, Valiente-Banuet and Verdú 2007, Mayfield and Levine 2010, McIntire and Fajardo 2014, Kunstler et al. 2016, Münkemüller et al. 2020).

Functional and phylogenetic diversity patterns are expected to reflect the processes that have shaped community assembly (Monnet et al. 2014, Kuczynski and Grenouillet 2018, Li et al. 2019). Functional traits capture ecological differences between organisms and relate communities to ecosystem processes (Naeem and Wright 2003, Petchey and Gaston 2006, Violle et al. 2007, Monnet et al. 2014, Jarzyna and Jetz 2017). However, despite the increasing use of functional diversity across ecology, the link between community diversity and underlying processes may be influenced by which traits are chosen (Weiher and Keddy 1995) as different traits are related to different ecological processes (Bernard-Verdier et al. 2012, Spasojevic et al. 2014, Münkemüller et al. 2020). Therefore, analyzing trait groups separately can result in signals that are hidden when analyzing all traits altogether (Saito et al. 2016, Côte et al. 2019, Münkemüller et al. 2020). Phylogenetic diversity, in contrast, captures total evolutionary relatedness between species (Gerhold et al. 2013). While some studies suggest that phylogenetic diversity is linked to ecosystem functioning (Cadotte et al. 2012), these patterns do not always clearly indicate an assembly process (Mayfield and Levine 2010). Both functional and phylogenetic diversity offer more insights into community diversity patterns than taxonomic richness alone, although neither metric is completely independent of it (Jia et al. 2021). For example, if functional richness increases with species richness, one can assume that as new species are introduced, new traits are also being introduced. However, opposite patterns in functional and taxonomic diversity could indicate that communities have high functional redundancy, that dominant species traits contribute more to functional diversity than rare ones (Wang et al. 2021), or that there is a loss of functional specialization (Villéger et al. 2010). To overcome this limitation, diversity indices can be standardized using a null model approach, after which trait and phylogenetic dispersion can be inferred in reference to a randomly structured community (Gotelli and Graves 1996). While there are limitations of both functional trait and phylogenetic based approaches to community assembly (Gerhold et al. 2013, Sobral and Cianciaruso 2016, Münkemüller et al. 2020), using both can offer complementary and multifaceted insights into diversity patterns (Mayfield and Levine 2010, Cadotte et al. 2013).

The state of Oklahoma in the central United States spans steep gradients in temperature and precipitation. Under climate change, Oklahoma is projected to see increased average annual temperatures (Zhang and Nearing 2005, Garbrecht et al. 2014), reduced annual precipitation (Zhang and Nearing 2005) and more extreme hydrological conditions such as droughts and floods (Bertrand and McPherson 2018). Thus, Oklahoma rivers provide a critical opportunity to understand how changes in climate may affect the diversity and assembly of freshwater fish communities. We combined climatic information and river fish abundance across Oklahoma to detect changes in community dispersion patterns through time in response to climate change stressors. Fish are good study organisms as their movement is limited by the dendritic networks of rivers, which results in trait selection based on local environmental constraints (Dias et al. 2014, Bower and Winemiller 2019). In addition, fish are ectotherms whose distribution is largely reliant on behavioral control of body temperature (Beitinger and Fitzpatrick 1979). Thus, local climate is essential in the reproduction and survival of species (Bütikofer et al. 2020). In addition, the well-studied and clearly defined traits of river fishes make them a model system to understand responses to environmental changes (Frimpong and Angermeier 2009, Bower and Winemiller 2019).

We explored how fish community diversity patterns changed over a minimum of eight years under the influence of climate related stressors using taxonomic, functional and phylogenetic diversity. Specifically, we hypothesized that under the influence of climate change stressors, fish communities would experience loss in diversity (i.e. shift towards under-dispersion) as species experience increased environmental harshness. Secondly, in response to increased environmental stress, we hypothesized that historically diverse communities (i.e. over dispersed) would be more likely to experience diversity loss over time, as these communities are likely to host rare or specialist species. Finally, we hypothesized that traits related to the abiotic niche (such as thermal tolerance) would show a stronger response to climate change than traits related to interspecific interactions (such as trophic position).

METHODS

Sites

To explore the temporal dynamics of taxonomic, functional and phylogenetic diversity in freshwater fish across Oklahoma, we compiled fish abundance data collected from 1972 to 2014 (Pigg 1987, Matthews and Marsh-Matthews 2017a, Supporting information). We restricted data to include observations from 69 locations that were sampled at least eight times over a minimum of eight years to document changes over a multi-year period while still retaining most sites. To understand how functional diversity within communities changed through time, we retained localities with at least four species, the minimum number necessary for estimating functional richness using a three-dimensional convex hull volume method. The final dataset included abundance observations of 159 species with sampling events occurring on average 11 times at each site over 13 years (Supporting information). As non-native species in our dataset represented on average 0.005% (SD = 0.02) of the total abundance of any given sample, and their relative abundance was steady over time based on a generalized least square models (GLS; estimate = 0.011, p = 0.5), we did not differentiate native from non-native species in our analyses (Miller and Robison 2004, Foster et al. 2008).

Functional and phylogenetic data

Analyzing trait groups separately may show signals that would be hidden when analyzing all traits together (Saito et al. 2016, Münkemüller et al. 2020). To identify which trait shifts are best predicted by climate change stressors, we used three functional trait categories: trophic ecology, life history and environmental tolerance based on those presented by Frimpong and Angermeier (2009) and previous studies (Supporting information). Trait information was extracted from Fish Traits, the most complete trait database for freshwater fish that covers multiple dimensions of the functional niche (Frimpong and Angermeier 2009). We performed a principal coordinates analysis (PCoA) on trophic and environmental functional distance matrices, using Gower distance (Gower 1971) with equally weighted traits. For trophic traits (100% completeness), we used those that describe fish species diet (Supporting information) and kept the first two PCoA axes (Supporting information). Environmental tolerance traits (100% completeness) were based on reproductive habitat, habitat preferences (Frimpong and Angermeier 2009) and temperature tolerance (Supporting information) and the two first PCoA axes were retained (Supporting information). For life history traits (97% completeness on average), we used age at maturity, body length and fecundity (Frimpong and Angermeier 2009; Supporting information) and kept the three axes (Supporting information). Finally, we ran a global PCoA based on all individual traits, weighing individual traits so categories were equally represented in the global PCoA (Supporting information), and kept the first three axes (Supporting information).

To quantify phylogenetic diversity, we used the most comprehensive time-calibrated phylogeny for fish available (Rabosky et al. 2013) and extracted the subset of species observed in our samples (100% completeness; Supporting information).

Interpretation of functional diversity patterns relies on all traits either being phylogenetically conserved or convergent (Webb et al. 2002). To interpret our results of functional diversity, we tested whether species' positions in functional space (i.e. PCoAs species' scores) were phylogenetically conserved using Blomberg's K, an estimate of the phylogenetic signal in traits (Blomberg et al. 2003) with the R package motmot (Puttick 2019). Species' scores across all axes showed a significant phylogenetic conservatism (all $p < 0.05$; Supporting information), indicating that closely related species exhibit similar values across all PCoA axes (i.e. position within the functional space). These values were thus used in subsequent analyses as the species-specific functional traits (Supporting information).

Diversity indices

We measured taxonomic diversity using species richness and estimated four diversity indices to quantify dispersion: functional richness, phylogenetic richness and functional and phylogenetic Rao's quadratic entropy (**Table 1**). We calculated functional richness (FR) using the convex hull volume, the multi-dimensional trait space defined by PCoA axes and occupied by species present in each sample (Cornwell et al. 2006, Villéger et al. 2008) with the ‘geometry' package (Roussel et al. 2019). A maximum of three axes were used to define the functional space based on which the convex hull volume is defined (Supporting information). We calculated phylogenetic diversity (PD) as the sum of branch lengths that link all species co-occurring in each sample (Faith 1992) with the picante package (Kembel et al. 2020). Rao's quadratic entropy offers a complementary understanding on diversity changes as it combines both dispersion (abundance) and richness (De Bello et al. 2010) and is less sensitive to outliers than either functional richness or Faith's PD (Laliberté and Legendre 2010). Functional Rao's quadratic entropy (Rao) was computed using the Gower distance matrix based on raw functional traits (Supporting information). We also used Rao's quadratic entropy (Rao) to calculate phylogenetic diversity using phylogenetic distance between species using the ade4 package (Villéger et al. 2008, Dray et al. 2021).

Community dispersion patterns: over- versus under-dispersion

Functional and phylogenetic diversity indices tend to be broadly correlated with species richness. Therefore, we used a null model approach can be used to standardize diversity indices (i.e.

removing the numerical artefact due to species richness; Gotelli and Graves 1996). The species pool for each assemblage was composed of all the species in the focal assemblage and all the species with which they co-occur anywhere in the study region at any point in time (i.e. pools were not time-series specific; **Figure 1: Step 1**). This assumes that if two species co-occur at some point within space and time, the two species can coexist (e.g. because of similar biogeographic origins and historic contingencies), indirectly incorporating dispersal into the models (i.e. the full dispersion field, Lessard et al. 2012b). From this assemblage-specific pool, the number of species equal to the species richness of the focal sample was randomly drawn. Moreover, we kept the abundance distributions fixed as in the focal assemblage (**Figure 1: Step 2**). From the dispersion field for each assemblage, we drew 999 random assemblages. The dispersion field approach allows for communities to vary in the size and composition of the species pool (Graves and Rahbek 2005), which is likely more realistic than using the same pool for assemblages distributed over large spatial scales or across environmental gradients (Lessard et al. 2012b).

For each null assemblage, we computed all 10 diversity indices (functional richness: FR_{global}, $FR_{trophic}$, FR_{env}, FR_{LHT}; functional Rao's quadratic entropy: Rao_{global}, $Rao_{trophic}$, Rao_{env}, Rao_{LHT}; phylogenetic diversity: PD; and phylogenetic Rao's: Rao_{phylo}) and calculated the average and standard deviation (X_{mean} and X_{std}, respectively) for each index (X) for each random assemblage (**Figure 1: Step 2**). We computed the standardized effect size of each index as $(X_{obs} - X_{mean})/X_{std}$ where X_{obs} is the observed value for the index X. Positive values indicate over-dispersion (more diversity than expected in a randomly assembled community) while negative values represent under-dispersion (less diversity than expected in a randomly assembled community; **Figure 1: Step 3**).

For each site, a time series of standardized effect sizes was generated based on the samples taken at each time point and the null models created from each sample. From each time series, overall trends were computed (see Temporal trends and relationship with climatic changes section; **Figure 1: Step 3**). To quantify the relationship between historical processes and changes over time, we calculated Pearson correlations between the historical standardized effect size (i.e. the standardized effect size calculated at the first sample point) and the slope of the standardized effect size time series for each diversity index. This comparison allowed us to view the overall changes in community diversity structure in relation to historical community structure. We ran a Kolmogorov–Smirnov test to compare differences between the distributions of historical and current values with the stats R-package (www.r-project.org) to test for changes in over- and under-dispersion over time.

Environmental data

We compiled environmental data for each site to identify the drivers of temporal changes in diversity patterns using the R package Stream Network Tools (Kopp 2019). We extracted nine physical and geological variables from each river that contained one of our 69 sites: the Strahler order for root node, number of headwater reaches, maximum and minimum elevation of the reach, slope of the reach, number of tributary junctions, the drainage area of the basin, the total length of network flowlines and drainage density. We kept two PCA axis (49.01 and 26.38% of explained variance) to represent the upstream–downstream gradient (UP–DOWN1 and UP–DOWN2) or the natural, spatially driven longitudinal changes in rivers (Vannote et al. 1980, Supporting information).

We quantified the climatic change experienced by fish communities using yearly climate data (precipitation and temperature) from the CHELSA database from 1969 to 2016 (Karger et al. 2017). From these data, we calculated the change in yearly maximum temperature (ΔTMAX), change in total annual precipitation (ΔPREC) and change in temperature range (the difference between the yearly maximum and yearly minimum; ΔTRANGE) over time. For each site, trends were estimated as the slope of the regression between a given climatic variable and time using GLS. The GLS incorporated temporal autocorrelation (autocorrelation structure of order 1 – corAR1), which take data from the previous year into account when calculating the regression. Using the slope allowed us to reduce the influence of extreme years as well as year-to-year fluctuations across the 42-year period.

Temporal trends and relationship with climatic changes

To quantify temporal trends in standardized diversity, we fit a GLS on each standardized effect size time series, using the standardized effect size as the response variable and the year as the explanatory variable. We extracted the slope of the model as a measure of the change in standardized effect size over time (hereafter Δ; **Figure 1: Step 3**). A positive slope value indicates that communities are becoming more over-dispersed over time, while a negative slope indicates communities are becoming more under-dispersed. ΔPD and $\Delta FR_{trophic}$ were minimally spatially autocorrelated (Moran's I = 0.08, −0.08, respectively), while the other eight indices were randomly distributed. We therefore did not consider spatial autocorrelation in our models. To better understand the mechanisms behind diversity trends, we tested Pearson correlations between changes in functional and phylogenetic diversity and changes in species richness.

To quantify climatic changes, we used environmental variables as response variables (ΔTMAX, ΔTRANGE, ΔPREC, UP–DOWN1 and UP–DOWN2). To investigate the relationship between temporal changes in diversity and environmental conditions, we used linear models with diversity changes as the response variable and environmental changes as explanatory variables with the lme4 package (Bates et al. 2015). We found no evidence of multicollinearity between the changes in environmental factors in the linear models (Supporting information). All analyses were done in R (www.r-project.org).

RESULTS

Our results showed that few sites exhibited a significant decline in species richness (SR), global functional richness (FR_{global}, Rao_{global}) or phylogenetic diversity (PD, Rao_{pylo}) over time (5 sites or fewer across 69 sites total). For each index, changes in diversity were significantly correlated with historical diversity (ΔSR: $r = -0.37$, $p = 0.002$; ΔFR_{global}: $r = -0.49$, $p < 0.001$; ΔRao_{global} $r = -0.63$, $p < 0.001$; ΔPD: $r = -0.45$, $p < 0.001$; and ΔRao_{phylo}: $r = -0.57$, $p < 0.001$; **Figure 2**). These changes were consistent across all diversity indices, where sites with low historical diversity became more over-dispersed and sites with high historical diversity became more under-dispersed over time.

We found increased under-dispersion for measures of global functional diversity (FR_{global} and Rao_{global}) by comparing Pearson correlations between historical and contemporary standardized effect sizes. Conversely, measures of phylogenetic diversity displayed different patterns: for PD, most sites showed a decrease in over-dispersion while Rao_{phylo} showed an overall decrease in under-dispersion (**Figure 3**). Despite these overall patterns, a Kolmogorov–Smirnov test showed that historical and current standardized effect size distributions were not significantly different ($p > 0.05$ for all indices).

Similar to global functional richness and phylogenetic diversity patterns, categorical functional richness indices showed that high historical richness was correlated with negative change in standardized effect size (increasing under-dispersion), and low historical richness was associated with positive change in standardized effect size (increasing over-dispersion; **Figure 4**). This pattern persisted for trophic richness ($\Delta FR_{trophic}$: $r = -0.37$, $p = 0.002$; $\Delta Rao_{trophic}$: $r = -0.39$, $p = 0.001$), life history richness (ΔFR_{LHT}: $r = -0.62$, $p < 0.001$; ΔRao_{LHT}: $r = -0.63$, $p < 0.001$) and environmental tolerance richness (ΔFR_{env}: $r = -0.30$, $p = 0.001$; ΔRao_{env}: $r = -0.34$, $p = 0.004$). There appeared to be an outlier for ΔFR_{LHT}, $\Delta Rao_{trophic}$ and ΔR_{LHT} (**Figure 4B, D** and **E**, respectively). We tested correlations without this point and found little change in our results (ΔFR_{LHT}: -0.31, $p = 0.01$; $\Delta Rao_{trophic}$: -0.34, $p = 0.005$; and ΔRao_{LHT}: -0.23, $p = 0.06$).

All trait categories demonstrated changes in under-dispersion over time. $\Delta FR_{trophic}$ and ΔFR_{env} both demonstrated decreasing under-dispersion over time (39 and 23% of sites, respectively). For all other indices, however, most sites demonstrated increasing under-dispersion over time (ΔFR_{LHT} 32%; $\Delta Rao_{trophic}$ 42%; ΔRao_{LHT} 49%; ΔRao_{env} 33%; Supporting information).

We found that ΔSR was positively correlated with two functional indices (ΔFR_{LHT}: 0.29, $p < 0.05$; and ΔFR_{env}: 0.38, $p < 0.01$) and one phylogenetic metric (ΔPD: 0.59, $p < 0.001$; **Figure 5**) using a Pearson test.

Over time, we found maximum temperature (TMAX) increased by 0.17°C, temperature range (TRANGE) increased by 0.19°C, and annual precipitation (PREC) increased by 14.86 mm on average per year. We found significant coefficients between models that compared $\Delta FR_{trophic}$ and ΔRao_{phylo} to $\Delta TMAX$ (-0.62, $p < 0.01$ and -0.30, $p = 0.04$, respectively) and ΔSR to the second UP–DOWN axis (-0.36, $p = 0.03$; **Table 2**). The other diversity indices were not significantly correlated with any environmental driver.

DISCUSSION

We found that changes in the functional and phylogenetic diversity of fish assemblages in Oklahoma were better predicted by historical patterns than climate change. We hypothesized that fish communities would experience functional and phylogenetic diversity loss (i.e. shift towards under-dispersion), that historically diverse communities (i.e. over dispersed) would be more likely to experience diversity loss, and that environmental tolerance traits would be increasingly more important in structuring communities as they respond to climate change. Supporting our first hypothesis, both global functional richness indices indicated a loss of diversity (i.e. increase in under-dispersion). Phylogenetic diversity, however, demonstrated an approach towards randomness, as PD and $\text{Rao}_{\text{phylo}}$ shifted in opposite ways. Additionally, we found that historical context had a stronger influence over how communities changed than environmental harshness, in contrast to our second hypothesis. Finally, our third hypothesis was not supported; trophic traits, rather than environmental traits, were correlated with environmental changes over time.

While our results show overall changes in diversity, functional richness and phylogenetic diversity demonstrated conflicting patterns. Indices for functional richness showed an increase of under-dispersion, following the stress dominance hypothesis. This suggests that as temperature and precipitation patterns change, communities adapted to previous conditions will face more environmental stress, limiting what species can be present at a given location. Contrary to this evidence, phylogenetic indices shifted towards randomness, contradicting our expectations under the stress dominance hypothesis. While diversity patterns often conflict (Gómez et al. 2010, Pavoine and Bonsall 2011, Cianciaruso et al. 2012, Sobral and Cianciaruso 2016), reasons behind these disconnects are not clear. In our study, causes for these conflicting patterns may be due to the limited spatial scale, which may not have provided a large enough species pool to detect climate change impacts on phylogenetic dispersion. Our spatial scale also limited the environmental gradient in our study, which could have constrained functional diversity, limiting the range of variation between our sites (Srivastava et al. 2012). However, we found that functional patterns were more sensitive than phylogenetic ones, suggesting that functional diversity may be more sensitive over limited spatial scales. In addition, human induced disturbances may act as an additional environmental filter, which tends to decrease phylogenetic diversity (Helmus et al. 2010). Regardless, our results indicate that fish assemblages are becoming more functionally similar while becoming less phylogenetically related. This could suggest that phylogenetic diversity is more reflective of changes in trait space of traits we did not measure, such as those related to phenology (Flynn et al. 2011, Galland et al. 2019). Thus, using phylogenetic diversity and functional richness can provide a more complete picture of community variation through space and time, despite not being proxies for one another (Pavoine and Bonsall 2011, Sobral and Cianciaruso 2016, Jia et al. 2021).

While functional and phylogenetic diversity indices provide more information on community diversity than taxonomic diversity alone, they are not independent (Jia et al. 2021). Our results suggest that variations in FR and PD are due to gains and losses of unique species, particularly with respect to life history and abiotic niche strategies. Trophic traits, however, were not related to species richness. This could be due to the smaller number of traits we used to define this category. However, the lack of co-variation between species richness and trophic traits in comparison to other trait categories suggests the trophic niche space was not a useful axis of variation for community comparison in our study. In contrast to FR, Rao's quadratic entropy indices were not significantly correlated with species richness, suggesting this index is independent of species richness and therefore potentially more useful in understanding diversity patterns through time.

Trophic traits were the only category to be significantly related to environmental change, refuting our hypothesis that environmental tolerance traits would be the most related to environmental change. One possible reason for a lack of relationship may be that our communities were not sampled from the margins of individual fish distributions, where species are more likely to be closer to the limits of their niche (Holt and Gaines 1992) and environmental changes may play a bigger role in community reassembly. Therefore, considering traits related to both the biotic and abiotic environment gives a fuller picture of community diversity than trait subsets, in part due to their interaction with environmental gradients across space. We argue that looking for patterns in functional richness across all traits, particularly when exploring larger spatial scales, is most useful for conservation and management to identify, for instance, hotspots of functional diversity.

We also found that changes in temperature had the strongest effect on diversity changes for two (out of eleven) indices, which parallels the findings of other studies relating fish communities and environmental stressors (Daufresne and Boët 2007, Whitney et al. 2016). Increases in maximum temperature led to loss of trophic diversity ($FR_{trophic}$) and phylogenetic diversity

($\text{Rao}_{\text{phylo}}$). As average and maximum temperatures continue to increase, more species are likely to experience temperatures outside their historical range, leading to extirpation and extinction in these vulnerable river systems (Matthews and Zimmerman 1990, Dodds et al. 2004). Additionally, community composition appears to change at a faster rate when communities approach thermal thresholds for multiple species (Comte et al. 2021). The relatively weak responses of Oklahoma fish communities to changes in temperature suggest that the largest impacts of temperature are yet to be observed.

While our results suggest that temperature is the most important driver of community reorganization where it occurred, most changes in diversity were not explained by any of the tested drivers. However, we found the upstream–downstream gradient drove changes in species richness, suggesting that species richness trends are changing along elevation gradients or across stream orders. Other diversity indices had no relationship to the upstream–downstream gradient, indicating that headwaters and lowland rivers are experiencing changes in diversity at similar rates or that species replacement is taking place with functionally and phylogenetically redundant species. While the longitudinal gradient of rivers is recognized as a driver of diversity (Vannote et al. 1980), as shown by its significant impact on species richness, the upstream–downstream gradient is likely to not be altered by climate change stressors. In addition, changing precipitation had no effect on changes in community structure despite the direct impact that precipitation can have on discharge (Power 1981, Favier et al. 2009). Discharge influences fish spawning behavior (Lytle and Poff 2004) and impacts food webs by altering nutrients (Reist et al. 2006) and therefore stream productivity (Power 1981). We also may have failed to detect stronger relationships with environmental changes because contemporary community diversity is also related to historical habitat conditions (Harding et al. 1998, Burcher et al. 2008), and land use change can increase environmental stress at a particular site. As land use changes can interact with climate change to alter communities (Mantyka-Pringle et al. 2014, Comte et al. 2021), further studies should investigate the role of change in land use and climate on assembly rules.

While our study detected changes in fish diversity patterns, we found that community changes were linked to historical processes. Across richness indices, we found that historically rich communities lost functional and phylogenetic diversity and shifted from over- to under-dispersion, supporting the stress dominance hypothesis. With more extreme climatic conditions expected over time (Daufresne and Boët 2007), sensitive or specialist species will likely be lost due to threshold responses (Brejão et al. 2018). On the other hand, sites that historically exhibited low diversity showed an increase in diversity over time, shifting from under- to over-dispersion. This pattern suggests that historically vacant niches have provided space and opportunity for new species to establish. This could indicate the spread of non-native species (Vitousek et al. 1997, Gavioli et al. 2019) which can compete with or predate upon natives within a river system, creating new species interactions (Lynch et al. 2016). The lingering impact of historical processes on contemporary community diversity in our results may dampen the effects of recent environmental change, which may be why we did not detect stronger support for the stress dominance hypothesis or more relationships between environmental drivers and diversity indices.

While null models are intended to standardize diversity changes across different assemblages, they also introduce biases. For example, our null models used a regional species pool spanning 40 years; had our null assemblages been specific to smaller sampling periods (i.e. 1–3 years), the species pool for each focal community may have been smaller, decreasing the standard deviation of the random communities and ultimately leading to larger standardized effect sizes. In addition, the dispersion field species pool definition accounts for dispersal barriers in addition to large scale habitat preferences (Graves and Rahbek 2005), thereby accounting for species dispersal ability. However, this species pool is dependent on the species in the focal sample, and may include species that never actually overlap with species in the focal community (Lessard et al. 2012a), which could lead to biases against over dispersion (i.e. limiting similarity; Carstensen et al. 2013). Finally, we assumed that no species invaded or became extirpated from the region during this sampling period, and that functional traits remained constant despite the known plasticity of fish traits (Crozier and Hutchings 2014). Future studies with more individual fish trait measurements would better illustrate the influences of changing climates on fish assemblages.

Our results demonstrate the importance of considering multiple indices of diversity, historical context and environmental drivers when testing community diversity patterns. Unlike in other studies, we did not find consistent patterns across our diversity indices (Jarzyna and Jetz 2017, Kuczynski and Grenouillet 2018), highlighting the need for careful consideration of indices and methods used to study various aspects of diversity. The Great Plains are a transition zone in the continental United States, encompassing a variety of biomes and a range of environmental gradients. The lack of consistent changes in diversity patterns highlights the need for further studies to better clarify the pressures acting on fish and other assemblages in transitional zones. Our study also demonstrates the importance of historical conditions on assemblages, highlighting the need for data consolidation and long-term studies. Understanding where historical conditions impact assemblage responses to environmental changes could allow managers better identify conservation needs under climate and environmental changes.

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TABLES

Table 1. Summary of diversity indices used, including what the index measures, how it is calculated, and expected results to the addition of a new species.

Diversity Index	Measures	Expected Results
Functional Richness	Measure the volume occupied by a community within trait space based on most extreme trait values, not weighted by abundance	Richness – increases as new species are added to a community only if species has extreme traits
Phylogenetic Diversity	Sum of branch lengths within a community, not weighted by abundance	Richness – increases as new species are added to the community
Rao's quadratic entropy	Measures variation among multiple traits / branch lengths, weighted by abundance	Richness and divergence – increases as new species are added to a community and / or as the abundances of current species increases

Table 2. Outcomes of GLS regression analyses relating environmental variables (ΔTMAX: change in maximum temperature; ΔTRANGE: change in temperature range; ΔPRECIP: change in precipitation; UP-DOWN: stable upstream-downstream gradient) to diversity indices. Coefficient of regression and p-values are listed. Significant relationships are highlighted in bold.

	ΔTMAX	ΔTRANGE	ΔPRECIP	UP-DOWN1	UP-DOWN2
ΔSR	-0.07, p = 0.69	-0.02, p = 0.89	-0.07, p = 0.72	0.10, p = 0.50	**-0.36, p = 0.03**
ΔFR_{env}	0.09, p = 0.58	-0.06, p = 0.73	0.09, p = 0.61	0.12, p = 0.41	-0.05, p = 0.73
ΔFR_{LHT}	-0.10, p = 0.53	-0.25, p = 0.12	-0.14, p = 0.46	0.14, p = 0.34	-0.21, p = 0.18
$\Delta FR_{trophic}$	**-0.62, p < 0.01**	0.11, p = 0.44	-0.01, p = 0.92	0.01, p = 0.96	-0.10, p = 0.46
ΔFR_{global}	-0.13, p = 0.41	-0.13, p = 0.41	-0.12, p = 0.52	0.15, p = 0.33	-0.21, p = 0.18
ΔRao_{env}	-0.07, p = 0.63	0.13, p = 0.41	0.03, p = 0.88	-0.01, p = 0.95	-0.29, p = 0.06
ΔRao_{LHT}	0.25, p = 0.13	-0.23, p = 0.16	-0.08, p = 0.68	0.04, p = 0.80	0.21, p = 0.19
$\Delta Rao_{trophic}$	0.06, p = 0.75	0.09, p = 0.59	-0.05, p = 0.78	0.14, p = 0.39	0.02, p = 0.89

$\Delta\mathrm{Rao}_{\mathrm{global}}$	0.14, p = 0.41	-0.13, p = 0.43	-0.09, p = 0.63	0.04, p = 0.81	-0.01, p = 0.94
$\Delta\mathrm{PD}$	0.25, p = 0.13	-0.12, p = 0.46	-0.06, p = 0.73	0.08, p = 0.61	-0.15, p = 0.35
$\Delta\mathrm{Rao}_{\mathrm{phylo}}$	**-0.30, p = 0.04**	0.10, p = 0.47	0.14, p = 0.38	0.05, p = 0.71	-0.17, p = 0.24

FIGURE CAPTIONS

Figure 1. Conceptual figure of the methods for these analyses, outlining the steps done for each individual focal community. Different fish outlines represent unique species. In Step 1, a focal community is selected, and focal species are identified. The species found in the focal community are highlighted in green and are inside a box. Shades of color represent different abundance levels, with darker shades indicating higher abundances. The focal community is then compared to all other community samples in the data set. Any fish that co-occurs with a species from the focal community at any point in time or space (purple fish) is included in the dispersion field species pool. In Step 2, 999 null models are created using species only from the dispersion field species pool. In addition, we ensured that the abundance distributions from the focal community sample are consistent in each null model, as shown by the shading of the fishes. Diversity indices are calculated for each random community to calculate the standardized effect size as shown in Step 3. Overall trends for each site were calculated using the slope of the timeseries ($m = \Delta X$). Fish silhouettes from PhyloPic.org.

Figure 2. Map of sites across Oklahoma (A) and correlations between the indices calculated for the first community sample (historical) and index changes as measured by the slope of a GLS regression of standardized effect size values over time for: species richness (SR; B), functional richness for all traits (FR_{global}; C), Rao's quadratic entropy (Rao_{global}; D), phylogenetic richness (PD; E), and Rao's quadratic entropy (Rao_{pylo}; F). Stream networks are displayed on the map as hydrographic networks (A) and sites are denoted with black circles. Historical refers to the Standardized Effect Size (SES) calculated at the first sample point for each site (C, D, E, F) or the species richness (B) at the first sampling point. SES calculations were not made for SR; thus, axes represent the first SR value at each site compared to the slope of SR values over time. Each black circle represents a site, with positive values demonstrating over-dispersion (OD) and those with negative values indicating under-dispersion (UD). The results of the Pearson correlation test are reported as r values along with p values.

Figure 3. Correlations between historical and contemporary standardized effect size (SES) values for (A) global Functional Richness (FR_{global}), (B) functional Rao's quadratic entropy (Rao_{global}), (C) Phylogenetic Diversity (PD), and (D) phylogenetic Rao's quadratic entropy (Rao_{phylo}) across each site over time. Historical and contemporary values demonstrate the SES at the first and last time point for each site, with an average of 13 years between them. Interpretations of changes in Standardized Effect Size are indicated by site position on the plot and matched in box plots: broadly, blue colors indicate an increase in over-dispersion (OD) while yellow colors indicate an increase in under-dispersion (UD). Sites in the upper left quadrant (blue) shift from UD to OD; possibly demonstrating a shift from environmental filtering to limiting similarity; UD -> OD), whereas sites in the bottom right quadrant (gold) show the opposite shift from OD to UD (OD -> UD). In the upper right and bottom left quadrants, sites

either increase in or decrease in UD or OD relative to their position against the 1:1 line (dashed line): light blue, decrease in UD (- UD); dark gold, increase in UD (+ UD); dark blue, increase in OD (+ OD); yellow, decrease in OD (- OD). Bar graphs indicate the number of sites which can be found in each subsection of the plot.

Figure 4. Correlations between the change in Standardized Effect Size (ΔSES) over time and the value of the first index calculated for a site (historical) for Functional Richness trait categories: $FR_{trophic}$, trophic ecology traits (A), FR_{LHT}, life history traits (B), FR_{env}, environmental niche traits (C), $Rao_{trophic}$, trophic ecology traits (D), Rao_{LHT}, life history traits (E), and Rao_{env}, environmental niche traits (F). ΔSES was measured by the slope of a GLS regression of richness changes over time. Historical refers to the SES calculated at the first sample point for each site. Each black circle represents a site, with positive values demonstrating a more important role of limiting similarity and negative values indicating a more important role of environmental filtering. In panels B, D, E the outlier is highlighted in gray. Correlations were performed including and excluding this point, and our results show that its inclusion did little effect on the strength or significance of the relationship (FR_{LHT} r = -0.31, p = 0.01 (B); $Rao_{trophic}$ r = -0.34, p = 0.005 (D), Rao_{LHT} r = -0.23, p = 0.06). The results of the Pearson correlation test are reported as r values along with p values.

Figure 5. Correlations between changes in species richness (ΔSR) and changes in functional (trophic traits: (A) $\Delta FR_{trophic}$ and (E) $\Delta Rao_{trophic}$; life history traits: (B) ΔFR_{LHT} and (F) ΔRao_{LHT}; environmental tolerance traits: (C) ΔFR_{env} and (G) ΔRao_{env}; all traits combined: (D) ΔFR_{global} and (H) ΔRao_{global}) and phylogenetic diversity indices ((I) ΔPD and (J) ΔRao_{phylo}). *'s indicate the significance of the correlation, with * indicating $p < 0.05$, ** indicating $p < 0.01$, and *** indicating $p < 0.001$.

FIGURES

Figure 1.

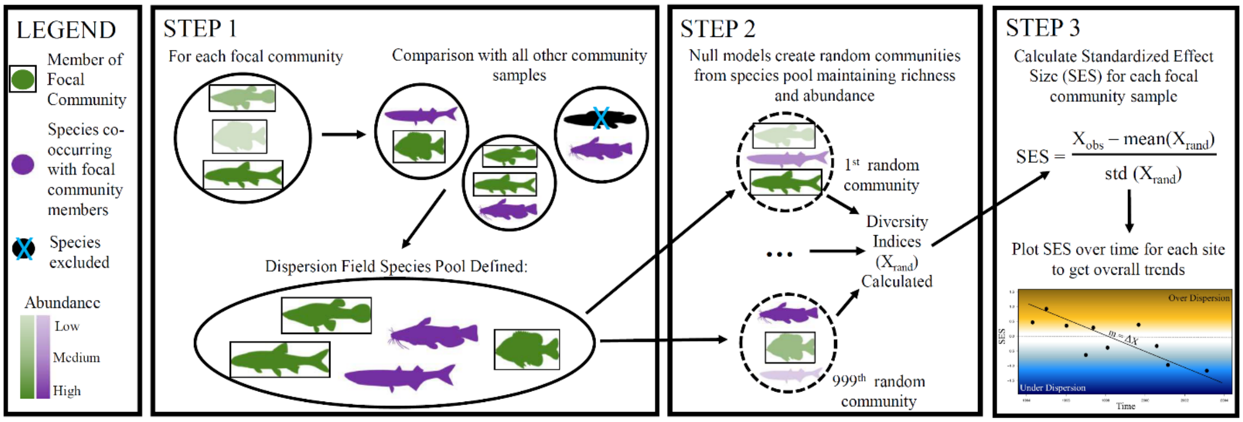


Figure 2.

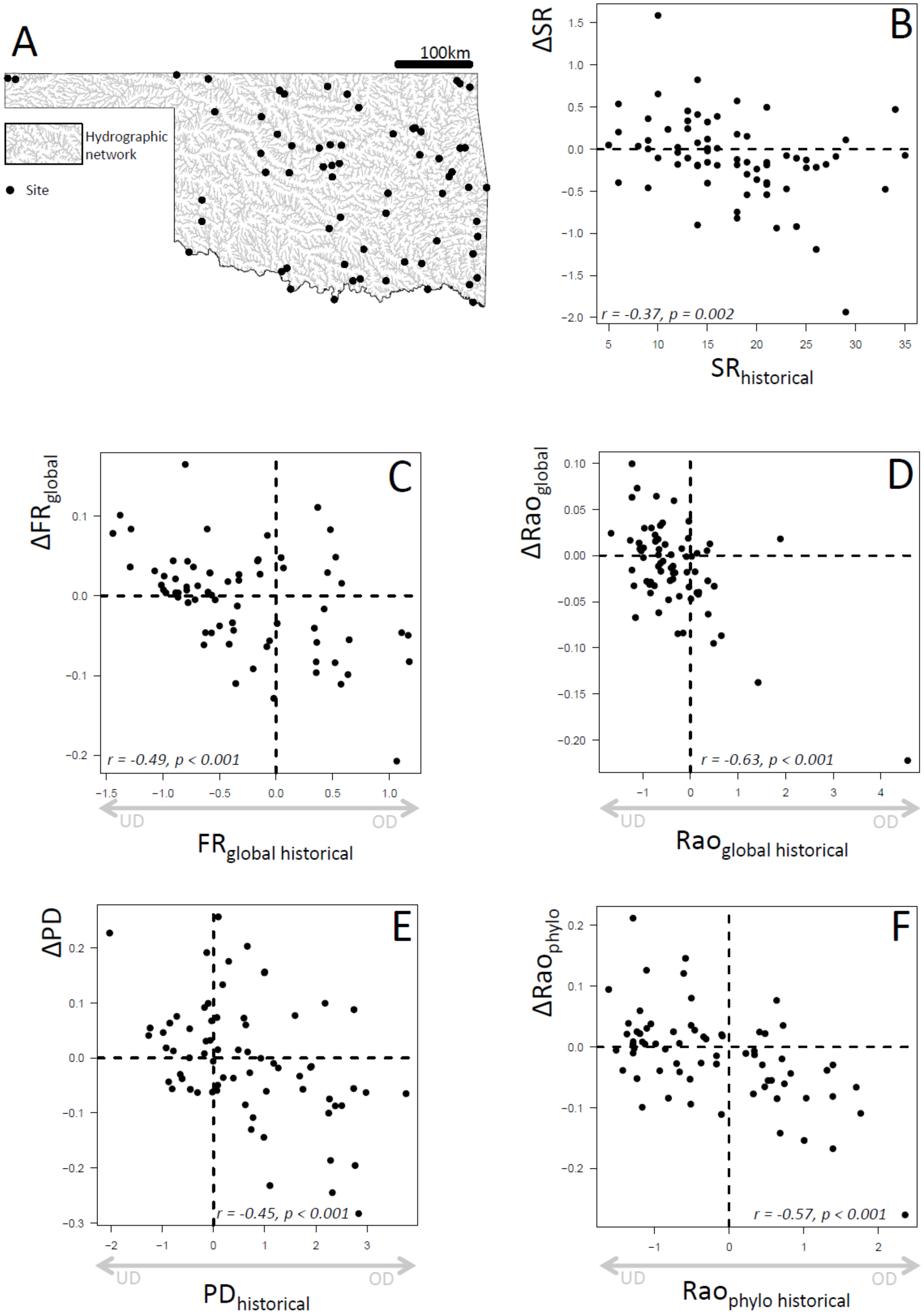

A
100km
Hydrographic network
Site
B
ΔSR
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
r = -0.37, p = 0.002
5
10
15
20
25
30
35
$SR_{historical}$
C
ΔFR_{global}
0.1
0.0
−0.1
−0.2
r = -0.49, p < 0.001
−1.5
−1.0
−0.5
0.0
0.5
1.0
UD
OD
$FR_{global\ historical}$
D
ΔRao_{global}
0.10
0.05
0.00
−0.05
−0.10
−0.15
−0.20
r = -0.63, p < 0.001
−1
0
1
2
3
4
UD
OD
$Rao_{global\ historical}$
E
ΔPD
0.2
0.1
0.0
−0.1
−0.2
−0.3
r = -0.45, p < 0.001
−2
−1
0
1
2
3
UD
OD
$PD_{historical}$
F
ΔRao_{phylo}
0.2
0.1
0.0
−0.1
−0.2
r = -0.57, p < 0.001
−1
0
1
2
UD
OD
$Rao_{phylo\ historical}$

Figure 3.

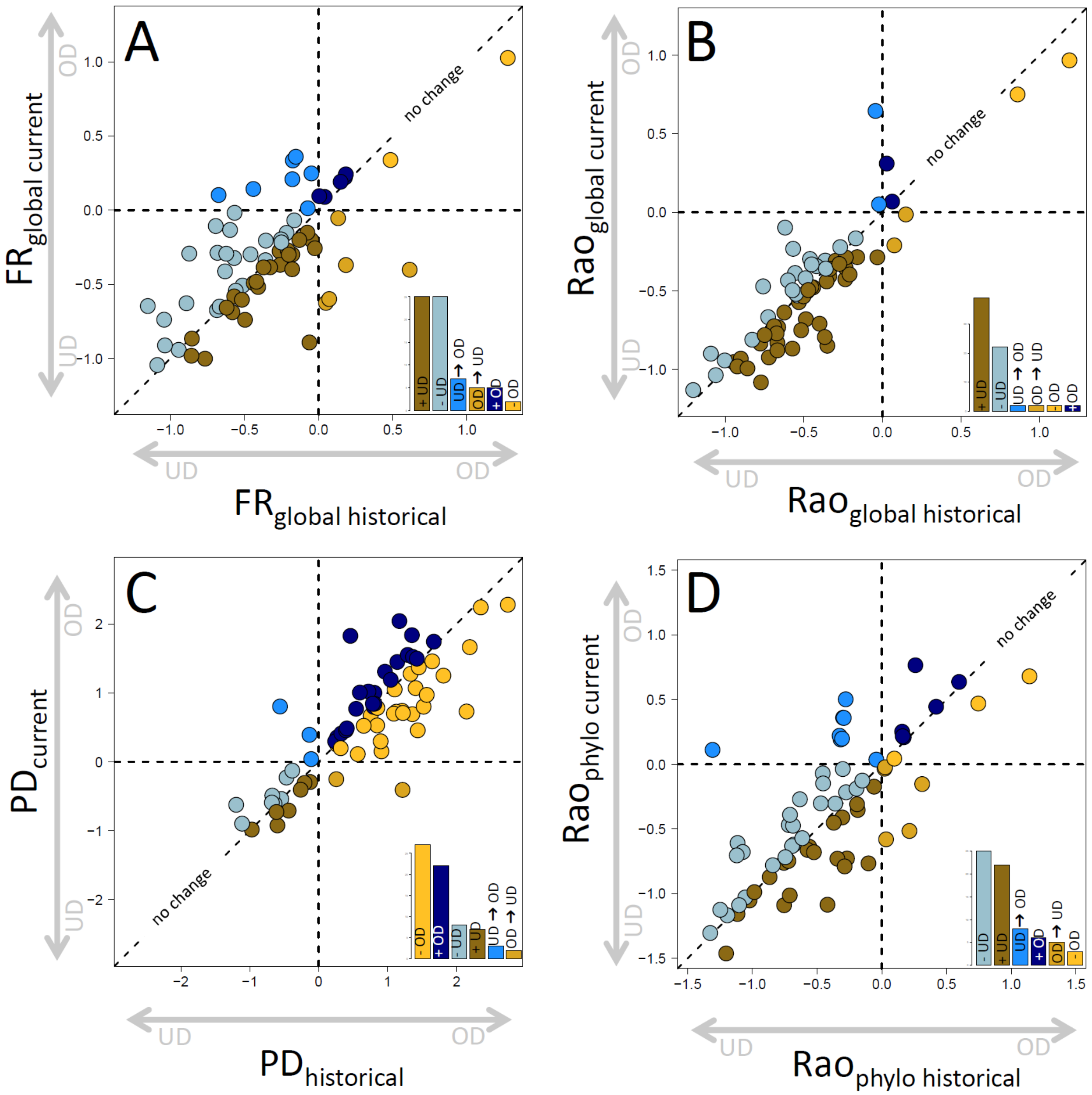

A
FR$_{global\ current}$
FR$_{global\ historical}$
no change
1.0
0.5
0.0
−0.5
−1.0
−1.0
−0.5
0.0
0.5
1.0
OD
UD
UD
OD
+ UD
- UD
UD → OD
OD → UD
+ OD
- OD
B
Rao$_{global\ current}$
Rao$_{global\ historical}$
no change
1.0
0.5
0.0
−0.5
−1.0
−1.0
−0.5
0.0
0.5
1.0
OD
UD
UD
OD
+ UD
- UD
UD → OD
OD → UD
- OD
+ OD
C
PD$_{current}$
PD$_{historical}$
no change
2
1
0
−1
−2
−2
−1
0
1
2
OD
UD
UD
OD
- OD
+ OD
- UD
+ UD
UD → OD
OD → UD
D
Rao$_{phylo\ current}$
Rao$_{phylo\ historical}$
no change
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
OD
UD
UD
OD
- UD
+ UD
UD → OD
+ OD
OD → UD
- OD

Figure 4.

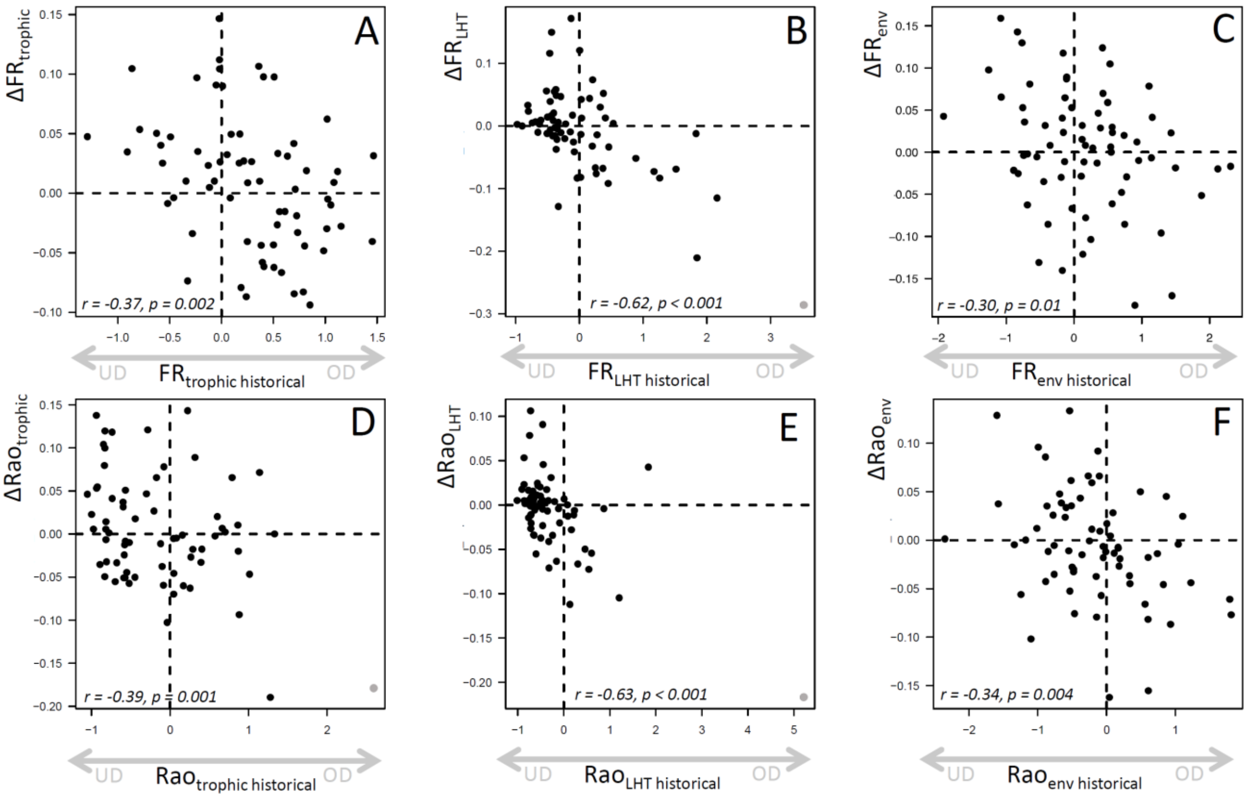
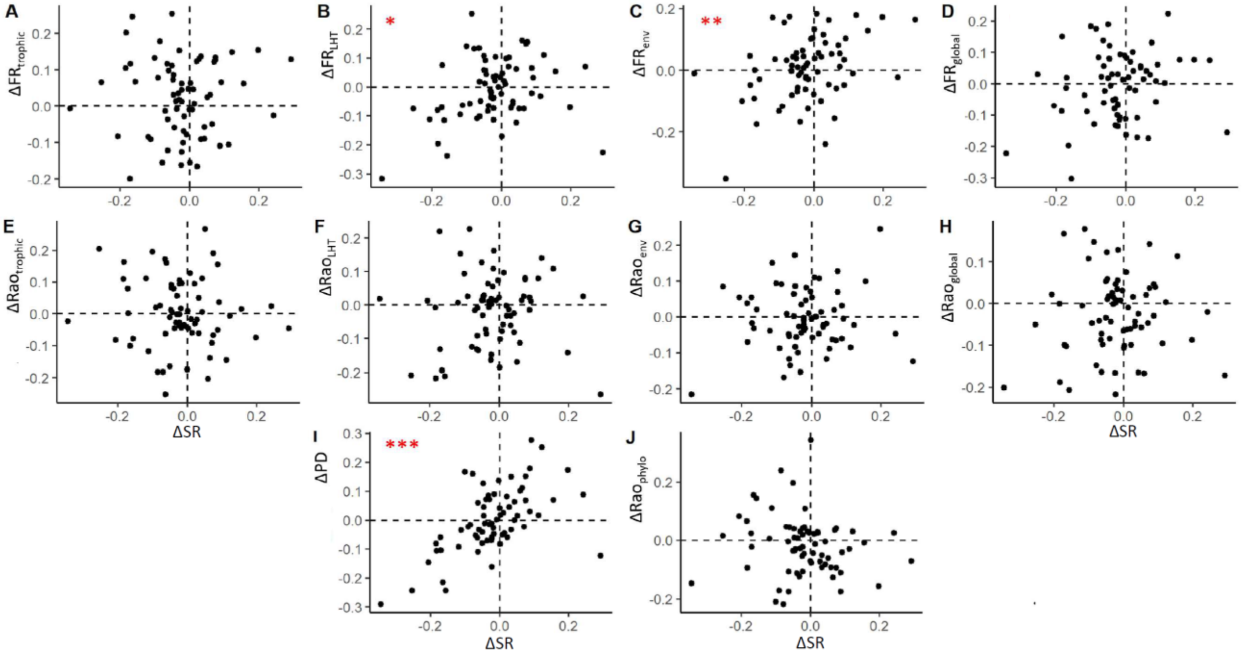

A
ΔFR trophic
FR trophic historical
r = -0.37, p = 0.002
B
ΔFR LHT
FR LHT historical
r = -0.62, p < 0.001
C
ΔFR env
FR env historical
r = -0.30, p = 0.01
D
ΔRao trophic
Rao trophic historical
r = -0.39, p = 0.001
E
ΔRao LHT
Rao LHT historical
r = -0.63, p < 0.001
F
ΔRao env
Rao env historical
r = -0.34, p = 0.004
UD
OD

Figure 5.


A
ΔFR_trophic
B
*
ΔFR_LHT
C
**
ΔFR_env
D
ΔFR_global
E
ΔRao_trophic
ΔSR
F
ΔRao_LHT
G
ΔRao_env
H
ΔRao_global
ΔSR
I
***
ΔPD
ΔSR
J
ΔRao_phylo
ΔSR

CHAPTER THREE

CHARACTERISTICS OF DRYING AND WETTING REGIMES DETERMINE ASSEMBLAGE STRUCTURE OF MACROINVERTEBRATES, SOFT-BODIED ALGAE, AND DIATOMS IN NON-PERENNIAL STREAMS

Keywords:

non-perennial stream, benthic macroinvertebrate, soft-bodied algae, diatom, hydrologic metrics

Under Review in *Freshwater Biology*

Busch M.H., Cook, S.C., Boersma, K.S., Jones, C.N., Loflen, C., Mazor, R.D., Price, A., Stubbington, R., Stancheva, R., Zimmer, M., Allen, D.C. Characteristics of drying and wetting regimes determine assemblage structure of macroinvertebrates, soft-bodied algae, and diatoms in non-perennial streams.

ABSTRACT

Biological communities in non-perennial streams are influenced by drying and wetting transitions. Although there has been increasing attention on how drying impacts stream organisms, few studies have investigated how specific characteristics of drying and wetting regimes influence biological assemblages. Here, we characterized hydrologic metrics quantifying drying and wetting regimes and explored how these metrics influenced three different aquatic assemblages in non-perennial streams in arid southern California: benthic macroinvertebrate, soft-bodied (non-diatom) algal, and diatom assemblages. We found that flow duration prior to sampling was correlated with macroinvertebrate and soft-bodied algal assemblage structures while their assemblage richnesses were not predicted by any hydrologic metric. The structure and richness of diatom assemblages, however, were predominantly influenced by the date of drying. Contrary to other studies, the duration of the dry phase preceding sampling did not influence assemblage structure or richness. While our study took place over a small region where each assemblage experienced approximately the same environmental conditions, we found no single metric that influenced all assemblages in the same way. The arid climate of southern California likely acts as a strong environmental filter, with taxa in this region relying on adaptations and life history cues to survive and recolonize non-perennial streams following rewetting. This study demonstrates how transitions between wetting and drying affect different components of stream ecosystems in different ways. Watershed managers should therefore consider multiple ecological and hydrologic benchmarks to meet biodiversity goals as non-perennial streams become increasingly dominant in global river systems.

INTRODUCTION

River ecosystems and their biodiversity are shaped by natural disturbances such as drying and flooding (Poff et al. 1997; Lake 2003; Chanut et al. 2020). Non-perennial streams, which cease to flow at some point in time or space (Busch et al. 2020), are largely defined by drying disturbances. Two distinct hydrologic states exist in non-perennial systems: a wet phase when surface water is connected and flowing, and a dry phase when the stream channel is dewatered, though non-flowing isolated pools may be present. These phases are linked via two hydrologic transitions: wetting, where surface water returns and flow resumes, and drying, when flow ceases and most or all surface water disappears. Hydrologists are developing methods to quantify these transitions, as they likely greatly influence the biological communities of non-perennial systems (Price et al. 2021). Wetting and drying regimes of non-perennial streams are rapidly changing at a global scale (Tramblay et al. 2021; Zipper et al. 2021). It is therefore essential to understand how communities respond to drying and wetting regimes in arid climates to predict how changes therein may shape biodiversity and management as aridification becomes more globally prevalent (Park et al. 2018).

Characteristics of stream drying, such as duration, timing, and rate of drying, influence biological communities across multiple levels of taxonomic organization in non-perennial streams (Gasith and Resh 1999; Fritz and Dodds 2004; Price et al. 2021), often leading to taxonomic turnover in macroinvertebrate and algal communities (Boulton 2003; Ledger et al. 2013; Aspin et al. 2018; Vander Vorste et al. 2021). As flow decreases and pools form, taxa typical of flowing water are replaced by taxa typical of still water (Sabater et al. 2017; Stubbington et al. 2017; Hill and Milner 2018). The loss of most or all surface water represents a profound shift in state when only desiccation-tolerant taxa can persist (Stubbington et al. 2017). The rate of drying likely affects biotic responses: slow drying onset may give motile organisms time to move into refuges such as isolated pools (Archdeacon and Reale 2020) or saturated subsurface sediments (DelVecchia et al. 2022). Similarly, biofilms can persist longer with slower drying rates (Robson 2000; Robson et al. 2008) which also give organisms time to make metabolic adjustments to promote desiccation tolerance (Strachan et al. 2015). As surface water is lost entirely, the composition of assemblages largely depends on the resistance adaptations of organisms to survive drying (Sabater et al. 2017; Stubbington et al. 2017), such as desiccation-tolerant life stages that allow organisms to persist through droughts (Lake 2000; Stancheva 2006; Stancheva et al. 2012; Stubbington and Datry 2013; Bogan, et al. 2017). Such adaptations are common in arid streams (Bogan et al. 2013). The duration of the dry period is known to be a primary driver of community diversity in non-perennial streams (Leigh and Datry 2017). As dry duration increases, the taxonomic richness of both macroinvertebrates (Datry et al. 2014; Sarremejane et al. 2020; Pineda-Morante et al. 2022) and biofilms (Sabater et al. 2016) declines, accompanied by a decrease in biofilm biomass and gross primary production (Colls et al. 2019; Miao et al. 2023). These drying patterns influence non-perennial communities at both local and regional scales (Colls et al. 2019; Sarremejane et al. 2020).

Although not as well studied, wetting regimes also influence biological communities in non-perennial streams (Price et al., in prep). Streams tend to rewet faster than they dry, sometimes through flash flood events (Ward and Stanford 1995; Mosisch 2001) that can mobilize substrate and displace organisms downstream (Poff et al. 1997), including those taxa that took refuge in the subsurface sediments (Olsen and Townsend 2005). Thus, the magnitude and rate of the wetting transition may influence the taxa of non-perennial streams as much as those of the drying transition, particularly in arid, mediterranean climates (Bonada and Resh 2013). During wetting, organisms can colonize from refuges (Stubbington 2012; Bogan and Boersma 2012; Sabater et al. 2017), and recovery times can vary widely across taxa (Bogan, et al. 2017). Diatoms and soft-bodied algae can rapidly regrow after floods (Gasith and Resh 1999) and provide food sources for recolonizing macroinvertebrates. Benthic macroinvertebrates have many adaptations for recolonization, including flying adult stages and passive drift from upstream refuges (Bogan et al. 2017). The duration that a stream has been rewetted is another important determinant of recolonization for both macroinvertebrates and soft-bodied algae (Matthaei et al. 2003; Fritz and Dodds 2004). Time since wetting influences the richness, density, and structure of macroinvertebrate (Doretto et al. 2020; Pineda-Morante et al. 2022), soft-bodied algae (Robson and Matthews 2004) and diatom assemblages (Barthès et al. 2015). Despite these indications of the importance of wetting regimes, studies of non-perennial streams have focused more on impacts of drying than wetting, and it is not clear which characteristics of drying and wetting processes influence community structure.

With increasing aridification and growing prevalence of non-perennial streams around the world (Jaeger et al. 2014; Pumo et al. 2016), studies that illuminate the relationships between hydrology and taxonomy are vital. However, few studies have directly examined how patterns in the timing, duration, and rate of drying and wetting influence biodiversity in non-perennial streams (but see Datry et al. 2012; Wyatt et al. 2014; Pineda-Morante et al. 2022). Here, we characterized multiple hydrologic metrics to quantify drying and wetting regimes (**Figure 1; Table 1**) in hydrologically diverse southern California and investigated how these metrics influence macroinvertebrate, soft-bodied algal, and diatom assemblages. We addressed two main questions: (1) How do the hydrologic characteristics of drying and wetting regimes influence aquatic biodiversity? and (2) Are the same hydrologic metrics consistent predictors of biodiversity across taxonomic assemblages? To answer these questions, we examined how benthic macroinvertebrate, soft-bodied algae, and diatom assemblages related to hydrologic metrics that characterize drying and wetting regimes. We hypothesized that the same metrics would consistently influence macroinvertebrate, soft-bodied algal, and diatom assemblage richnesses and structures: time assemblages have to recover after wetting (Wet Duration) and the length of the preceding dry period (Dry Duration; **Figure 1; Table 1**).

METHODS

Study area

Data were collected in southern California, between 34-32° North and 116.25-117.75° West in 2015-2017 (**Figure 2; S.I.1**). Southern California has a mediterranean climate with cool, wet winters and hot, dry summers, with almost all precipitation received between October and May (Luo et al. 2017). Precipitation in the study area is dominated by rainfall, with snow falling at levels insufficient to create a discernible snowpack. Most streams across this region are non-perennial (Mazor et al. 2014). The majority of the streams used in this study are classified as reference streams by the State of California (Ode et al. 2016, 2016b); they are located far from urban centers, have little anthropogenic activity within the watersheds, and have mostly natural surrounding land cover.

From 2012-2015, California experienced one of the worst droughts in state history (Williams et al. 2015; He et al. 2017). Our study spans from 2015-2017 and is therefore influenced by the legacy effects of this severe drought. The winter of 2015-2016 had lower-than-normal precipitation in southern California, but the following winter (2016-2017) was the second wettest winter on record (Singh et al. 2018). This extreme variability in precipitation is common in this region and is expected to amplify with climate change (Swain et al. 2018).

Study Taxa:

Data collection followed standard operating procedures for California stream biological assessments, sampling benthic macroinvertebrates, soft-bodied algae, and diatoms (Ode et al., 2016, 2016b). Each group of taxa is ubiquitous in freshwater systems, commonly used for stream assessments (Rosenberg and Resh 1993; Lowe and LaLiberte 2007; Stancheva and Sheath 2016; Fierro et al. 2017), and vital for stream ecosystem processes. In addition, benthic macroinvertebrate indices have been adopted for use as biocriteria in southern California (Loflen et al. 2020) and are used statewide for determining water body impairment under the United States Clean Water Act (State of California 2022).

As primary producers, soft-bodied algae and diatoms interface physicochemical and biotic components of aquatic food webs (Stevenson et al. 1996), although they serve different roles in stream ecosystems. Soft-bodied algal species tend to be larger than diatoms, creating relatively large, physical structures in the stream that provide habitat for many organisms (Dodds 1991). While soft-bodied algae are a potential food source for grazers, they are often less preferred than diatoms, which tend to be the preferred food source as they are small, easily digestible, non-motile, and rich in proteins and oils (Robson et al. 2008; Power et al. 2013).

Benthic macroinvertebrates link basal resources and primary producers to higher trophic levels such as fish (Hauer and Resh 2007) and provide important functions in streams such as nutrient cycling and transfer and detrital decomposition (Covich et al. 1999).

Data Collection:

Several California agencies (including the California Environmental Protection Agency: San Diego Regional Water Quality Control Board and the California Department of Fish of Wildlife) collected hydrologic and biological data as part of long-term reference stream monitoring programs. Onset HOBO® U20 pressure transducer loggers were installed in streams during the dry fall season to record average reach-scale flow conditions (avoiding pools and riffles) and recorded water stage level and temperature at 6-hour intervals for 2-5 years. Additional loggers were deployed above the banks to measure air pressure and enable stage level calculation using Onset HOBO® software. Sites were visited annually to measure stream flow and stage level to validate readings and to download data. In addition, conductivity loggers were deployed at a subset of sites to assess the wet and dry accuracy of loggers on zero flow days.

On each site visit, researchers measured physical and habitat variables, including wetted width, percent canopy cover, temperature, specific conductivity, pH, alkalinity (as $CaCO_3$), and the proportion of the reach that was riffle, pool, or run (as described in Ode et al. 2016, 2016b).

Benthic macroinvertebrates, soft-bodied (non-diatom) algae, and diatoms were collected between March and May, typically at least 4-6 weeks after the most recent wetting event, following standardized procedures (Ode et al. 2016, 2016b). For macroinvertebrate samples, each 150-m stream reach was divided into 11 transects. At each transect, a D-frame kick net was used to sample 0.09 m^2 of stream bed by kicking and scrubbing substrate to dislodge benthic macroinvertebrates from representative habitat types (riffles, pools, runs). Researchers sampled points at 25%, 50%, and 75% of the channel width in each transect and combined all 11 samples (1.1 m^2 total) into a single composite sample preserved in ethanol. The State of California's Aquatic Bioassessment Laboratory processed and identified benthic macroinvertebrate samples to the highest taxonomic resolution feasible: species for most insects, sub-family for Chironomidae, genera for mites and snails, and class for oligochaetes, flatworms, and nematodes (Richards and Rogers 2011). Ten percent of samples were subjected to secondary review by an independent taxonomist following the quality assurance plan of California's Surface Water Ambient Monitoring Program (Rehn and Slusark 2015).

Field crews collected benthic diatoms and soft-bodied algae quantitatively along the same 11 transects following standard operating procedures (Ode et al. 2016, 2016b). Benthic soft-bodied algae and diatoms were sampled along transects of standard area from available substrates (e.g., cobble, silt/sand, gravel, bedrock, wood). Field crews removed soft-bodied algae and diatoms by manual brushing or scraping and rinsing into a jar. Diatom samples were fixed using formalin and soft-bodied algae samples were fixed with glutaraldehyde. Algal samples were processed following Stancheva et al. (2015). At least 600 diatom valves from each sample were identified and counted on permanent slides prepared from cleaned material. Researchers calculated biovolumes for the soft-bodied macroalgae and microalgae samples. Due to fundamental differences in morphology, development, and functional roles, we analyzed soft-bodied algae separately from diatoms, and refer to the assemblages as either soft-bodied algae or diatoms. We calculated relative abundances for the quantitative samples of soft-bodied algae (macroalgae and microalgae samples combined) and diatoms.

In addition to quantitative samples, field crews collected qualitative soft-bodied algal samples by hand-picking or scraping soft-bodied algae that were visible within the 150-m reach. These additional samples were taken to ensure full algal assemblages were captured at each site, including those that do not attach to rocks (i.e., epiphytes that grow on in stream vegetation). These qualitative soft-bodied algae samples were identified and included in calculations of taxonomic richness, but not of abundance-based diversity metrics.

We resolved the final species list taxonomically for all three assemblages to ensure we did not count species more than once (e.g., in the family Baetidae, researchers identified most organisms to Genus, thus we excluded those identified to Family; Cuffney et al. 2007).

Data Selection:

We selected sites with macroinvertebrate, soft-bodied algae, and diatom samples that overlapped with the stage logger data (Loflen et al., *in prep.*) and included at least one dry and subsequent wet event. In total, we analyzed 27 biological samples across 20 sites between 2015 and 2017 (**Figure 2**).

Hydrologic Metrics

We created hydrographs for each site from the stage logger data (e.g., **Figure 1**). To isolate paired drying and wetting events, we set a start and end date for each drying and subsequent wetting event using the interactive ‘dygraphs’ package (Vanderkam et al. 2018). We visually defined the start date at the beginning of the preceding wet event, or as close to the start of the preceding event as the data allowed. Then we manually defined the end date as the date when the wet period containing the biological sample date had dried, or the last date of data collection.

This produced hydrographs for each site that contained two wetting events and the dry period between them (**Figure 1**).

We calculated hydrologic metrics from these hydrographs as described in **Table 1**. To calculate the metrics for each drying and subsequent wetting event, we filtered the logger data for each event to the records between the start and end dates and averaged the six-hourly stage data into daily values to reduce the noise in the data. We defined a stream as "dry" for days when the average daily water level equaled zero for at least 10 consecutive days. Dry periods were delineated as the number of dry days before the water level exceeded zero.

We created a hydrograph using daily water levels for each event to correct for any "false starts". In streams in this region, it is common for short, often violent precipitation events to cause pulse wetting events that persist for hours to a few days. For the majority of events included in this data, the duration of false stars were brief (1-3 days). However, one event included a longer "false start", which we manually corrected for (**S.I.2**). While we acknowledge that wet periods longer than 3 days may not indicate flashiness, we defined these as "false starts" to best capture the wetting stage that contained the biological sample date. In addition, this time period is less than most macroinvertebrates need to recolonize upon wetting, although recolonization varies between taxa (e.g., Otermin et al., 2002).

We used Pearson correlations to assess multicollinearity using the "performance" R package (Lüdecke et al. 2022) to identify which hydrologic metrics to use in subsequent analyses. We removed redundant variables with an absolute correlation coefficient of >0.70, retaining variables that were most relevant to our hypotheses (Hammond et al. 2021; Zipper et al. 2021; Price et al. 2021; **S.I.3**). This procedure produced a reduced set of ten hydrologic predictors (**Table 1**).

Modeling Predictors:

We also included environmental variables measured during biological sampling that are known to influence stream community composition: alkalinity (as $CaCO_3$), pH, specific conductance, temperature, canopy cover, water depth, wetted width, and the proportion of riffle, pool, and run habitat for each stream reach (**Table 2**). As above, we removed multicollinear environmental variables with an absolute Pearson correlation coefficient > 0.70. The final models included all environmental variables except for station water depth, which was correlated with the proportion of pool (r = 0.79). We chose to remove station water depth as it represents the habitat available, similar to wetted width (r = 0.67) and peak depth (r = 0.65; **S.I.3**).

Data Analysis:

We analyzed macroinvertebrates, soft-bodied algae, and diatom assemblages to understand how they are influenced by drying and wetting regimes. We calculated taxonomic richness, relative abundances, and Hill-Shannon values for all taxa. We calculated richness and the Hill-Shannon index using the R packages "vegan" (Oksanen et al. 2011) and "hillR" (Li 2021) respectively. We chose Hill-Shannon as a measure of alpha diversity because Hill numbers change in proportion with species gain and loss and Hill-Shannon diversity is more sensitive to both common and rare species in comparison with other Hill numbers (Roswell et al. 2021; Aspin and House 2022).

Six out of the 20 sites had more than one sample between 2015-2017, resulting in 14 out of 27 samples with a temporal component. In other climate zones, the pseudoreplication of multiple sampling events per location may prohibit the inclusion of these sites. However, the temporal and spatial stream fragmentation and extreme environmental filtering in this region means that aquatic communities are often more correlated spatially across streams than temporally within the same stream (Bogan et al. 2013). To test for sample independence and to quantify the effects of year on the assemblage data, we ran mixed effect models ("lme4" package; Bates et al. 2022) with all the predictor variables, including year as a fixed effect and site as a random effect on the 14 repeated samples. Year significantly predicted diatom Hill-Shannon diversity but had no significant influence on other assemblages or richness (**S.I.4**). Therefore, we included all 27 samples in further analyses and did not include year in models of richness or diversity. We also ran linear models for each hydrologic metric and environmental variable with year as the predictor to investigate potential effects of the 2012-2015 drought on the environment.

We examined associations between hydrologic metrics and assemblage structure using multivariate ordinations. For each assemblage, a non-metric multidimensional scaling (NMDS) ordination was created with a Bray-Curtis distance matrix of log-transformed relative abundance using "vegan" (Oksanen et al. 2011). Due to the low stress for each NMDS (all < 0.20), we retained all species in our analysis (McCune et al. 2002). The algal ordination excluded the qualitative samples without relative abundances. While we were mainly interested in the impacts of the hydrologic metrics, we also assessed how other environmental variables were associated with each assemblage. We used the ‘envfit’ function in the “vegan” package to fit linear correlations of environmental variables and hydrologic metrics ($p < 0.015$) to the NMDS ordinations with 999 permutations (Oksanen et al. 2011). We chose this alpha value to highlight only the variables with the strongest relationships to assemblage composition. We rotated all NMDS ordinations to align NMDS axis 1 with the hydrologic metric Wet Duration (time between the Rewet Date and Sample Date) to facilitate comparison across assemblages, because Wet Duration had the largest R^2 for 2 of the 3 ordinations. Finally, we tested the effects of the sampling year with multi-response permutation procedures (MRPP) with “vegan” (Oksanen et al. 2011).

To characterize the effects of the hydrologic metrics on alpha diversity (richness and Hill-Shannon), we ran general linear models. For each assemblage and diversity metric, we ran a global model that included all ten hydrologic metrics and the year the sample was taken as predictors and the diversity metric as the response. We also ran univariate models for each individual hydrologic metric and compared these with a null model without any hydrologic metrics (predictor = 1). Due to the relatively small number of sites relative to predictors, we did not include the environmental variables or a random effect to account for site identity. We justify this decision as site id had a negligible effect on our results when included as a random effect in our repeated sampling models, suggesting some level of sample independence (**S.I.4**). We compared models using Akaike Information Criteria (AIC) values corrected for small sample sizes (AICc; Warren and Seifert 2011; Galante et al. 2018), calculated by the “MuMIn" R package (Bartoń 2022). To determine if models differed from the baseline null models, we set an absolute AICc difference of 3 (Lu et al. 2016). Models of algal richness included qualitative and quantitative samples, while models of algal Hill-Shannon only included quantitative samples. We used R for all analyses (R Core Team 2022).

RESULTS

Hydrologic metrics and environmental variables

As expected for streams in arid regions, hydrologic metrics were highly variable across the three years and 27 hydrologic events (**Table 2A**). Peak depths occurred on average four weeks before the sample date, resulting in a negative Peak-to-Sample slope except for one event, in which the peak depth occurred after the sample date. On average, Dry Date occurred in late March, First Wet Date in late June, and Peak Date in mid-February. Of the variables measuring rates of change over time, Rewet Slope was the steepest (mean = 0.023 ∓ 0.059 m/day).

Study sites had similar pH values (mean = 8.1 ∓ 0.6) and wetted widths < 4.5 m (mean = 1.6 ∓ 0.9m), although alkalinity (mean = 120.0, range = 312.0) and specific conductivity (mean = 506.0 µS/cm, range = 1765.4 µS/cm) varied greatly (**Table 2B**). Generally, these streams exhibited low nutrient concentrations, with total nitrogen concentrations < 1 mg/L and total phosphorous concentrations < 0.1 mg/L, which is typical for undisturbed streams in coastal southern California (Mazor et al. 2022).

The models including year as a predictor indicate that the effects of year were observed in two hydrologic metrics (Peak Depth: $p < 0.01$, adjusted $R^2 = 0.32$; and Wet Duration: $p < 0.01$, adjusted $R^2 = 0.33$) and two environmental variables (proportion of riffle: $p < 0.01$, adjusted $R^2 = 0.32$ and wetted width: $p <=0.01$, adjusted $R^2 = 0.20$; **S.I.5**). Each of these variables were larger in years not affected by drought.

Biological diversity

Across the 27 samples in the study, 152 macroinvertebrate taxa, 207 soft-bodied algae taxa, and 225 diatom taxa were identified, with an average richness per sample of 13, 5, and 16, respectively (**Table 3**). An additional 11 soft-bodied algae taxa were collected with qualitative sampling. More specific information about the most and least common taxa for individual assemblages can be found in **S.I.6**.

Assemblage Structure and Association with Hydrologic Metrics: NMDS

All ordinations yielded stable two-dimensional solutions. The ordination for benthic macroinvertebrates (**Figure 3A**, stress = 0.127) demonstrates separation among years (A = 0.040, p = 0.002), whereas assemblage composition of soft-bodied algae and diatoms from different years overlapped (soft-bodied algae: **Figure 3B**, stress = 0.180, A = 0.0006, p = 0.94; diatoms: **Figure 3C**, stress = 0.148; A = 0.019, p = 0.64).

Across each assemblage, hydrologic metrics were more strongly related to variations in assemblages than environmental variables were (**Figure 3**, **Table 4**; **S.I.6**). We found that macroinvertebrates and soft-bodied algae had the strongest correlation with Wet Duration (R^2 = 0.59; R^2 = 0.49, respectively). However, this was not the case for diatoms, contrary to our hypotheses (Wet Duration R^2 = 0.15, p = 0.16). Rather, diatom assemblages had the strongest correlation with Dry Date (R^2 = 0.40, p = 0.005). Of the 19 hydrologic metrics and environmental variables we studied here, 10 were significantly correlated with the structure of at least one assemblage (**Table 4**). Diatom assemblages were associated with metrics and variables that were shared with at least one other assemblage, while macroinvertebrate and algal assemblages were associated with at least one unique predictor (macroinvertebrates: proportion of the reach comprised of riffles and alkalinity; soft-bodied algae: Peak-to-Sample Slope, Peak Date, and temperature). Contrary to our hypotheses, no assemblage was significantly correlated with Dry Duration (R^2 < 0.08; p > 0.40); and no single metric or variable was significantly correlated with all three assemblages.

Richness Responses to Hydrologic Metrics: Linear models

In the models containing a single hydrologic metric, Dry Date was predictive of diatom assemblage richness while Recession Slope was predictive of macroinvertebrate and soft-bodied algal richness (**Table 5**). Null models were important across all assemblages, indicating that factors other than those we included influenced taxonomic richness. Additionally, models including Recession Slope consistently performed better than null models (AICc difference > 3), although they explained little deviance for each assemblage (R^2 < 0.01). Dry Date predicted diatom richness (R^2 = 0.26) and performed better than the null model based on AICc values. Additionally, the deviance explained by the Dry Date was greater than the deviance explained by the global model. Contrary to our hypotheses, Wet Duration and Dry Duration did not have significant relationships with the richness of any assemblage. As with the NMDS analysis, we found no common metric that was important across all assemblages. We present results for Hill-Shannon diversity in Supplemental Information as results were largely redundant (**S.1.7**).

DISCUSSION

Although it has long been known that drying and rewetting influence biota in non-perennial streams (Gasith and Resh 1999; Datry et al. 2014; Sabater et al. 2017), the specific aspects of drying and wetting regimes that most strongly influence communities are not well characterized. Here we used hydrologic metrics to investigate biological responses to multiple aspects of drying and wetting regimes in non-perennial streams in arid, mediterranean southern California. We found inconsistencies across macroinvertebrate, soft-bodied algae, and diatom assemblages, demonstrating that taxonomic groups respond to drying and wetting in different ways. Specifically, we found that the time since initial wetting (Wet Duration) was important in structuring macroinvertebrate and soft-bodied algal assemblages, potentially highlighting the importance of recolonization and/or development time for these taxa. Contrary to our hypotheses, no assemblage had a significant response to the length of the dry period (Dry Duration) and diatom structure and richness was best predicted by the day when the stream went dry (Dry Date). Finally, we found that no single metric explained structure or richness for all three assemblages. Below, we review our original hypotheses, the at times contradictory results, and possible ecological explanations.

Assemblage responses to hydrologic metrics and environmental variables

We found some support for our hypothesis that Wet Duration (the duration of time that the stream was wet before sampling) and Dry Duration (the length of the dry period preceding sampling) would be the hydrologic metrics that were most predictive of biological assemblage structure. Wet Duration was the metric most correlated with the composition of macroinvertebrate and soft-bodied algal assemblages. The influence of Wet Duration on these groups may reflect the importance of flow duration for recolonization after flow resumes; the longer the streams flow, the greater the opportunity for taxa to recolonize. Some macroinvertebrates can recolonize over large distances, and aerial recolonization is typically the principal method of recolonization in arid land streams (Bogan and Boersma 2012). Similarly, some soft-bodied algae can recolonize via drift from perennial refuges (Sabater et al. 2017), while others have dormant, desiccation-resistant stages that contribute to repopulation upon rewetting (Garg and Maldener 2021). For example, *Zygnema*, a soft-bodied alga from non-perennial streams in southern California is able to recolonize quickly upon wetting due to quick germination of akinetes, their desiccation resistant spore-like cells (Fuller 2013). Some species of soft-bodied green algae can germinate within six days of flow resumption (O'Neal and Lembi 1983). The timing and sequence of colonization in two intermittent streams studied by Dodds et al. (2004) showed that algal assemblages recovered within two weeks after the floods, with diatoms colonizing early, followed by filamentous green algae. Similarly, recovery time for benthic macroinvertebrates can be as little as two to four weeks in small, non-perennial prairie systems (Fritz and Dodds 2004), although recovery time across families varies widely (Fowler 2004; Sarremejane et al. 2019). Our results suggest that macroinvertebrates and soft-bodied algae within this arid region are able to easily colonize streams upon wetting, and the duration of flow resumption is vital for non-perennial stream assemblages.

Contrary to our hypothesis, the length of the previous dry period (Dry Duration) did not influence the structure or richness of any assemblage. Our results clearly contradict the conclusions drawn from prior research (Sabater et al. 2016; Pineda-Morante et al. 2022; Miao et al. 2023). Biofilms that experienced longer drought periods had slower metabolisms and were less likely to recover to pre-drought rates than those exposed to shorter drought periods (Miao et al. 2023). Similarly, numerous studies have demonstrated the negative influence of longer dry periods on macroinvertebrate diversity (Datry et al. 2014; Soria et al. 2017; Sarremejane et al. 2020; Pineda-Morante et al. 2022), particularly with more sensitive taxa, such as Ephemeroptera, Plecoptera, and Trichoptera (Feminella 1996; Arscott et al. 2010). The lack of response to Dry Duration in our study suggests that the taxa in our dataset are well adapted to dry periods (Bogan et al. 2017).

Southern California is an arid region dominated by non-perennial streams (Mazor et al. 2014) and has strong aridity that acts as a "selective" regional filter on species distributions that favors organisms with adaptations which facilitate survival during dry periods (Weiher and Keddy 1995). For example, the larvae of the megalopteran *Neohermes filicornis*, which can tolerate multiple drying periods before pupating and can become active 2-3 days after rewetting (Cover et al. 2015). Other regionally important adaptations include the ability to drift from upstream perennial waterbodies, desiccation resistant eggs, and rapid development from egg stages laid by aerially dispersing adults (Bonada et al. 2007; Stubbington et al. 2017). Similarly, the soft-bodied algal assemblages in our study were characterized by cyanobacteria that are able to form thick-walled akinetes, which can withstand long dry periods and germinate quickly upon water availability (Garg and Maldener 2021) and filamentous algae such as *Zygnema,* which can survive in dry conditions up to 20 years (Transeau 1951). Another example is the very rare desiccation-tolerant alga *Tetrasporopsis*, which is physiologically adapted to inhabit only non-perennial streams in southern and central California (Stancheva et al. 2019). The strongly arid environment of southern California makes such adaptations necessary and limits the regional species pool to taxa able to persist during long dry periods.

We found no relationship between Wet Duration or Dry Duration and diatom assemblages. Rather, diatom structure and richness were most influenced with the earliest day of the preceding dry event (Dry Date), highlighting the importance of dry-phase timing for this taxonomic group. Mediterranean systems typically have predictable seasonal cycles of wetting and drying (Bonada and Resh 2013), and many taxa respond to environmental cues to initiate behavioral and life history transitions (Boersma et al. 2019). While hydrologic predictability explains biological responses in many taxa (Poff et al. 1997; Price et al. 2021), further research is needed to better understand the environmental cues used by diatoms. Like soft-bodied algae, diatoms can form double-walled internal resting spores that can persist throughout long periods of desiccation and can germinate within hours of rewetting (Sanyal et al. 2022). Evidence of diatom resting spore-formation has been observed in many taxa in this dataset (Stancheva, unpublished). Probable cues include water limitation, nutrient limitation, and temperature, though little is known about specific cues that encourage formation of desiccation-resistant life stages.

We also identified non-hydrologic environmental variables that influenced assemblage structure; for example, macroinvertebrate assemblage structure was correlated with canopy cover and wetted width. Canopy cover determines how much sunlight reaches the benthos of streams, which impacts algal and diatom assemblages (Pan et al. 1999; Atkinson and Cooper 2016; Jansen et al. 2020) and thus can influence macroinvertebrate food webs (Aguiar et al. 2017). Canopy cover is also related to the amount of carbon input into a stream and can increase habitat complexity through leaf litter and woody debris inputs (Kaufmann et al. 1999), which can provide additional resources and niches for macroinvertebrate taxa. Wetted width is positively correlated with habitat availability (Cowx et al. 1984; Dewson et al. 2007) and complexity (Cazaubon and Giudicelli 1999). More complex stream habitats can mediate the effects of predation and resource competition (Diehl 1992) and tend to have more refuges; this complexity generally leads to increased macroinvertebrate stability through time (Mykrä and Heino 2017). Further, it is known that increased habitat size and complexity often increases community diversity and abundance (Kovalenko et al. 2012). Thus, while we excluded environmental variables from our linear models due to statistical power, canopy cover and wetted width may be important determinants of richness that may have masked the effects of hydrologic metrics, in our study.

Responses across assemblages

We identified a single hydrologic predictor of taxonomic richness (Dry Date) and only for a single taxon (diatoms). Taxonomic richness can be a poor measure of biodiversity (Tuomisto 2010; Daly et al. 2018) as it cannot untangle rarity, abundance, turnover, and other factors important to community ecology and management (Fleishman et al. 2006; Tuomisto 2010). Richness notwithstanding, our hypothesis that we would find similar responses to hydrologic metrics across macroinvertebrate, soft-bodied algal and diatom assemblages was not supported. The lack of any single metric in the importance of assemblage structure and richness suggests that each assemblage is influenced by different predictors. Alternatively, the low correlation coefficients in the NMDS suggest other unmeasured variables may influence biodiversity, such as nutrient levels (Schneider et al. 2012), substrate (Sabater et al. 2017), and hydrologic connectivity (Sarremejane et al. 2020).

Ecological differences among taxonomic groups could explain the different responses of these taxa. Macroinvertebrates tend to be larger, have longer life cycles, and are capable of dispersal over farther distances than soft-bodied algae or diatoms. As consumers, many macroinvertebrates exhibit a delayed response to environmental stressors that primary producers may respond to first (Johnson and Hering 2009). While differences between macroinvertebrates and primary producers are expected, some studies suggest diatoms and soft-bodied algae can be proxies for one another (Kelly et al. 2008). In our study, however, diatoms and soft-bodied algae responded differently to different aspects of the hydrologic regime. Diatoms have higher dispersal rates and shorter generation times compared to soft-bodied algae, potentially explaining the different responses of these assemblages (Schneider et al. 2012). While soft-bodied algae have a variety of responses to drying, such as extracellular mucilage, accumulation of pigments as a protective screen against UV light, and formation of thick-walled zygospores, these desiccation resistance strategies are less common in diatoms (Aguirre et al. 2018). The differences between diatom and soft-bodied algal responses to hydrologic metrics could increase the resiliency of primary producers in non-perennial streams in this region. Our research suggests that some diatoms may be resistant to changes in the duration of wet periods, potentially providing functional redundancy in aquatic food webs during future climatic changes.

CONCLUSIONS

Taxonomic groups across the globe are facing a multitude of changes. Freshwater taxa are particularly vulnerable, as increased human water use and global climate change reduce surface water availability worldwide (Bogardi et al. 2012; Seagar et al. 2013), shifting once perennial streams to become non-perennial (Jaeger et al. 2014; Pumo et al. 2016). In addition, studies predict changes in hydrologic regimes, which could lead to unprecedented shifts in drying and wetting patterns (Tramblay et al. 2021; Zipper et al. 2021). Here we demonstrate that taxonomic groups vary in their responses to drying and wetting in an arid region. This variability indicates a need for further explorations of trait responses, which could provide more insights into the adaptations that allow taxa to persist in arid environments. In addition, more life history studies are required for many taxa to better understand responses to environmental cues. Finally, long term research is needed to address how variability in drying and wetting patterns may alter assemblage responses. With increasing aridification and growing prevalence of non-perennial streams around the world (Park et al. 2018; Tramblay et al. 2021; Zipper et al. 2021), our study illuminates the relationships between hydrology and taxonomy that will become increasingly important in a drier future.

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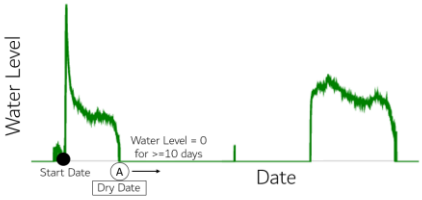
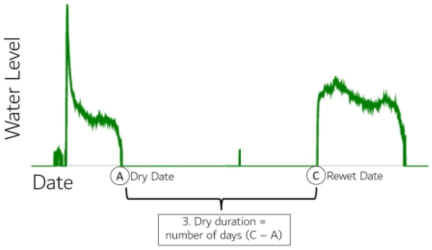
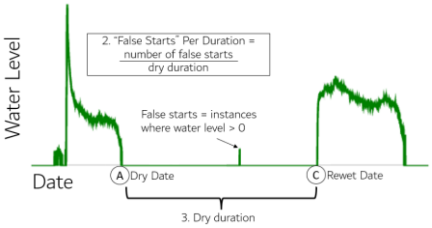
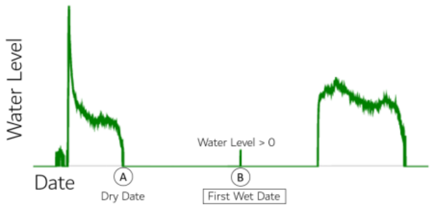
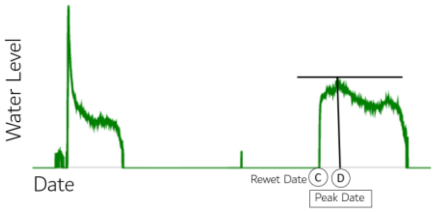
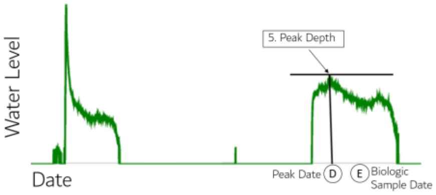
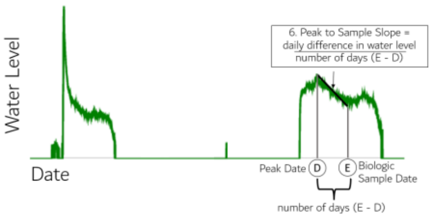
TABLES

Table 1. Description of hydrologic metrics. We calculated all metrics for each drying and subsequent wetting event. For a visual representation of metrics, refer to Figure 1. For the duration of the paper, hydrologic metrics are capitalized for easier identification.

Hydrologic Metric	**Calculation Explanation and Figure**	**Hypothesized Biological Significance**
Dry Date	First day after start date with >= 10 consecutive days with water level = 0  	• Typically predictable in mediterranean systems (Bonada and Resh 2013) • Deviations in the timing of dry date could reduce diversity and alter composition • Proxy for overall annual dryness of the year
Dry Duration	Number of days between the Dry Date and the Rewet Date  	• As the dry duration increases, desiccation stress increases on assemblages
"False Starts" per Duration	Number of periods between the dry date and the rewet date where water level was >1  	• Indication of stream flashiness • More false starts could break dormancy signal
First Wet Date	Earliest day after the Dry Date where water level was > 0, including false starts	• Highlights when organisms first get signals to end dormancy and trigger recolonization

		
Peak Date	The day after the Rewet Date with the maximum water level 	• Demonstrates peak water levels, when substrate mobilization would occur if peak was large enough
Peak Depth	Maximum depth of the time period where the sample was taken 	• A proxy for the amount of maximum habitat available
Peak-to-Sample Slope	Median of the daily differences of water level between the Peak Date and the sample day 	• Steeper slopes indicate timing and severity of scour
Recession Slope	Median of the daily differences of water level between the peak from the previous wet event and the dry date	• Shallower slopes indicate more time for organisms to find refuges (Gasith and Resh 1999; Bogan, et al. 2017) • Steeper slopes indicate aquatic habitat is being lost faster as flow declines and

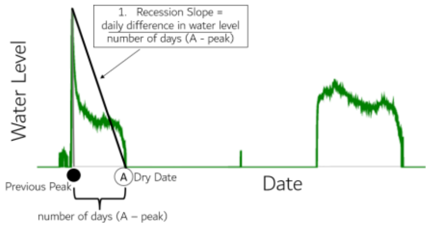
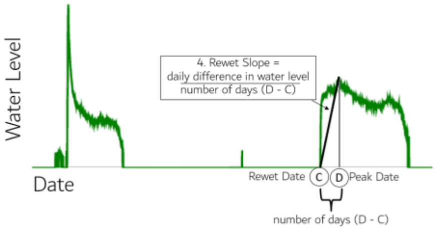
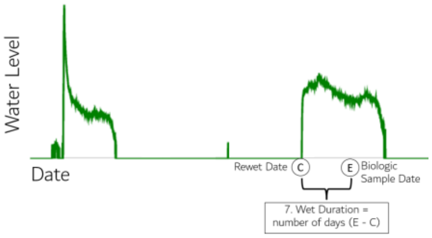
	 	the stream shrinks
Rewet Slope	Median of the daily differences of water level between the Rewet Date and the Peak Date  	• Steeper slopes indicate greater mobilization of sediments and displacement of organisms downstream (Murdock et al. 2010)
Wet Duration	Number of days between the Rewet Date and the sample day  	• Indicates how long the site has been wet, quantifying the time assemblages have to recover prior to sampling

Table 2. Summary statistics for hydrologic metrics (A) and environmental variables (B). SD = Standard deviation.

A. Hydrologic Metric	**Dry Date**	**Dry Duration**	**Peak Date**	**Peak Depth**	**Peak-to-Sample Slope**	**Recession Slope**	**False Starts per Duration**	**First Wet Date**	**Rewet Slope**	**Wet Duration**
	(Day in Water Year)	(days)	(Day in Water Year)	(m)	(m/day)	(m/day)		(Day in Water Year)	(m/day)	(days)
Minimum	100	22	65	0.39	-0.013	-0.009	0	6	0.002	6
Mean	218	209.8	117	0.39	-0.002	-0.003	0.007	117	0.052	110
Maximum	278	358	233	1.02	0.003	0	0.045	328	0.208	168
SD	48.8	76.1	33.6	0.25	0.003	0.002	0.01	81.6	0.059	40.8

B. Environmental Variable	**Alkalinity**	**pH**	**Specific Conductivity**	**Temperature**	**Canopy Cover**	**Pool**	**Riffle**	**Run**	**Wetted Width**
	(as CaCO3)		(µS/cm)	(°C)	(%)	(%)	(%)	(%)	(m)
Minimum	30	6.7	10.6	8.1	0.3	0	1	0	0.9
Mean	146.4	8.1	610.6	14.2	10.4	5.7	22.43	3.5	1.9
Maximum	342	9.7	1776	20.9	16.4	26	60.5	43.5	4.3
SD	71.6	0.6	395.8	3.1	5	6.6	15.7	10.3	0.9

Table 3. Summary statistics of taxonomic richness (A) and Hill-Shannon values (B) for macroinvertebrates, soft-bodied algae, and diatom assemblages. Algal richness includes quantitative and qualitative algal samples while soft-bodied algae Hill-Shannon values only include quantitative samples to account for relative abundances. SD = Standard deviation.

A. Richness	**Macroinvertebrates**	**Soft-Bodied Algae**	**Diatoms**
Minimum	13.0	5.0	16.0
Mean	33.4	28.9	36.9
Maximum	52.0	72.0	69.0
SD	8.8	14.7	16.1

B. Hill-Shannon	**Macroinvertebrates**	**Soft-Bodied Algae**	**Diatoms**
Minimum	1.7	1.1	3.8
Mean	13.4	5.8	15.8
Maximum	29.5	18.2	35.3
SD	6.1	4.5	9.6

Table 4. Correlations between hydrologic metrics (A) and environmental variables (B) and the NMDS axes for each assemblage. Metrics with P<0.015 are bolded.

A.	**Benthic Macroinvertebrates**		**Soft-Bodied Algae**		**Diatoms**	
Hydrologic Metric	R^2	p-val	R^2	p-val	R^2	p-val
Dry Date	0.103	0.264	0.303	0.017	**0.402**	**0.005**
Dry Duration	0.003	0.965	0.013	0.887	0.076	0.420
False Starts per Duration	0.003	0.968	0.114	0.230	0.001	0.984
First Wet Date	0.054	0.518	0.125	0.207	0.015	0.836
Peak Date	0.156	0.155	0.257	0.025	0.008	0.925
Peak Depth	0.320	0.017	0.116	0.241	0.031	0.695
Peak-to-Sample Slope	0.071	0.415	**0.270**	**0.012**	0.180	0.094
Recession Slope	0.038	0.640	0.042	0.589	0.138	0.188
Rewet Slope	0.207	0.060	0.138	0.192	0.256	0.031
Wet Duration	**0.594**	**0.001**	**0.493**	**0.001**	0.148	0.158

B.	**Benthic Macroinvertebrates**		**Soft-Bodied Algae**		**Diatoms**	
Environmental Variable	R^2	p-val	R^2	p-val	R^2	p-val
Alkalinity	0.257	0.035	0.186	0.108	0.056	0.518
Canopy Cover	**0.407**	**0.005**	0.046	0.589	0.142	0.173
pH	0.133	0.184	0.199	0.072	0.036	0.666
Pool	0.013	0.867	0.120	0.219	0.095	0.319
Riffle	**0.357**	**0.012**	0.032	0.687	0.037	0.668
Run	0.060	0.507	0.000	0.998	0.023	0.788
Specific Conductivity	0.079	0.379	0.025	0.748	0.180	0.111
Temperature	0.239	0.054	0.249	0.048	0.029	0.714
Wetted Width	0.285	0.021	0.083	0.353	0.175	0.122

Table 5. Linear model results of hydrologic metrics and assemblage richness. Columns indicate R^2 and AICc values. AICc values lower than null models by at least 3 are bolded.

	Benthic Macroinvertebrates		**Soft-Bodied Algae**		**Diatoms**	
Hydrologic Predictor	**R^2**	**AICc**	**R^2**	**AICc**	**R^2**	**AICc**
Dry Date	0.00	198.99	-0.02	227.14	**0.26**	**223.77**
Dry Duration	0.02	198.23	-0.04	227.72	0.01	231.59
False Starts Per Duration	0.06	197.31	-0.04	227.64	-0.02	232.42
First Wet Date	-0.03	199.64	-0.01	227.05	-0.02	232.24
Peak Date	0.05	197.41	0.01	226.46	-0.03	232.53
Peak Depth	-0.02	199.30	0.04	225.44	0.04	230.60
Peak-to-Sample Slope	-0.04	199.82	-0.03	227.50	0.05	230.38
Recession Slope	**-0.04**	**192.81**	**0.00**	**218.64**	-0.03	225.02
Rewet Slope	0.02	199.36	-0.02	227.19	-0.02	232.32
Wet Duration	0.01	198.70	-0.04	227.63	-0.03	232.67
Global	-0.10	222.99	-0.22	252.27	0.27	244.82
Null		**197.39**		**225.20**		**230.30**

FIGURE CAPTIONS

Figure 1. Conceptual hydrograph illustrating the hydrologic metrics. The preceding wet event, dry event, and the wet event containing the biological sample are identified at the top of the hydrograph. Hydrologic metrics related to rates, depth, and length of time are numbered, and arrows indicate which part of the hydrograph was used to calculate each metric. Metrics associated with dates are noted by letters. For detailed metric calculation descriptions, see **Table 1**.

Figure 2. Study site locations in southern California (16 sites in San Diego County, three in Orange County, and one in Riverside County; **S.I.1**).

Figure 3. Two dimensional NMDS ordinations for (A) macroinvertebrate, (B) soft-bodied algal, and (C) diatom assemblages. The NMDS stress and taxonomic richness for each assemblage are displayed. We rotated all ordinations so the Wet Duration metric aligned with NMDS1 for clearer comparability among assemblages. Significant environmental variables ($p < 0.015$) are also plotted with the length of the corresponding vector related to the strength of the relationship (R^2 value; **Table 4**).

FIGURES

Figure 1.

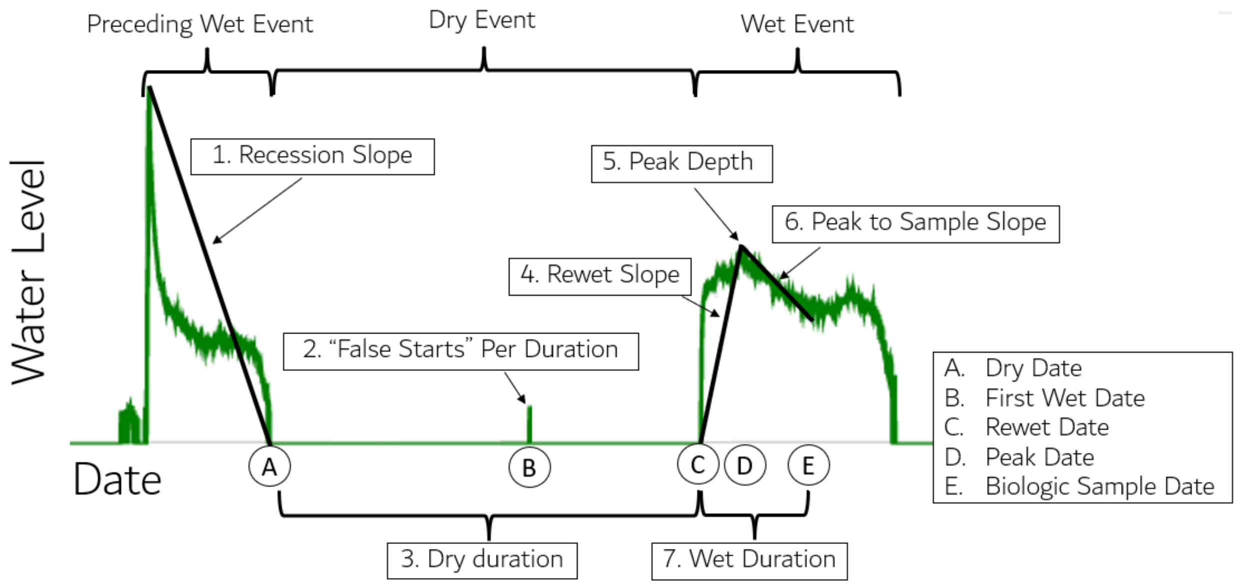


Figure 2.

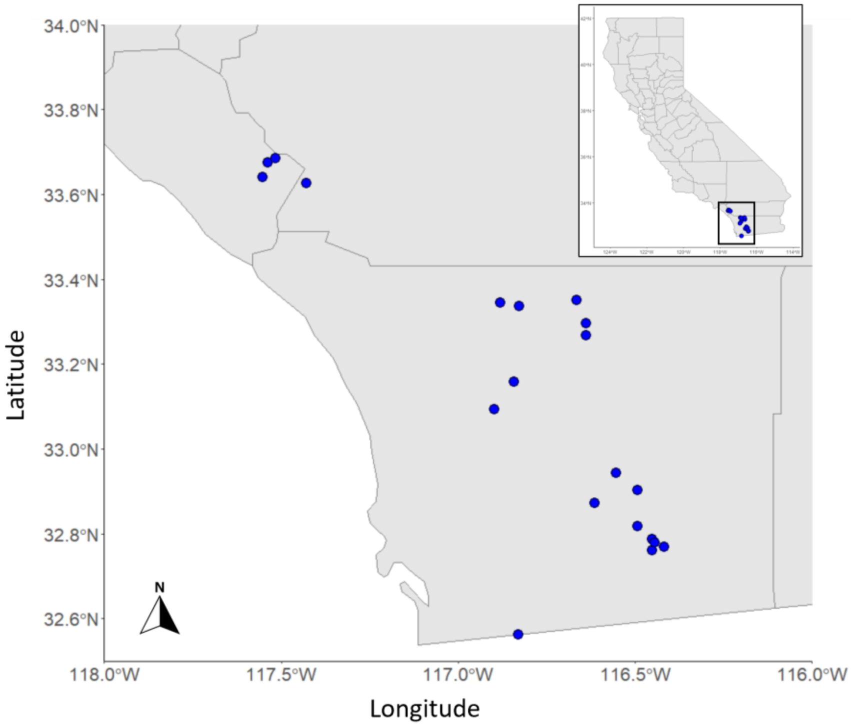
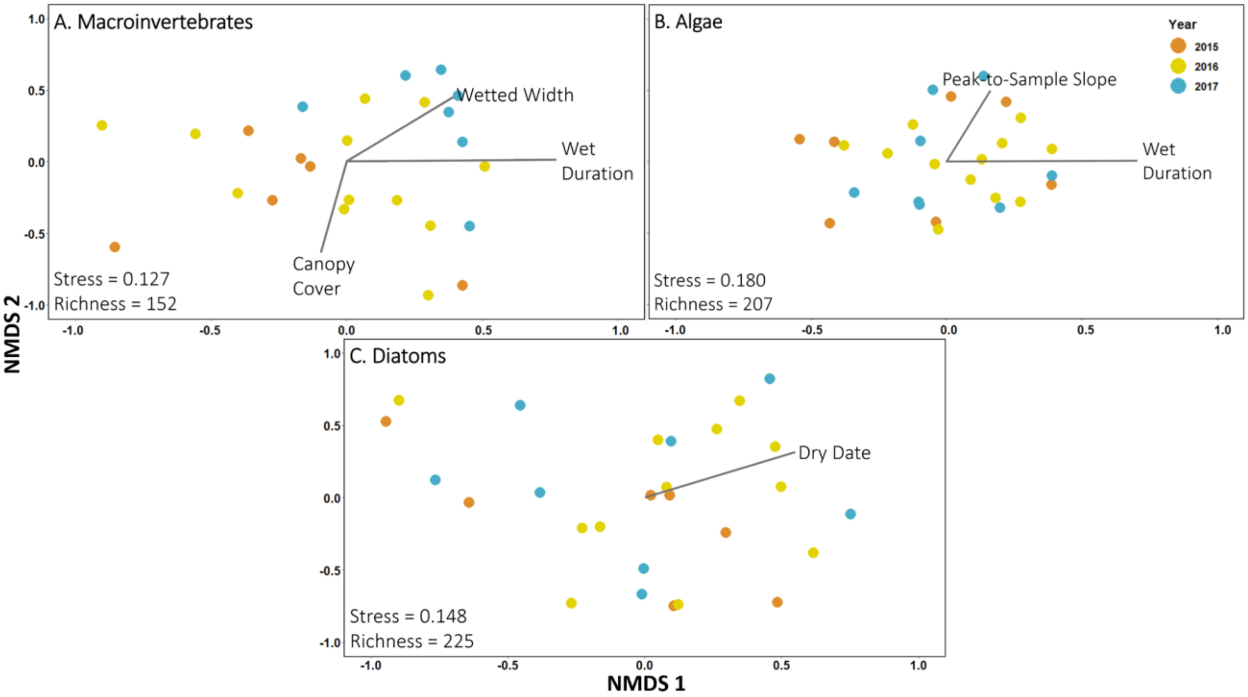

34.0°N
33.8°N
33.6°N
33.4°N
33.2°N
33.0°N
32.8°N
32.6°N
Latitude
118.0°W
117.5°W
117.0°W
116.5°W
116.0°W
Longitude
N

Figure 3.


A. Macroinvertebrates
Wetted Width
Wet Duration
Canopy Cover
Stress = 0.127
Richness = 152
B. Algae
Year
2015
2016
2017
Peak-to-Sample Slope
Wet Duration
Stress = 0.180
Richness = 207
C. Diatoms
Dry Date
Stress = 0.148
Richness = 225
NMDS 2
NMDS 1
1.0
0.5
0.0
-0.5
-1.0

CHAPTER FOUR

IMPACTS OF IMPOUNDMENTS OVERSHADOWED BY BIOGEOGRAPHY AND INTERANNUAL VARIABILITY

Keywords:

benthic macroinvertebrate, dams, land use, functional feeding groups, interannual variability

Formatted for *Freshwater Biology*

Busch M.H., Cook, S.C., Nelson, D., Bittner, S., Marske, K.A., Allen, D.C. Impacts of impoundments overshadowed by biogeography and interannual variability.

ABSTRACT

Dams are some of the world's largest contemporary threats to freshwater ecosystems. However, the ecological effects of dams largely depend on how they are managed, and studying rivers with similar biogeographical and geological histories may elucidate specific drivers of organismal responses to management. Here we studied four rivers in southeastern Oklahoma, three with dams that vary in management strategies, and one that is free flowing. We asked how macroinvertebrate assemblages, including biological metrics, ordinations, and functional feeding groups, are influenced by dams relative to other environmental factors. We used field surveys to sample sites above and below dams on three rivers, and along a comparable downstream gradient along the fourth un-impounded river. While biological metrics did not show differences among river or site types, ordinations with full assemblage data did indicate some effect of dams on assemblage composition. We also found differences between site type in full assemblage ordinations, but not in ordinations using functional feeding groups. In addition, our results demonstrated that ordinations showed greater correlations with environmental variables. We found that assemblage differences in this study were correlated to both local and watershed environmental variables. The higher elevation regions among these four watersheds may lead to biogeographic barriers, isolating the assemblages within each river. In addition, the strong aerial dispersal ability of many of the common taxa we found may allow for dispersal longitudinally along the rivers, damping the influence of dams on differences between communities upstream and downstream of the impoundment. The nuances among the results of our data highlight the importance of site-specific studies to fully understand how anthropogenic activities alter riverine ecosystems.

INTRODUCTION

Despite containing one of the world's most essential resources, freshwater bodies face multiple anthropogenic stressors and are one of the world's most threatened ecosystems (Vörösmarty *et al.*, 2010; Jun *et al.*, 2019). Among lotic systems, river impoundments, while providing benefits such as water storage, flood regulation, and hydroelectric power, have complex ecological impacts and are one of the most common contemporary threats to lotic (river) biodiversity (Power, Dietrich & Finlay, 1996; Nelson & Miller, 2023). Over 50% of all rivers are flow-regulated, and dam construction is predicted to continue to increase (Nilsson *et al.*, 2005). Therefore, it is essential to understand the influences of dams on riverine ecology.

While free-flowing rivers have been defined by the river continuum concept (Vannote *et al.*, 1980), dams lead to disruptions in the continuum, fragmenting river segments and disrupting ecological processes, ultimately resetting the river continuum downstream (Ward & Stanford, 1983; McCartney, 2009). In addition, dams reduce the downstream flow of sediments, nutrients, and organisms, eventually leading to downstream degradation and altered biological communities (Power *et al.*, 1996; Stanford & Ward, 2001; Thomson *et al.*, 2005). One of the most recognized influences of dams is their disruption of the natural flow regime; generally, they homogenize flow patterns and reduce current velocities (Poff *et al.*, 2007; Linares *et al.*, 2019). Similarly, dams can drastically alter temperature regimes. How both flow and temperature regimes change, however, depends on the purpose and, therefore, management of the dam (Roni, Hanson & Beechie, 2008; Vaughn, Atkinson & Julian, 2015). Thus, dams heavily alter the downstream riverine environment compared to the environment upstream (Maynard & Lane, 2012), though exact ecological effects differ based on specific dam management strategies.

Dams are constructed in response to human needs, and therefore the landscape surrounding rivers are usually influenced by other human impacts, such as changes in the surrounding land use. While often occurring at a larger watershed scale, land use can heavily alter freshwater ecosystems (Schilling & Spooner, 2006; Tayyebi, Pijanowski & Pekin, 2015; Gu *et al.*, 2019). For example, increased agricultural and developed land use have been identified as key contributors to river pollution and reduced water quality (Cooper, 1993; Mello *et al.*, 2018; Luo *et al.*, 2020). As water quality is altered or reduced, biological degradation quickly follows, leading to assemblages composed of limited pollution-tolerant species (Schofield, Seager & Merrlman, 1990; Kopp & Allen, 2021). In addition, timber harvesting in surrounding riparia often leads to increased sediment loading into streams due to the combined effects of vegetation loss, soil compaction, and erosion (Hood, 2000). Sedimentation in rivers can lead to many impacts on aquatic organisms. For example, increased sediments in the water column can reduce light penetration, reducing primary production for secondary consumers and increased sediments into the benthos alters substrate composition, altering habitat and refugia availability for benthic organisms (Jones *et al.*, 2012). Therefore, land use can heavily alter the physical and chemical environment leading to changes within biological assemblages.

Benthic macroinvertebrates are ubiquitous in freshwater systems and are commonly used to assess freshwater quality via bioassessments (Rosenberg & Resh, 1993). Benthic macroinvertebrates tend to show clear responses to harsh environmental conditions (Moreno *et al.*, 2009) and their assemblage structure often reflects their ecological conditions (Heino, Muotka & Paavola, 2003; Oliveira & Callisto, 2010). Macroinvertebrate fitness is influenced by many environmental variables including temperature, flow, water quality, and organic matter, all of which are indirectly impacted by anthropogenic stressors (Allan & Ibañez Castillo, 2009). Therefore, benthic macroinvertebrate distributions are dictated by both local variables, such as substrate and depth (Orth & Maughan, 1983), and regional variables, such as land use (Feld & Hering, 2007). Benthic macroinvertebrates also play an important role in food webs by linking basal food sources and primary producers to higher trophic levels (Hauer & Resh, 2007). Macroinvertebrates occupy many functional feeding groups and the proportion of such groups are influenced by the environmental conditions of their habitat (Oliveira & Callisto, 2010), including the disruption of natural longitudinal gradients due to dams (Nelson & Miller, 2023). Therefore, exploring the taxonomic and functional distribution of benthic macroinvertebrate assemblages can reveal how riverine ecosystems respond to dams and other environmental perturbations.

Numerous studies have explored the influences of dams (see review in Ellis & Jones, 2013) and land use (see reviews in Gál *et al.*, 2019; Schürings *et al.*, 2022) on freshwater macroinvertebrates. Despite many studies, understanding the influences of contemporary human impacts across streams that share biogeographic and geologic histories could provide further insights into characterizing anthropogenic impacts on stream biodiversity. For example, biogeography has been shown to be the main driver of differences between macroinvertebrate communities at larger spatial scales despite the prevalence of dams (Krajenbrink *et al.*, 2019). The Ouachita Mountains of southeastern Oklahoma provide a species-rich system in which to study the different effects of dams and land use on macroinvertebrate assemblages (Galbraith, Vaughn & Meier, 2008b). In addition to having similar biogeographic and geologic histories, each large river in southeastern Oklahoma experiences unique anthropogenic management, and previous work in the region has demonstrated different effects of dam management on biological assemblages (Allen *et al.*, 2013). Therefore, studying the impacts of different management strategies within a single biogeographic region could illuminate specific community responses.

Here, we used field surveys to characterize the ecological effects of dams on the taxonomic and functional structure of macroinvertebrate assemblages across various dam management strategies in southeastern Oklahoma. We address two major questions across the four rivers with these data: 1) what environmental factors lead to variation in macroinvertebrate assemblages in this region? and 2) what is the role of dams in structuring macroinvertebrate assemblages? We compared sites upstream and downstream on three dammed rivers with sites along a free-flowing river. We first investigated how dam management can lead to environmental differences. We then tested for relationships between biological metrics and environmental variables to identify potential environmental drivers of biological assemblages. Finally, we looked for differences between upstream and downstream sites to assess how dams may influence macroinvertebrate assemblages.

METHODS

Study area

We sampled four rivers within the Ouachita Highlands in southeastern Oklahoma: the Kiamichi, Little, Glover, and Mountain Fork Rivers (**Figure 1**; **S.I.1**). This region is largely contained within the Ouachita Mountain ecoregion, expanding from southeastern Oklahoma to central Arkansas. Largely underdeveloped, the region is primarily covered by forest and pasture although extensive logging occurs (Oeat, 2003; Atkinson, Julian & Vaughn, 2012). Known as a biodiversity hotspot within Oklahoma, this area is home to multiple endemic and endangered fish and mussel species (Mayden, 1985; Vaughn *et al.*, 1996; Galbraith, Spooner & Vaughn, 2008a; Allen *et al.*, 2013; Castro *et al.*, 2016). In addition to their high levels of biodiversity, these rivers also supply water to people across the region, making water rights a controversial topic (Vaughn *et al.*, 2015; Castro *et al.*, 2016; Burch *et al.*, 2020). The Glover and Mountain Fork Rivers are major tributaries to the Little River which, along with the Kiamichi River, are major tributaries to the Red River. Of these four major rivers, only the Glover River remains undammed (**Table 1**). The Kiamichi, Little, and Mountain Fork Rivers are hydrologically and geomorphically similar (Atkinson *et al.*, 2012), making this region and its various rivers amenable to a comparative study of the effects of dam management.

The three dams are rolled earth embankments built for various purposes such as flood control, water supply, recreation, and creation of fish and wildlife habitat. Despite these similarities, there are differences in management (**Table 1**). For example, Sardis Lake is primarily used for water supply, releasing water after high rain events but releasing no water during droughts (Vaughn *et al.*, 2015). Alternatively, Pine Creek Lake Dam releases water for a base flow to mitigate the impacts of a paper mill located downstream of the reservoir (Allen *et al.*, 2013). Finally, the Broken Bow Lake dam is hydroelectric, releasing water daily. Unlike Sardis Lake and Pine Creek Lake, the Broken Bow Lake dam has hypolimnetic releases, which also enables a cold-water trout fishery downstream that would otherwise not be possible in this warm region.

Sardis Lake is an impoundment located on Jackfork Creek, a major tributary to the Kiamichi River. However, the reservoir is located only about 62 kilometers from its confluence with the Kiamichi River, and therefore has major influences on the Kiamichi. The drainage area of Sardis Lake accounts for 24% of the runoff for the Kiamichi River and it has been found that Kiamichi flow downstream of the confluence with Jackfork Creek can be dictated by releases from Sardis Lake (Vaughn *et al.*, 2015).

We conducted field surveys at five sites below and five sites above the dams located on each river (**Figure 1**). As the Glover River is undammed, we identified five sites in the upper part of the watershed and five sites lower in the watershed to serve as an undammed comparison. We selected sites based on physical site similarity (substrate type, gradient, and flow) and site accessibility.

Field Sampling

We sampled the Little and Glover Rivers in July 2018 and the Kiamichi and Mountain Fork Rivers in July and August 2019. In July 2020 we returned to each river to collect chlorophyll *a* samples. While chlorophyll *a* was not collected at the same time as macroinvertebrates, chlorophyll growth and declines follow similar annual patterns between years (Skidmore, Maberly & Whitton, 1998)

Before sampling at each site, we set up a fine-meshed net (area: 0.0625 m^2, mesh size: 80 µm) directly upstream of the sample reach to collect seston, or fine particulate organic matter in the water column. We measured flow velocity upstream of the net once it was stabilized. The total time that the seston net was set up collecting material was recorded (mean = 55 minutes). After concluding sampling, we again measured flow velocity at the front of the net, and samples were put on ice and frozen. In the lab, we then freeze dried and weighed the samples. Samples were weighed, dried (60°C for 72+ hours), and ashed (500°C for 24 hours) to calculate ash free dry mass (AFDM) for half of the seston samples, saving the second half for future isotopic analyses (Nelson *et al.*, 2017).

At each site, we established two transects that spanned the width of the river along a 100-meter stream stretch. Transects were chosen that spanned multiple habitats and were spaced at least 50 meters apart. We measured temperature, depth, and flow velocity using a YSI probe and Hydrolab flow meter at the midpoint of both transects. Along each transect we estimated the percentage of the benthos composed of either silt, sand, gravel, cobble, boulder, or bedrock, as well as the percentage of the site that held large woody debris, leaf litter, and macrophytes. We measured the wetted and bankfull channel width with a rangefinder and estimated canopy cover using a densiometer at the midpoints of each transect. To minimize the number of variables describing the substrate, we calculated the substrate index for each site (S.I. [substrate index]= 0.08 bedrock + 0.07 boulder + 0.06 cobble + 0.05 gravel + 0.04 fine gravel + 0.03 sand and fines; Nelson & Lieberman, 2002). High values indicate a larger overall substrate (i.e., higher proportion of bedrock and boulder) while low values indicate a smaller substrate (i.e., a higher proportion of fine gravel and sand). Also, the substrate index allows for the combination of six variables into one, reducing the number of predictors (Bovee, 1982).

Along each transect we collected five cobble-sized rocks for chlorophyll *a* analyses at equidistant points. We removed benthic periphyton by scrubbing the top of each rock and rinsing each rock face vigorously. The slurry that resulted was placed in a dark bottle on ice. In the field, we used foil to outline the area of the rock face sampled, which we later used to estimate the surface area of each cobble with an aluminum foil mass-to-area conversion (Lamberti *et al.*, 1991; Cook *et al.*, 2018). Within 24 hours of collecting periphyton samples, we homogenized samples with a hand blender. Many sites had a large amount of bryophyte growth, which we included in each dark bottle and agitated thoroughly for at least a minute to detach any algae. After blending, we filtered the slurry through a 1 mm sieve to prevent any remaining clumps from clogging the pipette. While the slurry was suspended, we took six aliquots of 4-6mL each and filtered them onto 0.8 µm glass fiber filters to replicate chlorophyll *a* and ash free dry mass measurements three times each (AFDM; Biggs *et al.*, 2000; Cook *et al.*, 2018). Chlorophyll *a* as measured by a spectrophotometer reflects the amount of autotrophic organisms over a specific area (Biggs *et al.*, 2000).

To sample benthic macroinvertebrate assemblages, we collected samples with a Surber sampler (area: 0.09 m^2, mesh size: 500 µm). We took three targeted samples from pools and three targeted samples from riffles for a total of six samples per site (0.54 m^2 of total benthic area sampled). We elutriated samples in the field to remove large sediments and stored samples in Whirl-Paks with 95% ethanol for further processing.

In the lab, we aggregated samples by microhabitat (pools or riffles) and divided collected materials and invertebrates into large (>2 mm) and small (500 µm to 2 mm) size classes using nested sieves. All individuals in the large-size class were identified. When samples were particularly large, we split the small-size class samples using a plankton splitter to get a minimum of 300 organisms, which is enough to provide representative samples of the full assemblage (King & Richardson, 2002). Once sorted into large and small size classes, we identified individuals to genus when possible except for Oligochaeta, Platyhelminthes (to class), Acari, Amphipoda, Bivalvia, Hirudinea, Collembola, Decapoda, Isopoda (to order), and Chironomidae (separated by Chironomidae, Orthocladiinae, and Tanypoda). A subset of samples was sent to the National Aquatic Monitoring Center at Utah State University for QA/QC (https://namc-usu.org/; Logan, Utah). We taxonomically resolved the data to keep the majority of individuals in the study while ensuring taxa were not counted more than once (for example, within the Ephemeropteran family *Baetidae*, if the majority was identified to family while a small proportion was identified to genus, the individuals identified to genera were shifted to a family identification; Cuffney, Bilger & Haigler, 2007).

To estimate the organic matter found at each site, we separated material from the contents of >2 mm sieve fraction by organic matter type (woody debris, leaves, macrophytes, bryophytes, algae, and miscellaneous). We identified each type of organic matter as allochthonous or autochthonous depending on its origin. When unknown (i.e., miscellaneous), the organic material was noted as such. We broadly defined organic matter found in the 500 µm to 2 mm sieve fraction as fine particulate organic matter, categorized as miscellaneous. Once divided, we weighed, dried (60°C for 72+ hours), and ashed (500°C for 24 hours) each organic matter type to calculate AFDM (Nelson *et al.*, 2017).

Land use data

We calculated land use composition for the watershed area above each site using the National Land Cover Dataset (NLCD; USGS, 2019). We combined categories to limit the number of land use variables (forest: deciduous forest, evergreen forest, mixed forest; developed: developed open space, developed low intensity, developed medium intensity, developed high intensity; wetlands: woody wetlands, emergent herbaceous wetlands; agriculture: hay/pasture, cultivated crops; open: open water, barren land; miscellaneous: shrub/scrub). We then calculated the percentage of land use types within the area of the watershed above each site by taking the land cover for each land use and dividing it by the total watershed area. Each site downstream contained land area of the sites upstream to fully capture the influence of land use at each sampled point.

Analysis

We calculated the distance from each site to the corresponding dam using the "riverdist" package (Tyers, 2022) and recorded sites upstream of each dam as a negative distance to differentiate upstream and downstream sites. Sites were also identified categorically as "upstream" or "downstream". The location of the dam site for the Kiamichi River was placed at the confluence of Jackfork Creek and the Kiamichi River to recognize the impact tributaries have on the stream continuum (Ward & Stanford, 1983). As there was only one free flowing river, labeling the sites along the Glover as "free" as in other studies would have a confounding effect on river identification and site type. To avoid confounding variables during further analyses, we also labeled sites along the Glover River as either "upstream" or "downstream" based on their location along the river but did not calculate any river distances along the Glover River (i.e., all distances = NA). As direct comparisons of pre- and post-dam construction are not available, comparing downstream sites with those upstream from the dam or in neighboring un-impounded locations is common (Growns & Growns, 2001; Krajenbrink et al., 2019). Labeling sites along the Glover River to match the other rivers also allows for a more direct comparison between all four rivers. However, we also ran analyses with sites along the Glover River labeled as "free" to examine how analyses would change (**S.I.7**).

To maintain detailed differences between the data collected, we split the environmental data into three categories: 1. *Abiotic habitat* (substrate index, percent large woody debris, depth, flow, wetted channel width, canopy cover, and riffle and pool reach proportions), 2. *Organic matter* (AFDM of seston per liter, AFDM of organic material collected in surber samples (g/m^2), percentage of allochthonous and autochthonous surber organic matter, AFDM of benthic epilithic biofilm (g/m^2), and chlorophyll *a* measured by spectrophotometer (g/m^2)), and 3. *Land use* (proportion of the watershed covered by forest, development, wetlands, agriculture, open space, and miscellaneous shrubland).

To ensure we excluded significantly correlated environmental predictors, we used Principal Components Analysis (PCA) to identify collinearity and selected a subset of uncorrelated variables for analyses. For the abiotic habitat and land use categories, we ran PCAs with scaled and centered predictors using the "stats" package (R Core Team, 2020). We then rotated axes that described at least 90% of the variation and selected the predictors with the greatest loadings. To explore how different environmental variables drive macroinvertebrate differences, we selected three variables from each category. We selected variables with the highest loadings from the first three PCA axes (abiotic habitat PC1: 0.242, PC2: 0.138, PC3: 0.110, cumulative: 0.490; land use PC1: 0.544, PC2: 0.238; PC3: 0.121; cumulative: 0.903). From the abiotic habitat, we selected flow (PC1: 0.591), temperature (PC2: -0.928), and canopy cover (PC3: 0.867). From land use data, we selected the proportion of the watershed covered by forest (PC1: -0.673), wetlands (PC2: 0.594), and open (PC3: -0.985). Full loadings can be found in **S.I.2**. To capture the different sources of organic matter available at each site, we selected AFDM of seston (g/L), total organic matter collected during surber sampling (g/m^2), and chlorophyll *a* measured by the spectrophotometer (g/m^2). In addition, to capture how dams may alter these variables, we included the distance of each site from the dam. We used the “broom” package to test for correlations (Robinson *et al.*, 2023). After accounting for correlations, we chose to use the proportion of land cover that was developed, forested, and used for agriculture (**S.I.2**). The final 10 environmental variables used for analyses were temperature, flow, canopy cover, seston AFDM, surber AFDM, chlorophyll *a*, developed land cover, forested land cover, agricultural land cover, and distance from the dam (**S.I.3**). We included a limited number of environmental variables to minimize the number of variables included in general linear models (see below). We first looked at environmental variation among rivers and site types with General Linear Models (GLMs) to see how abiotic habitats varied among the interaction between river and site type as differences in abiotic variables may lead to differences in macroinvertebrate assemblages. We used different distributions depending on the variable to meet the assumptions of GLMs: temperature, Poisson distribution with identify link; flow, Poisson distribution with log link; canopy cover, Poisson distribution with log link; seston AFDM, Poisson distribution with identify link; surber AFDM, Poisson distribution with identify link; chlorophyll *a*, Poisson distribution with log link; proportion of forested, developed, and agricultural land use, binomial distribution with identity link; and distance from dam, gaussian distribution with identity link.

Next, to understand the impacts of dams on the macroinvertebrate assemblages of each river, we calculated 10 biological metrics for each site (**Table 2**). We calculated taxonomic richness as the number of unique taxa in each sample and calculated the log-transformed total absolute abundance across all taxa of each sample. In addition, we calculated the percent of the sample that was made up of Chironomidae by dividing the number of chironomid individuals by the total abundance of the sample. We followed the same method to calculate the percent of the sample composed of the Orders Ephemeroptera, Plecoptera, and Trichoptera (EPT). While chironomids have some sensitivity to anthropogenic stressors, they are often used as indicators of poor water quality (Moller Pillot, 2009; Serra *et al.*, 2017). Conversely, EPT taxa are recognized as indicators of high quality streams (Serra *et al.*, 2017). In addition to being important bioassessment indices, the relative proportions of these two taxonomic groups are commonly used to assess the impacts of dams on macroinvertebrate assemblages (Holt *et al.*, 2015; Mihalicz *et al.*, 2019; Mellado-Díaz *et al.*, 2019). Along with these metrics, we assigned each genus to its primary functional feeding group (collector-gatherer: CG; collector-filterer: CF; herbivore: HB; predator: PR; shredder: SH; Merritt, Cummings & Berg, 2008; Twardochleb *et al.*, 2021). When a genus had multiple primary feeding groups listed, the one with the highest affinity was selected. Unlike other functional feeding group assignments, Twardochleb et al. (2021) does not include a "scrapers" category, rather scrapers are listed as herbivores. Non-insect taxa (oligochaetes, mites, etc.) and insects to the family level were not assigned a functional feeding group (26 out of 104 taxa; 25%), with the exception of the Chironomidae and Orthocladiinae, which were assigned as collector-gatherers and the Tanypodinae, which were assigned as predators (Merritt *et al.*, 2008). After feeding groups were assigned, we calculated the proportion of feeding groups for each sample. Proportions of functional feeding groups are expected to vary longitudinally along rivers (Vannote *et al.*, 1980) and dams alter these natural gradients, changing the patterns of proportions of functional feeding groups downstream (Nelson & Miller, 2023).

To understand the role of dams in driving assemblage variation across each river and site type, we ran general linear models (GLMs) with river and site type as interactive effects. Again, different distributions were used depending on the variable to meet the assumptions of GLMs: taxonomic richness models used a negative binomial distribution, abundance models used Poisson distributions with log transformed abundances, and all other models used binomial family distributions with identity links as proportional data. Due to the low number of sites with shredders, we did not run models on the proportion of shredders (12 sites). GLMs in this study were run using the "stats" package and negative binomial GLMs were run using the "MASS" package (R Core Team, 2020; Ripley *et al.*, 2023). When models demonstrated significant results, we used the "emmeans" package to run post-hoc analyses (Lenth *et al.*, 2023).

To investigate relationships among all biological metrics and environmental variables, we again used GLMs. We ran one model with all environmental variables to test which variables drove biological responses. Because each river was only sampled once, we chose to not include river and site type in these full models to avoid confounding variables. Taxonomic richness models were negative binomial, abundance models used Poisson family distributions with log transformed abundances, and the proportion data all had binomial models. Proportion of chironomids, collector-filterers, and predators used a logit link while proportion of EPT, collector-gatherers, and herbivores used an identity link. To ensure the environmental variables would meet the assumptions of the models, we log transformed canopy cover, flow, and chlorophyll *a* measurements.

To investigate how ecological similarities varied across rivers and sites, we compared the Bray-Curtis distances among upstream, downstream, and upstream and downstream sites within each river with the "vegan" package (Oksanen *et al.*, 2011). We tested for differences among the dissimilarities of river and site type with an identity link binomial GLM using an interactive effect between river and site type.

We also ordinated the assemblages based on both the species matrix and functional feeding groups using non-metric multidimensional scaling procedures (nMDS) with log-transformed Bray-Curtis dissimilarity matrices. Due to the low stress of the ordination (species matrix stress = 0.126; functional feeding group stress = 0.084), we retained all species and feeding groups in our analyses (McCune, Grace & Urban, 2002). Using the 10 sub-categorized environmental predictors, we plotted significant environmental variables ($p < 0.05$) onto the ordinations with the "vegan" package (Oksanen *et al.*, 2011). Next, to understand the differences among the four rivers and their habitats, we used permutation analysis of multivariate dispersion (PERMIDSP; Anderson, Ellingsen & McArdle, 2006). The PERMDISP function tests for homogeneity of variances among groups (in this instance, river or site type) by comparing the distances from each sample to the group centroid (median). We then tested for differences between the centroids of the different groups and their interaction with a permutational analysis of variance (PERMANOVA; Anderson, 2001) with the "vegan" package (Oksanen *et al.*, 2011). These analyses enabled us to explore environmental drivers on assemblage variation and the influences of dams and rivers.

RESULTS

Taxonomic diversity summary

In total, we identified 97,208 individuals of 104 taxa across the four rivers. We found chironomids at every site sampled (100% of sites), while we found *Hydropsyche* (Trichoptera: Hydropsychidae), Oligochaeta, and Veneroida (Mollusca), *Stenelmis* (Coleoptera: Elmidae), *Caenis* (Ephemeroptera: Caenidae), *Baetidae* (Ephemeroptera: Baetidae), *Microcylloepus* (Coleoptera: Elmidae), Tanypodinae (Diptera: Chironomidae), *Dubiraphia* (Coleoptera: Elmidae), and Trombidiformes (Acari) at least at 80% of all sites (32 out of 40 sites). In contrast, 23 taxa were only found at single sites and eight taxa were found at two sites.

The Little River had the greatest total abundance (mean = 12546.10 ∓ 15308.56) while the Mountain Fork had the lowest average abundance (mean = 4590.60 ∓ 4477.08; **Table 4; Figure 2**). Additionally, the Little River had the highest percentage of chironomids (mean = 30.84 ∓ 16.83%), while the Mountain Fork River had the largest percentage of EPT mean = (55.17 ∓ 15.99%). Together, collector-gatherers (< 44%), and collector-filterers (< 11%) made up the greatest proportion of functional feeding groups across all rivers (**Table 4**). Shredders were absent only from the Little River and comprised the lowest proportion across functional feeding groups (**Figure 3**).

Differences in environment

We found significant variation in temperature, canopy cover, AFDM in surber samples, and river distances across the study area. Temperature differences appeared to be driven by variation between upstream and downstream sites on the Mountain Fork River (z.ratio = -2.38, $p = 0.017$). Differences in canopy cover and the amount of AFDM from surber samples occurred across multiple river comparisons and site types (**S.I.3**). Finally, upstream distances from dams were significantly different between the Mountain Fork River and the other two dammed rivers (Mt. Fork / Kiamichi: t.ratio = 6.631, $p < 0.01$; Mt. Fork / Little: t-ratio = 5.15, $p < 0.01$). In addition, significant differences in site distance from the dam were found across all rivers and their upstream and downstream sections (Kiamichi: t.ratio = 7.269, $p < 0.01$; Little: t.ratio = 7.38, $p < 0.01$; Mountain Fork River: t.ratio = 13.67, $p < 0.01$).

Biological Metrics and Environmental Drivers

Taxonomic richness was significantly driven by the amount of AFDM found in the surber samples ($z = 3.48$, $p < 0.01$). No other GLM of the biological metrics contributed a significant variable to the global models (**S.I.4**).

Biological Differences among Rivers and Site Types

We did not detect significant differences in any biological metrics among the four rivers or between site types (**Figure 2**, **Figure 3**, **S.I.5**).

The GLM using Bray-Curtis distances among the site categories showed no statistical differences among rivers or among the different site comparisons (**Figure 4**, **S.I.6**).

The nMDS ordination of the species matrix yielded a stable two-dimensional solution (stress = 0.126; **Figure 5**). We found no differences among rivers with the PERMDISP test ($p > 0.49$ for all comparisons among river and site type). The perMANOVA results, however, demonstrated significant assemblage differences among rivers ($F = 3.74$, $p < 0.01$), site types ($F = 2.040$, $p = 0.02$), and the interaction between river and site type ($F = 1.45$, $p = 0.05$). Of the 10 environmental metrics selected for these analyses, temperature ($R^2 = 0.28$, $p = 0.01$), flow ($R^2 = 0.39$, $p < 0.01$), proportion developed land cover ($R^2 = 0.25$, $p = 0.02$), proportion forested land cover ($R^2 = 0.26$, $p = 0.03$), and amount of AFDM in surber samples ($R^2 = 0.39$, $p < 0.01$) were significantly correlated to macroinvertebrate assemblage structure (**Table 4**).

The nMDS ordination of the functional feeding groups matrix also yielded a stable two-dimensional solution (stress = 0.084; **Figure 6**). We found no differences among the variances within each river with the PERMDISP test ($p > 0.57$ for all comparisons among river and site type). Like the species matrix, the perMANOVA results exhibited significant differences among rivers ($F = 6.10$, $p < 0.01$) and between site types ($F = 2.81$, $p = 0.04$). However, there was not a significant interaction between river and site type ($F = 1.37$, $p = 0.22$). In addition, the environmental variables with significant correlations to the functional feeding group matrix were all similar to the species matrix, although surber AFDM was not significant and proportion of agriculture land use was significant (Proportion developed area: $R^2 = 0.44$, $p < 0.01$; Proportion agriculture land: $R^2 = 0.41$, $p < 0.01$; Proportion forested area: $R^2 = 0.34$, $p < 0.01$; Temperature: $R^2 = 0.50$, $p < 0.01$; and Flow: $R^2 = 0.34$, $p < 0.01$ **Table 5**).

While there were some small differences between the results when sites along the Glover River were labeled as "free", this method largely did not change the qualitative results (**S.I.7**).

DISCUSSION

We investigated how varying dam management alters potential environmental drivers of macroinvertebrate assemblages in four rivers in southeastern Oklahoma. We found that local environmental variables varied across our sites and influenced diversity metrics more than watershed-scale variables, although both local and watershed variables were significant in ordinations. While all results demonstrated significant differences in assemblage composition across rivers, results comparing assemblage composition between site types (above/below dams) varied. This result suggests that variation in macroinvertebrate assemblages is largely due to differences among the rivers rather than due to impoundments on rivers. Broadly, ordination analyses found significant differences among rivers and site types, while analyses using univariate metrics did not. Therefore, careful considerations should be taken when analyzing assemblage data. This study indicated that interannual variability and differences in local and watershed variables may overpower the impact of dams on macroinvertebrate assemblages in this region.

Drivers of benthic macroinvertebrate assemblage differences

We found that only local-scale benthic organic matter (collected from surber sampling) was correlated to any biological metric. Similarly, local environmental variables accounted for most of the variation in the species matrix ordination (temperature, flow, surber organic matter), while the functional feeding group ordination demonstrated that each local-scale variable accounted for at least 25% of the variation (temperature, flow) among assemblage compositions. These results suggest that local-scale environmental variables dictate assemblage composition more than watershed-scale variables. Flow, a local-scale variable for example, has long been recognized as a major constraint on river biodiversity (Poff *et al.*, 1997). As organisms have adapted to the natural flow regime within a specific system, alterations to flow can have major consequences for assemblage composition (Lytle & Poff, 2004). Dams are well known to alter flow and temperature regimes (Lytle & Poff, 2004; Chandesris *et al.*, 2019). While flow regimes become permanently altered by dams, temperature gradients may take hundreds of kilometers to recover

(Ellis & Jones, 2013). Identifying the longitudinal recovery was beyond the scope of our study, but the effects of dams on temperature regimes are clearly seen. These differences were largely driven by the Mountain Fork, the only river in our study to receive hypolimnetic water releases from its reservoir. Finally, we measured the total organic matter collected during macroinvertebrate sampling, which varied widely across rivers and site type. This coarse particulate organic matter serves as a major energy source for stream ecosystems (Lamberti & Gregory, 2007). Restoration studies have shown that microhabitats with greater amounts of organic matter tend to house more macroinvertebrates, likely due to the additional food, shelter, and attachment sites organic matter provides (Downes *et al.*, 1998; Jähnig, Lorenz & Hering, 2008; Verdonschot *et al.*, 2016). Our results reflect those findings, as taxonomic richness was significantly related to surber AFDM. Previous research in this region found an equal amount of variation between assemblages were attributed to local and watershed variables, however, Galbraith et al. (2008) explored only one order of insects, whereas we examined the full assemblage.

While local-scale variables were correlated to the biological metrics we calculated here and to the ordination of species, land cover also influenced assemblage composition. Surrounding land cover and land use has many implications for water quality including nutrient concentrations and sedimentation (Cooper, 1993; Hood, 2000). We found that the functional feeding group ordination demonstrated significant correlation to agricultural land use. Agricultural land use has been linked to a decline in sensitive taxa and an increase in tolerant taxa (Schürings *et al.*, 2022). In addition, the proportion of developed land was correlated with the species ordination, accounting for 25% of the variation. As with agricultural land use, developed land has been identified as a source of pollution in rivers and can alter flow regimes due to increased impervious surfaces leading to greater runoff (Mello *et al.*, 2018; Luo *et al.*, 2020). Finally, the proportion of forest cover was significantly correlated with the results of both ordinations and had the largest R^2 value in the functional feeding group ordination. Previous studies have demonstrated the importance of forested land cover surrounding streams, highlighting the importance of natural land cover for water quality (Black, Munn & Plotnikoff, 2004). While the region of Oklahoma where our study takes place is largely forested, much of this land is reserved for logging companies. Logging can have multiple adverse effects on water quality (Hood, 2000). Without extensive surveying, we cannot understand what portion of each watershed had been recently logged at the time of sampling, limiting our understanding of how closely the forested designation for land cover reflected the conditions under which we sampled. Therefore, land cover, in addition to dams, has complex impacts on rivers and their surrounding watersheds/landscapes. Broadly, we found both local and watershed environmental variables should be considered when evaluating the environmental drivers of macroinvertebrate assemblages.

Impact of dams on benthic macroinvertebrate assemblages

While we found impacts of both local and watershed environments on macroinvertebrate assemblages, we broadly found that macroinvertebrate assemblages differ across rivers, but not always across sites upstream and downstream of dams. We found no significant differences in biological metrics or dissimilarity comparisons across river or site type. Both ordination analyses, however, demonstrated significant differences in the assemblages among the four rivers. Previous studies in this region have highlighted the importance of biogeography, which has suggested that the high elevation regions among the four rivers could limit aerial dispersal across rivers (Galbraith *et al.*, 2008b). Similarly, dam comparisons over larger spatial scales have demonstrated how the effects of river impoundment may be confounded by larger biogeographical signals (Krajenbrink *et al.*, 2019). In addition, site and sampling timing can explain more variance than smaller-scale variables, including those altered by dams (Laini *et al.*, 2019). While we found significant differences across rivers, these results may be skewed due to the timing of our sampling events. The Little and Glover Rivers were sampled in the summer of 2018, which was relatively dry when compared to conditions during the summer of 2019, when the Kiamichi and Mountain Fork Rivers were sampled. The spring of 2019 was much wetter than the spring of 2018, greatly altering flow between the two sampling years (sums from Battiest, Oklahoma weather station: April 2018: 3.97, April 2019: 6.63, May 2018: 2.88, May 2019: 11.19, June 2018: 4.98, June 2019: 10.10; NOAA, 2023). The importance of flow on ecological communities has been a focus in river ecology for many decades (Poff *et al.*, 1997; Lytle & Poff, 2004), and interannual variability often leads to variability within data analyses (Krajenbrink *et al.*, 2019). Thus, while our results suggest an important role for biogeography, they must be taken cautiously, as disentangling the effects of river and year was not possible. Future studies should incorporate temporal sampling to better incorporate climatic variations over time.

The importance of river and not of site type in this study, given the caveats of differences between sampling years, suggest that dam presence in the watershed appeared to be less important than interannual climate variability, which influences other local-scale factors, such as flow and temperature. The effects of specific dam management strategies were likely masked due to high interannual variability of flow. In addition, many taxa in our analyses have aerial adult stages, which allow for greater dispersal. Despite the biogeographic barriers that may be present among the rivers (Galbraith *et al.*, 2008b), aerial dispersal may enable these taxa to disperse above and below the dam, limiting the effects of management. Some of the most common taxa (present at 80% of the sites) in our study were ephemeropterans and trichopterans, including *Hydropsyche* (Trichoptera) and *Baetis* (Ephemeroptera), which have been shown to be abundant at sites downstream of dams in other regions (Armitage, 1978: Rocky Mountains; Rader & Ward, 1988: Colorado River). While many studies have found fewer Ephemeroptera, Plecoptera, and Trichoptera taxa below dams (Lessard & Hayes, 2003; Phillips *et al.*, 2015; Krajenbrink *et al.*, 2019), others have found greater abundance than above the dam (Armitage, 2006; Maynard & Lane, 2012; Gillespie, Brown & Kay, 2015). We also found different results among rivers; EPT taxa declined in abundance immediately below dams on the Kiamichi and Little Rivers but were more abundant below the dam on the Mountain Fork. The increase of EPT taxa below the dam on the Mountain Fork contradicts studies on other hydroelectric power dams, which found a complete absence of some or all EPT taxa (Boon, 1988; Jackson, Gibbins & Soulsby, 2007; Holt *et al.*, 2015). The wide variety of responses these sensitive taxa have to dams further highlights the need for site-specific studies due to the complex impacts of dams on river systems (Power *et al.*, 1996).

Despite the lack of influence of dams on the biological metrics we calculated for this study, we did see some influence of site type on assemblage composition in the ordination analyses, suggesting more subtle effects of dam management (Marchetti *et al.*, 2011). While we expected to see larger differences due to dam management, other studies have found that the impacts of flow alteration can be masked by other disturbances, such as water abstraction as in Miller et al. (2007) or interannual flow variation, as exemplified by our study. In addition, discrepancies between the general linear models and ordinations could be due to differences in the overall analyses (Marchetti *et al.*, 2011). The diversity metrics we used are fairly simple, and their use in the GLMs may fail to capture subtle differences among assemblages as well as ordination methods, which are likely more sensitive to assemblage dissimilarities (Marchetti *et al.*, 2011). This may also explain why the ordination with functional feeding groups did not reveal significant differences between the interaction of river and site type, as grouping species removes the fine-scale detail of assemblage differences. Including other traits, such as flow preference and dispersal ability, may reveal nuanced differences among assemblages and lead to more distinct assemblages, as has been suggested in previous literature (Demars *et al.*, 2012; White *et al.*, 2017).

In addition, results from the full assemblage ordination exhibited differences between site type, further suggesting that dams do affect taxa found within different river sections. However, the overall lack of differences among rivers and site types in this study suggests that the shared biogeographic and geologic histories of these rivers have led to a common species pool in this region. Generally, our results highlight the importance of careful consideration of statistical analyses, using those that incorporate full assemblage or community data to provide a more complete ecosystem perspective (Wang *et al.*, 2017).

CONCLUSIONS

As the human population continues to grow, so does the demand for fresh water, leading to the construction of dams on large and small rivers worldwide (Gleick & Cooley, 2021). Many studies have explored the complex and variable effects of dams on freshwater taxa, with mixed levels of responses (Ellis & Jones, 2013). This taxonomic variability could be attributed to characteristics of individual ecosystems or the variability of the flow regime and its concomitant impacts (Maynard & Lane, 2012). In addition, river communities vary across spatial and temporal scales (Galbraith *et al.*, 2008b). Here, we found that variation among individual rivers, rather than the presence of dams, played a larger role in shaping macroinvertebrate assemblages. This result suggests that the aerial dispersal ability of adult insects may overcome the drift dispersal barrier put in place by dams, but further in-depth analyses of dispersal ability is needed. However, this result could also be due to the limited sampling for this study, as we sampled each site once per year despite interannual variability in precipitation. We also found that environmental variables influenced biological assemblages at both local and watershed-wide scales. Thus, as for any ecological study, the importance of the environmental context and variability cannot be overstated. Understanding the effects of various stressors and drivers on macroinvertebrate assemblages is essential to better understand how to properly manage dam systems to properly conserve and manage riverine biodiversity (Laini *et al.*, 2019).

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TABLES

Table 1. Comparisons among the four rivers included in the present study, including information about the respective reservoirs located on each river. Full river lengths and drainage areas are displayed along with the length of the river included in the study (distance between most downstream and most upstream sites) and the drainage area from the most downstream study sites in parentheses. The Glover River is not dammed, thus contains NAs (non-applicable) for information regarding reservoir and dam information.

River	Full River Length (study length) (km)	Full Drainage Area (study drainage) (km^2)	Reservoir	Dam Activated Date	Reservoir Surface Area (km^2)	General Release Water Temp	General Release Timing
Kiamichi	285 (58.49)	4700 (2006.48)	Sardis	1982	58	warm	Variable, no releases during dry periods, but large releases during wet periods
Little	349 (51.36)	10890 (1902.16)	Pine Creek	1969	15.2	warm	Constant
Glover	54 (43.93)	876 (874.06)	NA	NA	NA	NA	NA
Mountain Fork	159 (92.73)	2181 (2143.55)	Broken Bow	1968	57	cold	Constant

Table 2. Biologic metrics used in analyses and how they were calculated.

Biologic Metric	Calculation
Taxonomic Richness	number of unique taxa in sample
Total Abundance	total absolute abundance in sample, log transformed
% Chironomidae	proportion of assemblage identified as Chironomids
% EPT	proportion of assemblage identified as Ephemeroptera, Plecoptera, and Trichoptera
% CF	proportion of collector-filterers in sample
% CG	proportion of collector-gatherers in sample
% HB	proportion of herbivores in sample
% PR	proportion of predators in sample
% SH	proportion of shredders in sample

Table 3. Summary statistics of macroinvertebrate assemblages for each river. EPT = Ephemeroptera, Plecoptera, and Trichoptera.

	Kiamichi			Little			Glover			Mountain Fork		
	Minimum	Mean (± SD)	Maximum	Minimum	Mean (± SD)	Maximum	Minimum	Mean (± SD)	Maximum	Minimum	Mean (± SD)	Maximum
Taxonomic Richness	14	31.00 (±7.89)	38	16	33.00 (±8.87)	45	25	36.30 (±6.27)	44	4	29.50 (±13.09)	42
Total Abundance	177.8	4934.80 (±3491.57)	11063	311.1	12546.10 (±15308.56)	41012.2	1152	6900.00 (±3897.18)	12622	22.22	4133.79 (±4461.40)	14248.54
% Chironomidae	7.69	22.27 (±11.43)	40.49	2.43	30.84 (±16.83)	52.91	4.28	22.71 (±13.32)	50	1.69	11.98 (±6.13)	22.09
% EPT	32.88	51.11 (±15.19)	78.05	19.7	35.93 (±13.04)	63.54	16.43	42.62 (±20.58)	74.45	16.67	54.92 (±20.20)	83.56
% Collector-Filterer	9.26	34.30 (±17.67)	67.35	1.92	11.89 (±12.00)	41.61	0.56	14.15 (±17.00)	55.14	0	29.90 (±15.85)	53.89
% Collector-Gatherer	12.24	44.20 (±17.00)	66.89	29.45	53.14 (±13.50)	73.51	7.29	50.41 (±21.74)	74.21	1.69	30.48 (±19.64)	62.5
% Herbivore	3.24	9.44 (±6.27)	20.2	1.33	10.34 (±9.40)	31.81	3.29	10.03 (±4.47)	17.4	0	6.21 (4.95)	17.42
% Predator	1.56	6.84 (±4.00)	14.29	3.01	10.47 (±5.85)	21.47	2.39	5.20 (±1.97)	7.47	0	3.85 (±4.28)	14.61
% Shredder	0	0.11 (±0.03)	1.03	0	0.00 (±0.00)	0	0	0.76 (±1.55)	4.29	0	0.96 (±1.55)	4.49

Table 4. Correlations among environmental variables and the species nMDS axes across all four rivers. Metrics with $p < 0.05$ are bolded.

	NMDS1	NMDS2	p-value	R^2
Temperature (°C)	**-0.354**	**0.390**	**0.011**	**0.277**
Flow (m/s)	**0.296**	**-0.549**	**0.001**	**0.389**
Canopy Cover (%)	-0.049	-0.125	0.773	0.018
Seston AFDM (g/L)	-0.202	-0.207	0.298	0.084
Surber AFDM (g/m^2)	**-0.618**	**0.053**	**0.003**	**0.385**
Chl *a* (g/m^2)	0.073	-0.008	0.922	0.005
Developed (%)	**-0.111**	**-0.493**	**0.029**	**0.255**
Forest (%)	**0.263**	**0.097**	**0.367**	**0.079**
Agriculture (%)	0.009	-0.500	0.020	0.250
Distance from dam (km)	0.159	0.179	0.470	0.058

Table 5. Correlations among environmental variables and the functional feeding group nMDS axes across all four rivers. Metrics with $p < 0.05$ are bolded.

	NMDS1	NMDS2	p-value	R^2
Temperature (°C)	**-0.423**	**0.567**	**0.001**	**0.501**
Flow (m/s)	**0.584**	**0.039**	**0.006**	**0.343**
Canopy Cover (%)	0.112	-0.125	0.746	0.028
Seston AFDM (g/L)	-0.262	-0.113	0.340	0.082
Surber AFDM ($g/m^{2)}$	-0.162	0.310	0.181	0.122
Chl *a* (g/m^2)	-0.063	-0.276	0.360	0.080
Developed (%)	**0.101**	**-0.578**	**0.004**	**0.345**
Forest (%)	**0.213**	**0.604**	**0.001**	**0.410**
Agriculture (%)	**0.418**	**-0.517**	**0.001**	**0.442**
Distance from dam (km)	0.166	-0.080	0.631	0.034

FIGURE CAPTIONS

Figure 1. Map of field sites in southeastern Oklahoma including a scale bar. Watersheds are outlined in purple. River and reservoir names are included in blue next to the associated water body. Site locations are noted as black circles.

Figure 2. Boxplots comparing taxonomic richness (A), log abundance (B), percent taxa from Chironomidae (C), and percent EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera; D) between sites downstream (purple) and upstream (pink) of dams along each river. No metrics were significantly different among rivers or site type (**S.I.5**).

Figure 3. Barplot depicting the proportion of each functional feeding group for compiled upstream and downstream sites per river. We found no differences among rivers or site type (**S.I.4**).

Figure 4. Bray-Curtis distances among the different sections of each river. Down-Down comparisons are between downstream sites only (purple), up-down comparisons are between downstream and upstream sites (dark pink), and up-up comparisons are between upstream sites only (light pink). We found no significant differences among the distance matrices.

Figure 5. Two-dimensional nMDS ordination of macroinvertebrate assemblages across each river (stress = 0.126). Significant environmental variables ($p < 0.05$) are also plotted with the length of the corresponding vector related to the strength of the relationship (R^2, **Table 4**).

Figure 6. Two-dimensional nMDS ordination of macroinvertebrate assemblages across each river (stress = 0.084). Significant environmental variables ($p < 0.05$) are also plotted with the length of the corresponding vector related to the strength of the relationship (R^2, **Table 5**).

FIGURES

Figure 1.

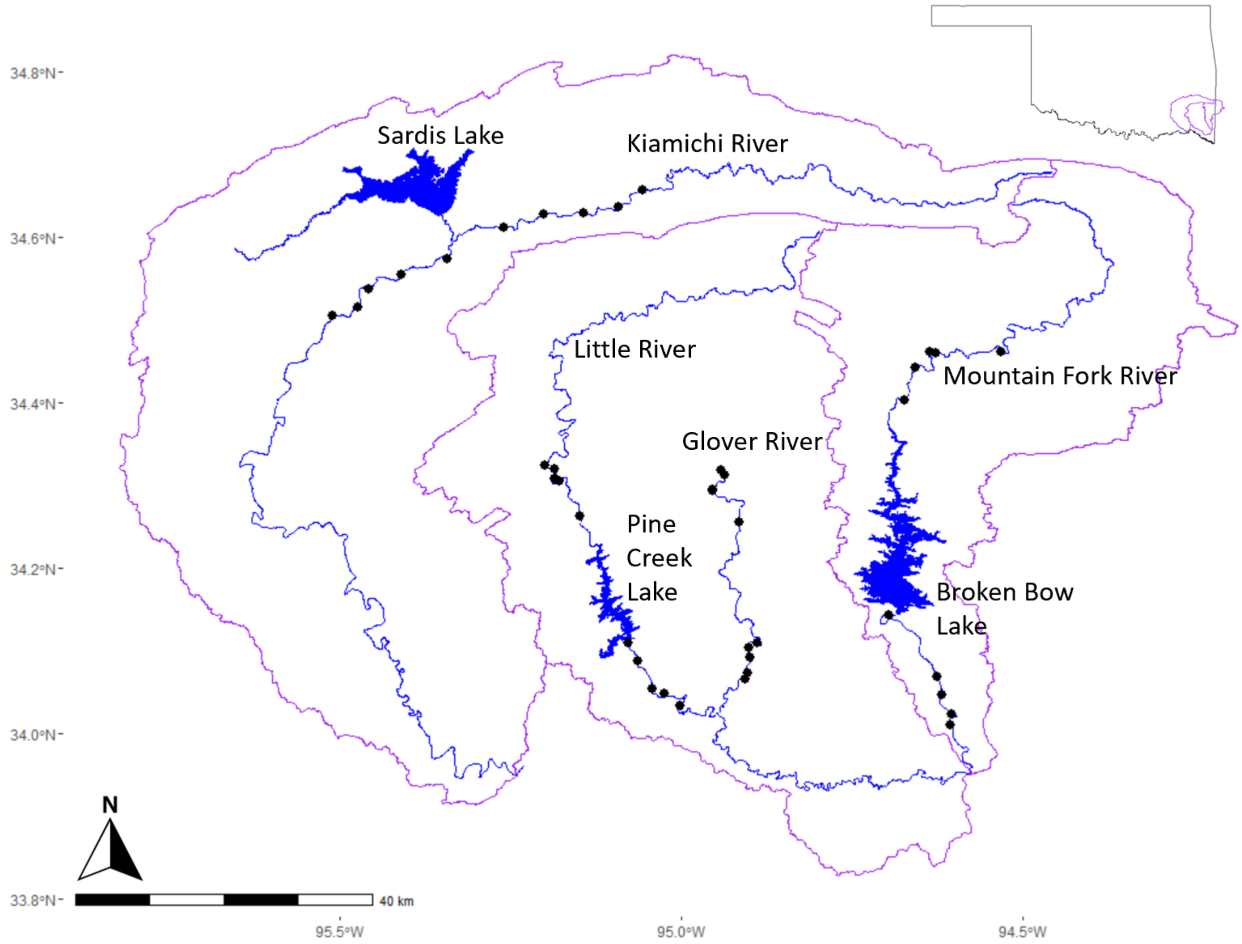
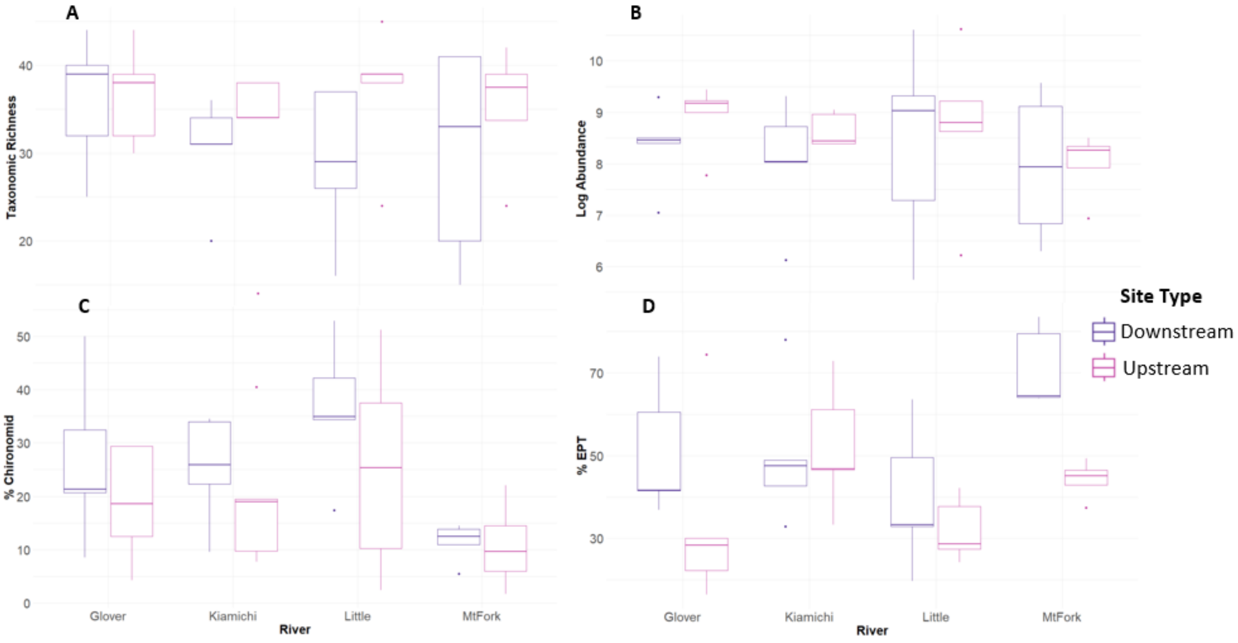


Figure 2.



A
B
C
D
Taxonomic Richness
Log Abundance
% Chironomid
% EPT
40
30
20
10
9
8
7
6
50
40
30
20
10
0
70
50
30
Glover
Kiamichi
Little
MtFork
River
Site Type
Downstream
Upstream

Figure 3.

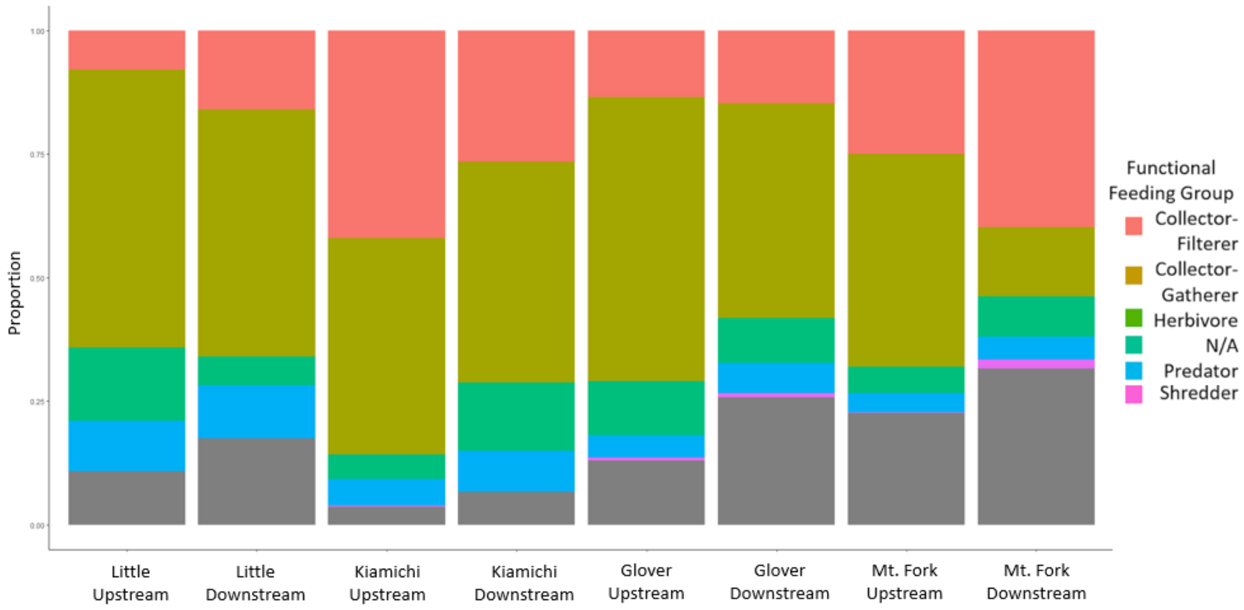

Proportion
1.00
0.75
0.50
0.25
0.00
Little Upstream
Little Downstream
Kiamichi Upstream
Kiamichi Downstream
Glover Upstream
Glover Downstream
Mt. Fork Upstream
Mt. Fork Downstream
Functional Feeding Group
Collector-Filterer
Collector-Gatherer
Herbivore
N/A
Predator
Shredder

Figure 4.

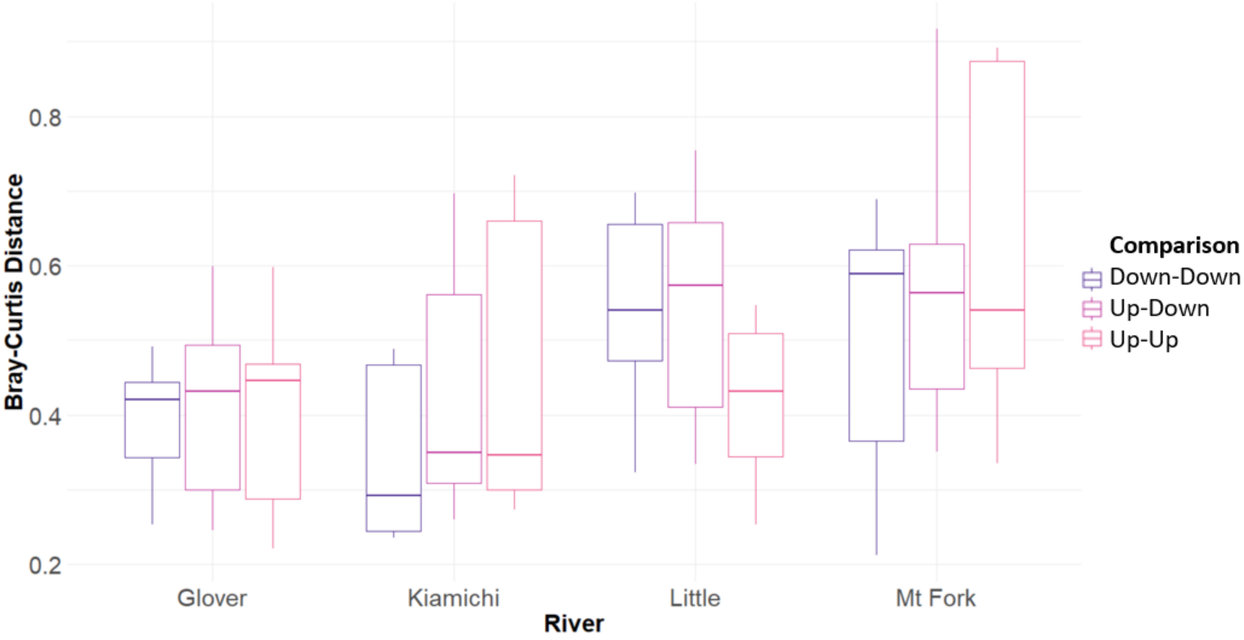
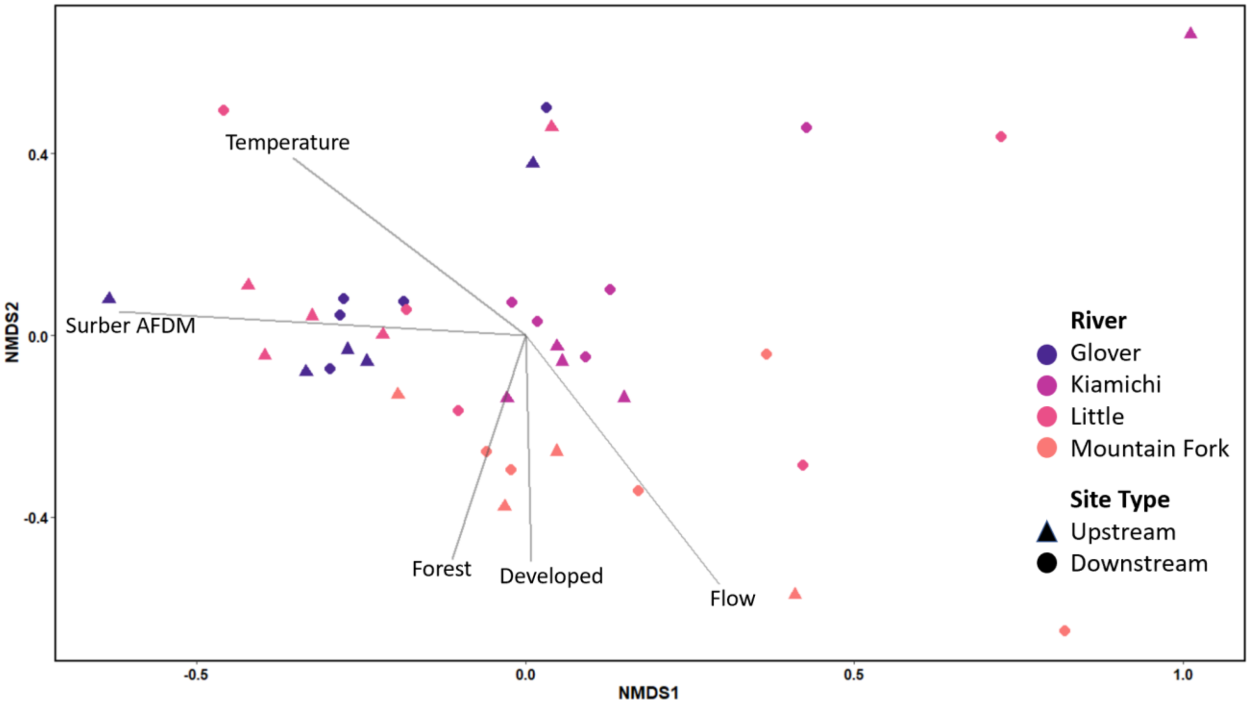
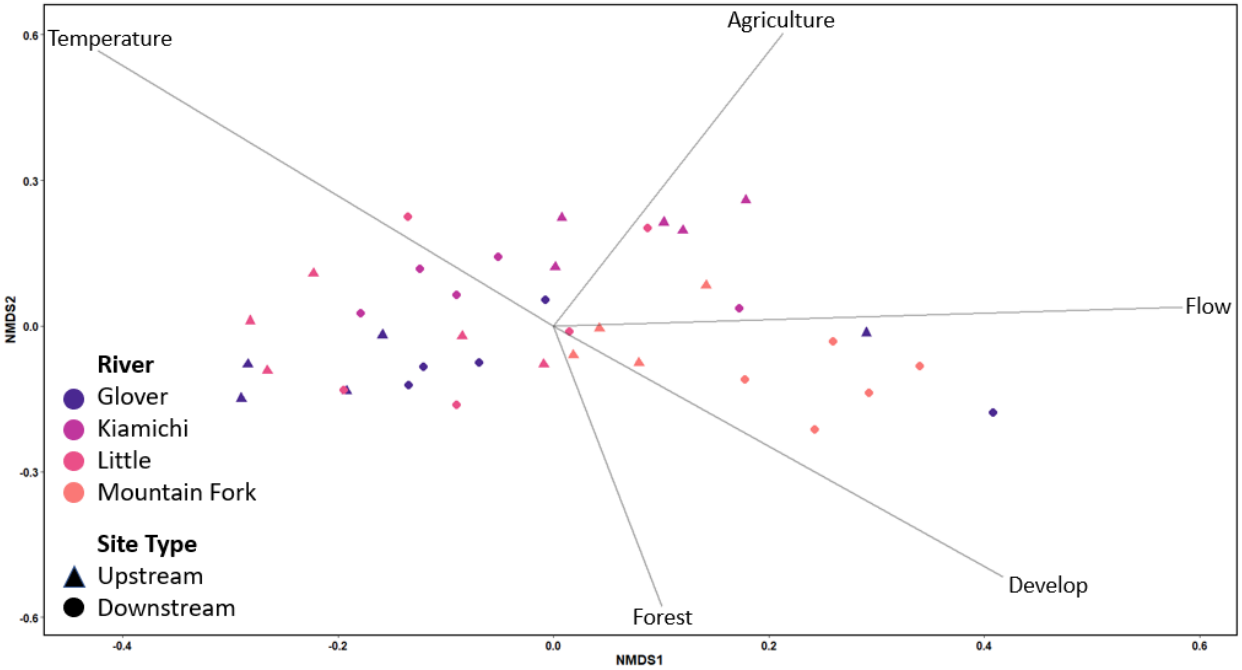

Bray-Curtis Distance
0.2
0.4
0.6
0.8
Glover
Kiamichi
Little
Mt Fork
River
Comparison
Down-Down
Up-Down
Up-Up

Figure 5.



Temperature
Surber AFDM
Forest
Developed
Flow
River
Glover
Kiamichi
Little
Mountain Fork
Site Type
Upstream
Downstream
NMDS2
0.4
0.0
-0.4
NMDS1
-0.5
0.0
0.5
1.0

Figure 6.


Temperature
Agriculture
Flow
Develop
Forest
0.6
0.3
0.0
-0.3
-0.6
NMDS2
-0.4
-0.2
0.0
0.2
0.4
0.6
NMDS1
River
Glover
Kiamichi
Little
Mountain Fork
Site Type
Upstream
Downstream

SYNTHESIS

One of the world's most threatened ecosystems, rivers are also one of the most biodiverse. Humans have multiple drastic impacts on rivers, many of which alter flow regimes, or the magnitude, frequency, duration, timing, and rate of change of streamflow. Altered flow regimes can be a product of dam construction, climate change, water abstraction, and other activities and lead to flow homogenization (reduced flow variability) and drying (lack of flow altogether). My dissertation assessed the effects of flow modification on riverine ecosystems and aquatic biodiversity.

My research focused on two major systems: non-perennial streams (at regional and global scales), and rivers in Oklahoma. As global climate patterns change, more perennial streams are expected to become non-perennial, and from there, their drying and wetting patterns are expected to change over time. In addition, the state of Oklahoma spans steep temperature and precipitation gradients and is expected to see increasingly harsh conditions with future climate projections. Both systems experience seasonal variations in flow and temperature: non-perennial streams undergo wetting and drying seasonally and Oklahoma streams experience large temperature swings throughout the year. River systems are also particularly vulnerable to climate change, as extreme conditions are expected to increase, resulting in even greater seasonal variability. My chapters illuminated how environmental pressures act on different components of freshwater ecosystems and how to connect scientific disciplines with common language to aid in conservation and management.

In my first dissertation chapter, I examined the terms scientists and managers use for streams that dry periodically in time and space. We found that, despite thematic overlaps, no single term was used within or across scientific disciplines. In an effort to unify research and management of these systems, I suggested and defined three terms be used throughout research and management. Having common definitions will facilitate communication between researchers, managers, and policy makers to enable better communication and protection of these dynamic systems.

While it is important to ensure clear and effective communication to protect rivers and streams, it is also important to understand how these ecosystems have changed through time to better understand management needs, particularly in the light of future global change. In my second chapter, we investigated how fish assemblages across the state of Oklahoma have changed over time. While many studies explore community assembly over spatial gradients, few have employed similar methods over longer time periods. We expected to see changes in taxonomic, functional, and phylogenetic diversity driven by changes in climate, but we found historical assemblage composition to be a better predictor of contemporary structure. This work highlights the importance of understanding historical conditions to better understand contemporary assemblages.

Climate change, in addition to altering precipitation and temperature patterns, is expected to increase aridity and therefore also increase the global prevalence of non-perennial streams. In my third chapter, I connected multiple aspects of drying and wetting patterns, which are expected to change with climate change, to assemblage responses. Our results suggest that different taxonomic groups will respond to drying in unique ways, suggesting the importance of regional environmental filters in determining limited species pools and highlighting the need for multiple benchmarks in ecological management. To the authors' knowledge, this study was the first to incorporate multiple aspects of wetting and drying regimes rather than focusing on one or two metrics to get a fuller understanding of biological responses to drying and wetting regimes.

My final chapter further highlighted the importance of environmental context in southeastern Oklahoma, where I found that interannual environmental variability can be more influential to ecological communities than river impoundments. In addition, I found that both local and watershed environmental variables drove patterns across ecological assemblages. As demands for freshwater resources continue to grow, understanding complex, anthropogenic impacts on rivers within the context of their environment is essential to preserve biodiversity and ecosystem functioning. This study can therefore offer some insights into how predicted increases in water abstraction and droughts can overshadow dam impacts on biological assemblages.

Complementary to water management, land use has multiple impacts on freshwater systems which strongly alter biological communities. Future research should incorporate land use changes into questions similar to my second chapter. Including land use changes could give better insights into what drives changes in assemblages. Future studies exploring temporal assembly changes in other climatic transition zones may further highlight drivers of assembly through time.

Additionally, while my third and fourth chapters focus on how taxonomic diversity patterns shift across space, future studies should also incorporate detailed analyses over longer periods of time. Including a temporal component to studies of dams and hydrologic patterns will highlight how these environmental variables are changing through time. Further, while a temporal component may highlight strong drivers of community diversity, incorporating more trait data into these analyses could also allow researchers to better understand functional ecosystem responses. Although species pools may vary spatially, functional traits of local communities can allow for direct comparisons across different regions. In addition, functional traits are strongly related to ecosystem functioning, which could lead to better understanding of how aquatic ecosystems may be impacted by environmental variation. As climate continues to change, capturing this variation and connecting it to community patterns and ecosystem functions may further highlight the importance of biological diversity.

Taken together, my dissertation has advanced the field of stream ecology: highlighting the importance of historical and environmental context for biological indices, unexpected drivers of ecological assemblages, and potential common language to better conserve and study these biodiverse and vulnerable ecosystems.

SUPPLEMENTAL INFORMATION

CHAPTER 1 SUPPLEMENTAL INFORMATION

Appendix A.

The six topics from all twelve epithets as identified with latent Dirichlet allocation (LDA) topic modeling from the complete corpus made up of 11,989 total abstracts. We assigned topic names to each topic after looking for similarities among the top twenty words from each topic. The top 20 words are stemmed, or, reduced to their base form (**Table A1**).

Table A1. Complete corpus topics.

Topic Number	**Topic Name**	**Top 20 Topic Words (stemmed)**
t_1	geomorphology	sediment*, channel*, flow*, water*, river*, deposit*, stream*, groundwat*, concentr*, surfac*, flood*, studi*, area*, season*, lake*, event*, basin*, transport*, process*, discharg*
t_2	vegetation	speci*, season*, flower*, plant*, burn*, tree*, fire*, popul*, forest*, habitat*, area*, site*, differ*, year*, studi*, veget*, seed*, growth*, us*, dry*
t_3	ecohydrology	stream*, flow*, river*, speci*, water*, dry*, commun*, fish*, intermitt*, site*, habitat*, season*, chang*, differ*, variabl*, studi*, increas*, us*, hydrolog*, temporari*
t_4	agriculture	soil*, water*, irrig*, yield*, us*, season*, crop*, increas*, eros*, treatment*, gulli*, plant*, differ*, year*, effect*, studi*, field*, ha*, product*, mm*
t_5	climate	water*, temperatur*, dry*, season*, rate*, increas*, us*, concentr*, degre*, differ*, leaf*, result*, effect*, flow*, plant*, activ*, cell*, growth*, studi*, co*
t_6	hydrology	water*, model*, us*, season*, chang*, flow*, data*, river*, streamflow*, climat*, studi*, runoff*, basin*, hydrolog*, result*, forecast*, simul*, watersh*, method*, area*

The 9 topics that resulted from LDA topic modeling across all six timeframe corpora. Timeframe corpora were based on WoS searches done after abstracts were common (1990) and broken up into 5-year timeframes (except the final 2016–2018 timeframe). We assigned topic names to each topic based on the top 20 words for each topic (**Table A2**).

Table A2. Time series corpus topics.

Topic Number	Topic Name	Top 20 Topic Words (stemmed)
t_1	community ecology	stream*, water*, river*, flow*, season*, fish*, commun*, site*, dry*, speci*, intermitt*, sampl*, habitat*, concentr,* lake*, assemblag, studi*, differ*, pool*, variabl*
t_2	hydrology	water*, model*, season*, chang*, river*, flow*, us*, climat*, streamflow*, basin*, forecast*, hydrolog*, increas, precipit*, manag*, region*, temperatur*, variabl*, runoff*, data*
t_3	water quality	flow*, water*, model*, us*, temperatur*, surfac*, dry*, result*, particl*, condit*, solut*, observ*, differ*, studi*, heat*, measur*, time*, process*, effect*, wave*
t_4	soil science	soil*, water*, season*, increas*, dry*, emiss*, content*, rate*, us*, moistur*, concentr*, drainag*, root*, potenti*, cm*, measur*, co*, rice*, carbon*, soil water*
t_5	agriculture	water*, irrig*, yield*, crop*, us*, season*, plant*, treatment*, increas*, stress*, product*, water us*, flower*, growth*, soi*l, differ*, leaf*, grain*, effici*, effect*
t_6	riparian	speci*, season*, forest*, burn*, fire*, veget*, tree*, plant*, site*, area*, habitat*, dry*, riparian*, us*, year*, increas*, effect*, water*, differ*, commun*
t_7	geomorphology	sediment*, channel*, deposit*, river*, gulli*, flow*, flood*, basin*, eros*, ephemer*, area*, format*, chang*, system*, lake*, bed*, sand*, surfac*, vallei*, studi*
t_8	modeling	water*, model*, us*, runoff*, groundwat*, soil*, area*, flow*, watersh*, data*, catchment*, studi*, sediment*, eros*, rainfal*, estim*, qualiti*, stream*, land*, result*
t_9	population ecology	speci*, popul*, flower*, fish*, temperatur*, differ*, habitat*, genet*, studi*, season*, femal*, egg*, rate*, us*, new*, male*, size*, growth*, degre*, reproduct*

S1. Example Search

Each epithet (**Table 1**) had an individual Clarivate Web of Science search done to collect the abstracts and papers used in the analyses. To limit search results to non-perennial river systems we limited the paired water body term to 41 based on conversation between authors. We also limited our search to 37 WoS categories. As an example, the search for epithet “arid” was:
TS = (*arid* NEAR/0 (river* OR stream* OR wadi* OR flow* OR "dry bed*" OR corridor* OR riverbed* OR branch* OR run* OR fork* OR brook* OR kill* OR bayou* OR swamp* OR wash* OR cañada* OR arroyo* OR rio* OR crik* OR creek* OR allt* OR water* OR burn* OR beck* OR afron* OR canal* OR prong* OR slough* OR lick* OR drain* OR coulee* OR outlet* OR ditch* OR waterbod* OR channel* OR rill* OR gull* OR tributar* OR hydrograph* OR headwater* OR watershed*) AND WC = (agricultural engineering OR agriculture multidisciplinary OR agronomy OR biodiversity conservation OR biology OR chemistry applied OR chemistry physical OR computer science interdisciplinary applications OR ecology OR engineering civil OR engineering environmental OR entomology OR environmental sciences OR environmental studies OR evolutionary biology OR fisheries OR forestry OR geography physical OR geology OR geosciences multidisciplinary OR green sustainable technology horticulture OR limnology OR marine freshwater biology OR materials science multidisciplinary OR meteorology atmospheric sciences OR microbiology OR multidisciplinary sciences OR oceanography OR physics applied OR physics multidisciplinary OR plant sciences OR public environmental occupation health OR remote sensing OR soil science OR water resources OR zoology).

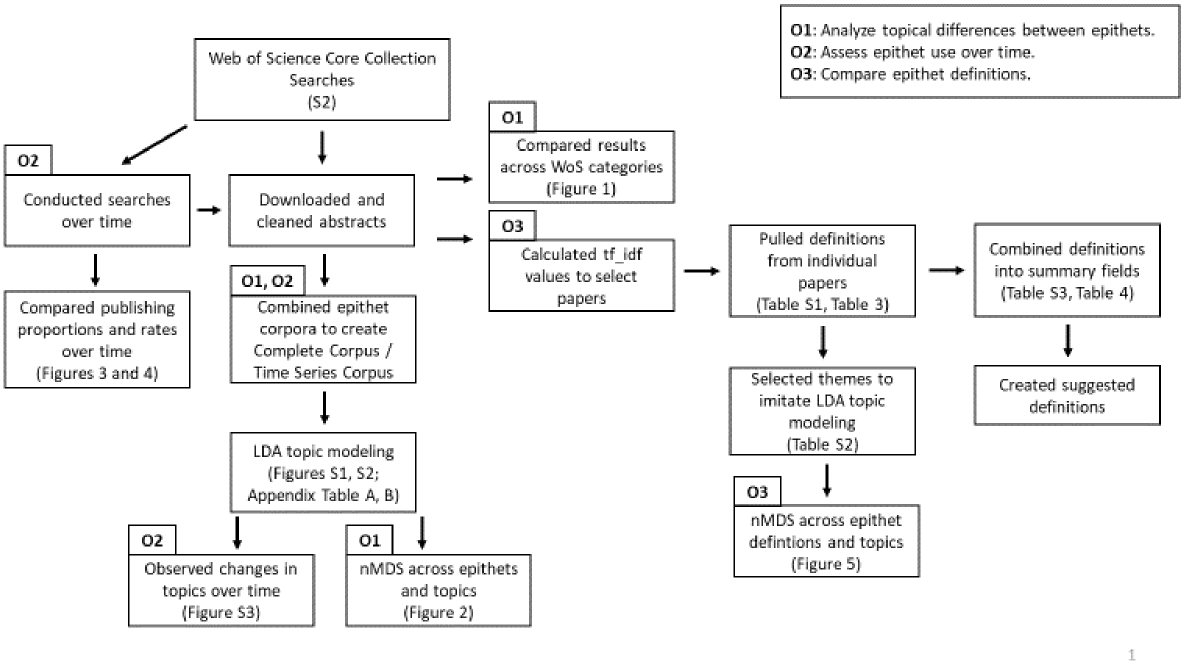


Figure S1. Methods Flow Chart.

A methods flow chart was created to provide additional clarity. All figures, tables, supplementary materials, and appendices are included in the flow chart to provide context. O1, O2, and O3 refer to the Objective number as listed in the manuscript. Full objectives are included within the flow chart to provide a complete overview of our analyses.

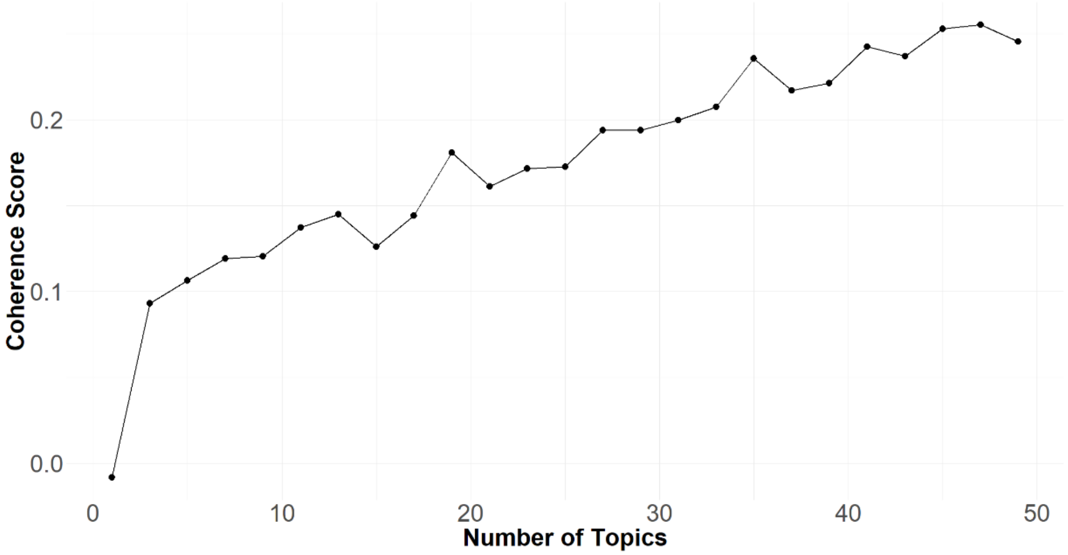


Figure S2. Coherence scores over number of topics for Complete Corpus.

A matrix was created to evaluate coherence scores from 1 to 50 topics by multiples of two before running LDA topic models. We selected six topics to explore further. While the coherence values continued to rise after 6 topics, the lack of a clear plateau in the graph indicated that coherence values could continue to rise with an increase in the number of topics. When exploring a higher number of topics, we found multiple cases of overlap where several of the same words were used for an increasing number of topics (for example, ten words that made up topic number 3 were also found to make up topic number 8). We chose 6 topics as the coherence value crossed the 0.1 threshold as well as a need to have a manageable number of topics to work with.

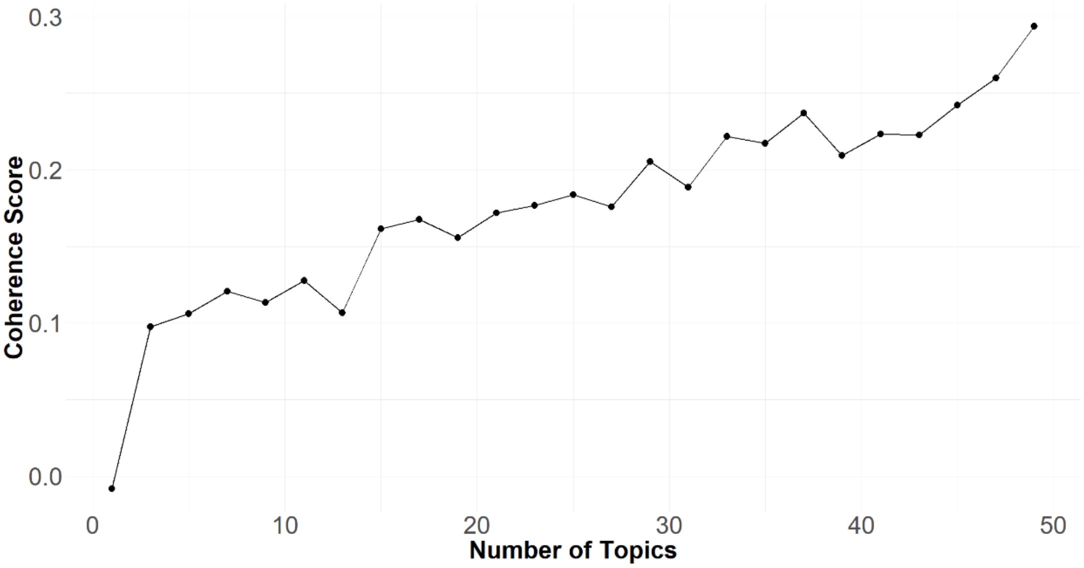


Figure S3. Coherence scores over number of topics for Time Series Corpus.

A matrix was created to evaluate coherence scores from 1 to 50 topics prior to running LDA topic modeling. We selected nine topics to explore further; once again based on a lack of a plateau, overlap of topics, and on the coherence plot while wanting a reasonable number of topics.

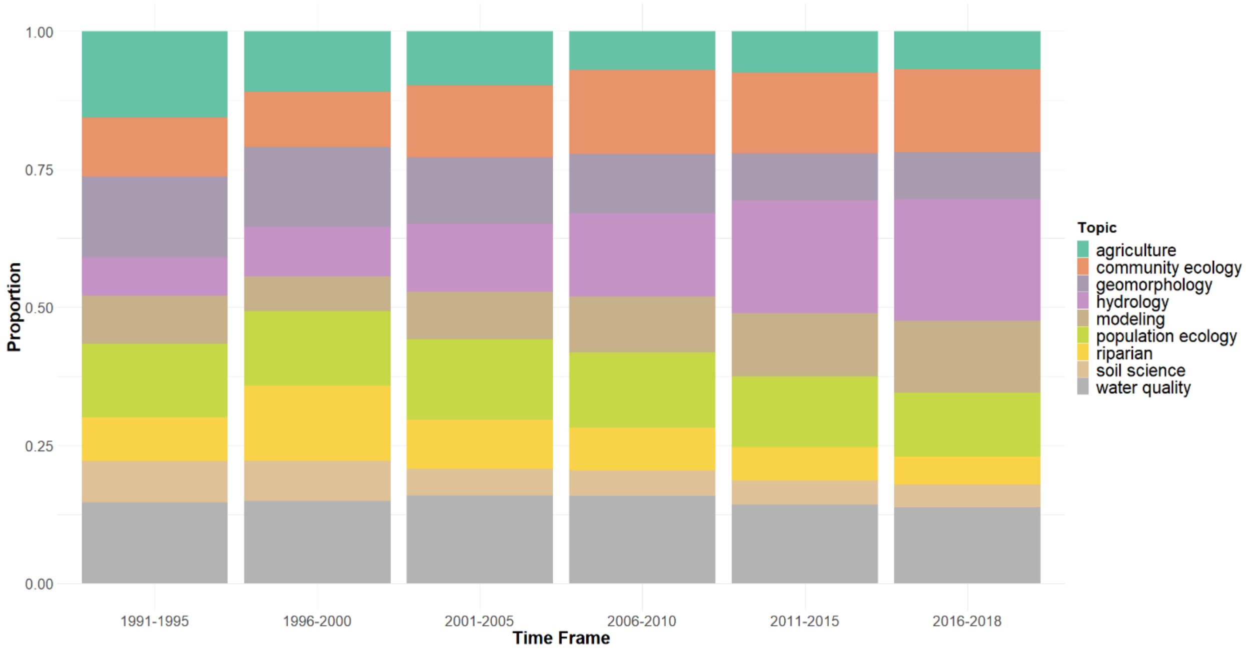


Figure S4. Time Series topics over time.

The proportion of each topic from the Time Series Corpus LDA topic modeling between 1991 and 2018. Colors represent different topics, named after reviewing the top 20 terms associated with each topic (**Appendix A2**).

The final list of papers used in our definition analysis grouped by epithet. A maximum of 50 papers were included in our original definition mining search. These original papers were limited to only using waterbody terms "river" and "stream" to exclude papers not about non-perennial rivers. Due to the lack of papers that held definitions in our original search, we included an addition randomly selected 25 papers that were not limited by waterbody terms (**Table S1.**). This gave us a total of 672 papers for definition mining. Authors were limited to include the first four in the spreadsheet. (Please see Excel file "TableS1-Definition Papers.csv" at https://www.mdpi.com/2073-4441/12/7/1980/s1 for full list of papers used in meta-analysis).

Table S2. Definition analysis themes.

Broad Theme	**Specific Theme**

Source	Precipitation / Runoff
Source	Groundwater
	Seasonality / Predictability
	Variability / Unpredictability
	Linked to Specific Timeframe
	Linked to Specific Landscape
	Related to Extremes (Floods / Droughts)
Phases of Drying	Low Flow
Phases of Drying	No Flow
Phases of Drying	Isolated Pools
Phases of Drying	No Surface Water
Phases of Drying	Not Specific

As definition corpora were too small to run LDA topic modeling, we selected the following themes that are common across non-perennial literature. Some themes were more related to each other than others, which is noted by the Broad Theme column.

Table S3. Web of Science categories by research field.

WoS Category	**Summary Field**

Ecology	Ecology
Water Resources	Hydrology
Civil Engineering	Hydrology
Geosciences	Hydrology
Geography	Hydrology
Environmental Studies	Eco-Hydrology
Limnology	Eco-Hydrology
Biodiversity and Conservation	Eco-Hydrology
Sustainability	Eco-Hydrology

WoS assigned categories for papers and the resulting summary fields they were placed into. Once mined definitions were placed into summary fields, definitions were reviewed to create summary definitions.

CHAPTER 2 SUPPLEMENTAL INFORMATION

SI.1. Study Sites: Additional Information

The state of Oklahoma in the central United States has steep climatic gradients, making streams in this area a model system to study the influences of environmental gradients and change: precipitation increases from the western panhandle (430 mm annual rainfall) to the eastern Ozark and Ouachita Mountains (1200+ mm annual rainfall), and temperature decreases from the southwest (100 annual mean days over 32.2C) to the Ozarks in the east (60 days; Matthews & Marsh-Matthews, 2017). Generally, streams in western Oklahoma have periodic low or no-flow periods while eastern streams trend towards more sustained flows throughout the year (Matthews & Marsh-Matthews, 2017).

To quantify temporal changes in diversity patterns of Oklahoman fish communities, we compiled freshwater fish abundance data collected in the state from 1972 to 2014. Data from 63 sites were collected using methods described in (Pigg 1987) and obtained from the Oklahoma Natural Heritage Inventory (http://www.oknaturalheritage.ou.edu/index.php). We obtained data from six additional sites (Matthews and Marsh-Matthews 2017b), which were collected using similar methods (Matthews and Marsh-Matthews 2017a). Both sources used similar sampling methods; briefly, 200m river sections were seined with a minnow seine for at least an hour. Jimmy Pigg, Dr. William Matthews, and Dr. Edie Marsh-Matthews are well known and respected fish researchers from the state of Oklahoma; they thoroughly sampled rivers and streams across the state and revisited sites multiple times to better understand how communities changed through time. In addition, their data is publicly available (see information above), though no analyses combining these two datasets has been done before to the authors' knowledge. Therefore, the analyses on these sites can offer a new, temporal view of fish community data across the state of Oklahoma. From these sites, we retained individual samples with at least 4 species, and sites with a minimum of 8 sampling events over at least 8 years (532 sampling occasions out of 2,216 lost due to species count restrictions, 24.1% of sampling events). Our final dataset compiled abundance observations of 159 species from 69 sites sampled across the state of Oklahoma from 1972 to 2014. On average, sites were sampled 11 times over 13 years (**Table S1**).

While we limited the number of species, samples, and total years for our analyses, sites with less than four species may be shifting dramatically through time in unique ways due to their relatively small species richness. While excluding these sites could bias our results, we found changes in species richness were significantly correlated with historical species richness (r = -0.37, p = 0.002; Figure 1B). The addition of sites with less than four species could have made this relationship stronger, with depauperate assemblages related to greater changes in diversity patterns through time. However, a minimum of four species was needed to calculate FR with the convex hull volume method. In the future, testing various thresholds would be useful to observe wholistic changes over time. Additionally, our findings might have been influenced by the reverting to the mean, which occurs in repeated measure studies (Barnett 2004). Our data lack multiple baseline measurements per community, so we were unable to analyze for a reversion to the mean phenomena.

Table S1. Site locations for all 69 sites included in the study, including timing of first and last samples (First Year and Last Year, respectively), time span (Last Year – First Year), total number of samples collected at each site over time, and who collected the data (Source).

Site ID	Latitude	Longitude	First Year	Last Year	Time Span	No. Samples	Source
site_id_12	33.941156	-94.758616	1976	1988	12	13	Jimmie Pigg
site_id_123	34.57526	-95.340679	1972	1988	16	10	Jimmie Pigg
site_id_127	34.639175	-94.612238	1972	1988	16	14	Jimmie Pigg
site_id_131	34.755054	-97.251481	1979	1988	9	10	Jimmie Pigg
site_id_143	34.858495	-99.509339	1978	1988	10	11	Jimmie Pigg
site_id_145	34.858985	-94.631428	1977	1987	10	9	Jimmie Pigg
site_id_158	34.919437	-97.050128	1979	1988	9	10	Jimmie Pigg
site_id_170	34.976265	-96.240809	1977	1989	12	13	Jimmie Pigg
site_id_193	35.167327	-99.507349	1978	1988	10	11	Jimmie Pigg
site_id_2	34.634776	-99.096812	1976	1988	12	13	Jimmie Pigg
site_id_201	35.262541	-95.239415	1979	1988	9	10	Jimmie Pigg
site_id_202	35.264522	-96.207538	1978	1988	10	11	Jimmie Pigg
site_id_2040	36.893098	-94.981193	2004	2014	10	8	Matthews

site_id_2041	36.170148	-92.061922	1972	2012	40	8	Matthews
site_id_2057	36.850503	-94.926738	2004	2014	10	8	Matthews
site_id_2058	36.146545	-92.070854	1972	2012	40	8	Matthews
site_id_207	35.347413	-94.453872	1977	1988	11	12	Jimmie Pigg
site_id_2076	34.02523	-96.697962	2005	2013	8	8	Matthews
site_id_2078	33.998079	-96.827416	1976	2012	36	16	Matthews
site_id_209	35.350046	-94.775305	1979	1988	9	10	Jimmie Pigg
site_id_219	35.500197	-97.194327	1976	1988	12	13	Jimmie Pigg
site_id_220	35.505574	-95.121672	1980	1988	8	9	Jimmie Pigg
site_id_227	35.562452	-97.959548	1976	1988	12	13	Jimmie Pigg
site_id_229	35.56726	-98.378399	1976	1988	12	13	Jimmie Pigg
site_id_230	35.572975	-95.068939	1977	1988	11	12	Jimmie Pigg
site_id_234	35.649559	-97.353914	1978	1988	10	11	Jimmie Pigg
site_id_235	35.666362	-97.20132	1980	1988	8	9	Jimmie Pigg
site_id_238	35.696491	-97.069024	1978	1988	10	11	Jimmie Pigg
site_id_241	35.767484	-95.29915	1978	1988	10	11	Jimmie Pigg

site_id_246	35.821108	-95.642552	1977	1988	11	12	Jimmie Pigg
site_id_247	35.841258	-98.463888	1978	1988	10	11	Jimmie Pigg
site_id_252	35.918923	-94.925733	1976	1988	12	12	Jimmie Pigg
site_id_253	35.919632	-97.426216	1978	1988	10	11	Jimmie Pigg
site_id_254	35.922784	-94.837314	1976	1988	12	8	Jimmie Pigg
site_id_258	35.951614	-97.914307	1979	1988	9	10	Jimmie Pigg
site_id_261	35.957936	-97.031858	1976	1988	12	13	Jimmie Pigg
site_id_266	35.967733	-97.230586	1981	1988	7	8	Jimmie Pigg
site_id_28	33.997682	-96.240944	1978	1988	10	10	Jimmie Pigg
site_id_287	36.119846	-98.168665	1979	1988	9	10	Jimmie Pigg
site_id_288	36.12363	-96.115899	1977	1988	11	12	Jimmie Pigg
site_id_296	36.154974	-95.61793	1980	1988	8	8	Jimmie Pigg
site_id_3	33.688511	-94.694788	1977	1988	11	12	Jimmie Pigg
site_id_304	36.203206	-95.758803	1978	1988	10	11	Jimmie Pigg
site_id_305	36.209331	-95.724817	1979	1988	9	10	Jimmie Pigg

site_id_318	36.371979	-98.451812	1979	1988	9	10	Jimmie Pigg
site_id_323	36.443805	-99.281997	1978	1988	10	11	Jimmie Pigg
site_id_327	36.504857	-96.724845	1977	1988	11	12	Jimmie Pigg
site_id_350	36.698661	-96.928446	1978	1988	10	11	Jimmie Pigg
site_id_351	36.701558	-98.047005	1979	1988	9	10	Jimmie Pigg
site_id_360	36.752585	-98.128518	1976	1988	12	13	Jimmie Pigg
site_id_368	36.800027	-94.751941	1980	1988	8	9	Jimmie Pigg
site_id_369	36.811432	-97.277944	1978	1988	10	10	Jimmie Pigg
site_id_37	34.041437	-94.621291	1977	1988	11	10	Jimmie Pigg
site_id_376	36.913228	-102.817903	1980	1988	8	8	Jimmie Pigg
site_id_378	36.918937	-99.396324	1977	1988	11	12	Jimmie Pigg
site_id_379	36.929553	-102.956258	1980	1988	8	9	Jimmie Pigg
site_id_382	36.977401	-99.958294	1981	1988	7	8	Jimmie Pigg
site_id_386	n/a	n/a	1975	1989	14	8	Jimmie Pigg
site_id_4	33.7272	-97.159046	1980	1988	8	9	Jimmie Pigg

site_id_5	33.875833	-95.501314	1978	1988	10	11	Jimmie Pigg
site_id_58	34.13287	-98.092216	1978	1988	10	11	Jimmie Pigg
site_id_6	33.878371	-97.934028	1977	1988	11	12	Jimmie Pigg
site_id_65	34.182653	-97.99998	1979	1988	9	10	Jimmie Pigg
site_id_69	34.233865	-96.977463	1976	1988	12	13	Jimmie Pigg
site_id_72	34.249214	-95.605325	1973	1988	15	13	Jimmie Pigg
site_id_74	34.271551	-95.911766	1976	1988	12	13	Jimmie Pigg
site_id_85	34.388376	-94.695746	1977	1988	11	11	Jimmie Pigg
site_id_89	34.413588	-99.737163	1980	1988	8	9	Jimmie Pigg
site_id_92	34.454369	-96.635665	1977	1988	11	11	Jimmie Pigg

SI.2. Functional Traits: Additional Information

Analyzing trait groups separately may show signals that would be hidden when analyzing all traits altogether (Saito et al. 2016, Münkemüller et al. 2020). To determine which traits react stronger to climate change, we used three functional trait categories: trophic ecology, life history, and environmental tolerance (**Table S2**) based on those presented by Frimpong and Angermeier (2009) and previous studies (**Table S3**).

Within the trophic ecology category (trophic), we selected traits that describe the diets of fish species (Table S2). To quantify species environmental niche (env), we used traits related to reproductive habitat (25 traits), habitat use (26 traits) and temperature tolerance (1 trait). Traits were extracted from Frimpong and Angermeier (2009; **Table S2**). Habitat related traits (i.e., reproductive and habitat use) were coded as binary, such that if a species prefers lotic water (PREFLOT) as opposed to lentic water (PREFLEN), the species got a score of 1 for PREFLOT and 0 for PREFLEN (**Table S2**). For each species, temperature tolerances were estimated as the maximum temperatures experienced across its range based on the IUCN distribution using range centroids (IUCN 2020; **Figure S2**). We reduced the dimensions of the environmental niche using a PCoA (**SI.3**). For life history traits (LHT), we used age at maturity, body length and fecundity (**Table S2**).

Table S2. Full list of fish functional traits used in our analyses (Frimpong and Angermeier 2009). We broke traits down into three categories: trophic, environmental tolerance, and life history. For both foraging and environmental tolerance traits we ran PCAs and noted the number of axes kept below. Cont. stands for continuous. Included in the "Traits" column is the multiplier used to weigh the traits for global trait analysis.

Traits			
Trophic (1/7)	Trophic habits – 2 PCA axes		
	NONFEED	BBinary	Adults do not feed (1/11 * 1/7)
	BENTHIC		Benthic feeder (1/11 * 1/7)
	SURWCOL		Surface or water column feeder (1/11 * 1/7)
	ALGPHYTO		Algae or phytoplankton, including filamentous algae (1/11 * 1/7)
	MACVASCU		Any part of macrophytes and vascular plants (1/11 * 1/7)
	DETRITUS		Detritus or unidentifiable vegetative matter (1/11 * 1/7)
	INVLVFSH		Aquatic and terrestrial invertebrates including zooplankton, insects, microcrustaceans, annelids,

			mollusks, etc. This group also includes larval fishes (1/11 * 1/7)
	FSHCRCRB		Larger fishes, crayfishes, crabs, frogs, etc. (1/11 * 1/7)
	BLOOD		For parasitic lampreys that feed mainly on blood (1/11 * 1/7)
	EGGS		Eggs of fishes, frogs, etc. (1/11 * 1/7)
	OTHER		Other diet components distinct from the preceding classes (1/11 * 1/7)
Environmental Tolerance (1/7)	Reproduction habitat – 1 PCA axis		
	A_1_1	Binary	Nonguarders; Open substratum spawners; Pelagophils (1/25 * 1/7)
	A_1_2		Nonguarders; Open substratum spawners; Litho-pelagophils (1/25 * 1/7)
	A_1_3A		Nonguarders; Open substratum spawners; Lithophils (rock-gravel) (1/25 * 1/7)
	A_1_3B		Nonguarders; Open substratum spawners; Lithophils (gravel-sand) (1/25 * 1/7)
	A_1_3C		Nonguarders; Open substratum spawners; Lithophils (silt- mud) (1/25 * 1/7)
	A_1_4		Nonguarders; Open substratum spawners; Phyto-lithophils (1/25 * 1/7)
	A_1_5		Nonguarders; Open substratum spawners; Phytophils (1/25 * 1/7)
	A_1_6		Nonguarders; Open substratum spawners; Psammophils (1/25 * 1/7)
	A_2_3A		Nonguarders; Brood hiders; Lithophils (rock-gravel) (1/25 * 1/7)
	A_2_3B		Nonguarders; Brood hiders; Lithophils (gravel-sand) (1/25 * 1/7)
	A_2_3C		Nonguarders; Brood hiders; Lithophils (mud) (1/25 * 1/7)

A_2_4A		Nonguarders; Brood hiders; Speleophils (rock cavity) (1/25 * 1/7)
A_2_4C		Brood hiders; Speleophils (cavity generalist rock crevices, and also under log bark, openings in vegetation, metal cans, etc.) (1/25 * 1/7)
B_1_3A		Guarders; Substratum choosers; Lithophils (1/25 * 1/7)
B_1_4		Guarders; Substratum choosers; Phytophils (1/25 * 1/7)
B_2_2		Guarders; Nest spawners; Polyphils (1/25 * 1/7)
B_2_3A		Guarders; Nest spawners; Lithophils (rock-gravel) (1/25 * 1/7)
B_2_3B		Guarders; Nest spawners; Lithophils (gravel-sand) (1/25 * 1/7)
B_2_4		Guarders; Nest spawners; Ariadnophils (1/25 * 1/7)
		Guarders; Nest spawners; Phytophils (1/25 * 1/7)
B_2_6		Guarders; Nest spawners; Psammophils (1/25 * 1/7)
B_2_7_A		Guarders; Nest spawners; Speleophils (rock cavity/roof) (1/25 * 1/7)
B_2_7_B		Guarders; Nest spawners; Speleophils (bottom burrows or natural holes associated with structure or bank) (1/25 * 1/7)
B_2_7C		Guarders; Nest spawners; Speleophils (cavity generalist) (1/25 * 1/7)
C1_3_4_C2_4		A lumping of all bearers. May also be regarded as substrate-indifferent (1/25 * 1/7)
Habitat use – 2 PCA axes		
MUCK	Binary	Muck substrate (1/26 * 1/7)
CLAY/SILT		Clay or silt substrate (1/26 * 1/7)
SAND		Sand substrate (1/26 * 1/7)

GRAVEL	Gravel substrate (1/26 * 1/7)
COBBLE	Cobble or pebble substrate (1/26 * 1/7)
BOULDER	Boulder substrate (1/26 * 1/7)
BEDROCK	Bedrock substrate (1/26 * 1/7)
VEGETAT	Aquatic vegetation (1/26 * 1/7)
DEBRDETR	Organic debris or detrital substrate (1/26 * 1/7)
LWD	Large woody debris (1/26 * 1/7)
PELAGIC	Open water (1/26 * 1/7)
PREFLOT	Lotic and lentic systems but more often in lotic (1/26 * 1/7)
PREFLEN	Lotic and lentic systems but more often in lentic (1/26 * 1/7)
LARGERIV	Medium to large river (1/26 * 1/7)
SMALLRIV	Stream to small river (1/26 * 1/7)
CREEK	Creek (1/26 * 1/7)
SPRGSUBT	Spring or subterranean water (1/26 * 1/7)
LACUSTRINE	Lentic systems (1/26 * 1/7)
POTANADR	Potamodromous or anadromous. Species that exhibit significant movement related to spawning. We concentrated on movements between marine and freshwater or within freshwater from large river, reservoirs, or lakes to tributary streams (1/26 * 1/7)
LOWLAND	Lowland elevation (1/26 * 1/7)
UPLAND	Highland elevation (1/26 * 1/7)
MONTANE	Mountainous physiography (1/26 * 1/7)
SLOWCURR	Slow current (1/26 * 1/7)
MODCURR	Moderate current (1/26 * 1/7)
FASTCURR	Fast current (1/26 * 1/7)

	MINTEMP	Cont.	The 30-year average minimum January temperature at range centroid in degrees Celsius. Range centroids were used to extract values from 400-m resolution temperature grids obtained from Climate Source, Inc., Oregon (1/26 * 1/7)
	MAXTEMP	Cont.	The 30-year average maximum July temperature at range centroid in degrees Celsius. Range centroids were used to extract values from 400-m resolution temperature grids obtained from Climate Source, Inc., Oregon (1/26 * 1/7)
	MINPRECIP	Cont.	The 30-year average minimum January precipationa at range centroid in millimeters. Range centroids were used to extract values from 400-m resolution precipitation grids obtained from Climate Source, Inc., Oregon (1/26 * 1/7)
	MAXPRECIP	Cont.	The 30-year average maximum July precipitation at range centroid in degrees Celsius. Range centroids were used to extract values from 400-m resolution temperature grids obtained from Climate Source, Inc., Oregon (1/26 * 1/7)
Life History (1/7)	MAXTL	Cont.	Maximum total length in centimeters. Some records may estimate asymptotic length. We assumed that the difference between maximum observed length and asymptotic length is negligible (1/7)
	MATUAGE	Cont.	Mean, median, or modal age at maturity in years for females. Where different ages at maturity were obtained for distinct populations, the clearly supported records were averaged. Male maturity age was accepted where female data were not available (1/7)
	FECUNDITY	Cont.	(1/7)
	LONGEVITY	Cont.	Longevity in years based on life in the wild wherever available. Where not indicated, the record was assumed to be from the wild. If wild records were not known, a record from captivity was accepted (1/7)

Once PCoAs were run for trophic and environmental tolerance traits, the axes were tested for phylogenetic conservatism (**S1.3**). Only those that were phylogenetically conserved (**Table S3**) were kept, satisfying the assumptions made by Webb et al. (2002). Blomberg's K is an estimate of the phylogenetic signal in traits (Blomberg et al. 2003) and was calculated from the R package 'motmot' (Puttick 2019).

Table S3. Classification of the functional traits used and their rationale. PC refers to Phylogenetic Conservatism (✓ indicates that the corresponding trait is phylogenetically conserved based on Blomberg's K) and Bloomberg's K values are shown in the final column.

Designation	Rationale	References	PC	Bloomberg's K
Trophic niche	**Feeding strategy** – Trophic habits related to trophic interspecific interactions between species	Saito et al., 2016; Lopez et al. 2016; Côte et al. 2019, Pease et al. 2012; Ingram and Shurin, 2009; Adam et al. 2015	Axis 1 ✓ Axis 2 ✓	K = 0.17, p = 0.001 K = 0.08, p = 0.004
Environmental niche	**Habitat use –** The set of environmental conditions needed for survival and reproduction	Saito et al., 2016; Lopez et al. 2016; Côte et al. 2019	Axis 1 ✓ Axis 2 ✓	K = 0.1, p = 0.001 K = 0.12, p = 0.001
	Reproduction habitat – Although reproduction habitat relates to reproduction, it refers to habitat use and requires a given set of environmental conditions	Winemiller 2005; Pool et al., 2014		
	Thermal niche – physical factor influencing species ability to survive and persist in a given habitat patch	Pease et al. 2012; Blanck et al. 2007; Tzanatos et al. 2020		

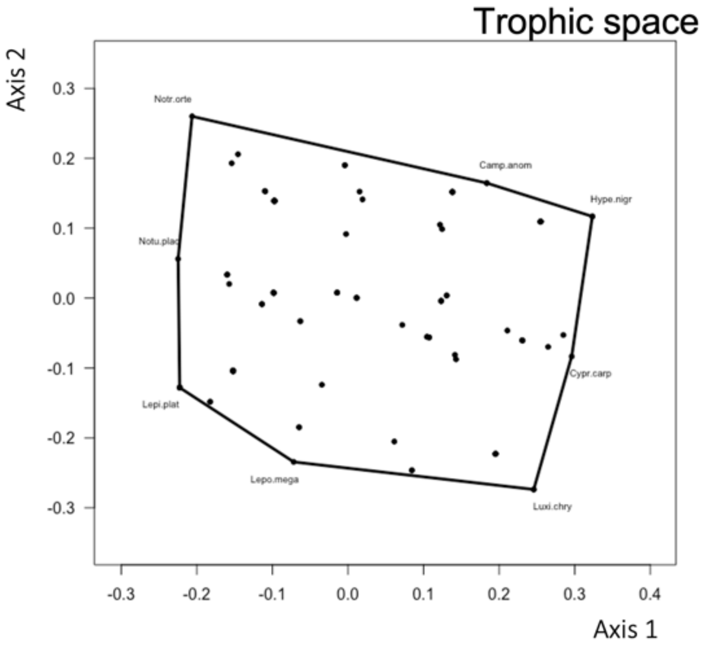
Life History Traits	**Habitat use, feeding strategy, life history and dispersal** – Body size is known to be integrative of several traits	Gatz 1979; Webb 1984; Pease et al. 2012; Lopez et al. 2016; Hitt and Roberts 2011	Axis 1 ✓ Axis 2 ✓ Axis 3 ✓	K = 0.89, p = 0.001 K = 0.17, p = 0.011 K = 0.14, p = 0.001
	Life history – Longer longevity results in a more important place in the trophic structure of communities (i.e. relates to interspecific interactions) while it confers more resistance to environmental stress	Hitt and Roberts 2011; Pool et al., 2014; Tzanatos et al., 2020; Kaiser et al., 2006; Rijnsdorp et al., 2016		
	Life history – Higher fecundity results in higher abundances of young stages that can be resources for other trophic levels	Côte et al. 2019; Pease et al. 2012; Hitt and Roberts 2011; Tzanatos et al. 2020		

SI.3. Functional Trait Diversity: Additional Methods

We computed functional richness from the trait database as the convex hull volume of the multi-dimensional trait space occupied by species present in each sample. We calculated convex hull volumes from all traits combined (FR_{global}) and on the three different subsets of functional traits (i.e. trophic, environmental preference and life history traits; $FR_{trophic}$, FR_{env}, FR_{LHT}, respectively; Cornwell et al., 2006; Villéger et al., 2008). This index corresponds to the portion of the maximal volume that species can occupy that is filled by the co-occurring species in a given sample. We used Principal Coordinates Analyses (PCoAs) to reduce the number of traits so that convex hull volumes were derived from a similar number of axes across trait categories (SI.2). We used the "conhulln" function from the 'geometry' package (Roussel et al. 2019). This index corresponds to the portion of the maximal volume that species can occupy that is filled by the co-occurring species in each sample. To account for outliers, which can strongly alter the convex hull volume method, we also calculated Rao's quadratic entropy (Rao), which is less effected by species numbers or outliers (De Bello et al. 2010, Kingrani et al. 2017) using the functions "Qdecomp" (Villéger et al. 2008; modified by Wilfried Thuiller) and "disc" in the 'ade4' package (Dray et al. 2021). As with the FR calculations, we computed Rao's quadratic entropy across trait categories ($Rao_{trophic}$, Rao_{env}, Rao_{LHT}) and for all traits (Rao_{global}).

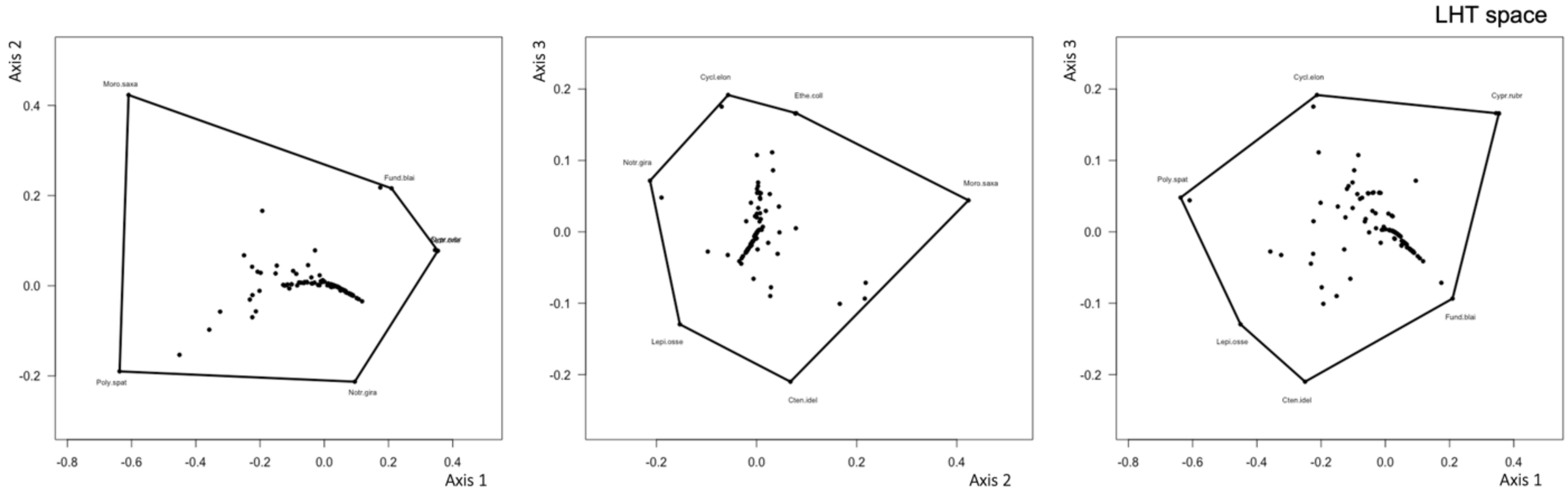
The trophic PCoA was based on equally weighted 11 traits with the first two axes retained (**Table S2**). The first axis represented 58% of the variance and the second PCoA axis explained 37% of the variance (**Figure S1**).

Figure S1. Functional space based on PCoA axes from trophic habits of species. Each dot represents a species that has been sampled at least once. The enclosed area represents the convex hull, the index of functional richness, based on the two axes. Full species names can be found in **Table S4**.



Three traits were selected to represent life history (**Table S2**) and were all equally weighted in the PCoA (**Figure S2**). From the PCoA, we kept three axes representing 19%, 15% and less than 1%, respectively (**Figure S3**).

Figure S2. Functional species based on the traits categorized as life history traits based on (a) maximum size and fecundity, (b) age at maturity and size, and (c) longevity and fecundity. Each dot is a species that has been sampled at least once. The enclosed areas represent the convex hull based on the pair of dimensions represented. Full species names can be found in Table S4.


LHT space
Axis 2
Axis 1
Axis 3
Axis 2
Axis 3
Axis 1
0.4
0.2
0.0
-0.2
0.1
-0.1
-0.8
-0.6
-0.4
Moro.saxa
Fund.blai
Cypr.rubr
Poly.spat
Notr.gira
Cycl.elon
Ethe.coll
Lepi.osse
Cten.idel

Three aspects were used to determine the environmental tolerance of species (**Figure S3**): reproductive habitat, habitat use and temperature tolerance. Each of them, although based on a different number of traits, represents an equal weight in the PCoA (i.e., 1/3 each to be sure the PCoA axes represent equally all categories (i.e., environmental niche components). The 25 reproductive habitat-related variables were given a weight of 1/3 * 1/25; the 26 habitat use-related variables were given a weight of 1/3 * 1/26 and finally, the temperature tolerance, which was only one variable, was given a weight of 1/3. The first two axes were kept as the third one was not phylogenetically conserved. Two axes were kept representing 39% and 17% respectively of the total variance.

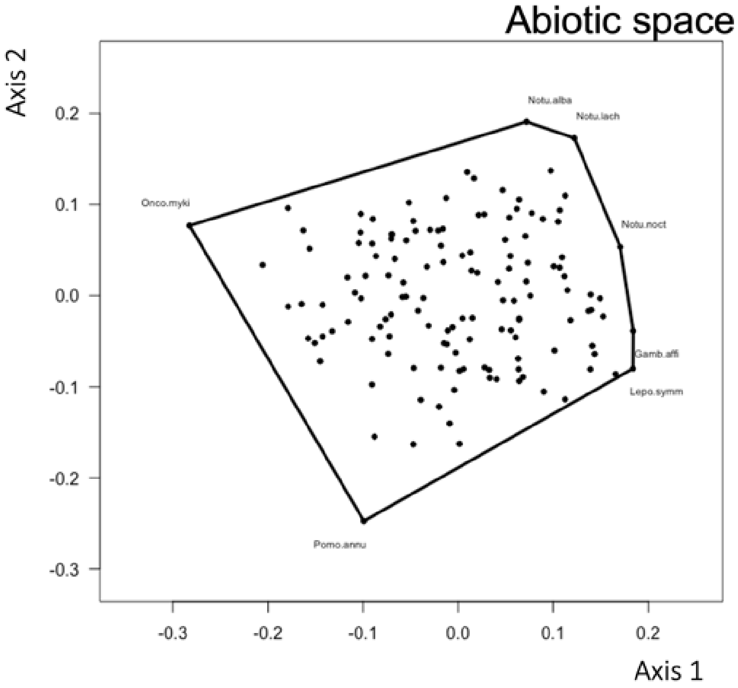


Figure S3. Environment tolerance trait space based on (a) habitat use and reproductive habitat, (b) temperature tolerance and habitat use, and (c) temperature tolerance and reproductive habitat. Each dot is a species that has been sampled at least once. The enclosed areas represent the convex hull based on the two axes. Full species names can be found in **Table S4**.

Finally, we ran a global PCoA (global) based on all traits (**Table S2**). We weighted traits in such way that different hypothesized functions were equally weighted:

1/7 * 1/11 for each of the 11 trophic traits,

1/7 for each life history traits (i.e., 3),

1/7 * 1/25 for each of the 25 reproductive habitat related traits,

1/7 * 1/26 for each of the 26 habitat use related traits and,

1/7 for the temperature tolerance.

With this weighting scheme, each trait category was equally represented in the rest of the analyses. The three kept axes represented 38%, 17% and 15% of the total variance (**Figure S2d**; **Table S3**; **Figure S4**).

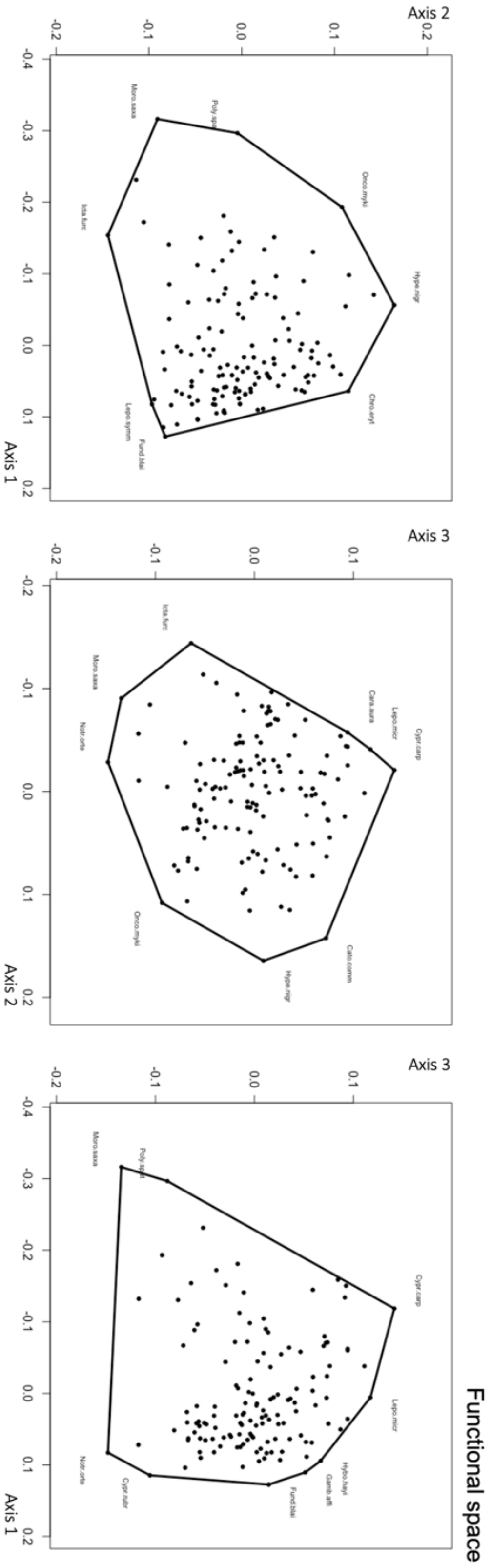


Figure S4. Functional space based on global traits (all raw traits included in individual categories) based on all raw traits included in each category based on (a) axes 1 and 2, (b) axes 1 and 3, and (c) axes 2 and 3. The total variance explained by the three axes is 23% (axis 1: 11%, axis 2: 7%, axis 3: 5%). Each dot is a species that has been sampled at least once. The enclosed areas represent the convex hull based on the pair of dimensions represented. Full species names can be found in **Table S4**.

Table S4. Abbreviations (Abr. name) and full species names for figures S2-S5

Full name	**Abr. name**
Ambloplites.ariommus	Ambl.ario
Ambloplites.constellatus	Ambl.cons
Ambloplites.rupestris	Ambl.rupe
Ameiurus.melas	Amei.mela
Ameiurus.natalis	Amei.nata
Amia.calva	Amia.calv
Ammocrypta.clara	Ammo.clar
Ammocrypta.vivax	Ammo.viva
Aphredoderus.sayanus	Aphr.saya
Aplodinotus.grunniens	Aplo.grun
Campostoma.anomalum	Camp.anom
Campostoma.oligolepis	Camp.olig
Carassius.auratus	Cara.aura
Carpiodes.carpio	Carp.carp
Carpiodes.velifer	Carp.veli
Catostomus.commersonii	Cato.comm
Centrarchus.macropterus	Cent.macr
Chrosomus.erythrogaster	Chro.eryt
Cottus.carolinae	Cott.caro
Ctenopharyngodon.idella	Cten.idel
Cycleptus.elongatus	Cycl.elon
Cyprinella.camura	Cypr.camu
Cyprinella.galactura	Cypr.gala
Cyprinella.lutrensis	Cypr.lutr
Cyprinella.spiloptera	Cypr.spil
Cyprinella.venusta	Cypr.venu
Cyprinella.whipplei	Cypr.whip
Cyprinodon.rubrofluviatilis	Cypr.rubr
Cyprinus.carpio	Cypr.carp
Dorosoma.cepedianum	Doro.cepe
Elassoma.zonatum	Elas.zona

Erimystax.dissimilis	Erim.diss	Gambusia.affinis	Gamb.affi
Erimyzon.oblongus	Erim.oblo	Hiodon.alosoides	Hiod.alos
Erimyzon.sucetta	Erim.suce	Hybognathus.hayi	Hybo.hayi
Esox.niger	Esox.nige	Hybognathus.nuchalis	Hybo.nuch
Etheostoma.asprigene	Ethe.aspr	Hybognathus.placitus	Hybo.plac
Etheostoma.blennioides	Ethe.blen	Hybopsis.amblops	Hybo.ambl
Etheostoma.caeruleum	Ethe.caer	Hybopsis.amnis	Hybo.amni
Etheostoma.chlorosomum	Ethe.chlo	Hypentelium.nigricans	Hype.nigr
Etheostoma.collettei	Ethe.coll	Ictalurus.furcatus	Icta.furc
Etheostoma.flabellare	Ethe.flab	Ictalurus.punctatus	Icta.punc
Etheostoma.fusiforme	Ethe.fusi	Ictiobus.bubalus	Icti.buba
Etheostoma.gracile	Ethe.grac	Ictiobus.cyprinellus	Icti.cypr
Etheostoma.histrio	Ethe.hist	Ictiobus.niger	Icti.nige
Fundulus.blairae	Fund.blai	Labidesthes.sicculus	Labi.sicc
Fundulus.catenatus	Fund.cate	Lepisosteus.osseus	Lepi.osse
Fundulus.notatus	Fund.nota	Lepisosteus.platostomus	Lepi.plat
Fundulus.olivaceus	Fund.oliv	Lepomis.auritus	Lepo.auri
Fundulus.sciadicus	Fund.scia	Lepomis.cyanellus	Lepo.cyan
Fundulus.zebrinus	Fund.zebr	Lepomis.gulosus	Lepo.gulo

Lepomis.humilis	Lepo.humi
Lepomis.macrochirus	Lepo.macr
Lepomis.marginatus	Lepo.marg
Lepomis.megalotis	Lepo.mega
Lepomis.microlophus	Lepo.micr
Lepomis.miniatus	Lepo.mini
Lepomis.punctatus	Lepo.punc
Lepomis.symmetricus	Lepo.symm
Luxilus.cardinalis	Luxi.card
Luxilus.chrysocephalus	Luxi.chry
Luxilus.pilsbryi	Luxi.pils
Lythrurus.fumeus	Lyth.fume
Lythrurus.snelsoni	Lyth.snel
Lythrurus.umbratilis	Lyth.umbr
Macrhybopsis.aestivalis	Macr.aest
Macrhybopsis.storeriana	Macr.stor
Micropterus.dolomieu	Micr.dolo
Micropterus.punctulatus	Micr.punc
Micropterus.salmoides	Micr.salm
Minytrema.melanops	Miny.mela
Morone.chrysops	Moro.chry
Morone.saxatilis	Moro.saxa
Moxostoma.carinatum	Moxo.cari
Moxostoma.erythrurum	Moxo.eryt
Moxostoma.macrolepidotum	Moxo.macr
Nocomis.asper	Noco.aspe
Nocomis.biguttatus	Noco.bigu
Notemigonus.crysoleucas	Note.crys
Notropis.atherinoides	Notr.athe
Notropis.blennius	Notr.blen
Notropis.boops	Notr.boop
Notropis.buchanani	Notr.buch
Notropis.girardi	Notr.gira
Notropis.nubilus	Notr.nubi
Notropis.ortenburgeri	Notr.orte
Notropis.perpallidus	Notr.perp
Noturus.albater	Notu.alba
Noturus.eleutherus	Notu.eleu

Noturus.exilis	Notu.exil
Noturus.flavus	Notu.flav
Noturus.gyrinus	Notu.gyri
Noturus.lachneri	Notu.lach
Noturus.miurus	Notu.miur
Noturus.nocturnus	Notu.noct
Noturus.placidus	Notu.plac
Oncorhynchus.mykiss	Onco.myki
Percina.caprodes	Perc.capr
Percina.copelandi	Perc.cope
Percina.macrolepida	Perc.macr
Percina.maculata	Perc.macu
Percina.nasuta	Perc.nasu
Percina.pantherina	Perc.pant
Percina.phoxocephala	Perc.phox
Percina.sciera	Perc.scie
Percina.shumardi	Perc.shum
Phenacobius.mirabilis	Phen.mira
Pimephales.notatus	Pime.nota
Pimephales.promelas	Pime.prom
Pimephales.tenellus	Pime.tene
Pimephales.vigilax	Pime.vigi
Platygobio.gracilis	Plat.grac
Polyodon.spathula	Poly.spat
Pomoxis.annularis	Pomo.annu
Pomoxis.nigromaculatus	Pomo.nigr
Pylodictis.olivaris	Pylo.oliv
Sander.vitreus	Sand.vitr
Scaphirhynchus.platorynchus	Scap.plat
Semotilus.atromaculatus	Semo.atro

SI.4. Phylogenetic Diversity: Additional Methods

To quantify phylogenetic diversity (PD), we used the most comprehensive time-calibrated phylogeny for fish available (Rabosky et al., 2013) and then extracted the subset of species observed in our samples (100% completeness; **Figure S5**). We calculated PD as the sum of branch lengths that link all species co-occurring in a given sample (Faith, 1992) with the "pd" function in the 'picante' package (Kembel et al. 2020). In addition to Faith's PD, we also used Rao's quadratic entropy to calculate phylogenetic diversity ($\text{Rao}_{\text{phylo}}$) using phylogenetic distance between species.

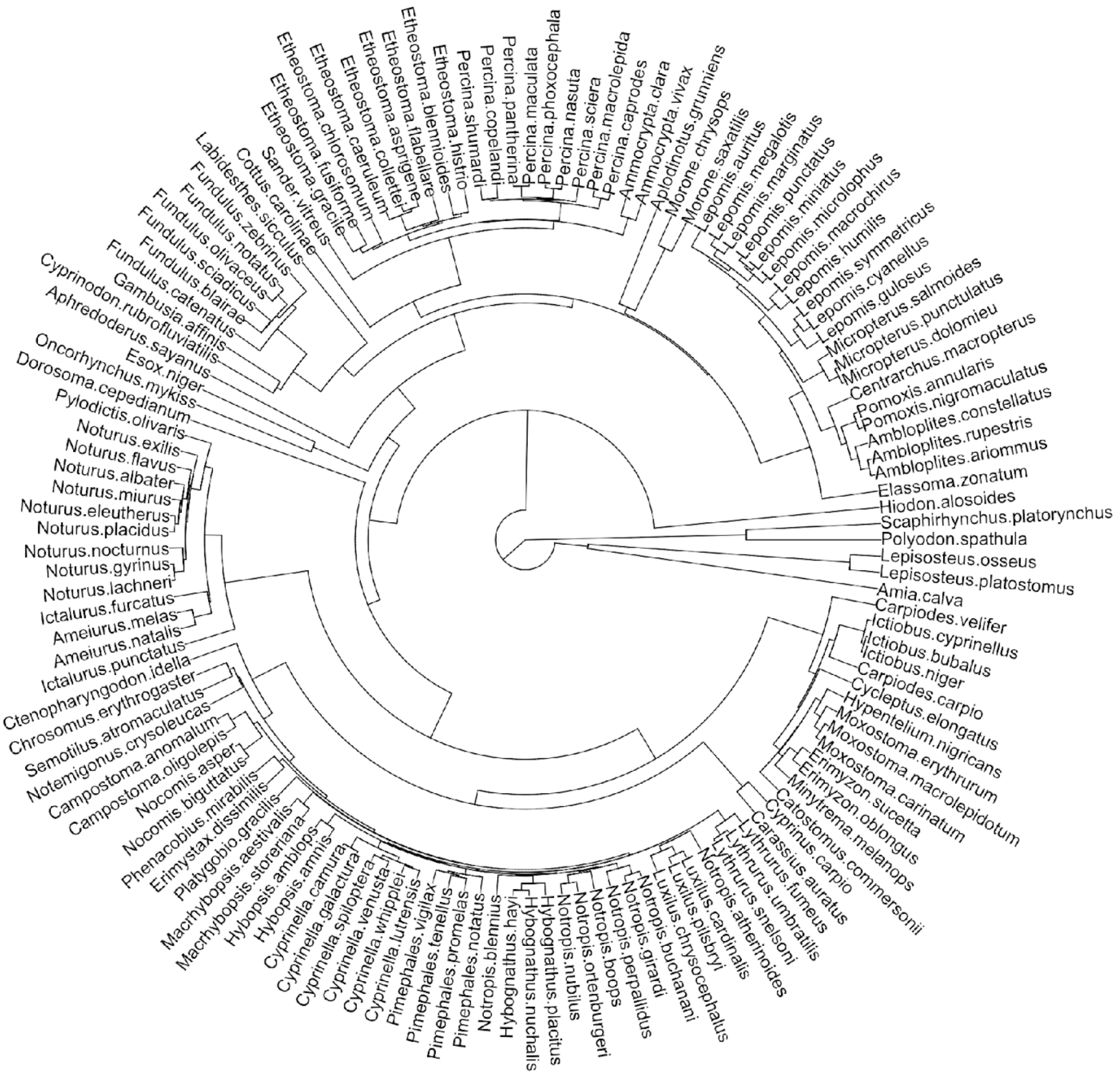


Figure S5. Complete phylogeny of fish included in study (Rabosky et al., 2013).

To infer patterns from phylogenetic diversity, traits must be either all phylogenetically conserved or phylogenetically converged (Webb et al. 2002). We tested whether the traits or trait axes presented above were phylogenetically conserved using Blomberg’s K from the R package ‘motmot’ (Blomberg et al., 2003; Puttick, 2019). Blomberg's K provides an estimate of the phylogenetic signal in traits and compares it to a random Brownian evolution of the traits. In our case, all traits showed a significant phylogenetic conservatism (all $p < 0.05$; **Table S3**) indicating that species closely related exhibit similar values for all traits (**Figure S6 - S9**; **Table S4**).

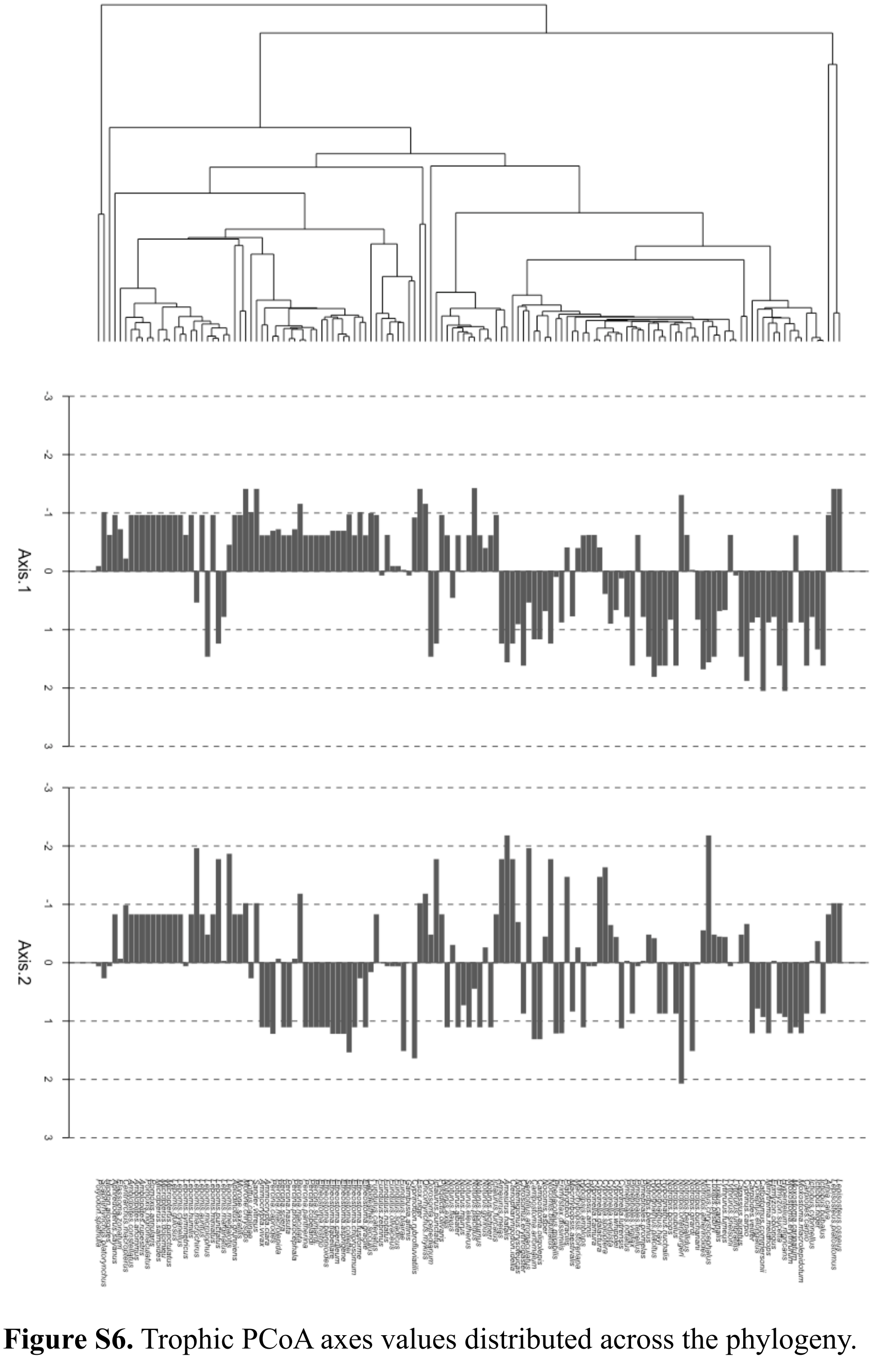


Figure S6. Trophic PCoA axes values distributed across the phylogeny.

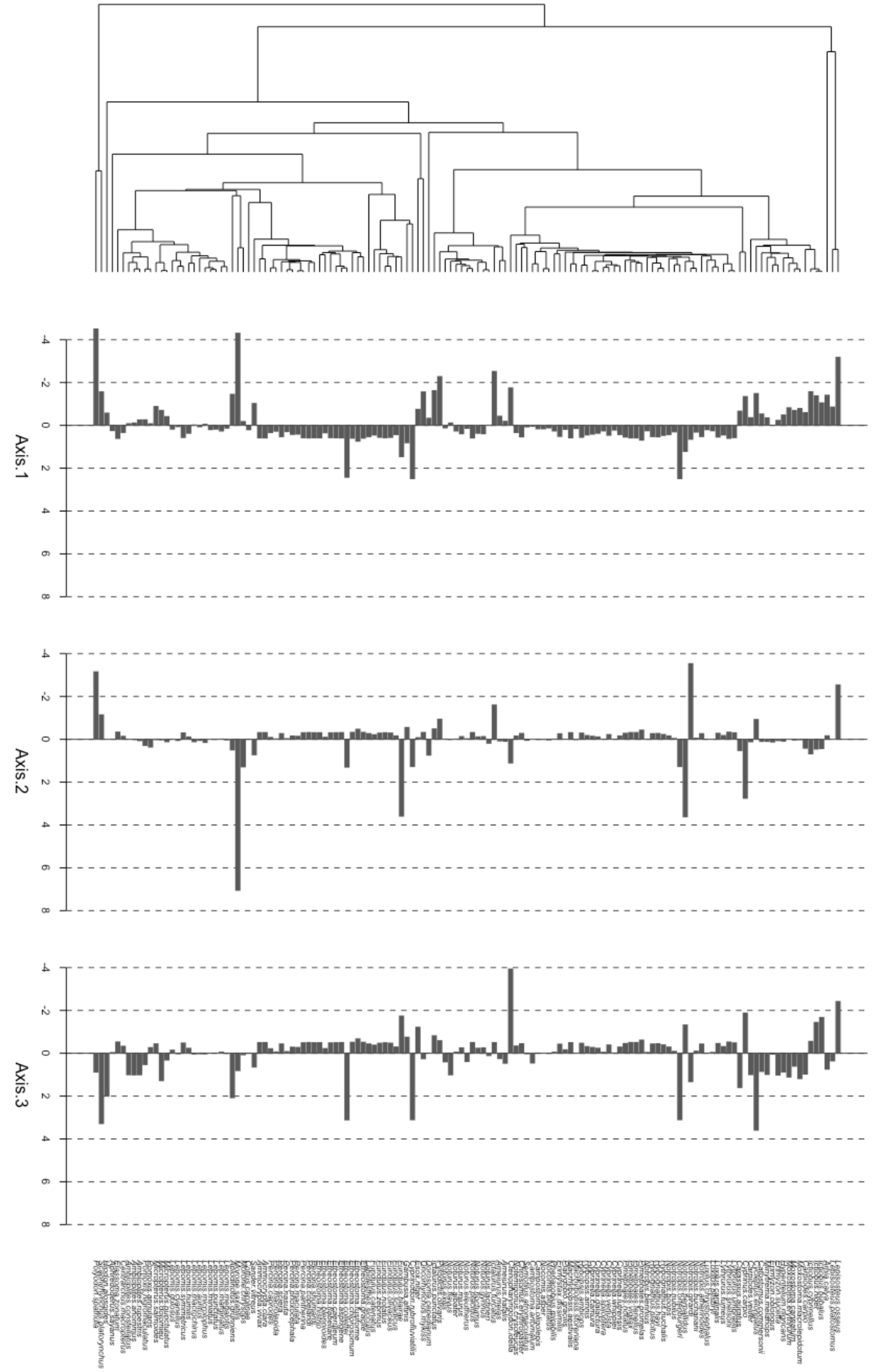


Figure S7. Life history trait based PCoA axes values distributed across the phylogeny.

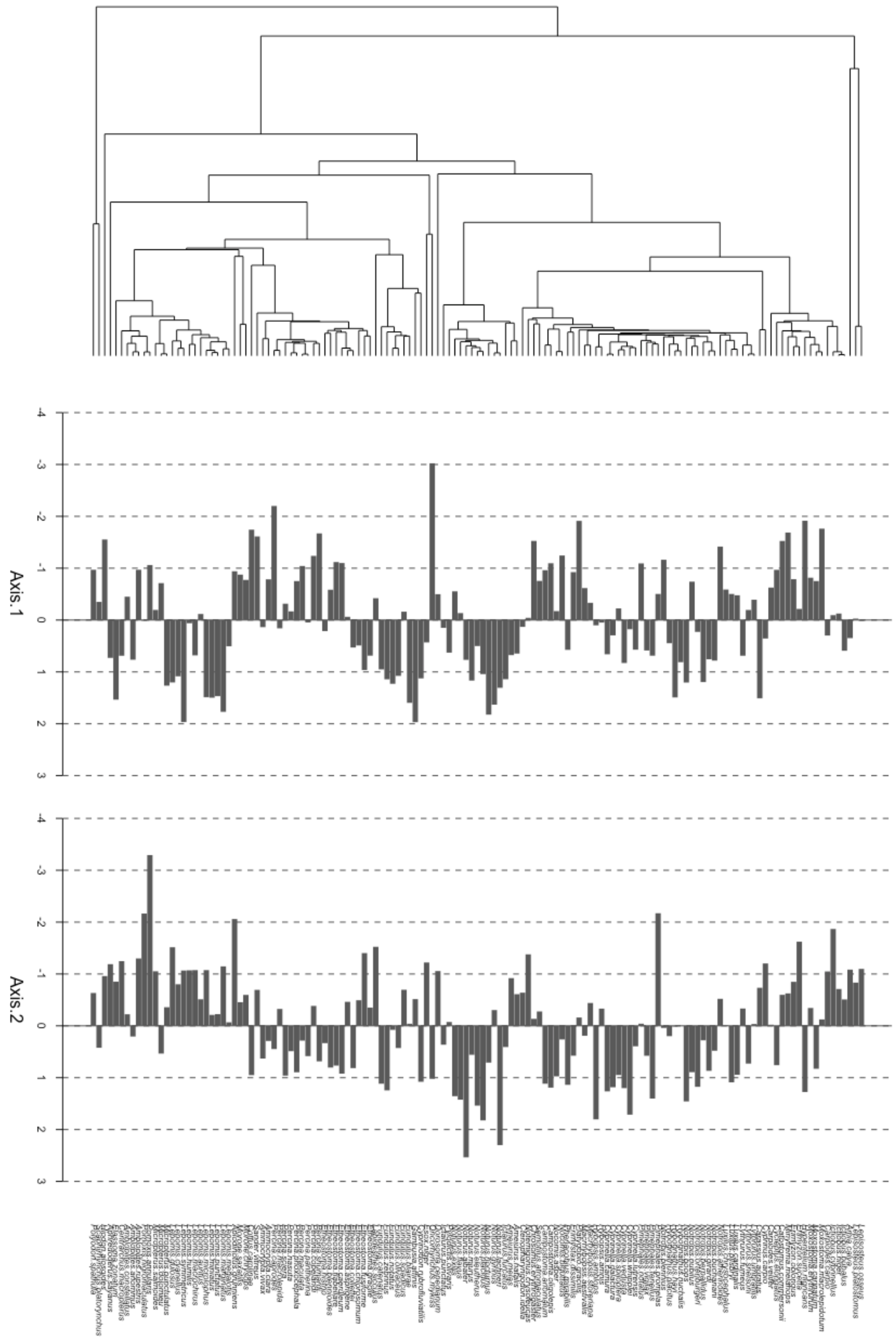


Figure S8. Environmental tolerance based PCoA axes values distributed across the phylogeny.

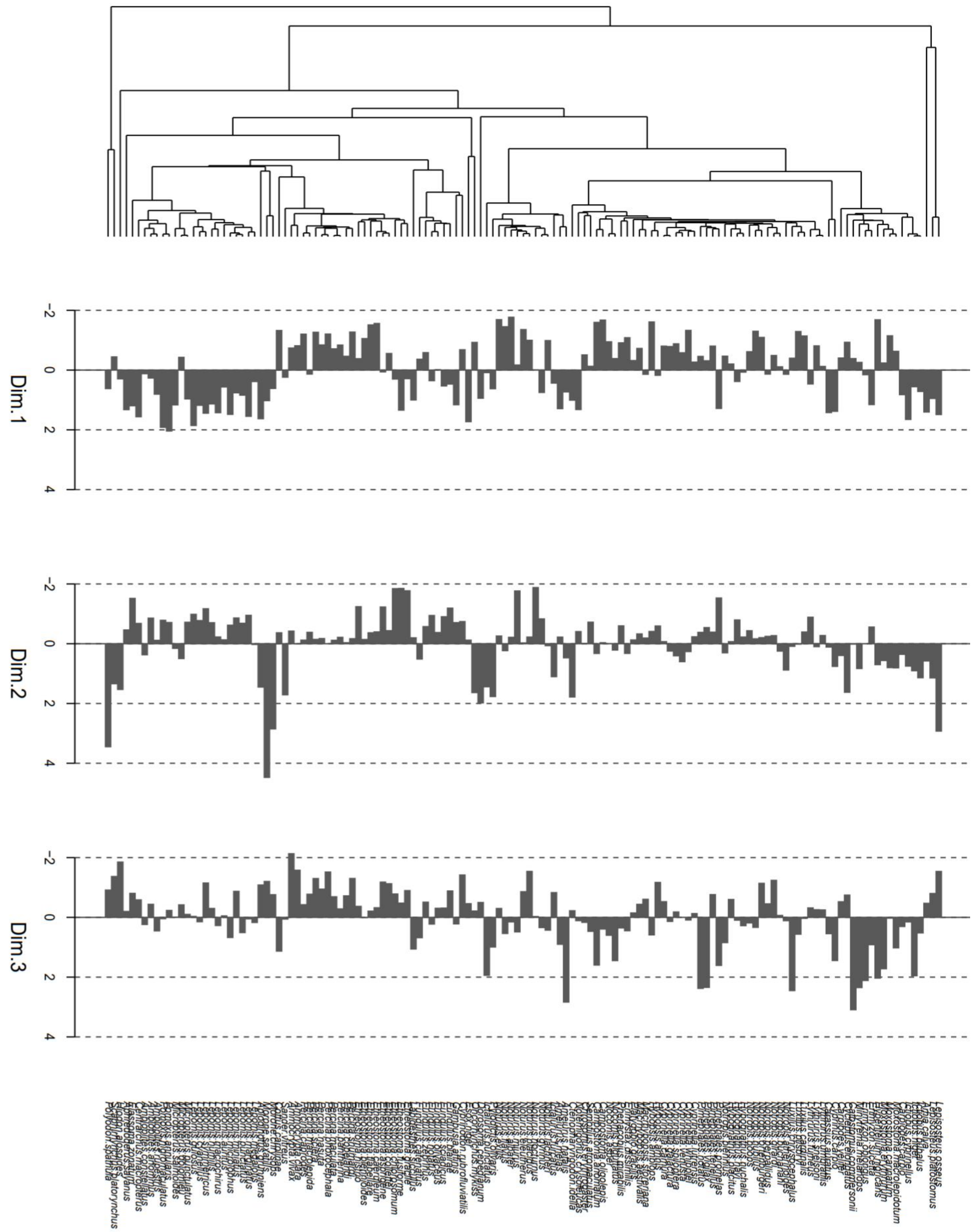


Figure S9. Global PCoA values distributed across the phylogeny. All values were phylogenetically conserved across the three axes ($K_{axis.1} = 0.96$, $K_{axis.2} = 0.13$, $K_{axis.3} = 0.15$ and all p values = 0.001).

SI.5. Environmental Drivers: Additional Methods

We collected environmental data for each site to investigate potential drivers of temporal changes in processes. First, we extracted 9 river network topology variables (the Strahler order for root node, number of headwater reaches, maximum and minimum elevation of the reach, slope of the reach, number of tributary junctions, the drainage area of the basin, the total length of network flowlines, and drainage density) using the R package 'Stream Network Tools' (Kopp and Allen 2019). We used a PCA, keeping the first axis for further use in our analysis, which represented 49.01% of the total variance. This axis was positively correlated with the number of headwater reaches, tributary junctions, area, order and river length so we use this axis as a proxy for the position of a given site along an upstream-downstream gradient (**Figure S10**).

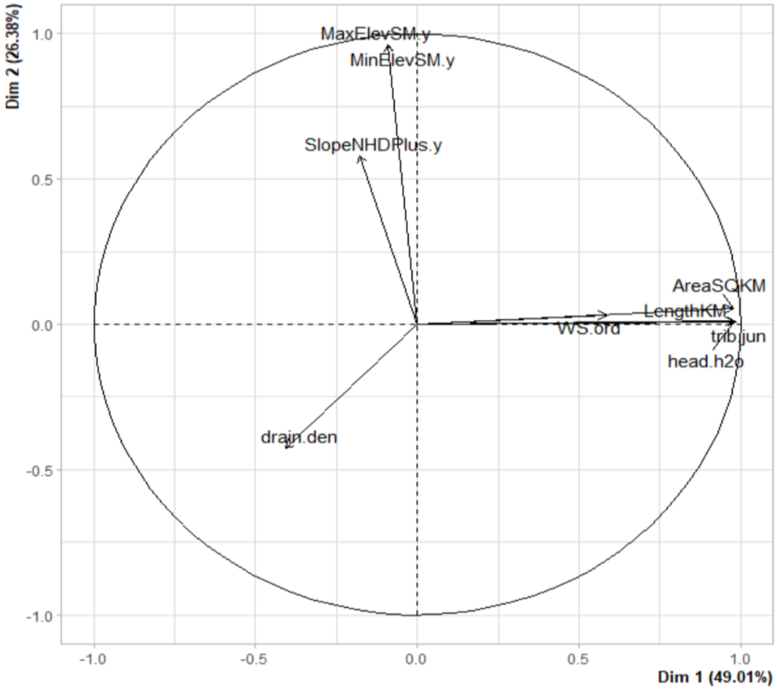


Figure S10. Environmental PCA from variables extracted from the Stream Network Tools package. Axis 1 explained 49% of the variance and is positively correlated with the number of headwater reaches, tributary junctions, area, order and river length. We therefore used this axis as a proxy of the upstream-downstream gradient to assess environmental drivers in our analyses. (The second axis is displayed here for graphical representation only but not used in our analyses)

We tested for multicollinearity between our environmental drivers within our linear models. We calculated variance inflation factors for each variable with "vif" in the 'car' package (Fox et al. 2022). All variance inflation factors were less than 2 (ΔTMAX: 1.34, ΔTRANGE: 1.22, ΔPREC 1.21, UP-DOWN1: 1.07 and UP-DOWN2: 1.18). Cutoff points for variance inflation factors range from 5 to 10 (Craney and Surles 2002), therefore we concluded we do not have to worry about multicollinearity.

SI.6. Functional Trait Correlations: Additional Methods

To understand how the different indices were associated with each other, we tested the correlations between ΔFR_{global} and $\Delta FR_{trophic}$, ΔFR_{env}, and ΔFR_{LHT} in addition to the correlations between ΔRao_{global} and $\Delta Rao_{trophic}$, ΔRao_{env}, and ΔRao_{LHT} with a Pearson correlation test. We also used Pearson correlation tests between the trends and the historical values of each index separately to investigate potential legacy effect of processes on the observed trends.

Similar patterns of high historical values associated with negative ΔSES and low historical values associated with positive ΔSES across all functional indices: trophic values ($\Delta FR_{trophic}$: $r = -0.37$, $p = 0.002$; $\Delta Rao_{trophic}$: $r = -0.39$, $p = 0.001$), life history values (ΔFR_{LHT}: $r = -0.62$, $p < 0.001$; ΔRao_{LHT}: $r = -0.63$, $p < 0.001$), environmental tolerance values (ΔFR_{env} : $r = -0.30$, $p = 0.001$; ΔRao_{env}: $r = -0.34$, $p =0.004$), and all traits together (ΔFR_{global} : $r = -0.49$, $p < 0.001$; ΔRao_{global}: $r = -0.63$, $p < 0.001$; **Figure 3**).

The most common change for all functional indices was either a decreased effect in under-dispersion ($\Delta FR_{trophic}$ 39% and ΔFR_{env} 23% of sites, respectively) or increased effect of under-dispersion (ΔFR_{LHT} 32%; $\Delta Rao_{trophic}$ 42%; ΔRao_{LHT} 49%; ΔRao_{env} 33%).

When exploring changes in assembly rules, only life history traits showed a higher or equal percentage of sites shifting from over-dispersion to under-dispersion (ΔFR_{LHT}: 6% under-dispersion to over-dispersion and 7% over-dispersion to under-dispersion; ΔRao_{LHT}: 1% under-dispersion to over-dispersion and 1% over-dispersion to under-dispersion). Conversely, trophic traits and environmental traits had more sites shifting from under-dispersion to over-dispersion ($\Delta FR_{trophic}$: 14% under-dispersion to over-dispersion and 3% over-dispersion to under-dispersion; $\Delta Rao_{trophic}$:10% under-dispersion to over-dispersion and 7% over-dispersion to under-dispersion; ΔFR_{env}: 20% under-dispersion to over-dispersion and 14% over-dispersion to under-dispersion; ΔRao_{env}: 14% under-dispersion to over-dispersion and 6% over-dispersion to under-dispersion). Life history traits showed the most consistency with global trends (**Figure S11**).

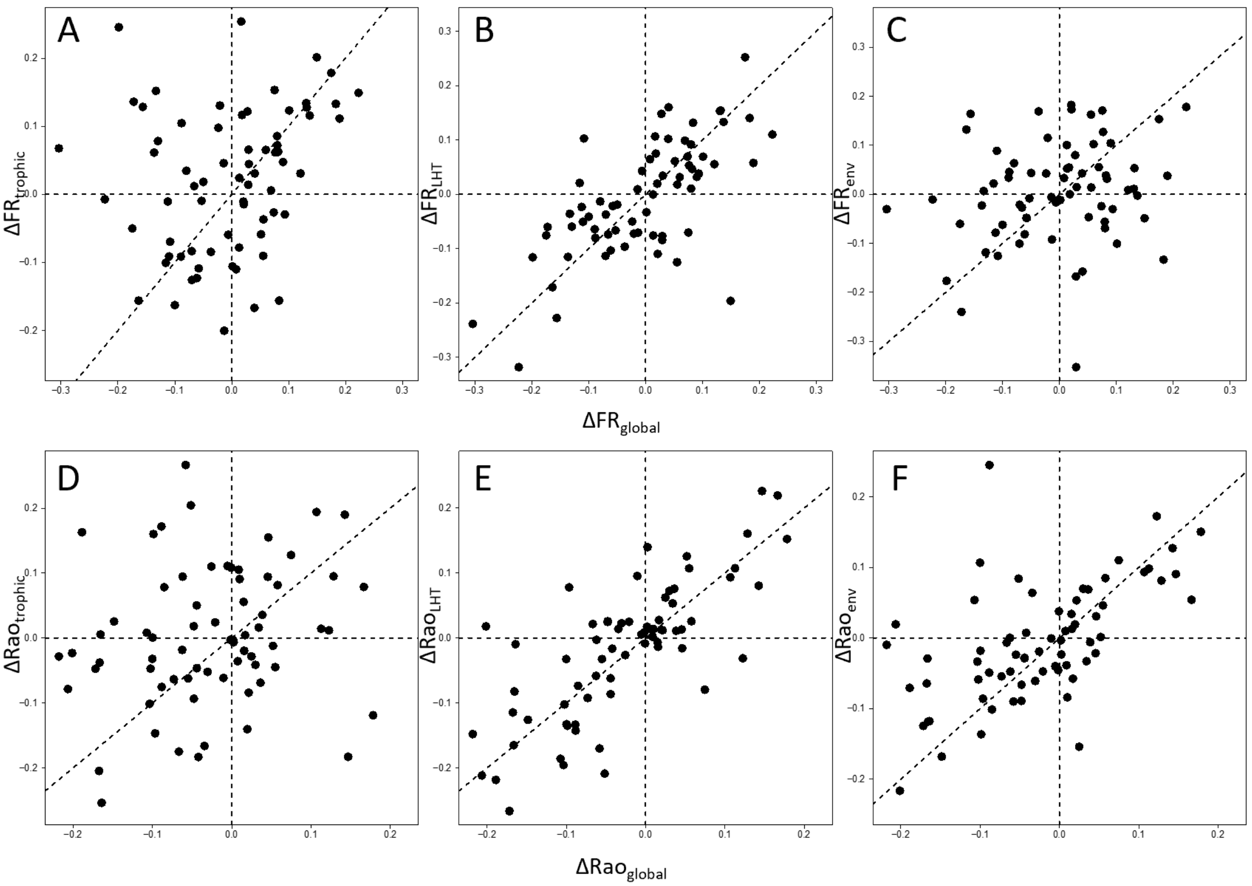


Figure S11. ΔFR_{global} compared across the three trait categories: (A) $\Delta FR_{trophic}$, (B) ΔFR_{LHT}, and (C) $\Delta FR_{environ}$ and ΔRao_{global} compared to (D) $\Delta Rao_{trophic}$, (E) ΔRao_{LHT}, and (F) $\Delta Rao_{environ}$. Each point represents a site, with the 1:1 line indicating no difference in trends between FR and the corresponding trait category.

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CHAPTER 3 SUPPLEMENTAL INFORMATION

S.I.1 Study Sites

To quantify the influence of wetting and drying regimes on biological communities in non-perennial streams, we analyzed macroinvertebrate, soft-bodied algae, and diatom data across 20 streams in Southern California (**Table S.I.1**). Data are available through the California Environmental Data Exchange Network (CEDEN, www.ceden.org).

Table S.I.1. Site locations for the 20 sites included in the study.

Station Code	**Latitude**	**Longitude**
901BELOLV	33.64	-117.55
901NP9FLC	33.68	-117.54
901NP9HJC	33.68	-117.52
901NP9LCC	33.63	-117.43
903ACPCT1	33.30	-116.64
903CVPCT	33.27	-116.64
903NP9SLR	33.35	-116.67
903SLFRCx	33.34	-116.88
903WE0798	33.34	-116.83
905DGCC1x	33.16	-116.84
905SDBDN9	33.09	-116.90
909S00282	32.87	-116.61
909SWCASR	32.94	-116.55
911COPPER	32.56	-116.83
911KCKCRx	32.79	-116.45
911NP9ATC	32.77	-116.42
911NP9UCW	32.82	-116.49
911S00858	32.90	-116.49
911TJKC1x	32.76	-116.45
911TJLCC2	32.78	-116.44

S.I.2 Example Hydrographs

We created a hydrograph for each event to correct for any "false starts" where water rewetted a stream for less than ten days before drying again. One event (site number 905DGCC1x) did not have a previous wet event that lasted longer than ten days, thus we did not calculate recession slope from this event. All other samples had enough logger data to calculate all hydrologic metrics. Presented here are examples of hydrographs with important dates highlighted showing different scenarios: a straight-forward hydrograph (**Figure S.I.1**), a hydrograph with no false starts during the dry period (**Figure S.I.2**), and a hydrograph that required a manually defined Rewet Date (**Figure S.I.3**).

Gray lines indicate the start date of the event, defined as the earliest day of the previous wet period captured by the loggers. Green lines represent the peak day of the previous wetting event and red lines indicate the Dry Date, the first day that the previous event went dry. The Recession Slope was calculated as the rate of change between the green (peak) and red lines (Dry Date). Light blue lines show the First Wet Date while dark blue lines represent the Rewet Date. Purple lines indicate the date where the Peak Depth was reached. Finally, the black lines show when the samples were taken. These dates were largely used to calculate the other metrics in **Table 1**. All plots demonstrate the water level in meters on the corresponding days.

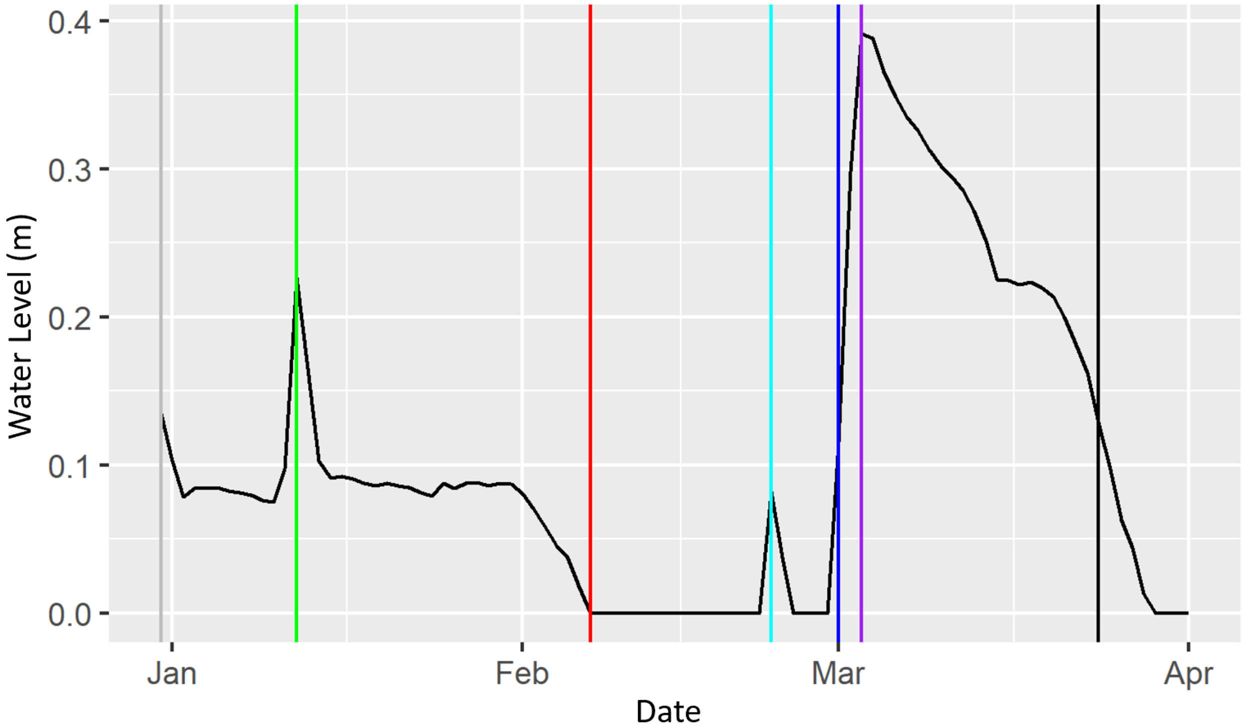

Figure S.I.1. Hydrograph for site 911COPPER with a March sampling date. Example hydrograph with one "false start" during the dry duration.

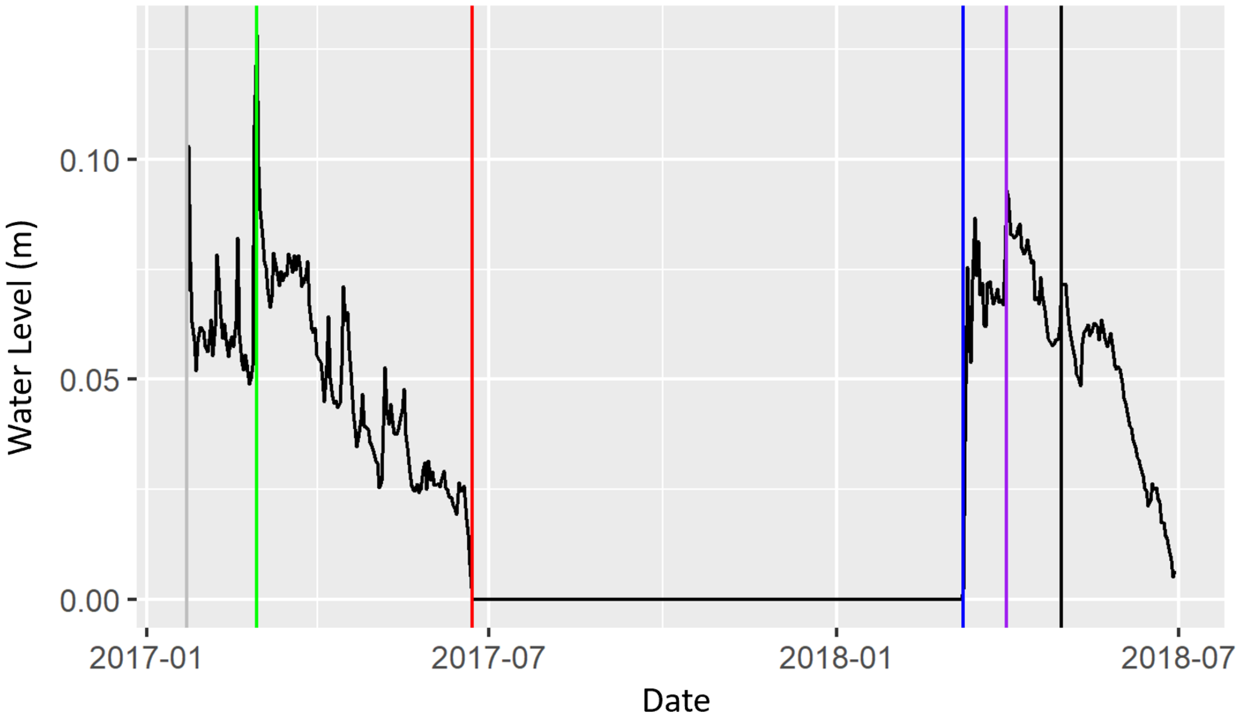

Figure S.I.2. Hydrograph for site 903CVPCT with an August sampling date. Example hydrograph with no "false starts" during the dry duration, as shown by the absence of a light blue line.

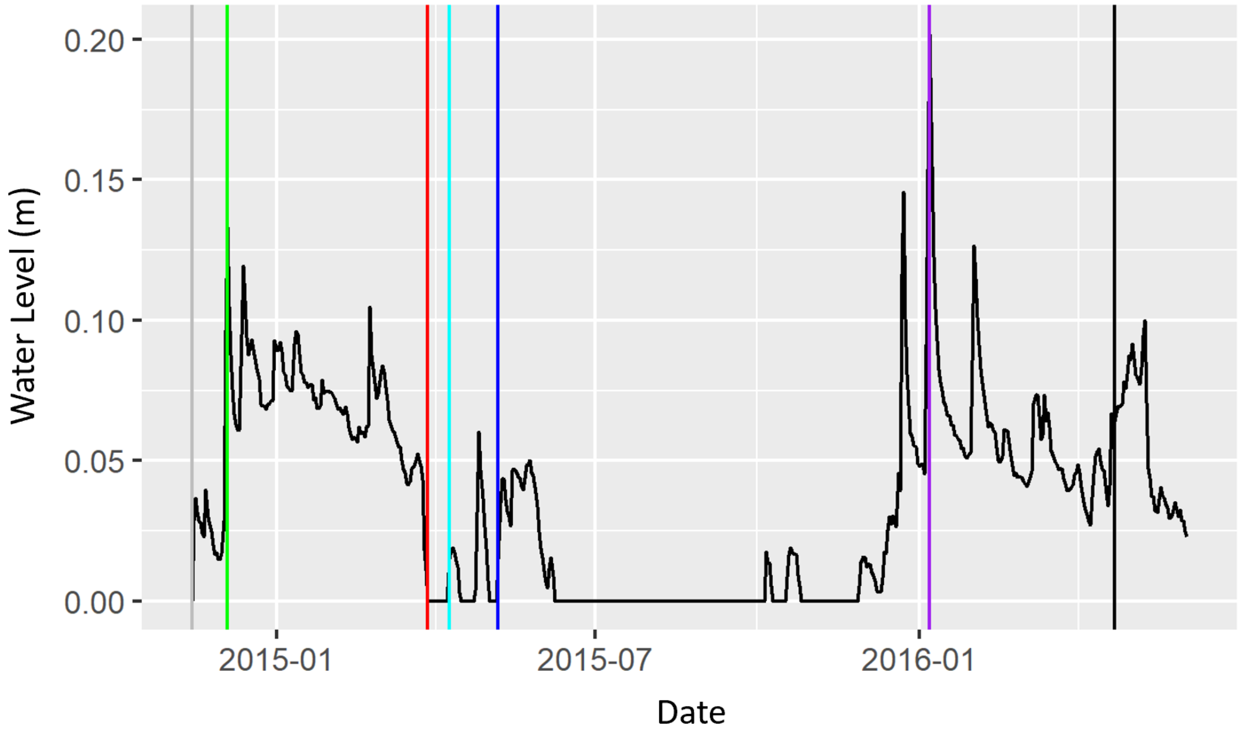

Figure S.I.3. Hydrograph for site 901NP9FLC with an April sampling date. Example hydrograph that required a manual definition of the Rewet Date. Note that there was a period of wetting for at least ten days before the wetting event of interest (which contains the Sample Date) as noted by the position of the dark blue line. For these drying and subsequent wetting events, the Rewet Date was manually set as the first day of the wetting event of interest using the interactive “dygraphs” package. In this example, the dry period contained five false starts.

S.I.3 Correlated Variables

In total, we calculated 15 hydrologic variables to better understand what hydrologic variables influence BMI, algae, and diatom assemblages. We calculated the Dry Duration, Peak Depth, Peak to Sample Duration, Peak to Sample Slope, Proportion of Dry Days, Proportion of Wet Days, the Recession Coefficient (along with it's modeled R^2 value, Recession R^2), Recession Slope, False Starts per Duration, Time to Peak, Rewet Slope, and Wet Duration.

In addition to these hydrologic metrics, we included environmental data collected during the sampling collection: alkalinity (as CaCO3), pH, specific conductivity, temperature, percent canopy cover, station water depth, wetted width, and the percentage of the reach comprised of riffles, pools, and runs. Other water chemistry variables, such as nitrogen and phosphorus amounts, were excluded in 25% of the samples and were therefore excluded from all analyses.

For analyses, we checked Pearson correlations between all the variables listed above and removed variables that were >0.70 or <-0.70 correlated (Price et al. 2021) using the performance package (Lüdecke et al. 2022). Wet Duration was correlated with Peak to Sample Duration (0.79), Rewet Date (-0.90), and the Proportion of Dry (-0.70) and Wet (0.70) days. We chose to keep the Wet Duration in favor of the other three hydrologic variables as we hypothesized Wet Duration to have the largest influence on assemblages. In addition, the proportion of pools was correlated to station water depth (0.79). Because we calculated Peak Depth via the logger information, we removed station water depth prior to further analyses. In addition, of the 27 events, 12 of the R^2 values of the Recession Coefficient had a value < 0.10 (44.4% of all events). Due to the low explanatory value of the linear model, we removed Recession Coefficient (along with Recession R^2) and used Recession Slope to assess how the rate of drying influenced biodiversity.

In total, ten hydrologic metrics were used in subsequent analyses: Dry Date, Dry Duration, False Starts per Duration, First Wet Date, Peak Date, Peak Depth, Peak to Sample Slope, Recession Slope, Rewet Date, Wet Duration, (**Figure 1; Table 1**).

S.I.4 Linear Models - Effects of Year, Repeated Samples

In total, we found 27 biological sampling events (including samples of benthic macroinvertebrates, algae, and diatoms) that overlapped with hydrologic data across 20 sites in southern California. Of these 27 events, 14 were repeated at 6 of the 20 sites (**Figure S.I.4**).

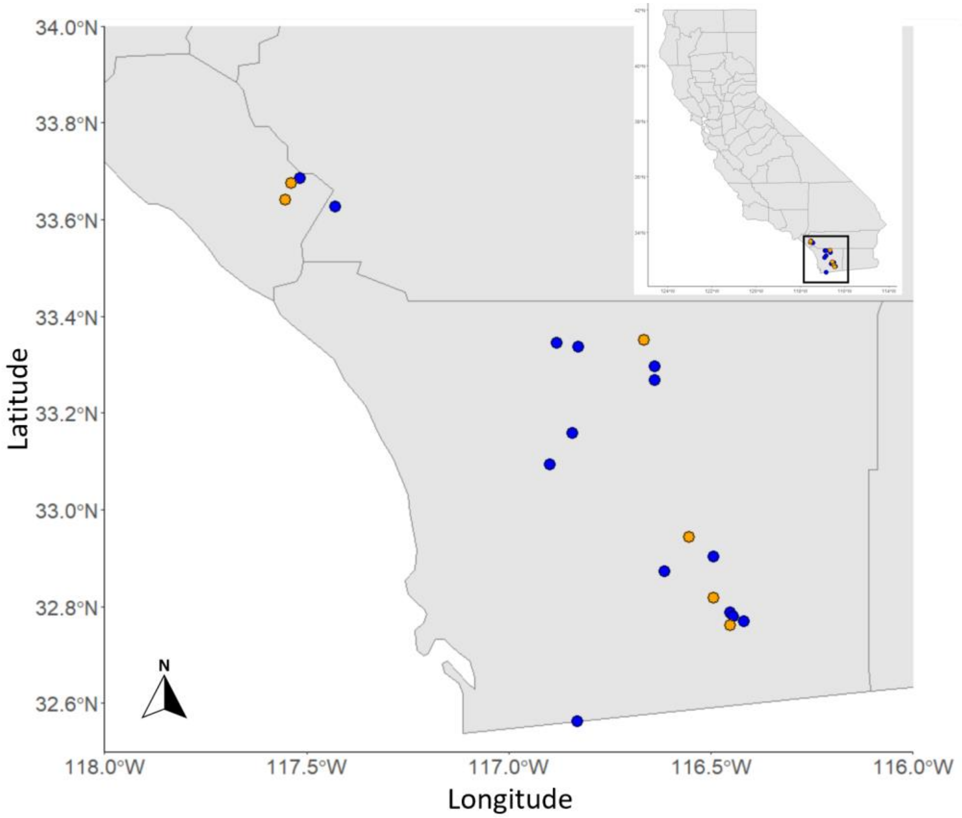

Figure S.I.4. Map of study sites within the State of California. Sites in orange are the six sites with repeated samples used to test for the impacts of year on biodiversity.

To test for sample independence, we selected only these six sites and ran the global linear models (which included all 10 hydrologic metrics as predictors) on this subset of data. We ran linear models without random effects in addition to linear models with site id as a random effect, although the models with site id as a random effect produced more warnings and errors. Year had a significant effect on algae Hill-Shannon diversity values, however, with the addition of site as a random effect, year no longer predicted algal Hill-Shannon diversity (**Table S.I.2**). The lack of significance of year within these models suggests some degree of independence year to year.

Table S.I.2. Summary table for linear models run for the six sites with repeated samples including p-values, R^2 values, AICc, and p-values for year within the global models for richness without a random effect, richness with site as a random effect, Hill-Shannon without a random effect, and Hill-Shannon with site as a random effect.

	Macroinvertebrates			**Soft-Bodied Algae**			**Diatoms**		
	p-val	**R^2**	**AICc**	**p-val**	**R^2**	**AICc**	**p-val**	**R^2**	**AICc**
Richness	0.751	-0.074	112.785	0.755	-0.074	122.629	0.517	-0.044	120.438
Richness (1|site)	0.822	0.003	106.910	0.576	0.019	117.672	0.664	0.006	109.920
Hill-Shannon	0.6911	-0.069	104.21	0.379	-0.013	94.869	**0.041**	**0.070**	**90.829**
Hill-Shannon (1|site)	0.873	0.001	99.990	0.325	0.060	92.173	0.191	0.066	106.165

S.I.5 Effect of Year on Hydrologic Metrics and Environmental Variables

To explore how the 2012-2015 drought may have impacted the hydrology and environment, we ran linear models for each hydrologic metric and environmental variable with year as the predictor. We found year significantly predicted Peak Depth, Wet Duration, proportion of Riffle, and Wetted Width (**Table S.I.3**).

Table S.1.3. Summary of linear model results exploring the effects of year on each hydrologic metric (A) and environmental variable (B), sorted by p value. Significant results are bolded.

A. Hydrologic Predictor	**p-val**	**R^2**
Dry Date	0.42	-0.01
Dry Duration	0.22	0.22
False Starts Per Duration	0.41	-0.01
First Wet Date	0.58	-0.27
Peak Date	0.82	-0.04
Peak Depth	**0.00**	**0.55**
Peak-to-Sample Slope	0.80	-0.03
Recession Slope	0.32	0.00
Rewet Slope	0.24	0.02
Wet Duration	**0.00**	**0.33**

B. Environmental Variable	**p-val**	**R^2**
Alkalinity	0.67	-0.03
Canopy Cover	0.17	0.04
pH	0.52	-0.02
Pool	0.27	0.01
Riffle	**0.00**	**0.32**
Run	0.40	-0.01

Specific Conductivity	0.49	-0.02
Temperature	0.42	-0.01
Wetted Width	**0.01**	**0.20**

S.I.6 Results - Biologic Diversity, Common and Rare Taxa

Across the 27 events sampled, we found 152 macroinvertebrate species. We found 12 taxa during at least 70% of all sampling events, 9 of which are in the family Chironomidae, 10 in the order Diptera, and 1 in the order Ephemeroptera (at least 19 sampling events; Corynoneura (family Chironomidae), 92.5% of all events; Parametriocnemus (family Chironomidae), 92.5%; Simulium (family Simuliidae), 88.9%; Eukiefferiella (family Chironomidae), 85.2%; Micropsectra (family Chironomidae), 85.5%; Zavrelimya-Paramerina (family Chironomidae), 85.2%; Baetis (family Baetidae), 81.5%; Orthocladinnae (family Chironomidae), 81.5%; Tanypodinae (family Chironomidae), 81.5%; Brillia (family Chironomidae), 81.5%, Oligochaeta, 81.5%, and Thienemanniella (family Chironomidae), 81.5%). Conversely, we found 51 taxa present at only 1 sampling event (3.7% of all sampling events). Across all samples, the maximum richness was 52 in 2016 and the minimum was 13 in 2015.

The final 27 events had 207 algal species. We found four taxa during at least 70% of all sampling events (*Heteroleibleinia sp1* (family Pseudanabaenaceae), 96.3%; *Chroococcus minmus* (family Chroococcaceae), 77.8%; *Aphanocapsa delicatissima* (family Merismopediaceae), 70.4%; and *Aphanothece minutissima* (family Aphanothecaceae), 70.4%) and 89 taxa present during only one sampling event. The maximum number of species found in the quantitative samples was 62 in 2016 and the minimum was 5 species in 2017.

Finally, we found 225 diatom species across all samples. We found 10 taxa during at least 70% of all sampling events (at least 19 sampling events; *Planothidium frequentissimum* (family Achnanthidiaceae), 92.6%; *Planothidium lanceolatum* (family Achnanthidiaceae), 92.6%; *Achnanthidium minutissimum* (family Achnanthidiaceae), 85.2%; *Ulnaria ulna* (family Fragilariaceae), 85.2%; *Nitzschia linearis* (family Bacillariaceae), 77.8%; *Nitzschia palea* (family Bacillariaceae), 77.8%; *Cocconeis placentula* (family Cocconeidaceae), 74.1%; *Halamphora veneta* (family Amphipleuraceae), 74.1%; *Gomphonema micropus* (family Gomphonemataceae), 74.1%; and *Navicula veneta* (family Naviculaeceae), 74.1%). We found 100 taxa during only one sampling event (3.7%). Maximum richness was 69 (2016) and minimum richness was 16 (2016).

S.I.7 Results - Hill-Shannon Diversity Linear Models

Algal linear models for Hill-Shannon diversity included only quantitative samples, but linear models for algal richness included both quantitative and qualitative samples.

As with richness models, the Null model was the most significant for all assemblages (**Table S.I.4**). Richness (**Table 5**) and Hill-Shannon model results were similar, with Dry Date predicting diatom Hill-Shannon Diversity and no significant predictors of macroinvertebrate or algal richness.

Table SI.4. Results from linear models of hydrologic metrics and assemblage Hill-Shannon Diversity. Columns indicate R^2 and AICc values. Bolded values with $p < 0.05$.

	Benthic Macroinvertebrates		**Soft-Bodied Algae**		**Diatoms**	
Hydrologic Predictor	**R2**	**AICc**	**R2**	**AICc**	**R2**	**AICc**
Dry Date	-0.04	180.09	-0.03	163.45	**0.22**	**197.32**
Dry Duration	-0.02	179.69	-0.02	163.28	0.08	201.80
False Starts Per Duration	0.03	178.39	-0.04	163.67	-0.04	205.03
First Wet Date	0.02	178.45	-0.04	163.68	0.01	203.82
Peak Date	0.00	178.97	-0.01	162.92	-0.03	204.84
Peak Depth	-0.02	179.65	-0.04	163.74	0.00	204.01
Peak-to-Sample Slope	-0.04	180.13	-0.03	163.48	0.02	203.55
Recession Slope	0.00	173.56	-0.04	159.00	-0.02	198.24
Rewet Date	-0.03	179.78	0.00	162.71	0.06	202.64
Total Rewet	-0.03	179.88	-0.04	163.77	0.00	204.09
Global	-0.03	209.64	0.27	200.06	0.16	228.33
Null		**177.60**		**161.25**		**202.52**

References

Lüdecke D, Makowski D, Ben-Shachar MS, Patil I, Waggoner P, Wiernik BM, Arel-Bundock V, Thériault R, Jullum M. 2022. performance: Assessment of Regression Models Performance. https://CRAN.R-project.org/package=performance

CHAPTER 4 SUPPLEMENTAL INFORMATION

S.I.1 Site Locations

We sampled four rivers within the Ouachita Highlands in southeastern Oklahoma: the Kiamichi, Little, Glover, and Mountain Fork Rivers. This region is largely contained within the Ouachita Mountain ecoregion, expanding from southeastern Oklahoma to central Arkansas. We conducted field surveys at five sites below and five sites above the dams located on each river. We selected sites based on physical site similarity (substrate type, gradient, and flow) and site accessibility (**Table S.I.1**).

Table S.I.1. Locations of each site along the four rivers included in the study. One site along the upper portion of the Mountain Fork River had significantly reduced taxonomic richness and was excluded in analyses (marked with *).

River	Dam Location	Longitude	Latitude	Distance from Dam (km)
Glover	upstream	-94.941	34.319	NA
Glover	upstream	-94.936	34.313	NA
Glover	upstream	-94.954	34.295	NA
Glover	upstream	-94.954	34.293	NA
Glover	upstream	-94.915	34.255	NA
Glover	downstream	-94.888	34.109	NA
Glover	downstream	-94.901	34.103	NA
Glover	downstream	-94.899	34.092	NA
Glover	downstream	-94.903	34.073	NA
Glover	downstream	-94.907	34.065	NA
Kiamichi	upstream	-95.056	34.657	-32.808
Kiamichi	upstream	-95.092	34.636	-27.787
Kiamichi	upstream	-95.143	34.630	-21.692

Kiamichi	upstream	-95.200	34.627	-15.820
Kiamichi	upstream	-95.260	34.611	-8.492
Kiamichi	downstream	-95.343	34.574	3.385
Kiamichi	downstream	-95.409	34.555	10.735
Kiamichi	downstream	-95.457	34.537	16.954
Kiamichi	downstream	-95.473	34.516	21.229
Kiamichi	downstream	-95.511	34.506	25.678
Kiamichi	dam	-95.336	34.597	0.000
Little	upstream	-95.199	34.325	-33.811
Little	upstream	-95.186	34.320	-32.342
Little	upstream	-95.184	34.308	-30.635
Little	upstream	-95.179	34.305	-28.707
Little	upstream	-95.148	34.263	-20.986
Little	downstream	-95.078	34.110	0.278
Little	downstream	-95.064	34.087	3.326
Little	downstream	-95.042	34.055	8.015
Little	downstream	-95.024	34.048	11.696
Little	downstream	-95.001	34.034	17.553
Little	dam	-95.079	34.113	0.000
Mountain Fork	upstream	-94.532	34.462	-67.715
Mountain Fork	upstream	-94.628	34.460	-55.956
Mountain Fork	upstream	-94.635	34.461	-55.163
Mountain Fork	upstream	-94.657	34.442	-49.322

Mountain Fork*	upstream*	-94.673*	34.403*	-44.253*
Mountain Fork	downstream	-94.696	34.143	1.250
Mountain Fork	downstream	-94.625	34.069	16.102
Mountain Fork	downstream	-94.617	34.048	18.574
Mountain Fork	downstream	-94.605	34.023	22.110
Mountain Fork	downstream	-94.605	34.010	25.013
Mountain Fork	dam	-94.684	34.145	0.000

S.I.2 Environmental PCA Loadings

For the abiotic habitat and land use categories, we ran PCAs with scaled and centered predictors using the “stats” package (R Core Team, 2020b). We then rotated each axis and selected the predictor with the greatest loading. To keep a consistent number of variables across each category described above, we only selected from the first three PCA axes (abiotic habitat PC1: 0.297, PC2: 0.181, PC3: 0.114, cumulative: 0.592, **Table S.I.2**; land use PC1: 0.544, PC2: 0.238; PC3: 0.121; cumulative: 0.903, **Table S.I.3**). From the abiotic habitat, we selected flow (PC1 0.692), canopy cover (PC3 -0.789), and temperature (PC2 0.991; **Table S.I.2**). From land use data, we selected the proportion of the watershed covered by forest (PC1 -0.673), wetlands (PC2 0.594) and open (PC3 -0.985; **Table S.I.3**). However, the proportion of open land use was correlated with river distance (r = 0.79). As we were interested in examining how distance from dams may influence taxa, we selected developed land, the predictor with the highest loading from the fourth PCA axis (variance 0.091). The proportions of developed vs wetland land cover were also correlated (r = 0.72). As developed land cover has been shown to influence macroinvertebrate assemblages (Mello *et al.*, 2018; Luo *et al.*, 2020) and forested land cover was already selected, we kept agricultural land cover (loading = 0.579), the second largest loading from PC2.

Table S.I.2. Loadings of abiotic habitat predictor variables for the PCA axes that explained at least 90% of the variation among sites. The overall proportion of variance and cumulative variance are included at the bottom of the table.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Temperature (°C)			**0.911**				
pH	-0.188			-0.583	0.115		
Specific Conductivity (µS/cm)	0.127			-0.771	-0.166		
Large Woody Debris (%)		-0.612	0.165	0.112	-0.129	0.293	0.168
Depth (m)	0.627		0.146				
Flow (m/s)	**0.692**		-0.204	0.101			

Wetted Channel Width (m)	0.223		0.209	-0.151	0.384	0.376	-0.535
Canopy Cover (%)		**-0.789**	-0.136			-0.226	-0.121
Bankfull Width (m)	-0.126			0.104	-0.188	-0.126	-0.809
Riffle Proportion (%)						-0.827	
Substrate Index					0.864		0.107
Proportion of Variance	0.297	0.112	0.057	0.181	0.114	0.099	0.053
Cumulative Proportion	0.297	0.704	0.859	0.478	0.592	0.802	0.912

Table S.I.3. Loadings of land cover and land use predictor variables for each PCA axes. The overall proportion of variance and cumulative variance are included at the bottom of the table.

	PC1	PC2	PC3	PC4
Developed (%)	0.51	-0.18		**-0.838**
Forest (%)	**-0.673**	-0.49	0.104	-0.334
Agriculture (%)	-0.164	**0.579**		-0.282
Wetlands (%)		0.594		-0.163
Miscellaneous Habitat (%)	0.503	-0.195		0.283
Open Habitat (%)			-0.985	
Proportion of Variance	0.544	0.238	0.121	0.091
Cumulative Proportion	0.544	0.782	0.903	0.994

S.I.3. Environmental Variables

Based on PCA axes, predictor loadings, and tests of multicollinearity, we selected 10 environmental variables: temperature, flow, canopy cover, seston AFDM, surber AFDM, chlorophyll *a*, distance of each site to the dam, and proportion of land cover that is developed, forested, and agricultural. Mean water temperatures were fairly consistent across the Kiamichi, Little, and Glover Rivers, while temperatures in the Mountain Fork were generally lower (**Table S.I.4**). Flows in the Kiamichi (mean = 0.87 ∓ 0.284 m/s) and Mountain Fork (mean = 1.18 ∓ 0.293 m/s) were higher than the Little (mean = 0.17 ∓ 0.129 m/s) and Glover (mean = 0.17 ∓ 0.100 m/s), likely related to the difference in rainfall in sampling years (2019 and 2018, respectively). Land cover proportions were similar across the four rivers; the Glover had the highest percent of developed land (4.7%), the Little had the highest percent forested (86.3%) and the Kiamichi had the highest percent devoted to agriculture (13.8%). Finally, seston AFDM values were consistently low for each river, while the amount of AFDM found in surber samples was lowest in the Glover (mean = 30.86 ∓ 21.395 g/m^2) and highest in the Little (mean = 66.38 ∓ 12.024 g/m^2; Mountain Fork mean = 55.16 ∓ 41.899 g/m^2; Kiamichi mean = 52.07 ∓ 44.617 g/m^2).

Table S.I.4. Summary statistics for the environmental variables selected across each river.

	Kiamichi			Little			Glover			Mountain Fork		
	Minimum	Mean (±SD)	Maximum	Minimum	Mean (±SD)	Maximum	Minimum	Mean (±SD)	Maximum	Minimum	Mean (±SD)	Maximum
Temperature (°C)	28	29.7 (1.06)	31	23.3	29.1 (3.22)	32	26.5	29.5 (1.94)	32.5	22	26.9 (4.55)	32
Flow (m/s)	0.53	0.87 (0.28)	1.41	0.04	0.17 (0.13)	0.48	0.02	0.17 (0.10)	0.39	0.81	1.18 (0.29)	1.76
Canopy Cover (%)	0	5.13 (5.65)	16.93	0	16.38 (12.02)	31.9	0	7.61 (10.14)	31.75	0.33	14.36 (20.58)	68.6
Seston AFDM (g/L)	2.33E-05	7.04E-05 (6.79E-05)	2.18E-04	2.31E-06	9.04E-05 (9.99E-05)	3.28E-04	2.04E-05	6.00E-05 (3.38E-05)	1.41E-04	3.34E-05	8.99E-05 (5.71E-05)	2.09E-04
Surber AFDM (g/m^2)	5.09	52.07 (44.62)	160.76	12.64	66.87 (45.78)	150.92	5.17	30.86 (21.40)	68.93	7.35	55.16 (41.90)	138.96
Chl A (g/m^2)	0.01	0.02 (0.02)	0.06	0.01	0.03 (0.02)	0.08	0.03	0.07 (0.40)	0.15	0.01	0.03 (0.018)	0.06
Developed	0.02	0.0 2 (0.14)	0.03	0.03	0.03 (0.17)	0.03	0.05	0.05 (0.07)	0.05	0.03	0.03 (0.12)	0.03
Forest	0.72	0.73 (1.17)	0.76	0.72	0.86 (1.19)	0.79	0.69	0.72 (2.07)	0.74	0.78	0.79 (0.82)	0.81
Agriculture	0.13	0.14 (0.32)	0.14	0.02	0.03 (2.66)	0.05	0.04	0.05 (1.28)	0.07	0.06	0.07 (1.55)	0.1
Distance (km)	-32.81	-2.86 (21.30)	25.68	-33.81	-10.56 (20.54)	17.55	-53.31	-31.38 (19.82)	-9.39	-67.71	-18.84 (38.42)	25.01

We found significant differences between temperature, canopy cover, AFDM in surber samples, and river distances (**Table S.I.5**). Temperature differences appeared to be driven by differences between upstream and downstream sites on the Mountain Fork River (z.ratio = -2.38, p = 0.017;

Table S.I.6). Differences in canopy cover occurred across multiple river comparisons and site types (**Tables S.I.7**, **S.I.8**). Similarly, differences in AFDM found in surber samples were driven by differences across upstream sites of the Glover River compared to the other three dammed rivers (**Tables S.I.9**, **S.I.10**). There were also significant differences between upstream and downstream sites within all four rivers (**Table S.I.11**). Upstream distances from dams were significantly different between the Mountain Fork River and the other two dammed rivers (Mt. Fork / Kiamichi: t.ratio = 6.631, $p < 0.01$; Mt. Fork / Little: t-ratio = 5.15, $p < 0.01$). In addition, significant differences were found across all rivers and their upstream and downstream sections (Kiamichi: t.ratio = 7.269, $p < 0.01$; Little: t.ratio = 7.38, $p < 0.01$; Mountain Fork River: t.ratio = 13.67, $p < 0.01$; **Table S.I.12**). We found no significant differences among flow, seston AFDM, chlorophyll *a* AFDM, and proportions of land cover (**Tables S.I.13-18**).

Table S.I.5. Temperature differences among river and site type general linear model output. Comparisons with significant p values ($P < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**30.90**	**2.49**	**12.43**	**<2e-16**
Riverkiamichi	-1.30	3.48	-0.37	0.71
Riverlittle	-3.90	3.40	-1.15	0.25
Rivermtfork	**-8.24**	**3.27**	**-2.52**	**0.01**
Dam_Locationupstream	-2.75	3.44	-0.80	0.42
Riverkiamichi:Dam_Locationupstream	2.95	4.87	0.61	0.54
Riverlittle:Dam_Locationupstream	7.00	4.84	1.45	0.15
Rivermtfork:Dam_Locationupstream	**11.09**	**4.91**	**2.26**	**0.02**

Table S.I.6. Emmeans post-hoc results for differences in temperature. Comparisons with significant p values (P < 0.05) are bolded.

Contrast	Estimate	Standard Error	Degrees Freedom	Z Ratio	P Value
Dam_Location = downstream:					
glover - kiamichi	1.30	3.48	Inf	0.37	0.98
glover - little	3.90	3.40	Inf	1.15	0.66
glover - mtfork	8.24	3.27	Inf	2.52	0.06
kiamichi - little	2.60	3.36	Inf	0.77	0.87
kiamichi - mtfork	6.94	3.23	Inf	2.15	0.14
little - mtfork	4.34	3.15	Inf	1.38	0.51
Dam_Location = upstream:					
glover - kiamichi	-1.65	3.40	Inf	-0.49	0.96
glover - little	-3.10	3.45	Inf	-0.90	0.81
glover - mtfork	-2.85	3.66	Inf	-0.78	0.86
kiamichi - little	-1.45	3.49	Inf	-0.42	0.98
kiamichi - mtfork	-1.20	3.70	Inf	-0.32	0.99
little - mtfork	0.25	3.74	Inf	0.07	1.00
River = Glover:					
downstream - upstream	2.75	3.44	Inf	0.80	0.42
River = Kiamichi:					
downstream - upstream	-0.20	3.45	Inf	-0.06	0.95
River = Little:					
downstream - upstream	-4.25	3.41	Inf	-1.25	0.21

River = Mountain Fork:					
downstream - upstream	**-8.34**	**3.50**	**Inf**	**-2.38**	**0.02**

Table S.I.7. Canopy cover differences among river and site type general linear model output. Comparisons with significant p values (P < 0.05) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**2.25**	**0.15**	**15.52**	**< 2e-16**
Riverkiamichi	**-1.38**	**0.32**	**-4.26**	**0.00**
Riverlittle	**0.77**	**0.18**	**4.36**	**0.00**
Rivermtfork	**0.82**	**0.17**	**4.68**	**0.00**
Dam_Locationupstream	**-0.51**	**0.24**	**-2.15**	**0.03**
Riverkiamichi:Dam_Locationupstream	**1.70**	**0.41**	**4.18**	**0.00**
Riverlittle:Dam_Locationupstream	0.00	0.29	0.01	0.99
Rivermtfork:Dam_Locationupstream	**-0.71**	**0.32**	**-2.18**	**0.03**

Table S.I.8. Emmeans post-hoc results for differences in canopy cover. Comparisons with significant p values (P < 0.05) are bolded.

Contrast	Estimate	Standard Error	Degrees Freedom	Z Ratio	P Value
Dam_Location = downstream					
glover - kiamichi	-1.46	1.10	Inf	-1.33	0.54

glover - little	0.06	1.42	Inf	0.04	1.00
glover - mtfork	-1.75	1.07	Inf	-1.63	0.36
kiamichi - little	1.52	1.13	Inf	1.35	0.53
kiamichi - mtfork	-0.29	0.63	Inf	-0.45	0.97
little - mtfork	-1.81	1.10	Inf	-1.64	0.35
Dam_Location = upstream					
glover - kiamichi	-1.89	1.34	Inf	-1.42	0.49
glover - little	-0.15	1.70	Inf	-0.09	1.00
glover - mtfork	-2.08	1.34	Inf	-1.56	0.40
kiamichi - little	1.75	1.25	Inf	1.39	0.50
kiamichi - mtfork	-0.19	0.69	Inf	-0.28	0.99
little - mtfork	-1.94	1.26	Inf	-1.54	0.41
River = Glover:					
downstream - upstream	0.46	1.59	Inf	0.29	0.77
River = Kiamichi:					
downstream - upstream	0.03	0.68	Inf	0.04	0.97
River = Little:					
downstream - upstream	0.25	1.54	Inf	0.17	0.87
River = Mountain Fork:					
downstream -	0.12	0.64	Inf	0.19	0.85

upstream					

Table S.I.9. Ash free dry mass from surber samples differences among river and site type general linear model output. Comparisons with significant p values (P < 0.05) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**16.76**	**1.83**	**9.15**	**< 2e-16**
Riverkiamichi	**29.63**	**3.55**	**8.34**	**< 2e-16**
Riverlittle	**42.00**	**3.89**	**10.81**	**< 2e-16**
Rivermtfork	**36.89**	**3.75**	**9.83**	**< 2e-16**
Dam_Locationupstream	**28.20**	**3.51**	**8.03**	**0.00**
Riverkiamichi:Dam_Locationupstream	**-16.84**	**5.76**	**-2.92**	**0.00**
Riverlittle:Dam_Locationupstream	**-11.98**	**6.25**	**-1.92**	**0.06**
Rivermtfork:Dam_Locationupstream	**-17.10**	**6.27**	**-2.73**	**0.01**

Table S.I.10. Emmeans post-hoc results for differences in surber ash free dry mass. Comparisons with significant p values (P < 0.05) are bolded.

Contrast	Estimate	Standard Error	Degrees Freedom	Z Ratio	P Value
Dam_Location = downstream					
glover - kiamichi	**-29.63**	**3.55**	**Inf**	**-8.34**	**<.0001**
glover - little	**-42.00**	**3.89**	**Inf**	**-10.81**	**<.0001**

glover - mtfork	**-36.89**	**3.75**	**Inf**	**-9.83**	**<.0001**
kiamichi - little	**-12.37**	**4.59**	**Inf**	**-2.70**	**0.04**
kiamichi - mtfork	-7.26	4.47	Inf	-1.62	0.37
little - mtfork	5.12	4.74	Inf	1.08	0.70
Dam_Location = upstream					
glover - kiamichi	**-12.79**	**4.53**	**Inf**	**-2.82**	**0.02**
glover - little	**-30.02**	**4.90**	**Inf**	**-6.13**	**<.0001**
glover - mtfork	**-19.78**	**5.02**	**Inf**	**-3.94**	**0.00**
kiamichi - little	**-17.23**	**5.15**	**Inf**	**-3.34**	**0.00**
kiamichi - mtfork	-6.99	5.27	Inf	-1.33	0.55
little - mtfork	10.24	5.58	Inf	1.83	0.26
River = Glover:					
downstream - upstream	**-28.20**	**3.51**	**Inf**	**-8.03**	**<.0001**
River = Kiamichi:					
downstream - upstream	**-11.40**	**4.56**	**Inf**	**-2.49**	**0.01**
River = Little:					
downstream - upstream	**-16.20**	**5.17**	**Inf**	**-3.14**	**0.00**
River = Mountain Fork:					

downstream - upstream	**-11.10**	**5.19**	**Inf**	**-2.14**	**0.03**

Table S.I.11. Differences in distance from the dams among river and site type general linear model output. Comparisons with significant p values (P < 0.05) are bolded.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**15.60**	**3.59**	**4.34**	**0.00**
Riverlittle	-7.42	5.08	-1.46	0.16
Rivermtfork	1.01	5.08	0.20	0.84
Dam_Locationupstream	**-36.92**	**5.08**	**-7.27**	**0.00**
Riverlittle:Dam_Locationupstream	-0.55	7.18	-0.08	0.94
Rivermtfork:Dam_Locationupstream	**-36.73**	**7.40**	**-4.96**	**0.00**

Table S.I.12. Emmeans post-hoc results for differences in site distance from dams. Comparisons with significant p values (P < 0.05) are bolded.

Contrast	Estimate	Standard Error	Degrees Freedom	Z Ratio	P Value
Dam_Location = downstream					
kiamichi - little	7.42	5.08	23.00	1.46	0.33
kiamichi - mtfork	-1.01	5.08	23.00	-0.20	0.98
little - mtfork	-8.44	5.08	23.00	-1.66	0.24
Dam_Location = upstream					

kiamichi - little	7.98	5.08	23.00	1.57	0.28
kiamichi - mtfork	**35.72**	**5.39**	**23.00**	**6.63**	**<.0001**
little - mtfork	**22.74**	**5.39**	**23.00**	**5.15**	**0.00**
River = Kiamichi:					
downstream - upstream	**36.90**	**5.08**	**23.00**	**7.27**	**<.0001**
River = Little:					
downstream - upstream	**37.50**	**5.08**	**23.00**	**7.38**	**<.0001**
River = Mountain Fork:					
downstream - upstream	**73.60**	**5.39**	**23.00**	**13.67**	**<.0001**

Table S.I.13. Differences in flow among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.59	0.99	-1.61	0.11
Riverkiamichi	1.46	1.10	1.33	0.18
Riverlittle	-0.06	1.42	-0.04	0.97
Rivermtfork	1.75	1.07	1.63	0.10
Dam_Locationupstream	-0.46	1.59	-0.29	0.77
Riverkiamichi:Dam_Locationupstream	0.43	1.73	0.25	0.81
Riverlittle:Dam_	0.20	2.21	0.09	0.93

Locationupstream				
Rivermtfork:Dam_Locationupstream	0.33	1.71	0.19	0.85

Table S.I.14. Differences in seston ash free dry mass among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	6.5E-05	3.6E-03	1.8E-02	0.99
Riverkiamichi	-3.7E-06	5.0E-03	-1.0E-03	1.00
Riverlittle	-4.0E-05	4.2E-03	-9.0E-03	0.99
Rivermtfork	5.9E-06	5.2E-03	1.0E-03	1.00
Dam_Locationupstream	-9.9E-06	4.9E-03	-2.0E-03	1.00
Riverkiamichi:Dam_Locationupstream	2.8E-05	7.2E-03	4.0E-03	1.00
Riverlittle:Dam_Locationupstream	1.4E-04	7.8E-03	1.8E-02	0.99
Rivermtfork:Dam_Locationupstream	6.0E-05	8.3E-03	7.0E-03	0.99

Table S.I.15. Differences in chlorophyll *a* free dry mass among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.42	1.50	-1.61	0.11
Riverkiamichi	-0.92	2.80	-0.33	0.74

Riverlittle	-0.57	2.49	-0.23	0.82
Rivermtfork	-1.03	2.92	-0.35	0.72
Dam_Locationupstream	-0.64	2.55	-0.25	0.80
Riverkiamichi:Dam_Locationupstream	-0.57	5.57	-0.10	0.92
Riverlittle:Dam_Locationupstream	-0.46	4.73	-0.10	0.92
Rivermtfork:Dam_Locationupstream	0.59	4.59	0.13	0.90

Table S.I.16. Differences in the proportion of forested land cover among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**0.735**	**0.197**	**3.726**	**0.000**
Riverkiamichi	-0.008	0.280	-0.028	0.978
Riverlittle	0.003	0.278	0.013	0.990
Rivermtfork	0.049	0.270	0.181	0.856
Dam_Locationupstream	-0.037	0.285	-0.130	0.897
Riverkiamichi:Dam_Locationupstream	0.056	0.398	0.141	0.888
Riverlittle:Dam_Locationupstream	0.084	0.392	0.216	0.829
Rivermtfork:Dam_Locationupstrea	0.049	0.394	0.124	0.901

m				

Table S.I.17. Differences in the proportion of developed land cover among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.047	0.094	0.494	0.621
Riverkiamichi	-0.025	0.115	-0.216	0.829
Riverlittle	-0.018	0.120	-0.146	0.884
Rivermtfork	-0.013	0.124	-0.106	0.916
Dam_Locationupstream	0.001	0.134	0.008	0.993
Riverkiamichi:Dam_Locationupstream	0.001	0.164	0.009	0.993
Riverlittle:Dam_Locationupstream	-0.004	0.169	-0.022	0.982
Rivermtfork:Dam_Locationupstream	-0.002	0.180	-0.009	0.993

Table S.I.18. Differences in the proportion of agricultural land cover among river and site type general linear model output.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.039	0.087	0.450	0.652
Riverkiamichi	0.098	0.177	0.556	0.578
Riverlittle	-0.002	0.121	-0.012	0.990
Rivermtfork	0.019	0.135	0.138	0.891

Dam_Locationupstream	0.020	0.136	0.145	0.885
Riverkiamichi:Dam_Locationupstream	-0.018	0.257	-0.071	0.943
Riverlittle:Dam_Locationupstream	-0.037	0.172	-0.215	0.830
Rivermtfork:Dam_Locationupstream	0.009	0.221	0.039	0.969

S.I.4. General Linear Model Results - Biological Metrics and Environmental Variables

To test for relationships between the biologic metrics and environmental variables, we ran general linear models of each biological metric and all the environmental variables. Taxonomic richness was significantly driven by the amount of AFDM in the surer samples (**Table S.I.19**). All other metrics did not have a significant driver in their models (**Tables S.I.20-S.I.26**)

Table S.I.19. Taxonomic richness GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.33	3.40	0.69	0.49
Temperature (C)	0.02	0.02	0.67	0.50
Flow (m2)	0.00	0.04	0.08	0.94
Canopy Cover (%)	0.34	0.36	0.95	0.34
Seston AFDM (g/L)	310.00	737.00	0.42	0.67
Surber AFDM (g/m2)	**0.00**	**0.00**	**3.41**	**0.00**
Chl A (g/m2)	0.41	2.97	0.14	0.89

Developed	-12.90	19.10	-0.67	0.50
Forest	0.97	4.36	0.22	0.82
Agriculture	-1.58	2.52	-0.63	0.53
Distance (km)	0.00	0.00	-0.02	0.98

Table S.I.20. Log abundance GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	22.50	44.40	0.51	0.61
Temperature (C)	0.14	0.32	0.45	0.66
Flow (m2)	0.13	0.57	0.23	0.82
Canopy Cover (%)	3.46	4.73	0.73	0.47
Seston AFDM (g/L)	-1,390.00	10,200.00	-0.14	0.89
Surber AFDM (g/m2)	0.02	0.01	1.20	0.23
Chl A (g/m2)	-11.70	37.40	-0.31	0.76
Developed	-52.70	257.00	-0.21	0.84
Forest	-23.00	57.50	-0.40	0.69
Agriculture	-24.60	33.30	-0.74	0.46
Distance (km)	0.00	0.04	0.02	0.99

Table S.I.21. Proportion of chironomid GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)

(Intercept)	24.00	39.60	0.61	0.54
Temperature (C)	-0.08	0.27	-0.30	0.77
Flow (m2)	-0.15	0.56	-0.27	0.79
Canopy Cover (%)	-0.85	4.17	-0.20	0.84
Seston AFDM (g/L)	6,660.00	8,890.00	0.75	0.45
Surber AFDM (g/m2)	0.00	0.01	-0.32	0.75
Chl A (g/m2)	4.08	33.30	0.12	0.90
Developed	-3.80	227.00	-0.02	0.99
Forest	-29.30	51.80	-0.57	0.57
Agriculture	-7.30	30.10	-0.24	0.81
Distance (km)	-0.01	0.03	-0.25	0.80

Table S.I.22. Proportion of EPT taxa GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.00	7.45	-0.54	0.59
Temperature (C)	0.01	0.05	0.20	0.85
Flow (m2)	0.01	0.09	0.11	0.91
Canopy Cover (%)	-0.25	0.79	-0.32	0.75
Seston AFDM (g/L)	-209.00	1,660.00	-0.13	0.90

Surber AFDM (g/m2)	0.00	0.00	-0.37	0.71
Chl A (g/m2)	-1.30	6.51	-0.20	0.84
Developed	29.50	42.60	0.69	0.49
Forest	4.37	9.63	0.45	0.65
Agriculture	3.98	5.59	0.71	0.48
Distance (km)	0.01	0.01	0.99	0.32

Table S.I.23. Proportion of collector-filterers GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-5.98	37.30	-0.16	0.87
Temperature (C)	-0.03	0.27	-0.10	0.92
Flow (m2)	-0.15	0.47	-0.32	0.75
Canopy Cover (%)	-1.29	3.74	-0.35	0.73
Seston AFDM (g/L)	-1,110.00	9,120.00	-0.12	0.90
Surber AFDM (g/m2)	-0.01	0.01	-0.49	0.62
Chl A (g/m2)	-10.20	31.80	-0.32	0.75
Developed	224.00	241.00	0.93	0.35
Forest	-1.22	47.40	-0.03	0.98
Agriculture	25.00	28.10	0.89	0.37
Distance (km)	0.01	0.03	0.37	0.71

Table S.I.24. Proportion of collector-gatherers GLM model results. Significant results (p < 0.05) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.75	6.89	0.54	0.59
Temperature (C)	0.01	0.05	0.26	0.79
Flow (m2)	0.03	0.09	0.32	0.75
Canopy Cover (%)	0.27	0.69	0.39	0.69
Seston AFDM (g/L)	-12.30	1,630.00	-0.01	0.99
Surber AFDM (g/m2)	0.00	0.00	1.01	0.31
Chl A (g/m2)	0.94	6.41	0.15	0.88
Developed	-24.00	41.40	-0.58	0.56
Forest	-4.20	8.86	-0.47	0.64
Agriculture	-3.04	4.98	-0.61	0.54
Distance (km)	0.00	0.01	-0.67	0.50

Table S.I.25. Proportion of herbivores GLM model results. Significant results (p < 0.05) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.39	4.15	-0.33	0.74
Temperature (C)	0.00	0.03	0.14	0.89
Flow (m2)	-0.01	0.05	-0.14	0.89

Canopy Cover (%)	-0.02	0.46	-0.05	0.96
Seston AFDM (g/L)	-69.70	912.00	-0.08	0.94
Surber AFDM (g/m2)	0.00	0.00	-0.25	0.80
Chl A (g/m2)	0.89	3.61	0.25	0.81
Developed	-11.40	22.60	-0.51	0.61
Forest	2.25	5.00	0.45	0.65
Agriculture	0.00	3.05	0.00	1.00
Distance (km)	0.00	0.00	0.31	0.76

Table S.I.26. Proportion of predators GLM model results. Significant results ($p < 0.05$) are bolded.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.51	62.90	-0.02	0.98
Temperature (C)	0.04	0.43	0.10	0.92
Flow (m2)	-0.15	0.83	-0.18	0.86
Canopy Cover (%)	-1.40	6.78	-0.21	0.84
Seston AFDM (g/L)	1,270.00	14,800.00	0.09	0.93
Surber AFDM (g/m2)	-0.01	0.02	-0.27	0.79
Chl A (g/m2)	6.37	51.90	0.12	0.90
Developed	11.00	349.00	0.03	0.98

Forest	-1.97	80.40	-0.02	0.98
Agriculture	-0.97	48.00	-0.02	0.98
Distance (km)	0.01	0.05	0.11	0.91

S.I.5. General Linear Model Results - Biological Metrics and River / Site Type

General Linear Model Results showed no differences among any biologic metric and river or site type (**Tables S.I.27-34**).

Table S.I.27. Taxonomic richness GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.584	0.105	34.118	<2e-16
Riverkiamichi	-0.169	0.152	-1.113	0.266
Riverlittle	-0.216	0.153	-1.413	0.158
Rivermtfork	-0.182	0.152	-1.198	0.231
Dam_Locationupstream	0.017	0.148	0.112	0.911
Riverkiamichi:Dam_Locationupstream	0.022	0.214	0.104	0.917
Riverlittle:Dam_Locationupstream	0.227	0.213	1.068	0.286
Rivermtfork:Dam_Locationupstream	0.145	0.219	0.660	0.509

Table S.I.28. Log abundance GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	8.339	1.291	6.457	0.000
Riverkiamichi	-0.293	1.810	-0.162	0.871
Riverlittle	0.060	1.830	0.033	0.974
Rivermtfork	-0.391	1.805	-0.217	0.829
Dam_Locationupstream	0.585	1.858	0.315	0.753
Riverkiamichi:Dam_Locationupstream	-0.626	2.581	-0.242	0.808

Riverlittle:Dam_Locationupstream	-0.289	2.621	-0.110	0.912
Rivermtfork:Dam_Locationupstream	-0.541	2.653	-0.204	0.838

Table S.I.29. Proportion of chironomid GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.266	0.198	1.346	0.178
Riverkiamichi	-0.013	0.277	-0.048	0.962
Riverlittle	0.097	0.292	0.334	0.739
Rivermtfork	-0.151	0.244	-0.622	0.534
Dam_Locationupstream	-0.078	0.264	-0.295	0.768
Riverkiamichi:Dam_Locationupstream	0.018	0.372	0.048	0.962
Riverlittle:Dam_Locationupstream	-0.032	0.392	-0.083	0.934
Rivermtfork:Dam_Locationupstream	0.071	0.338	0.210	0.834

Table S.I.30. Proportion of EPT taxa GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.509	0.224	2.278	0.023
Riverkiamichi	-0.009	0.316	-0.028	0.978
Riverlittle	-0.111	0.313	-0.355	0.722
Rivermtfork	0.202	0.302	0.668	0.504
Dam_Locationupstream	-0.166	0.308	-0.539	0.590
Riverkiamichi:Dam_Locationupstr	0.188	0.442	0.425	0.671

eam				
Riverlittle:Dam_Locationupstream	0.089	0.432	0.205	0.837
Rivermtfork:Dam_Locationupstream	-0.102	0.445	-0.230	0.818

Table S.I.31.Proportion of collector-filterer GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.147	0.158	0.929	0.353
Riverkiamichi	0.119	0.253	0.469	0.639
Riverlittle	0.012	0.228	0.052	0.958
Rivermtfork	0.251	0.270	0.929	0.353
Dam_Locationupstream	-0.012	0.220	-0.052	0.958
Riverkiamichi:Dam_Locationupstream	0.165	0.369	0.446	0.655
Riverlittle:Dam_Locationupstream	-0.069	0.300	-0.229	0.819
Rivermtfork:Dam_Locationupstream	-0.137	0.379	-0.362	0.717

Table S.I.32. Proportion of collector-gatherer GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.435	0.222	1.962	0.050
Riverkiamichi	0.011	0.314	0.034	0.973
Riverlittle	0.065	0.315	0.206	0.836
Rivermtfork	-0.295	0.271	-1.090	0.276
Dam_Locationupstream	0.138	0.313	0.442	0.659

Riverkiamichi:Dam_Locationupstream	-0.146	0.444	-0.329	0.742
Riverlittle:Dam_Locationupstream	-0.075	0.444	-0.170	0.865
Rivermtfork:Dam_Locationupstream	0.152	0.428	0.355	0.722

Table S.I.33. Proportion of herbivores GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.090	0.128	0.704	0.481
Riverkiamichi	0.048	0.201	0.241	0.809
Riverlittle	-0.032	0.166	-0.190	0.849
Rivermtfork	-0.009	0.177	-0.051	0.960
Dam_Locationupstream	0.020	0.190	0.106	0.916
Riverkiamichi:Dam_Locationupstream	-0.109	0.263	-0.414	0.679
Riverlittle:Dam_Locationupstream	0.069	0.269	0.258	0.797
Rivermtfork:Dam_Locationupstream	-0.048	0.252	-0.189	0.850

Table S.I.34. Proportion of predators GLM results.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.061	0.107	0.570	0.569
Riverkiamichi	0.022	0.163	0.135	0.892
Riverlittle	0.046	0.175	0.263	0.793
Rivermtfork	-0.015	0.142	-0.105	0.917

Dam_Locationupstream	-0.017	0.141	-0.120	0.904
Riverkiamichi:Dam_Locationupstream	-0.012	0.213	-0.058	0.954
Riverlittle:Dam_Locationupstream	0.013	0.239	0.052	0.958
Rivermtfork:Dam_Locationupstream	0.009	0.195	0.049	0.961

S.I.6. General Linear Model Results - Bray Curtis dissimilarity and River / Site Type

The GLM using Bray-Curtis distances among the site categories showed no differences among river or the different site comparisons (**Figure 4, Table S.I.35**). While site comparisons did not statistically differ, visually the distances between downstream site comparisons and the upstream site comparisons are more variable in the Kiamichi and Mountain Fork Rivers than the Glover and Little Rivers.

Table S.I.35. General linear model results comparing Bray Curtis dissimilarities across rivers and site types.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.391	0.154	2.532	0.011
riverKiamichi	-0.045	0.215	-0.211	0.833
riverLittle	0.154	0.220	0.698	0.485
riverMt Fork	0.113	0.221	0.512	0.609
comparisonup-down	0.016	0.183	0.087	0.931
comparisonup-up	0.010	0.219	0.045	0.964
riverKiamichi:comparisonup-down	0.065	0.257	0.253	0.800
riverLittle:comparisonup-down	-0.016	0.261	-0.061	0.951
riverMt Fork:comparisonup-down	0.054	0.261	0.205	0.837
riverKiamichi:comparisonup-up	0.102	0.309	0.329	0.742
riverLittle:comparisonup-up	-0.135	0.311	-0.435	0.664
riverMt Fork:comparisonup-up	0.107	0.310	0.345	0.730

S.I.7. Alternative methods - Glover River sites labeled as “free”

The authors had some discussion about whether to label sites along the Glover River as “free” or as “upstream” and “downstream”, depending on their location along the river. The authors decided that labeling sites on the Glover River as “free” would lead to confounding variables and therefore present the “upstream” / “downstream” results in the main text. As the overall qualitative results do not change regardless of how the sites are labeled, below we present each figure from the results section to clarify the slight differences between the analyses.

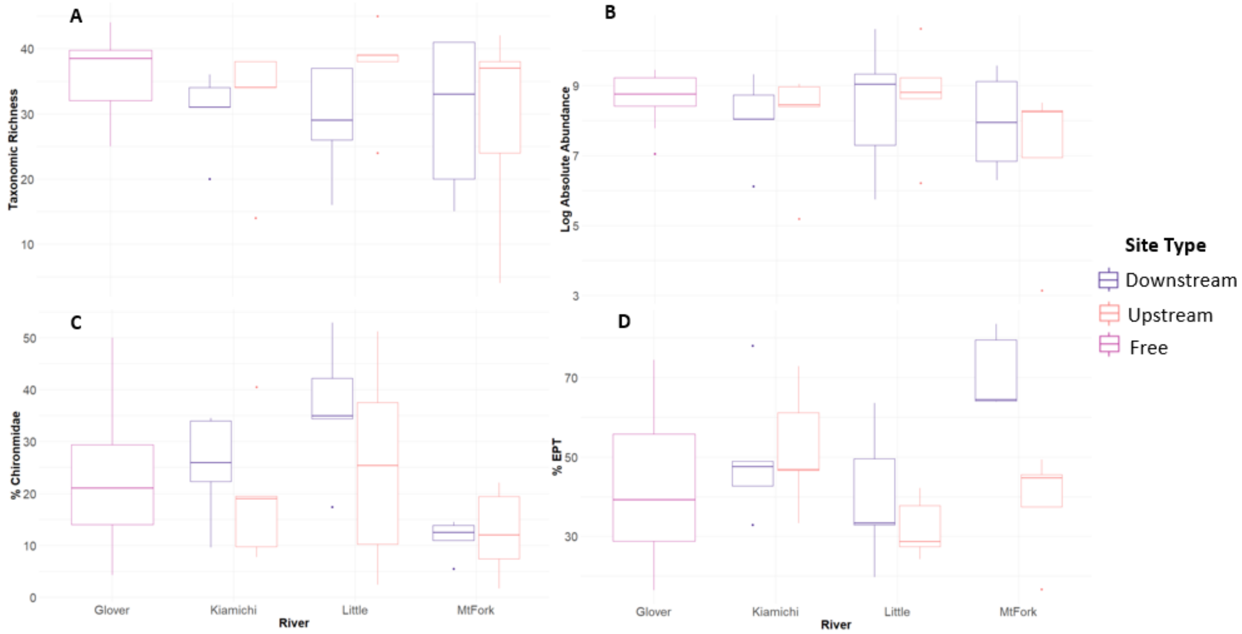

Figure S.I.1. Boxplots comparing taxonomic richness (A), log abundance (B), percent taxa from Chironomidae (C), and percent EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera; D) among free sites along the Glover River (dark pink) to sites downstream (purple) and upstream (orange) of dams along the other three rivers.

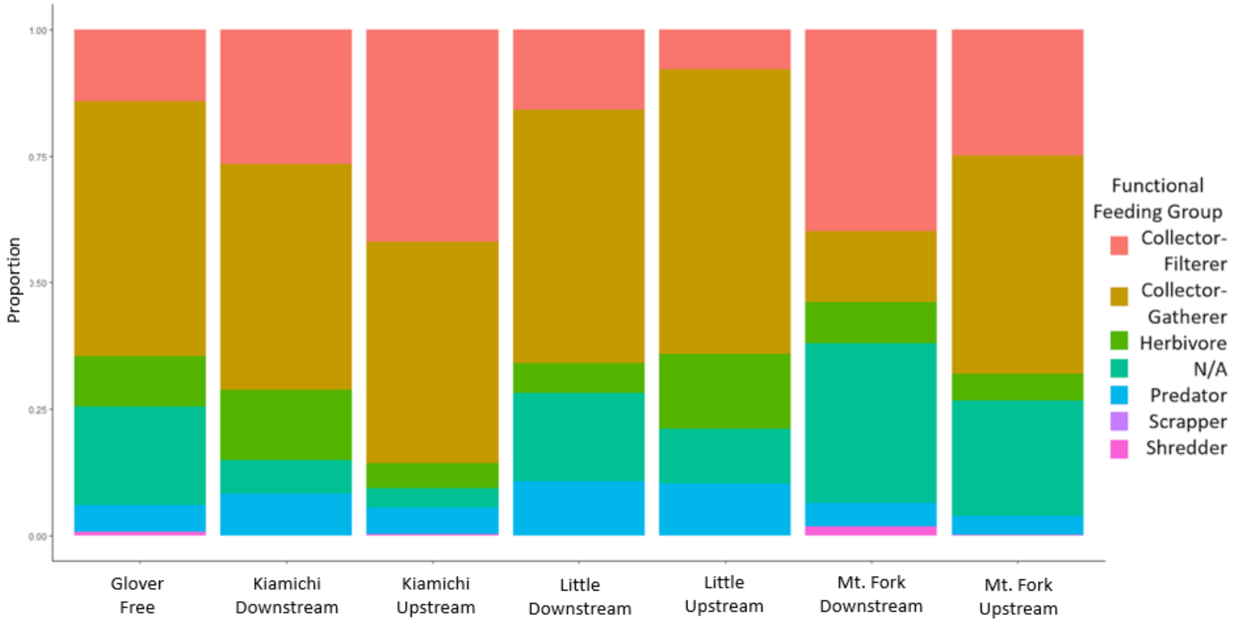

Figure S.I.2. Barplot depicting the proportion of each functional feeding group for compiled upstream and downstream sites per river.

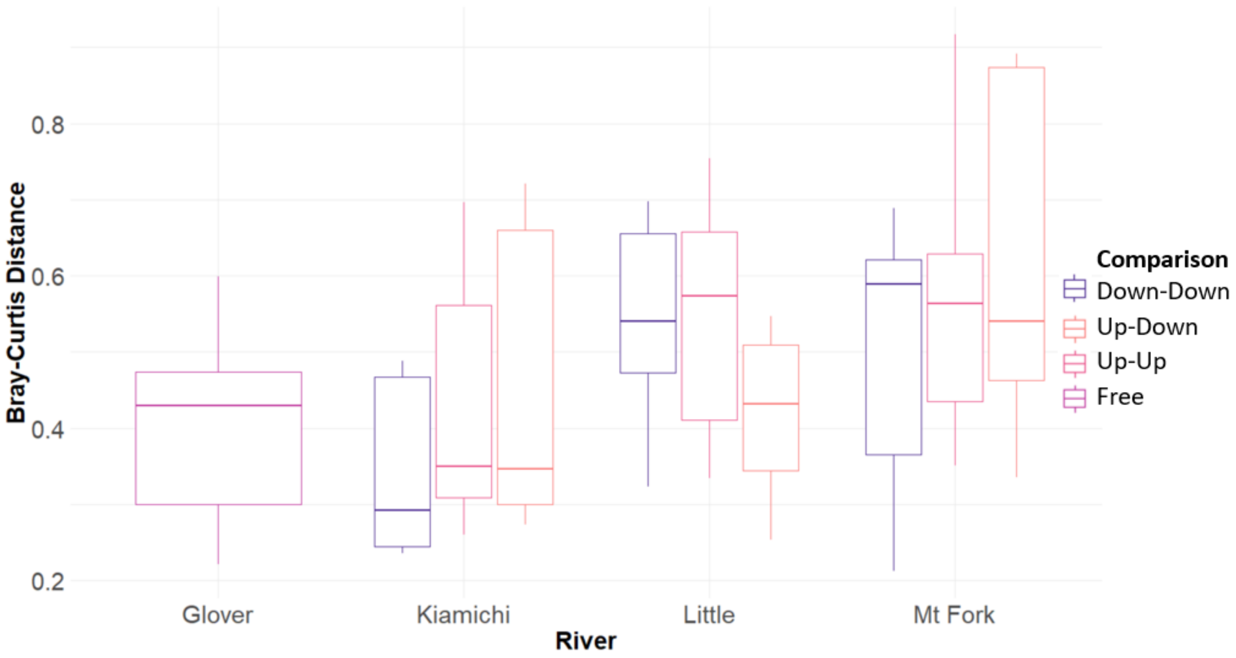

Figure S.I.3. Bray-Curtis distances among the different sections of each river. Glover River sites were all labeled as "free" (purple). Down-Down comparisons are between downstream sites only (blue), up-down comparisons are between downstream and upstream sites (light pink), and up-up comparisons are between upstream sites only (orange).

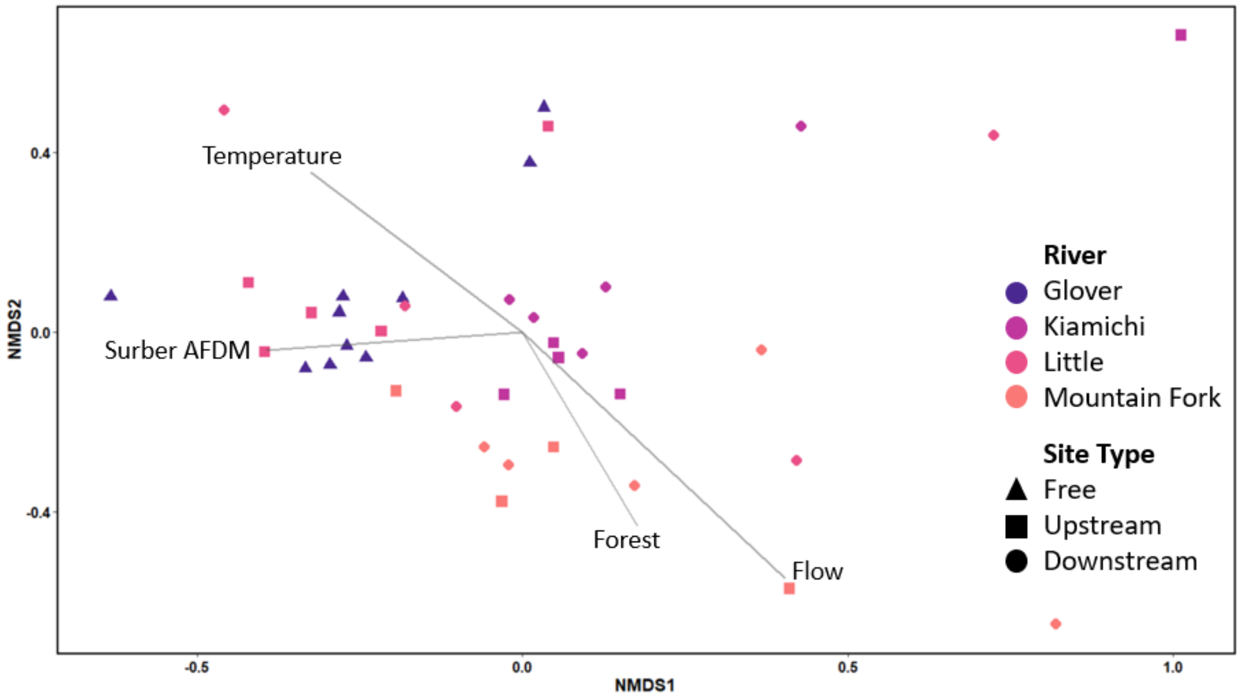

Figure S.I.4. Two-dimensional nMDS ordination of macroinvertebrate assemblages across each river (stress = 0.126). Significant environmental variables ($p < 0.05$) are also plotted with the length of the corresponding vector related to the strength of the relationship (R^2, **Table S.I.36**).

Table S.I.36. Correlations among environmental variables and the species nMDS axes across all four rivers. Metrics with $p < 0.05$ are bolded.

	NMDS 1	NMDS 2	pval	r2
Temperature (C)	**-0.326**	**0.356**	**0.009**	**0.233**
Flow (m2)	**0.403**	**-0.549**	**0.001**	**0.464**
Canopy Cover (%)	-0.005	-0.166	0.588	0.028
Seston AFDM (g/L)	-0.112	-0.240	0.249	0.070
Surber AFDM (g/m2)	**-0.394**	**-0.041**	**0.045**	**0.157**
Chl a (g/m2)	-0.205	0.056	0.421	0.045
Developed (%)	0.176	-0.434	0.013	0.219
Forest (%)	0.327	0.013	0.159	0.107

Agriculture (%)	**-0.384**	**-0.020**	**0.054**	**0.148**
River Distance (km)	0.298	0.108	0.146	0.101

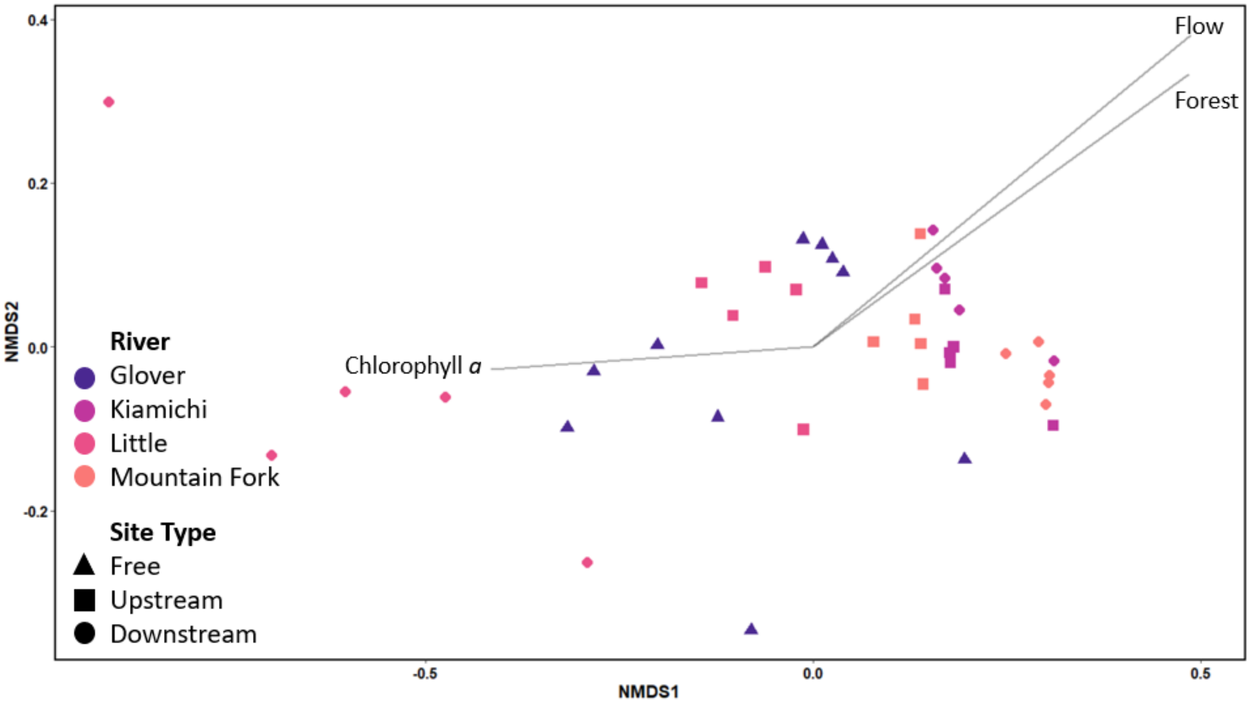

Figure S.I.5. Two-dimensional nMDS ordination of macroinvertebrate assemblages across each river (stress = 0.126). Significant environmental variables ($p < 0.05$) are also plotted with the length of the corresponding vector related to the strength of the relationship (R^2, **Table S.I.37**).

Table S.I.37. Correlations among environmental variables and the functional feeding group nMDS axes across all four rivers. Metrics with $p < 0.05$ are bolded.

	NMDS 1	NMDS 2	pval	r2
Temperature (C)	-0.026	-0.017	0.981	0.001
Flow (m2)	**0.487**	**0.381**	**0.001**	**0.382**
Canopy Cover (%)	-0.117	-0.114	0.587	0.027
Seston AFDM (g/L)	0.054	0.223	0.402	0.053
Surber AFDM (g/m2)	0.028	0.142	0.685	0.021
Chl a (g/m2)	**-0.415**	**-0.028**	**0.035**	**0.173**

Developed (%)	0.177	-0.02	0.545	0.032
Forest (%)	**0.484**	**0.333**	**0.002**	**0.345**
Agriculture (%)	-0.061	-0.225	0.361	0.054
River Distance (km)	-0.031	-0.201	0.473	0.041