

Hydrogeomorphic drivers of functional diversity in riverine fishes at an intercontinental scale

By

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Abstract

Functional diversity (FD) has been used as a metric to gauge the health and stability of fish communities in many different environments, but few studies have examined FD on an intercontinental scale. This study formally examined the FD of riverine fishes at a macrosystem scale based on hydrogeomorphic features in similar climates between two continents. To accomplish this goal, I sampled fish in five systems representing three ecoregions (terminal basin, mountain steppe and grasslands) across the United States of America and Mongolia. I then investigated how FD changed between and within each continent and ecoregion type.

As expected, FD was strongly correlated with species diversity. Additionally, I found that FD, specifically functional richness, was higher in wider, deeper rivers and decreased with faster, more sloped systems. This suggests that FD increases similarly to species richness as one moves from high elevation headwaters toward larger, lowland systems. However, a community containing redundant species that offer no novel traits to the community can complicate this generality. This project should serve as a complement to earlier work as well as provide a foundation for future studies that attempt to more thoroughly understand functional diversity at a macrosystem scale.

Keywords: functional diversity, hydrogeomorphology, fish, Mongolia, river, macrosystem

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Introduction

Functional diversity (FD), which represents the range and values of species traits that influence ecosystem function, has been studied at length over the last few decades (Tilman, 2001). Investigators have examined the FD of many different taxa including plants, mammals and insects (Díaz & Cabido, 2001; Blackburn et al., 2005; Tschardt et al., 2008). In addition to these previously mentioned groups, fishes may be a particularly useful group for FD studies. Fishes are a highly speciose group with more diversity than any other class of vertebrates and almost half of their diversity is found in freshwater systems. This diversification not only demonstrates species richness within the group, but functional richness as well. Studying fishes, particularly in functional studies, also provides the benefit of a robust knowledge base of trait literature (Angermeier & Frimpong, 2011; Froese & Pauly, 2018). FD studies of fishes alone have been conducted across a wide array of environments including studies completed in marine and freshwater systems located in tropical to desert ecoregions (Pool et al., 2010; Pease et al., 2012; Wiedmann et al., 2014; Colin et al., 2018). These studies also span a variety of spatial scales ranging from the examination of a single river to multi-river basins, though less work has been conducted on larger scales and there is very limited work in terms of intercontinental studies (Lamouroux et al., 2002).

Early FD analyses relied heavily on functional dendrograms (Petchey & Gaston, 2002; Petchey & Gaston, 2006). These operate in a similar fashion to evolutionary distance trees and other hierarchical analyses where groups with similar characters or traits are clustered together to form a tree and branches that are closer to each other are either more related in phylogenetic analyses or similar in functional dendrograms. The total branch length (BL) of a community then

is used to represent that assemblage's functional diversity. However, this technique does not take into account species abundances and the resulting tree can change depending on the clustering method used (Petchey and Gaston, 2006). Functional dendrograms benefit from allowing the use of multiple traits in a study and do not have a minimum number of required unique species to perform an analysis (Petchey & Gaston, 2002).

A later trend focused on building multidimensional functional spaces to visualize community function (Villéger et al., 2008). These multidimensional spaces are formed by using trait-species matrices to plot species in space relative to the traits of other species. The more traits that species share, the smaller the functional space is, while having many species with distinct trait attributes will create a larger space. A multitude of metrics can then be extracted from this functional space including functional evenness (FEve), divergence (FDiv), and richness (FRic). Constructing multidimensional spaces yields better, more reliable results than constructing dendrograms (Maire et al., 2015).

The particular traits used in FD studies determine what functions of the community the models account for and whether the traits are categorical or continuous can strongly influence the type of analysis needed. In a comparison of various functional diversity approaches, continuous and mixed trait data sets were found to produce higher quality results than solely categorical trait data (Maire et al., 2015). Traits selected frequently center on an organism's reproductive, feeding, or locomotive characteristics (Villéger et al., 2013; Toussaint et al., 2018). An ideal set of traits would fully illustrate a species' function in an ecosystem while avoiding traits that become redundant when combined with certain other traits (Petchey & Gaston, 2006; Wiedmann et al., 2014).

Many studies have connected species richness or presence to aspects of hydrogeomorphology or stream gradients (Schlosser 1982, Lamouroux 2002; Bey & Sullivan, 2014). However, functional diversity is not typically an exact product of species richness, especially when functionally redundant species are present (Petchey & Gaston, 2002). Lamouroux et al. (2002) helped pave the way for large-scale functional studies when they investigated intercontinental convergence of fish traits along hydraulic and geomorphic gradients in similar communities between France and the United States. However, they examined only one type of ecoregion and focused on microhabitat aspects as opposed to larger reach and valley level scales.

The drivers of functional diversity remain relatively unknown in many types of systems. Pool et al. (2010) found that watershed land use, hydrologic alteration and local climate were significantly related to functional diversity in fishes of the Colorado River Basin while Lamouroux et al. (2002) noted that the Froude number (relating ‘calmness’ of flow) was significant in influencing fish traits in North American and French rivers. Salinity has also been significantly related to functional diversity in coastal lagoon fishes (Mouillot et al., 2007). There has yet to be an approach that examined multiple types of freshwater ecoregions for any overarching drivers and very little functional diversity work has been conducted in particularly unique or remote ecoregions, such as the terminal basin systems of the United States and Mongolia.

This study is a subset of a National Science Foundation-funded project, from this point referred to as the MACRO project, which investigated these larger scales. MACRO is an effort to conduct the first empirical macrosystem ecology study across multiple continents. Studies of macrosystem ecology are very rare in the literature; in fact, macrosystem ecology lacks even a

common, concrete definition among ecologists. For the purpose of this study, riverine macrosystems are defined as spatially large, hierarchical networks composed of multiple ecosystems whose biological, geophysical or sociocultural processes interact with one another at various scales (Heffernan et al., 2014; Thorp, 2014). The MACRO project explored macrosystem ecology across five ecoregions from two continents. The project consisted of collaborators from 11 different universities with research interests spanning all domains of riverine ecology from carbon sources and system metabolism to methane utilization, parasite ecology, and invertebrate traits.

Here, I focus on the fish trait and hydrogeomorphic data sets that were collected in connection with the MACRO project. The data collection was conducted primarily by a team of researchers representing the University of Kansas, Ball State University, South Dakota School of Mines and Technology, and the National University of Mongolia.

In this paper, I used a combination of functional dendrograms and multidimensional functional space to evaluate FD of riverine fishes across a variety of hydrogeomorphic variables from several ecoregions in the United States and Mongolia. To evaluate the relationships between FD and hydrogeomorphology, I examined FD metrics within and between continents. I compared FD within paired ecoregions as well as across different ecoregions. I proposed multiple hypotheses to evaluate based on this study design. First, I predicted the functional richness metrics (BL and FRic) will increase with species richness. Second, I hypothesized that my hydrogeomorphic predictors would significantly explain the FD metrics (BL, FRic, FDiv, and FEve). Furthermore, I expected these drivers of FD would be consistent based on ecoregion type and independent of continent.

Methods

Study area

This study includes sites in terminal basin, mountain steppe, and grassland ecoregions nested within the temperate steppe biomes on two continents (Figure 1). The terminal basin systems in this study are the Carson, Bear and Humboldt Rivers of the U.S. Great Basin and the Khovd and Zavkahn Rivers in western Mongolia. The mountain steppe of the United States is represented by the Little Bighorn River and Tensleep Creek in Wyoming, both part of the Yellowstone, Missouri, Mississippi basins, respectively. The Mongolian mountain steppe was sampled in central Mongolia within the Eg River of the Selenge River basin. This study also included sites along the Niobrara and Little Missouri Rivers in the U.S. Great Plains grasslands. In total, I present data from a total of 79 sites located either along the mainstems or tributaries of these rivers (Table 1).

General site localities were initially selected remotely based on riverine and valley scale characteristics using the RESonate tool in ArcGIS (Williams et al., 2013). The RESonate tool takes into account several variables including precipitation, parent geology, valley floor width, and down valley slope among others. The goal of this was to provide a set of sites representative of a wide range of hydrogeomorphic variables. Specific sites and reaches were selected in the field just prior to sampling based on current flows, site accessibility, and sampling safety.

Fish collection

We sampled fishes using single-pass electrofishing surveys along reaches that were 20 times the average wetted width of the stream. Electrofishing settings varied with water

chemistry, but test sampling was conducted prior to shocking at each site to maximize capture efficiency while minimizing mortality. We electrofished all habitat types present in each reach. This improved our ability to accurately characterize each community. Electrofishing was supplemented by seining, gill netting, and angling to maximize species detection when electrofishing was not feasible. This was the case in streams, particularly in the U.S. mountain steppe, that had extremely low conductivity ($< 20 \mu\text{S}/\text{cm}$). Collected fishes greater than 30mm total length were identified to species, measured for standard length, and weighed. Most of these individuals were released, but up to ten individuals of each species at each site were retained for gut content analysis.

Individuals that needed to be sacrificed were euthanized shortly after capture using MS-222 in a solution of at least 250mg/L. The stomachs, when present, were taken from sacrificed individuals and sealed in bags of 85% ethanol. In fishes that lack true stomachs, the gut of the individual was taken until the first loop of the midgut. These samples were then dissected under a microscope to identify as specifically as possible any visible food items that remained inside. Each food item was classified and weighed.

Assigning functional traits

To limit redundancy in my traits, I focused on a diversity of traits regarding a species' trophic group, spawning method, life history attributes and habitat preferences. The majority of trait values used in this paper were found through the FishBase and also FishTraits databases (Angermeier & Frimpong, 2011; Froese & Pauly, 2018). When these lacked the desired species information, an extensive literature search typically provided trait values. No value was assigned

in cases where the trait could not be found in the literature or confidently derived from our own data.

The ten traits used in this study include trophic group, aquatic position, parental guild, spawning guild, spawning substrate, rheophily, water column position when feeding, body length, age at sexual maturity, and maximum recorded longevity (Table 2). Each trait used in this study had several modalities, or unique conditions of that trait, that were assigned to each individual based solely on that individual's species and independent of its life stage or size (Table 3A-3C). Without knowledge of the contributions of individual traits to FD relative to other traits, I assumed that all traits influenced ecosystem function equally and as such were all weighted identically.

A number of Mongolian fishes, especially certain *Barbatula* species which were only described in 2016, had relatively little previous research from which to acquire trait information (Prokofiev, 2016). In these cases, I resorted to using our personally collected data to assign or estimate trait characters. For instance, type of food item and amount of debris found within the gut assisted in filling knowledge gaps such as trophic group and feeding position for the purpose of this study. I used directly recorded standard lengths to represent species size as an indicator for energy demand and productivity. Reproductive traits such as parental protection, preferred spawning substrate and spawning method were all derived from previous literature or from information about a close relative of the species.

Selecting hydrogeomorphic data

Hydrogeomorphic metrics were measured concurrently with fish sampling at all sites. Reaches, likewise with fish sampling, were designated as 20 times the wetted width.

Hydrogeomorphological measurements focused on stream discharge, pool-riffle-run composition, substrate size and distribution, and a variety of other geomorphic features.

I selected metrics that would represent the diversity of hydrogeomorphic measures examined at each site (Table 4). All hydrogeomorphic data were continuous. I used principal component analysis (PCA) to visualize collinearity between hydrogeomorphic variables and to select interpretable variables that were also representative of a large portion of the variance in overall reach-scale stream hydrogeomorphology (instead of using difficult-to-interpret PCA axes as predictors). Each hydrogeomorphic metric used in PCAs was standardized across all the sites for the mean to equal zero with a standard deviation of one.

Calculating functional diversity

All FD calculations were conducted using R version 3.5.3 (R Core Team, 2019). FD was measured via both multidimensional functional spaces and functional dendrograms. These methods follow Petchey & Gaston (2002) and Villéger et al. (2008).

Functional dendrogram analyses rely on constructing a single dendrogram that represents the entire possible species pool of a community; this can also be viewed as that site's gamma diversity and is a particularly sensitive aspect of the study. Depending on species presence, total branch length of a given community is calculated based on the lengths of all the branches needed to connect all the present species. This initial tree had to be inclusive enough from which conclusions could be drawn, but specific enough that it did not artificially inflate branch lengths. For instance, adding Mongolia species that are functionally similar, but absent in the U.S. to the species pool of a site within the United States' terminal basin would have created increased branch lengths between species actually present in that system. Therefore, I settled on ecoregion

as logically representing the gamma diversity of a particular site which produced five functional dendrograms and five functional spaces for my analyses.

To create multidimensional functional spaces, I used the *FD* – displayed in italics to differentiate from FD as a functional diversity acronym – package, function “dbFD” in R (Laliberté & Legendre, 2010; Laliberté et al., 2014). This requires a species-trait matrix as well as a species abundance matrix. Within the “dbFD” function, I employed Gower’s distance, rather than Euclidean distance, to create a distance matrix based on the species-trait matrix because Gower’s distance works well with categorical or mixed data such as the fish trait data in this study (Podani & Schmera, 2006). Euclidean distance on the other hand is best suited to continuous data sets only. *FD* runs a principal coordinate analysis (PCoA) to provide the desired functional space while also producing FRic, FEve, and FDiv (functional richness, evenness, and divergence respectively) values for each site as defined by Villéger et al. (2008) (Laliberté & Legendre, 2010; Laliberté et al., 2014). Each of these functional metrics correspond to an aspect of the functional space. FRic is the minimum volume of functional space needed to include all the species; FEve is a measure of evenness between abundances within the functional space, and FDiv measures the extent that species’ traits diverge from a central point within the functional space (Villéger et al., 2008). FRic, FEve, and FDiv increase with a larger functional space, more similar abundances, and more extreme trait values, respectively.

The functional dendrogram construction was not entirely unlike the functional space model. It requires the same species-trait matrix, but it does not take into account abundances and instead relies only on presence-absence data. I used Gower’s distance, function “gower.dist”, package *MatchStats*, to create a dissimilarity matrix because the traits included categorical values (D’Orazio, 2019). I clustered the matrix using an unweighted pair group method with

arithmetic mean (UPGMA), as recommended by Podani & Schmera (2006), within the function “hclust” to create a functional tree based on the distance matrix. I then measured branch length to calculate the diversity of each site using the “treedive” function from the *vegan* package in R (Oksanen et al., 2019). A branch length of zero indicates a site with only one species present (Petchey & Gaston, 2007).

Evaluating FD across hydrogeomorphic variables

The functional diversity-hydrogeomorphic factor analyses were conducted within a combination of Minitab and R. First, I ran a Pearson’s correlation test to visualize the relationships between the factors. I then conducted the principal component analyses (PCAs) discussed earlier on the hydrogeomorphic data set. The prominent hydrogeomorphic factors were then selected as predictors in my regression and nested general linear models. In my analyses, I used the hydrogeomorphic predictors in separate models. This study focused on the effects of hydrogeomorphology on trait diversity at various scales and incorporated interactive aspects of the selected hydrogeomorphic variables.

Decreasing my total number of factors used in each model not only simplified the analysis, but also likely decreased the likelihood of Type I error by eliminating superfluous and redundant variables. Factors selected were those that contributed the most to the first few PCA axes and included stream width, percent of fast water within the reach, and stream sinuosity. I used biplots generated by the PCAs to focus on variables perpendicular to each other to minimize correlation and account for more variability within the dataset.

I used a nested ANOVA to investigate functional diversity as a result of ecoregion and country with each ecoregion nested fully in its respective country. The assumptions of ANOVA

and linear regression were met through the accounting of outliers, normality and autocorrelation. When outliers were present, the model was run with and without the outlier and any notable difference is noted with the result (e.g. significance only when the outlier is included). The residual plots typically suggested the data followed the assumption of normality. In cases that were not normal, I log transformed the data to allow a better fit to the assumptions. All regression and GLM analyses had Durbin-Watson values between the minimum and maximum bounds that indicated no acceptable levels of autocorrelation between sites at a 95% confidence level 1.5 and 2.5 which indicated manageable levels of autocorrelation between sites (Durbin & Watson, 1951; Field, 2009).

Results

A total of 52 species were found throughout all five ecoregions (Table 5). Species richness was heavily skewed towards the United States over Mongolia with the latter only having 13 species. One species, northern pike (*Esox lucius*), possesses a circumpolar native range and was present in both countries.

I used a nested ANOVA model to examine the functional diversity metrics of all five ecoregions nested within their respective countries (Table 5). Community branch lengths (BL) were calculated from five individual ecoregion-level dendrograms (Figure 2A-2C). BLs differed significantly based on both country ($p = .037$) and ecoregion ($p < .001$) while the functional richness and divergence values from the multidimensional space (FRic and FDiv) respectively were both affected similarly by ecoregional constraints on each continent ($p < .05$). It is worth noting that if the US grassland system was removed, then the effect of Country on BL and of ecoregion on FRic both lost their significance ($p > .05$). I observed no discernable relationships regarding functional evenness at either the ecoregional or continental scale.

Community branch length and FRic were significantly explained by species richness even when including country and ecoregion effects within the model (general linear model, $p < 0.001$, $R^2 = 96\%$ and 67% respectively). Thus, the more speciose ecoregions such as the grasslands and terminal basin of the U.S. were also the more functionally rich systems (Table 7). BL and FRic themselves were also significantly correlated with a Pearson's correlation of 0.72. Neither FDiv nor FEve was found to be significantly related to species richness.

Hydrogeomorphology as a predictor of functional diversity

The results of the Pearson's correlation test between the ten hydrogeomorphic variables showed several significant results among the variables (Table 8). Of the 45 correlation tests run among variables, 21 tests were found to be significant. As expected, the most notable correlations occur between stream depth and width, slope and fast water, discharge and width, and fast water and substrate. Examination of the PCAs of the variables associated with the various ecoregions typically reinforced these earlier findings (Figure 3). Evaluating the PCAs reveals two major and fairly consistent hydrogeomorphic complexes across all the PCAs where the factors they contain share both similar eigenvalues and eigenvectors across the most explanatory principal components. The first of these include stream depth, width, and discharge while the other contains amount of fast water, slope, and substrate size. To avoid redundancy in my models, I focused my hydrogeomorphic analyses on stream width, amount of fast water, and also sinuosity as my selected predictors.

BL was found to decrease with the amount of fast water within terminal basin communities (general linear model, $p < 0.05$). However, in the mountain steppe ecoregions, BL was found to increase with the average wetted width of the river (general linear model, $p < 0.05$). The single grassland ecoregion of the U.S. Great Plains demonstrated no significant hydrogeomorphic metrics in relation to BL. Both width and amount of fast water significantly affected BL when all sites were analyzed together. The interaction between these two variables also showed significance and was investigated further (Figure 4). The interaction indicated that stream width is only significant to BL in streams with high amounts of fast water (greater than 40%).

Due to low species richness, multidimensional spaces could not be built for several communities. The following multidimensional space results focus only on the communities with

three or more functionally distinct species as that was a prerequisite for the analysis. As a result, the U.S. mountain steppe sample size was greatly decreased to only three sites. However, when combining these with the Mongolian mountain steppe sites, I still found that, like BL relationships, Fric increased with stream width.

The only significant factor to FRic for the U.S. grassland ecoregion was percent fast water (linear regression, $p < 0.05$). Like the BL analysis earlier, both stream width and percent fast water significant to FRic in the terminal basin systems (general linear model, $p < .05$). The interaction between these two effects was also significant. However, upon further investigation, I did not find a definitive effect of this interaction on FRic of the community and as such focus on the significance of the main effects (Figure 5). FRic significantly decreased with percent fast water and increased with average stream width. Examining FRic across all sites also mirrored the same strong positive and negative relationship with wetted width and amount of fast water, respectively.

Discussion

I hypothesized that the functional richness metrics of community branch length (BL) and multidimensional richness (FRic) would increase with species richness and that hydrogeomorphic predictors would significantly explain all functional diversity (FD) metrics, including BL, FRic, functional evenness (FEve) and functional divergence (FDiv). I also expected that the combination of significant hydrogeomorphic predictors would vary based on ecoregion (terminal basin, mountain steppe, or grassland) and be independent of country (Mongolia, USA). While my first hypothesis was significantly supported by the relationship between species richness and BL and FRic, my second hypothesis was not well supported as multiple ecoregions lacked any significant hydrogeomorphic predictor. The last hypothesis was somewhat supported as certain ecoregions differed in their observed hydrogeomorphic drivers; but due to the lack of significance in certain systems, this claim could not be entirely supported.

Functional richness and species richness

One of the strongest relationships I observed was the positive relationship between species richness and both functional richness metrics. Species richness had a stronger relationship with community branch lengths than functional spaces, but both were significant. This relationship supports previous hypotheses that increasing or preserving the number of species in a system will have similar effects on its functional diversity (Halpern & Floeter, 2008). As natural systems are increasingly threatened, findings such as these underscore the importance of species preservation especially when the species in question provides unique function to a system or belongs to a sparsely filled functional group (Micheli & Halpern, 2005).

There was also a strong positive relationship between FRic (functional richness computed through the use of multidimensional space) and BL (functional richness derived from a trait-based dendrogram). These analyses have differences in regards to their methodologies and assumptions (see Villéger et al., 2008), but this result suggests they both produce consistent functional richness values relative to the communities within a study.

Functional diversity and hydrogeomorphology

I used functional dendrograms and multidimensional functional space to gauge functional diversity of riverine fishes across a variety of ecoregions between two continents. Although I found evidence that related hydrogeomorphology to both BL and FRic, I did not find strong evidence to support conclusions regarding hydrogeomorphology with either FDiv or FEve – a result which suggests that functional evenness and divergence vary greatly within similar environments. While FRic is strongly correlated with BL, there is no significant correlation between FRic, FEve, and FDiv. This strengthens the arguments of Mason et al. (2005) and Villéger et al. (2008) that functional diversity, like species diversity, can be further broken down into richness, evenness, and divergence as they each measure a unique aspect of functional ecology.

My approach centered on extensively using one aspect of the environment, hydrogeomorphology, as the basis for my predictors against functional diversity, but this yielded no significant relationships in multiple ecoregions (both the U.S. and Mongolian mountain steppes). This indicates that functional diversity is being driven by a factor not included in my analysis. An alternate approach was used in a study by Pool et al. (2010) where they incorporated land use, hydrologic alterations, and local climate to investigate functional diversity. Keck et al.

(2014) incorporated an array of buffer land cover and catchment basin data to investigate how fish traits change with environmental variables. Their approach of including variables from multiple aspects of the environment may increase the likelihood of discovering a driving relationship.

Proportion of fast water (e.g. riffles, rapids, and falls) and average wetted width within each reach were the strongest predictors of functional diversity, especially within the terminal basin rivers. Keeping in mind the strong correlations of the fast water-complex (amount of fast water, substrate size, and stream slope) and the stream width complex (stream width, depth, and discharge) mentioned previously, these findings suggest functional diversity is lower in mountainous headwater-like systems and higher in systems more similar to wide, lowland rivers.

Future Studies

Future studies should endeavor to apply more holistic approaches to discovering FD drivers, such as examining not only hydrogeomorphology but also land use, habitat quality, disturbance regime, climate change, and invasive species presence to determine their combined effect on functional diversity of fishes. Although focusing in on one category of traits, as done in this study, allows for a high level of detail, it may also increase the likelihood of missing strong signals between FD and other major drivers. Future studies may benefit from taking more inclusive approaches such as those used by Pool et al. (2010) or Keck et al. (2014).

A unique aspect of functional diversity that I did not incorporate into my current study is that of functional redundancy. Functional redundancy involves several species performing similar roles within a system so a loss of one species may not include a loss in ecosystem function (Loreau, 2004). While functional redundancy has been studied for several decades,

some researchers advise caution when exploring the concept. Rosenfield (2002) suggested avoiding placing too much emphasis on the power of functional redundancy studies until more reliable methodologies are produced. Moreover, Loreau (2004) stated functional redundancy may not be sustainable in nature over long temporal scales given the habitat variability within complex systems.

Micheli & Halpern (2005) found functional redundancy, albeit in low levels, in coastal marine systems. However, they noted that the redundancy was not abundant enough to sufficiently buffer certain functional groups from overfishing. This case may be more evident of functional vulnerability rather than functional redundancy which supports the hypothesis that the former is actually the more common of the two (Mouillot et al., 2014). Even in this study, despite the terminal basin in Mongolia having fewer species on average at each site, it still had greater Fric values than both the Mongolian mountain steppe and the US terminal basin which had higher average species richness (Table 7). This implies a higher functional redundancy in these latter two systems than in the Mongolian terminal basin. New studies tying functional redundancy to hydrogeomorphology, for instance, could greatly help prioritize species in need of conservation. Being able to relate certain functional groups to specific hydrogeomorphic criteria may also increase efficiency and effectiveness of ongoing conservation efforts.

Conclusions

This study is unique in several ways. First, most river models do not consider atypical systems such as those found in terminal basins, which provides a limited basis from which to derive endorheic basin river theory. Second, this study provided opportunities to investigate biotic processes in some of the most remote, pristine, and relatively understudied river systems in the world, as present in Mongolia. Third, the diversity and scale of ecoregions sampled allowed for an extensive and thorough analysis of both intercontinental and intracontinental hydrogeomorphic drivers of functional diversity. Lastly, many FD studies take place in species-rich areas, whereas our study included several naturally species-poor ecoregions (e.g. the U.S. mountain steppes).

While hydrogeomorphology has high explanatory power in certain ecoregions, especially in terms of the atypical terminal basin systems, there remains large amounts of variation within functional diversity that requires further explanation. Hydrogeomorphology should be used as a base while novel categories of factors are included in new studies to get a more thorough grasp of the principal drivers of functional diversity within riverine fishes. Fish trait knowledge on a global scale represents an area of this field that needs considerable expansion. Many species, particularly those in remote areas, are greatly overlooked in the literature. Advances in building this knowledge base will consequently lead to increased quality in trait studies, more informed depictions of communities, and a better understanding of how fishes play a role in ecosystem function.

Tables

Table 1A. United States Site Information

Site	Ecoregion*	Latitude	Longitude	Date Sampled	Site	Ecoregion*	Latitude	Longitude	Date Sampled
CLEUC1	MS	44.32069	-106.95271	7/18/2017	CARUC1	TB	38.71667	119.91667	7/7/2016
CLEUC2	MS	44.30332	-106.95730	7/18/2017	CARUW1	TB	38.68333	119.91667	7/8/2016
CLEUC3	MS	44.27422	-106.95486	7/20/2017	CARUC2	TB	38.77618	119.89561	7/10/2016
CRAUW1	MS	44.16877	-106.91708	7/14/2017	CARUC3	TB	38.57886	119.70781	7/17/2016
CRAUW2	MS	44.19500	-106.92977	7/13/2017	CARUW2	TB	38.75284	119.93605	7/6/2016
LAKUW1	MS	44.19328	-107.20975	7/17/2017	CARUW3	TB	38.58747	119.68818	7/17/2016
LBHUW1	MS	44.73770	-107.68915	7/26/2017	CARLC1	TB	39.10872	119.71220	7/18/2016
LBHUW2	MS	44.80764	-107.72067	7/26/2017	CARLC2	TB	39.12947	119.70344	7/13/2016
LBHUW3	MS	44.79832	-107.76392	7/27/2017	CARLC3	TB	39.17861	119.67773	7/15/2016
SOUUW1	MS	44.25081	-106.95454	7/15/2017	CARLW1	TB	39.24841	119.58410	7/15/2016
TENUW1	MS	44.24600	-107.22352	7/11/2017	CARLW2	TB	39.28570	119.41741	7/14/2016
TENUW2	MS	44.20645	-107.23387	7/12/2017	CARLW3	TB	39.28925	119.28848	7/12/2016
TONUC1	MS	44.71969	-107.44781	7/25/2017	LMRLC1	GRS	46.89561	-103.54046	9/9/2018
TONUC2	MS	44.68626	-107.44680	7/25/2017	LMRLC2	GRS	46.32733	-103.91998	9/10/2018
TONUC3	MS	44.76820	107.46864	7/27/2017	LMRLC3	GRS	46.96043	-103.50781	9/11/2018
BEAUC1	TB	42.13735	111.64340	8/1/2016	LMRLC4	GRS	47.59385	-103.32861	9/12/2018
BEAUC2	TB	40.87426	110.83650	8/3/2016	LMRUW1	GRS	45.43550	-104.05275	9/18/2018
BEAUC3	TB	40.88673	110.79817	8/3/2016	LMRUW2	GRS	45.55176	-103.96494	9/15/2018
BEAUW1	TB	42.52645	111.57890	7/30/2016	LMRUW3	GRS	45.77347	-103.89005	9/16/2018
BEAUW2	TB	42.52721	111.57804	7/31/2016	NIOLC1	GRS	42.89278	-100.30759	9/22/2018
BEAUW3	TB	40.92834	110.73631	8/3/2016	NIOLC2	GRS	42.67156	-99.76611	9/21/2018
HUMUC1	TB	40.66423	115.44775	7/21/2016	NIOLC3	GRS	42.54460	-99.70952	9/23/2018
HUMUC2	TB	40.65824	115.43296	7/24/2016	NIOLC5	GRS	42.78879	-100.06271	9/25/2018
HUMUC3	TB	40.68977	115.47697	7/24/2016	NIOLC6	GRS	42.92400	-100.74689	9/26/2018
HUMLC1	TB	40.72666	116.00958	7/25/2016	NIOLC7	GRS	42.54732	-100.10766	9/27/2018
HUMLC2	TB	40.57910	116.27739	7/26/2016	NIOLC8	GRS	42.77072	-98.44424	9/28/2018

*Ecoregion refers to either the terminal basin (TB), mountain steppe (MS) or grassland (GRS) system

Table 1B. Mongolian Site Information.

Site	Ecoregion	Latitude	Longitude	Date Sampled
KVDUW1	TB	49.18442	89.20778	8/5/2018
KVDUW2	TB	48.89408	89.64806	8/5/2018
KVDUW4	TB	48.86969	90.17083	8/7/2018
KVDUC1	TB	48.87231	89.67972	8/7/2018
KVDUC2	TB	48.83667	89.53333	8/6/2018
ZAKLC1	TB	48.27817	93.48083	7/31/2018
ZAKLW1	TB	48.30842	93.49417	7/31/2018
ZAKUC1	TB	47.17819	97.72139	7/24/2018
ZAKUC2	TB	47.10900	97.63816	7/21/2018
ZAKUC3	TB	47.03756	97.60639	7/23/2018
ZAKUC4	TB	47.27700	98.05694	7/24/2018
ZAKUC5	TB	46.58222	97.25278	7/27/2018
ZAKUW1	TB	47.22553	97.61611	7/22/2018
ZAKUW2	TB	47.15400	97.62778	7/22/2018
ZAKUW4	TB	46.61628	97.30639	7/27/2018
DELLW1	MS	49.62519	99.59083	9/5/2017
DELLW2	MS	49.62417	99.68833	9/4/2017
DELLW3	MS	49.63736	99.92417	9/2/2017
DELUC1	MS	50.17340	98.48914	9/7/2017
DELUC2	MS	50.17575	98.48293	9/7/2017
DELUC3	MS	50.09867	98.58125	9/8/2017
DELUC4	MS	50.12066	98.64066	9/10/2017
EGILS1	MS	50.52122	101.43498	9/17/2017
EGILS2	MS	50.50444	101.75060	9/18/2017
EGILS3	MS	50.09532	101.59291	9/22/2017
EGILS4	MS	50.31178	101.94071	9/23/2017
EGILW1	MS	50.56733	101.52973	9/16/2017

*Ecoregion refers to either the terminal basin (TB) or mountain steppe (MS) system

Table 2. Fish trait categories and respective modalities

TRAIT CATEGORY	MODALITY	MODALITY ABBREVIATION
TROPHIC GROUP	Omnivore	OMN
	Invertivore	INV
	Piscivore	PIS
FEEDING POSITION	Benthic specialist	BS
	Water column generalist	WCG
	Water column specialist	WCS
RHEOPHILY	Limnophilic	LIM
	Eurytopic	EUR
	Rheophilic	RHE
AQUATIC POSITION	Demersal	DEM
	Bentho-pelagic	BP
	Pelagic	P
	Pelagic-neritic	PN
SPAWNING	Brood-hider	BH
	Nest spawner	NS
	Open substratum	OC
	Substrate chooser	SC
	Live bearer	LB
SPAWNING SUBSTRATE	Lithophil	LTH
	Phytolithophil	PHL
	Speleophil	SPL
	Generalist	GEN
	Polyphil	POL
	Lithopelagophil	
	Psammophil	PSM
	Phytophil	PHY
PARENTAL GUILDS	Guarder	G
	Nonguarder	NG
	Live bearer	B
MAX LENGTH	Millimeters	Continuous
AGE AT MATURITY	Years	Continuous
MAX LONGEVITY	Years	Continuous

Table 3A. Fish species and assigned traits.

Species	Trophic Group	Aquatic Position	Parental Guild	Spawning Guild	Spawning Substrate	Rheophily	Water Column Feeding	Max Length	Age at Maturity	Longevity	Trait Data Sources
<i>Oncorhynchus mykiss</i>	PIS-INV	BP	NG	BH	LTH	EUR	WCG	400	3	11	1,2
<i>Salvelinus fontinalis</i>	PIS-INV	BP	NG	BH	LTH	EUR	WCG	249	2	24	1,2
<i>Salmo trutta</i>	PIS-INV	PN	NG	BH	LTH	EUR	WCG	292	3	38	1,2
* <i>S. trutta</i> X <i>S. fontinalis</i>	PIS-INV	BP				EUR	WCG	431			3,9
<i>Prosopium williamsoni</i>	PIS-INV	BP	NG	BH	LTH	EUR	WCG	347	4	11	1,2
<i>Oncorhynchus clarkii</i>	PIS-INV	D	NG	BH	LTH	EUR	WCG	307	3	10	1,2
<i>Rhinichthys osculus</i>	OMN	D	G	NS	LTH	EUR	WCG	106	1.5	3.5	1,2
<i>Cyprinus carpio</i>	OMN	BP	NG	OS	PHL	LIM	WCG	430	2	38	1,2
<i>Pimephales promelas</i>	OMN	D	G	NS	SPL	LIM	WCG	67	0.5	5	1,2
<i>Richardsonius earegius</i>	OMN	BP	NG	OS	LTH	EUR	WCG	77	2	5	1,2
<i>Rhinichthys cataractae</i>	OMN	D	G	SC	LTH	RHE	BS	109	2.5	5	1,2
<i>Catostomus tahoensis</i>	OMN	D	NG	OS	LTH	EUR	WCG	214	5	15	1,2
<i>Catostomus platyrhynchus</i>	OMN	D	NG	OS	LTH	EUR	BS	256	4	9	1,2
<i>Ameiurus melas</i>	OMN	D	G	NS	LTH	LIM	WCG	230	2.5	10	1,2
<i>Gambusia affinis</i>	OMN	BP	B	LB	GEN	LIM	WCG	47	0.3	1	1,2
<i>Cottus beldingi</i>	OMN	D	G	NS	SPL	RHE	BS	102	3	5	1,2
<i>Micropterus dolomieu</i>	PIS-INV	BP	G	NS	POL	EUR	WCG	295	3.5	26	1,2
<i>Lepomis macrochirus</i>	PIS-INV	BP	G	NS	POL	LIM	WCG	119	2	10	1,2
<i>Lepomis cyanellus</i>	PIS-INV	BP	G	NS	POL	LIM	WCG	126	2	9	1,2
<i>Micropterus salmoides</i>	PIS-INV	BP	G	NS	POL	LIM	WCG	245	2.5	23	1,2

Refer to Table 1 for modality abbreviations.

**S. trutta* X *S. fontinalis* is a sterile hybrid and does not reproduce

1= FishBase (Froese & Pauly 2018), 2=FishTraits (Angermeier & Frimpong, 2011), 3=Measured directly with fish diet data, 9= Tramilton 2017.

Table 3B. Fish species and assigned traits

Species	Trophic Group	Aquatic Position	Parental Guild	Spawning Guild	Spawning Substrate	Water		Age at Maturity	Longevity	Trait Data Sources
						Rheophily	Column Feeding			
<i>Carpiodes carpio</i>	OMN	D	NG	OS	PHL	LIM	BS	3	10	1,2
<i>Catostomus commersonii</i>	OMN	D	NG	OS	LTH	LIM	BS	3	12	1,2
<i>Culex inconstans</i>	INV	D	G	NS	LTH		BS	1	2	1,2,3
<i>Cyprinella lutrensis</i>	OMN	BP	NG	OS	PHL	EUR	BS	1.5	3	1,2
<i>Dorosoma cepedianum</i>	OMN	PN	NG	OS	PHL	LIM	WCG	2	10	1,2
<i>Esox americanus</i>	PIS-INV	D	NG	OS	PHY	LIM	WCS	2.5	7	1,2
<i>Esox lucius</i>	PIS-INV	D	NG	OS	PHY	LIM	WCS	2	30	1,2
<i>Fundulus sciadicus</i>	OMN	BP	NG	OS	PHY	LIM	WCS	1.5	3.5	1,2
<i>Hiodon alosoides</i>	INV	P	NG	OS	LPG	LIM	WCG	5	14	1,2
<i>Hybognathus grayi</i>	OMN	D	NG	OS	LTH	LIM	BS	1.5	3	1,2
<i>Hybognathus hankinsoni</i>	OMN	D	NG	OS	PHL	LIM	WCG	2	3	1,2
<i>Ictalurus punctatus</i>	OMN	BP	NG	NS	SPL	EUR	WCG	3.5	24	1,2
<i>Lepomis gibbosus</i>	OMN	BP	NG	NS	POL	LIM	WCG	2	12	1,2
<i>Maxostoma macrolepidotum</i>	OMN	D	NG	OS	LTH	EUR	BS	3.5	12	1,2
<i>Notropis stramineus</i>	OMN	BP	NG	OS	PSM	EUR	WCG	1	3	1,2
<i>Noturus flavus</i>	OMN	D	G	NS	SPL	EUR	BS	3	8	1,2
<i>Perca flavescens</i>	PIS-INV	BP	NG	OS	PHL	LIM	WCG	4	12	1,2
<i>Pimephales notatus</i>	OMN	D	G	NS	SPL	EUR	WCG	1	3.5	1,2
<i>Platygobio gracilis</i>	OMN	D	NG	OS	LTH	EUR	WCG	1.5	6	1,2
<i>Sander canadensis</i>	PIS-INV	D	NG	OS	LPG	EUR	WCS	3	18	1,2
<i>Semotilus atromaculatus</i>	OMN	D	NG	BH	LTH	EUR	WCG	2	8	1,2

Refer to Table 1 for modality abbreviations

1= FishBase (Froese & Pauly 2018), 2=FishTraits (Angermeier & Frimpong, 2011), 3= NatureGate brook stickleback page (Brook stickleback 2019)

Table 3C. Fish species and assigned traits

Species	Trophic Group	Aquatic Position	Parental Guild	Spawning Guild	Spawning Substrate	Rheophily	Water Column Feeding	Max Length	Age at Maturity	Longevity	Trait Data Sources
<i>Thymallus arcticus</i>	INV	BP	NG	OS	LTH	EUR	WCS	327	4	12	1,2
<i>Phoxinus phoxinus</i>	OMN	D	NG	OS	LTH	EUR	WCG	91	2	11	1,3,8
<i>Percu fluviatilis</i>	PIS-INV	D	NG	OS	PHL	LIM	WCG	65	2	22	1,3,8
<i>Barbatula golubstovi</i>	INV	D	NG	OS	LTH	RHE	BS	131			1,3,4,5
<i>Brachymystax lenok</i>	PIS-INV	BP	NG	OS	LTH	EUR	WCG	402	6	13	1,3,8
<i>Thymallus brevirostris</i>	OMN	BP	NG	OS	LTH	EUR	WCG	306	5	17	1,3
<i>Oreoleuciscus potanini</i>	OMN	D	NG	OS	LTH	EUR	WCG	118	8	40	1,3
<i>Barbatula conilobus</i>	INV	D	NG	OS	LTH	RHE	BS	162			3,4,5,7
<i>Leuciscus leuciscus</i>	OMN	BP	NG	OS	LTH	EUR	WCG	174	3	16	1,3,8
<i>Barbatula toni</i>	INV	D	NG	OS	LTH	RHE	BS	99	2		1,3,4,8
<i>Cobitis taenia</i>	INV	D	NG	OS	PSM	LIM	BS	106	2	5	1,3,4

Refer to Table 1 for modality abbreviations.

1= FishBase (Froese & Pauly 2018), 2=FishTraits (Angermeier & Frimpong, 2011), 3=Measured directly with fish diet data, 4=Implied from anatomical features (e.g. barbels, dorsoventrally compressed body). 5= Traits inferred from similar species (*Barbatula toni*). 7= Prokofiev 2016, 8= Mendsaikhan et al. n.d.

Table 4. Hydrogeomorphic variables used in the study to represent the structure of the rivers

Hydrogeomorphic Metric	Definition	Description
SINU	Channel sinuosity	Reach length divided by straight line between endpoints
XWIDTH	Stream width	Mean wetted width over reach
XSLOPE	Stream slope	Water surface gradient over reach (%)
DSCHRG	Stream discharge	Mean discharge from site
XDEPTH	Stream depth	Mean thalweg depth
PCTFAST	Percent fast water	Percent of reach composed of fast water
PCTPOOL	Percent pools	Percent of reach composed of all pool
SUB_X	Substrate size	Mean substrate size (mm)
ENTRATIO	Entrenchment ratio	Width of flood prone area divided by bankfull width
XBKA	Bank angle	Mean bank angle

Table 5. Fish species sampled of the U.S. and Mongolian temperate steppe

Family	Species Name	Family	Species Name
Catostomidae	<i>Catostomus tahoensis</i>	Cyprinidae	<i>Oreoleuciscus potanini</i>
Catostomidae	<i>Catostomus platyrhynchus</i>	Cyprinidae	<i>Leuciscus leuciscus</i>
Catostomidae	<i>Catostomus commersonii</i>	Esocidae	<i>Esox americanus</i>
Catostomidae	<i>Moxostoma macrolepidotum</i>	Esocidae	<i>Esox lucius</i>
Centrarchidae	<i>Micropterus dolomieu</i>	Fundulidae	<i>Fundulus sciadicus</i>
Centrarchidae	<i>Lepomis macrochirus</i>	Gasterosteidae	<i>Culea inconstans</i>
Centrarchidae	<i>Lepomis cyanellus</i>	Hiodontidae	<i>Hiodon alosoides</i>
Centrarchidae	<i>Micropterus salmoides</i>	Ictaluridae	<i>Ameiurus melas</i>
Centrarchidae	<i>Lepomis gibbosus</i>	Ictaluridae	<i>Ictalurus punctatus</i>
Clupeidae	<i>Dorosoma cepedianum</i>	Ictaluridae	<i>Noturus flavus</i>
Cobitidae	<i>Cobitis taenia</i>	Nemacheilidae	<i>Barbatula golubstovi</i>
Cottidae	<i>Cottus beldingi</i>	Nemacheilidae	<i>Barbatula conilobus</i>
Cyprinidae	<i>Rhichthys osculus</i>	Nemacheilidae	<i>Barbatula toni</i>
Cyprinidae	<i>Cyprinus carpio</i>	Percidae	<i>Perca flavescens</i>
Cyprinidae	<i>Pimephales promelas</i>	Percidae	<i>Sander canadensis</i>
Cyprinidae	<i>Richardsonius egregius</i>	Percidae	<i>Perca fluviatilis</i>
Cyprinidae	<i>Rhinichthys cataractae</i>	Poeciliidae	<i>Gambusia affinis</i>
Cyprinidae	<i>Carpiodes carpio</i>	Salmonidae	<i>Oncorhynchus mykiss</i>
Cyprinidae	<i>Cyprinella lutrensis</i>	Salmonidae	<i>Salvelinus fontinalis</i>
Cyprinidae	<i>Hybognathus argyritis</i>	Salmonidae	<i>Salmo trutta</i>
Cyprinidae	<i>Hybognathus hankinsoni</i>	Salmonidae	<i>S. trutta</i> X <i>S. fontinalis</i>
Cyprinidae	<i>Notropis stramineus</i>	Salmonidae	<i>Prosopium williamsoni</i>
Cyprinidae	<i>Pimephales notatus</i>	Salmonidae	<i>Oncorhynchus clarkii</i>
Cyprinidae	<i>Platygobio gracilis</i>	Salmonidae	<i>Thymallus arcticus</i>
Cyprinidae	<i>Semotilus atromaculatus</i>	Salmonidae	<i>Brachymystax lenok</i>
Cyprinidae	<i>Phoxinus phoxinus</i>	Salmonidae	<i>Thymallus brevirostris</i>

Table 6. Summary of nested ANOVA results of country and ecoregional effects on functional diversity measures.

Factor	Branch Length	Fric	Feve	Fdiv
Country	$F_{1,74} = 4.53,$ $p = .037$	$F_{1,54} = 0.03,$ $p = .856$	$F_{1,54} = 0.31,$ $p = 0.582$	$F_{1,54} = 0.03,$ $p = .853$
Ecoregion (Country)	$F_{3,74} = 27.27,$ $p < .001$	$F_{3,54} = 2.83,$ $p = .048$	$F_{3,54} = 1.13,$ $p = 0.345$	$F_{3,54} = 7.48,$ $p < .001$

TABLE 7. Average species and functional richness per site in each ecoregion

Ecoregion	Number of Sites	Number of Species Mean \pm SE	Branch Length Mean \pm SE	FRic Mean \pm SE
U.S. terminal basin	23	4.13 \pm 0.455	1.69 \pm 0.215	0.12 \pm 0.0154
U.S. mountain steppe	15	2.07 \pm 0.206	0.51 \pm 0.093	0.08 \pm 0.0380
U.S. grasslands	14	7.57 \pm 0.810	3.02 \pm 0.258	0.19 \pm 0.0275
Mongolia terminal basin	15	3.07 \pm 0.248	1.15 \pm 0.093	0.15 \pm 0.0257
Mongolia mountain steppe	12	4.00 \pm 0.389	1.56 \pm 0.153	0.10 \pm 0.0317

Table 8. Pearson correlation values between hydrogeomorphic variables.

	XDEPTH	XWIDTH	PCTFAST	SINU	XSLOPE	SUB_X	DSCHRG	POOL	XBKA
XWIDTH	0.533***								
PCTFAST	-0.422***	-0.345**							
SINU	-0.003	-0.169	-0.284*						
XSLOPE	-0.352**	-0.299**	0.505***	-0.214					
SUB_X	-0.218	-0.277*	0.564***	-0.367***	0.48***				
DSCHRG	0.56***	0.733***	-0.237*	-0.152	-0.253*	-0.095			
POOL	0.339**	0.151	-0.403***	0.128	-0.195	-0.085	0.151		
XBKA	-0.114	-0.128	0.026	-0.019	0.195	0.115	-0.212	-0.079	
ENTRATIO	-0.308**	-0.312**	0.158	-0.076	0.163	0.233*	-0.261*	-0.09	0.069

Significance levels $p < 0.05$, $p < 0.01$, and $p < 0.001$ are indicated by *, **, and *** respectively. Refer to Table 2 for hydrogeomorphic definitions

Figures

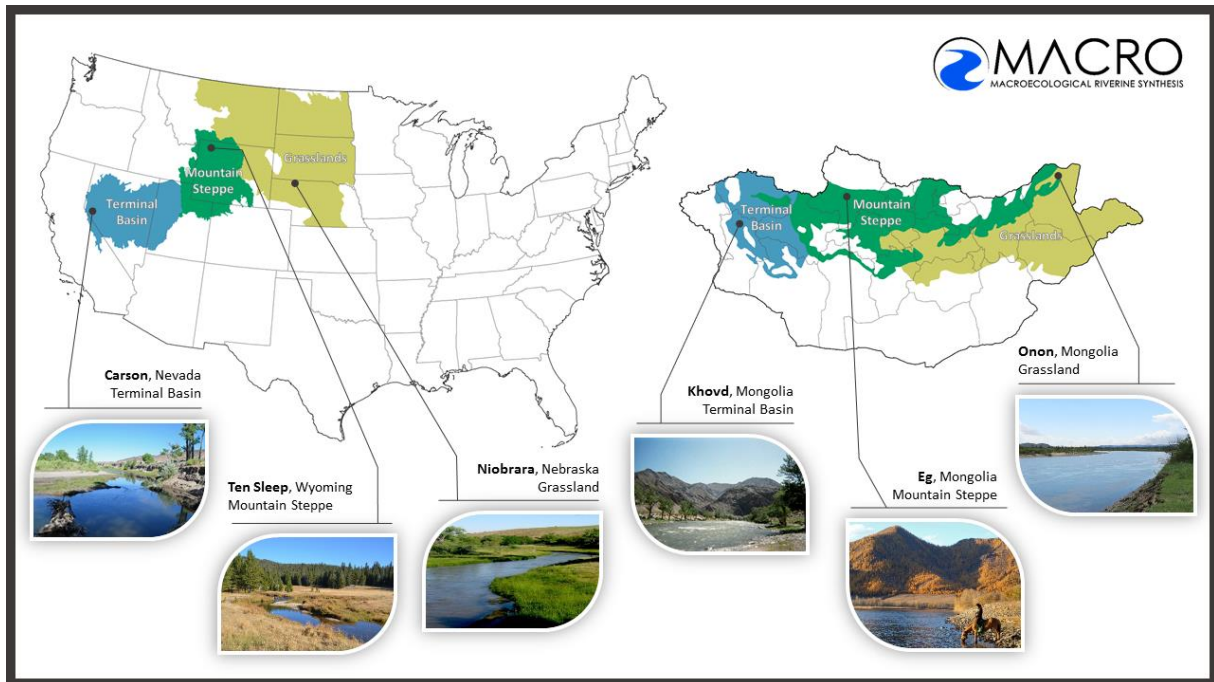


Figure 1. Paired ecoregions of the United States of America (left) and Mongolia (right) (MACRO: Study Sites, n.d.).

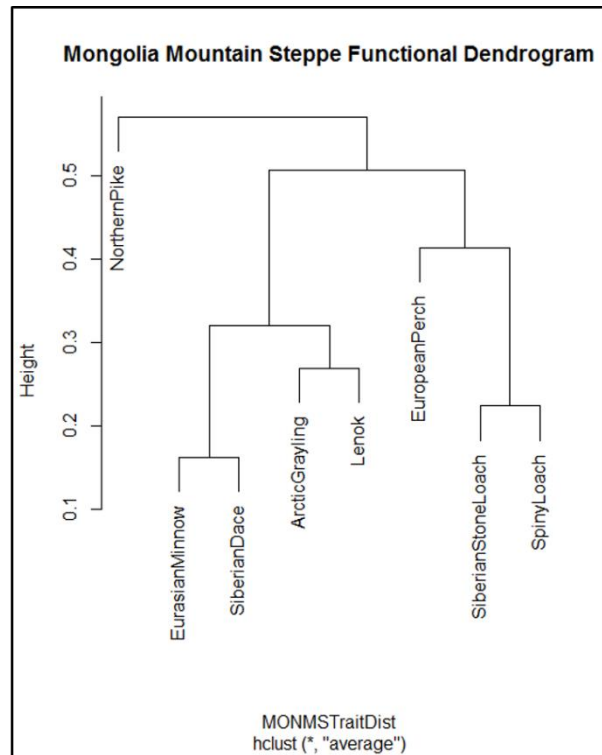
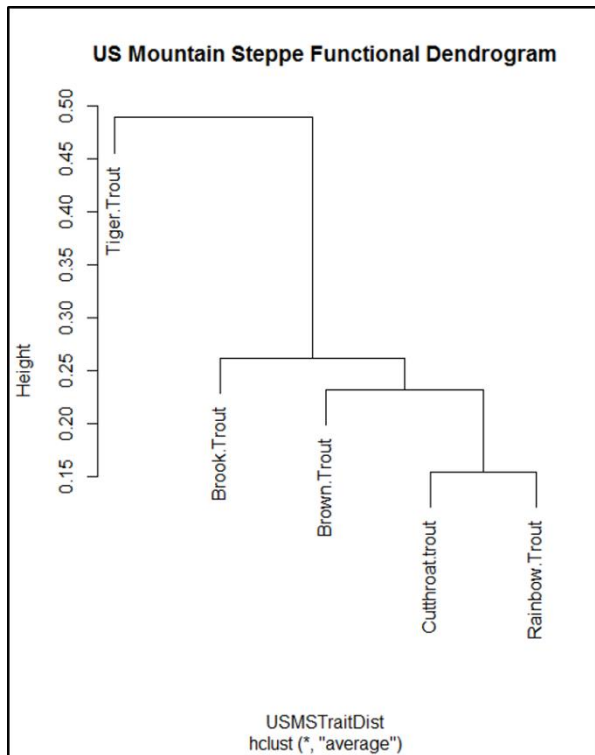


Figure 2A. Mountain steppe functional dendrograms for the United States (left) and Mongolia (right). The US mountain steppe represents the least functionally diverse ecoregion within my study.

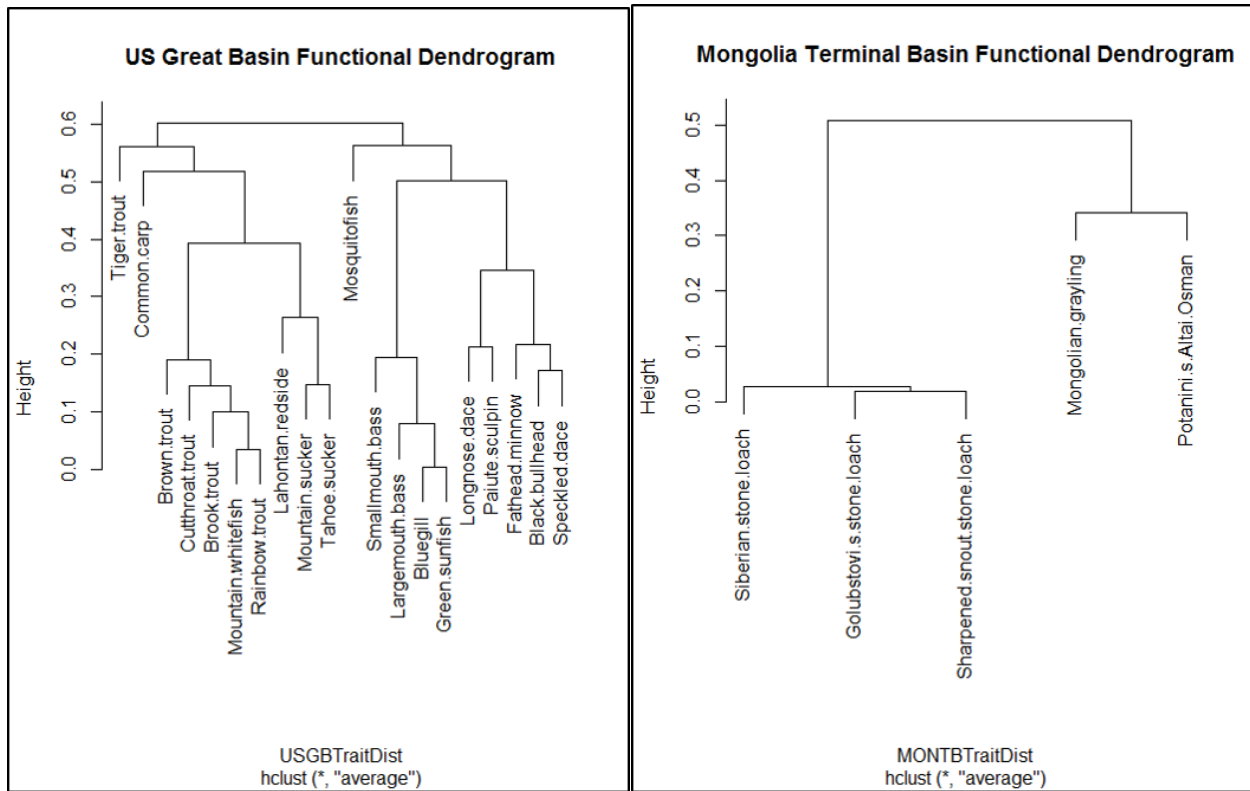


Figure 2B. Terminal basin dendrograms of the United States (left) and Mongolia (right).

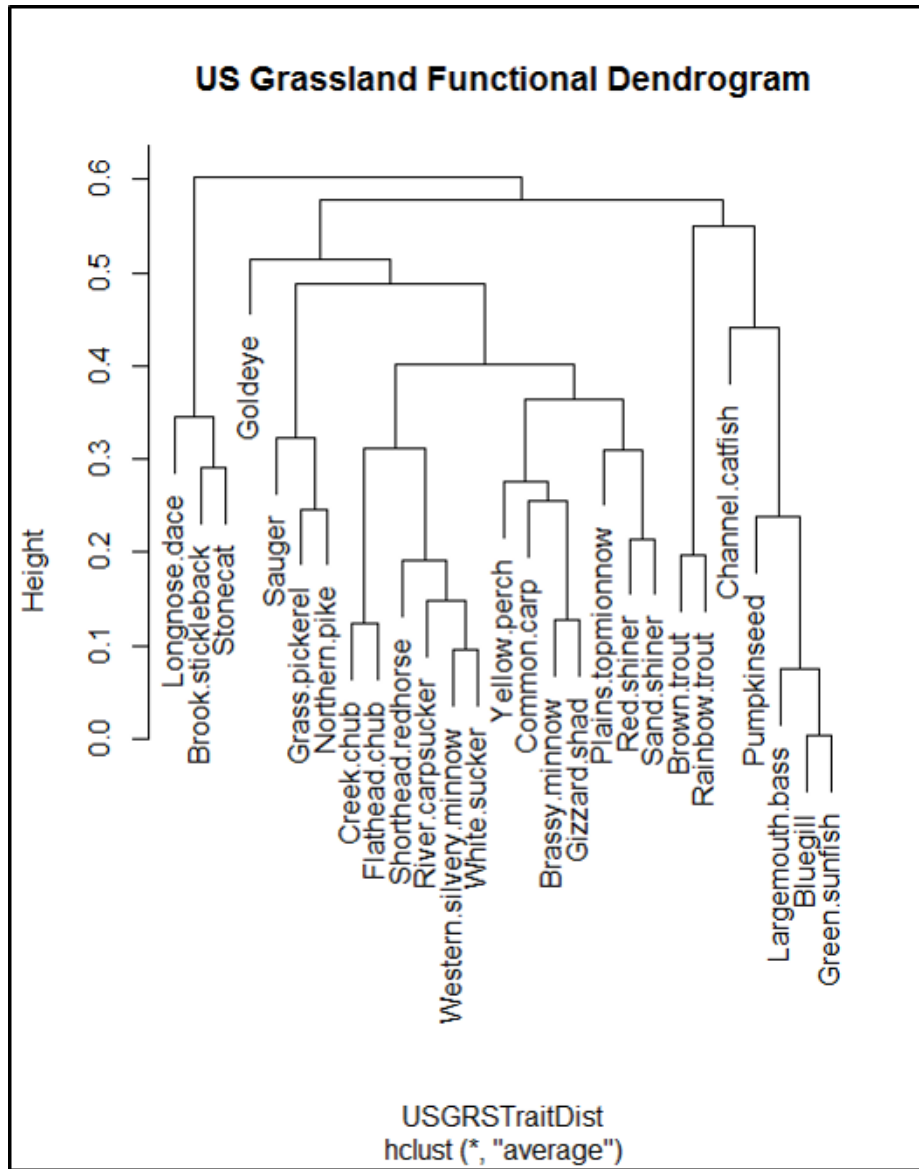


Figure 2C. US Grassland functional dendrogram. This represents the most diverse system within my study with a variety of functional groups present.

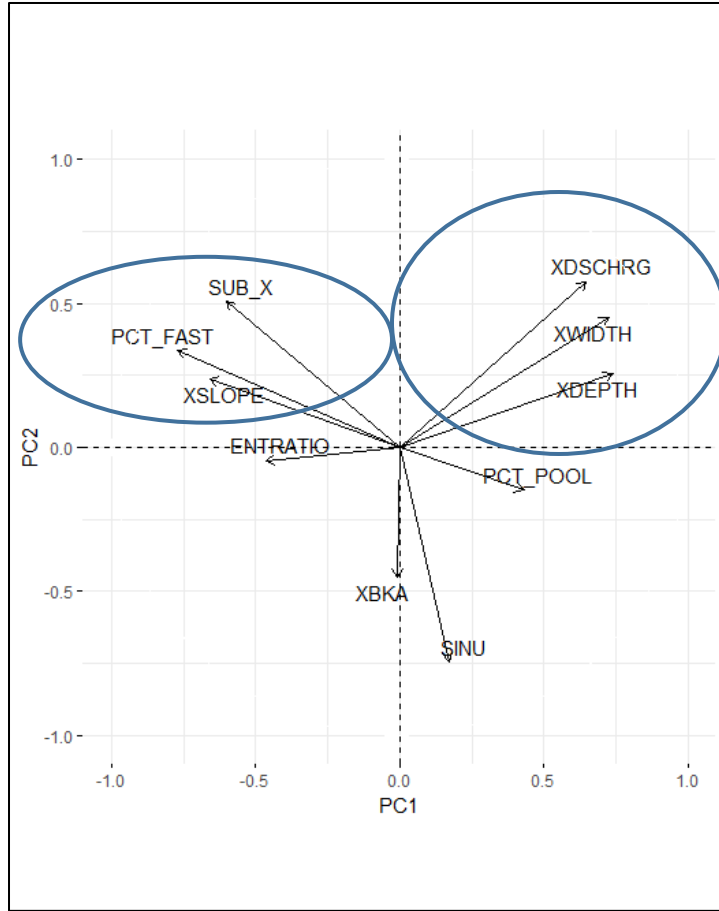


Figure 3. PCA of hydrogeomorphic variables. The two main complexes of hydrogeomorphic variables are each circled with definitions of abbreviations provided in Table 2. Members of each complex accounted for very similar variation within the dataset and were significantly correlated with one another.

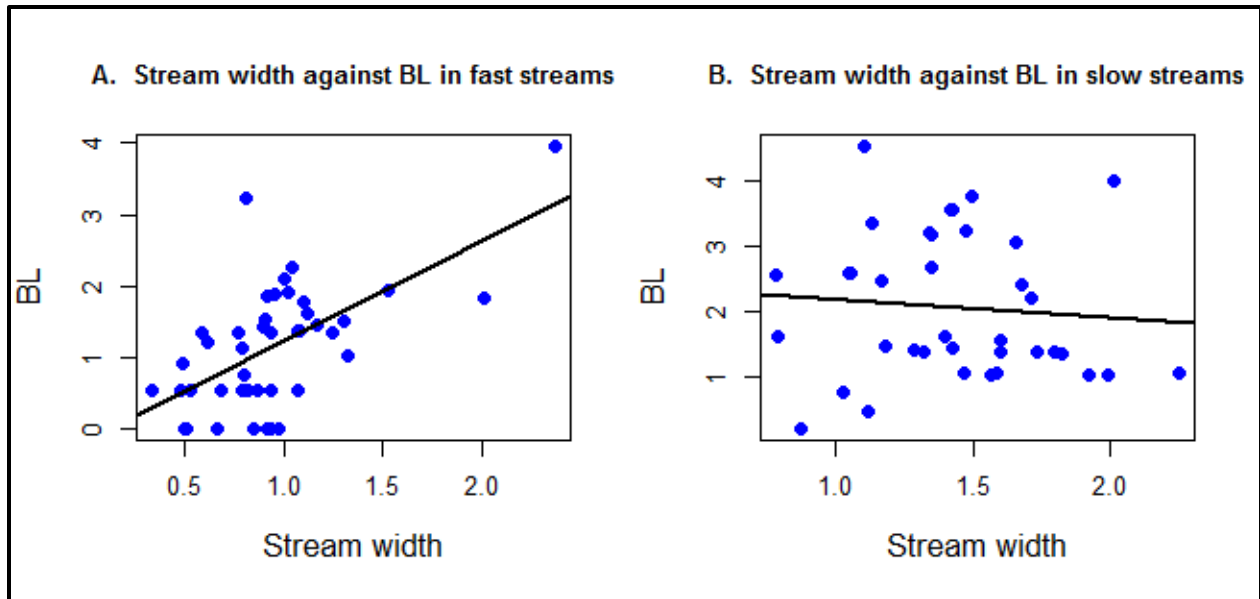


Figure 4. Interactive effects of stream width and amount of fast water on BL across all sites. The effect of width on BL was significant in streams with more fast water (A) and not significant in streams with less fast water (B).

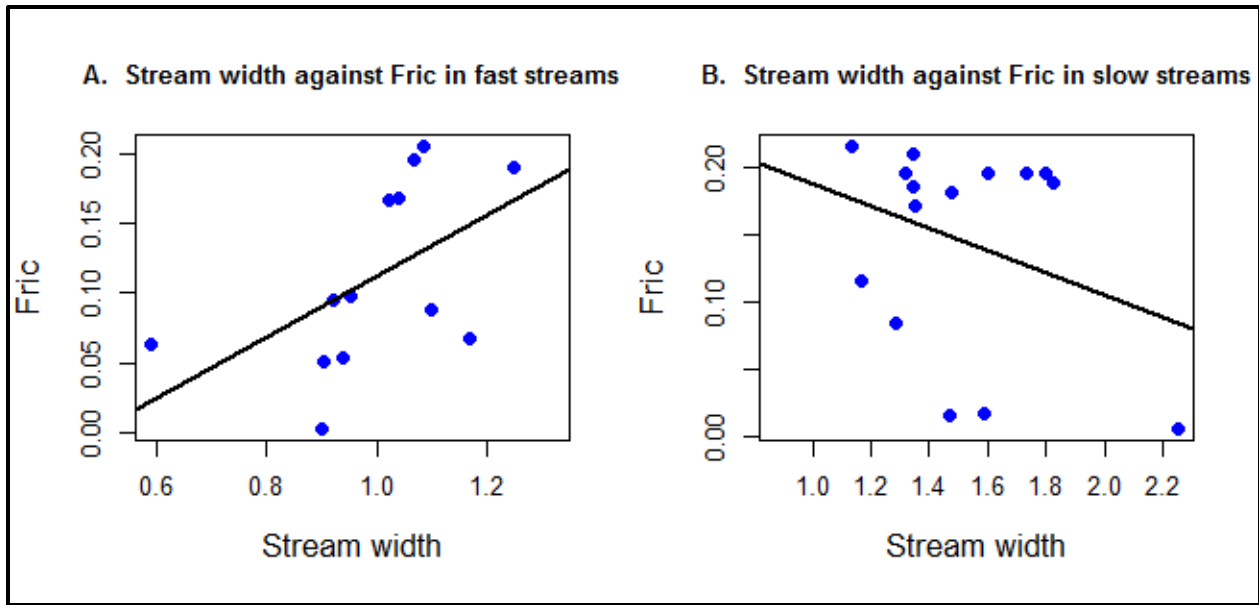


Figure 5. Interactive effect of stream width and amount of fast water on Fric in terminal basin systems. Neither type of system showed a significant effect of stream width on Fric.

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