CONVERGENCE AND COMMUNITY ASSEMBLY OF STREAM FISHES: AN INTERCONTINENTAL ANALYSIS

A Dissertation

by

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ABSTRACT

A mechanistic understanding of general community assembly is crucial for predicting how species will respond to future environmental changes. My dissertation explores general ecological patterns of stream fish assemablages based on intercontinental comparisons using new quantitative approaches. In this study, I tested for convergent trait-environment patterns across regional faunas in response to consistent sets of environmental filters acting on functional traits. I found similar patterns of trait-environment patterns across all five regions, implying common environmental filters acted on local community assembly. The congruent trait-environment patterns implied that water velocity and habitat structural complexity act as universal environmental filters. These universal filters appear to produce similar trait distributions of fish assemblages in streams across all regions. In my study, I also tested for convergence of species traits within similar microhabitats. This study revealed a high prevalence of convergence of functional traits among fish species occupying similar microhabitats of small, low-gradient streams. The prevalence of convergent suites of functional traits implies that adaptation to similar environmental conditions resulted in repeated patterns of evolution along multiple niche dimensions. Fishes occupying areas with relatively fast water velocity or little structural complexity generally occupied a restricted morphological space and exhibited the highest degrees of convergence. Finally, I test for similar patterns of functional trait and phylogenetic dispersion across regions and along environmental gradients. Here, under-dispersion was consistently more prevalent than over-dispersion in all regions regardless of null model or functional metric. Functional metrics tended to decrease with high water velocity, shallow water depth, and non-structured substrates microhabitats. Together, these results emphasize that environmental filtering plays an important role in structure stream fish assemblages. Furthermore, I detected more instances of functional trait under-dispersion coupled with phylogenetic under-dispersion, which may reflect a signal of phylogenetic niche conservation or stabilizing selection acting on species' traits and ecology at the local scale. Overall, the results of my study implied that steam fish assemblages were structured by relatively consistent deterministic mechanisms.

DEDICATION

To my loving parents, Alan and Caryn, for their continued support.

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NOMENCLATURE

FRic	Functional richness
MNND	Mean nearest neighbor distance
MPD	Mean pairwise distance
MNTD	Mean nearest taxon distance
NTI	Nearest taxon index
NRI	Net relatedness index
FD	Functional diversity

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CHAPTER I

INTRODUCTION

Robert MacArthur proposed that the goal of all science should be to search for general patterns or rules (MacArthur, 1972). Community ecology is no exception, even though individuals like Lawton have suggested that community ecology is “a mess” because the immense variation in ecology, natural history, and evolutionary history of different species prevent broad generalizations (Lawton, 1999). Some feel that communities are too variable and complex to allow for formulation of general rules (Lawton, 1999; Simberloff, 2004). However, the search for general patterns in community ecology may not be out of reach, and this dissertation explores the structure of stream fish communities based on intercontinental comparisons using some of the newest quantitative approaches.

Newly developed theories and methods for analysis of community functional trait variation have the potential to reveal general, predictable patterns in community ecology (McGill et al., 2006; Verberk et al., 2008; Webb et al., 2010; Verberk, 2013). In contrast to taxonomic methods of community ecology (e.g. taxonomic composition, species richness), trait-based methods should enhance predictions about ecology because functional traits mediate the interaction between organisms and their environment (Weiher and Keddy, 1995; McGill et al., 2006; Algar et al., 2011l; Mouchet et al., 2013). Additionally, different functional traits are associated with different niche dimensions (Gatz, 1979; Violle et al., 2007; Winemiller et al., 2015). This allows researchers to interpret patterns for either a single or multiple niche dimensions (Trisos et al., 2014), thus improving our understanding of how traits shape community assembly and species coexistence. Ultimately, analysis of functional traits distributions of communities from different habitats and regions provides a means to reveal mechanisms driving community assembly that may facilitate predictions about the effects of anthropogenic impacts on biodiversity (Suding et al., 2005; McGill et al., 2006). Before we can predict how communities will change in response to anthropogenic alteration of habitats, we must first understand how communities vary along environmental gradients.

Community convergence also can reveal general ecological and evolutionary patterns (Winemiller, 1991; Lamouroux et al., 2002; Winemiller et al., 2015). General ecological or evolutionary processes should influence species and communities in the same way regardless of geographic location or evolutionary history. Therefore, convergence of assemblage trait distributions would indicate general ecological processes that help shape repeated patterns of adaptive evolution among geographic and evolutionary independent regions. My study attempts to elucidate general ecological patterns using two approaches. First, consistent methods were used to test for similar patterns of assembly processes in stream fish assemblages from five zoogeographic regions on four continents. Second, I used convergent trait-environment patterns to infer similar ecological mechanisms acting on species traits.

Ecologists have long sought to understand the mechanisms that account for local community assembly, species coexistence, and biodiversity patterns involving various dimensions at various scales. These mechanisms, termed community assembly processes, have been widely studied using a variety of approaches, but most recent attention has been on methods to infer the relative contribution of niche-based processes (environmental filtering and limiting similarity) to neutral processes (Hubbell, 2001; Chase and Myers, 2011). In chapter one, I explore the patterns that may reveal niche-based processes of community assembly along environmental gradients of streams in the five regions. My goal was to test if the same processes influence stream fish assemblages in a similar way across the different zoogeographic regions. Patterns of functional trait dispersion are used to infer the ecological processes that structure local assemblages. Under the environmental filtering hypothesis, local environmental conditions limit successful establishment of species to those with certain sets of functional traits, leading to species assemblages with traits that are more similar, or under-dispersed, than expected by change alone (Figure 1; Weiher and Keddy, 1995; Cornwell and Ackerly, 2009). Alternatively, if co-occurring species have traits that are less similar (over-dispersed) than expected at random, then this can be interpreted as an indication of limiting similarity (Brown and Wilson, 1956; Weiher and Keddy, 1995). Under the limiting similarly hypothesis, species avoid competitive exclusion through niche and functional trait differentiation, resulting in assemblage trait over-dispersion (Figure 1; MacArthur and Levins, 1967). The neutral theory posits that species either are ecologically equivalent and coexist and persist independent of their traits (Hubbell, 2001). In this case, assemblage trait distributions would be indistinguishable from random. Also, an assemblage structured entirely by a neutral process, such as random dispersal, should have a distribution of functional traits reflecting random assembly.

Community assembly processes are intrinsically scale dependent, and it has been suggested that different processes influence assemblage taxonomic and functional structure depending on the scale of study (Levin, 1992; Oberdoff et al., 1995; Smith et al., 2013; Blanchet et al., 2014). For instance, at a regional scale, two populations may never interact and therefore cannot be influenced by competition. At the local scale, it is generally assumed that community assembly and population persistence are heavily influenced by environmental variability, species interactions, environmental stress and productivity, whereas historical biogeography, dispersal, speciation, and abiotic environmental factors play a major role at the regional scale (Brooker et al., 2009; Algar et al., 2011). Ascertaining the scale at which niche-based processes operate is crucial for understanding community assembly processes and species co-occurrence.

Both regional and local processes interact to shape species coexistence and community structure (Ricklefs, 2004; Algar et al., 2011); however, the relative contributions of each across geographic scales is less known (Algar et al., 2011; Heino et al., 2015). The question is no longer whether niche-based or stochastic processes determine community structure, but rather what is the relative contribution of each to species coexistence patterns and community structure at different scales (Vellend, 2010; Weiher et al., 2011). Unfortunately, investigation into these mechanisms has produced mixed results. Some studies have suggested that environment filtering is the predominant process at the local scale, resulting in co-occurring species with similar functional traits (Schlosser, 1987; Mouillot et al., 2007; Weiher et al., 2011; Baraloto et al., 2012; Dimitriadis et al., 2012; Mouchet et al., 2013; Troia and Gido, 2015; Córdova-

Tapia et al., 2018). For example, only environmental filtering, and not limiting similarity, was shown to be the predominant factor shaping fish assemblages in Neotropical streams (Córdova-Tapia et al., 2018). In contrast, other studies have found trait over-dispersion at the local scale, suggesting limiting similarity as the predominant process (Ingram and Shurin, 2009; Montaña and Winemiller, 2014). It also is possible that both processes can play a major role in determining community structure simultaneously (Cornwell and Ackerly, 2009; Troia et al., 2015; Mendez et al., 2012; Montaña et al., 2014).

In my second and third chapters, I explore the strength and frequency of convergent evolution in stream fishes along environmental gradients among five zoogeographic regions. Convergent evolution can arise when taxa from divergent lineages undergo adaptive change in response to similar selective pressures, with the degree and frequency of convergence depending on available genotypic and phenotypic variation, strength of selection, and passage of time. Convergent evolution can occur at all biological levels, from DNA sequences to communities, and is thought to be common throughout the tree of life (Conway Morris, 2003; Losos, 2011; McGhee, 2011; Winemiller et al., 2015). Yet, few studies have rigorously tested for convergence over large geographic and evolutionary scales (e.g. Wiens et al., 2006; Moen et al., 2016).

Species that evolve in response to similar selective pressures should share many convergent traits, and communities that assemble in response to similar environmental filters should have similar trait distributions, regardless of geographic proximity or evolutionary history. Habitat features often act as environmental filters that restrict establishment and persistence of organisms based on the suitability of their traits for survival under a given set of conditions (Weiher and Keddy, 1995; Cornwell and Ackerly, 2009; Lebrija-Trejos et al., 2010; Kraft et al., 2015). Therefore, I hypothesized that streams with similar environmental conditions in different geographic locations should have fish assemblages with similar trait distributions. Assemblage trait convergence among geographically and evolutionarily independent systems would infer a common response to selection producing repeated patterns of adaptive evolution as well as consistent processes of local community assembly. By assessing patterns of functional trait dispersion and convergent evolution, I seek evidence for general rules that structure steam fish assemblages. In the final chapter, I briefly explore some of the broader implications of my findings, including future directions for community ecology research and ecological applications.

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CHAPTER II

FISH ASSEMBLAGE CONVERGENCE ALONG STREAM ENVIRONMENTAL GRADIENTS: AN INTERCONTINENTAL ANALYSIS

Introduction

Although evolution plays a major role in establishing trait distributions in species assemblages (Webb et al., 2002; Cavender-Bares et al., 2009), contemporary ecological processes also have a significant influence, especially at local scales (Lebrija-Trejos et al., 2010; Kraft et al., 2015). For example, habitat template theory posits that spatial and temporal variation of habitat features selects for certain traits and, therefore, influence the structure of local communities (Southwood, 1977; Poff, 1997). In this manner, habitat features act as environmental filters that shape trait distributions of species assemblages by restricting establishment and persistence of organisms based on the suitability of their traits for a given environment (Weiher and Keddy, 1995; Cornwell and Ackerly, 2009; Lebrija-Trejos et al., 2010; Kraft et al., 2015). Therefore, it is predicted that species that pass through similar environmental filters, regardless of geographic proximity or evolutionary history, should share many convergent traits, and local assemblages should reflect nonrandom assembly. Assemblage trait convergence among geographic and evolutionary independent systems would indicate common responses to selection producing repeated patterns of adaptive evolution as well as consistent processes of local community assembly. Here we examine the degree of convergent environmental-trait relationships in fish assemblages of lowland streams with similar environmental gradients in five different zoogeographic regions.

Stream fish are excellent model organisms for addressing questions about assemblage trait convergence in response to environmental conditions. First, stream fish often are isolated within a single drainage basin, which results in adaptation to local-regional conditions. Second, many functional traits of fish are well studied and therefore robustly quantified and interpreted (Gatz, 1979; Winemiller, 1991). Third, local fish assemblages are strongly structured by environmental filters acting at multiple spatial and temporal scales (Poff and Allan, 1995; Poff, 1997; Hoeinghaus et al., 2007). Certain selective pressures, such as costs associated with hydraulic drag as a function of body shape, are universal in fluvial habitats and should produce convergent assemblage structure. Several regional and local environmental filters have been found to be associated with fish assemblage structure. For example, hydraulic and geomorphic aspects of streams explain a large proportion of the trait variance between fish assemblages in North America and Europe at stream-reach and basin scales (Lamouroux et al., 2002). Finally, fluvial habitats, such as small streams, have similar characteristics worldwide, making them excellent model systems for comparing convergence across different zoogeographic regions.

Although there is great potential for finding general ecological patterns through the study of assemblage trait convergence in fishes (Winemiller, 1991; Lamouroux et al., 2002), these studies face several challenges. First, assemblage-wide convergence studies require large data sets. Specifically, studies of different biogeographic regions are often problematic, with inconsistent site selection, scale of sampling, and collection methods leading to incongruent data sets. Another potential problem arises from the data type and quality, where broad qualitative data for traits or habitat variables are often used rather than quantitative data (Lamouroux et al., 2002; Ernst et al., 2012). Finally, commonly used methods such as community-weighted trait means or, to a lesser extent, niche centroids have been shown to be poor tests of trait-environment relationships and should be replaced with multivariate approaches such as RLQ and fourth-corner analyses (Peres-Neto et al., 2017).

Another factor that could contribute to lack of evidence of assemblage convergence is historical contingency. The unequal distribution of evolutionary lineages in different biogeographic regions may result in local assemblages with disparate functional trait distributions and niches due to evolutionary histories and phylogenetic niche conservatism. Phylogenetic niche conservatism occurs when linages retain ancestral niches over time (Harvey and Pagel, 1991; Wiens and Graham, 2005; Wiens et al., 2010) and has been shown to be common in various taxa, including mammals (Cooper et al., 2011; Peixoto et al., 2017), birds (Rangel et al., 2007), amphibians (Hof et al., 2010), and plants (Ackerly, 2003; Crisp et al., 2009). Phylogenetic niche conservatism is often key to understanding niche-trait patterns observed in local assemblages (Vamosi et al., 2009; Wiens et al., 2010). For example, Ernst et al., (2012) inferred that trait-environment relationships were explained more by niche conservatism rather than convergent evolution. However, a review by Losos (2008) found that most studies of phylogenetic niche conservatism focus on only a few species at small geographic scales. He concluded that niche conservatism is not universal and should not be assumed.

Investigations testing for universal environmental filters based on congruent methods and data are rare, most research on community structure and assembly has been site specific. Research that compares assemblages in similar habitats from different regions using functional traits could reveal assemblage-level convergence and general ecological patterns (Lamouroux et al., 2002; McGill et al., 2006). If local environmental conditions are an important driver of community structure (Ricklefs, 2006), assemblages that pass through similar environmental filters should display similar patterns of trait distribution regardless of evolutionary history or geographic location. If these environmental filters are globally consistent, they should yield similar trait-environment relationships across geographically isolated and evolutionarily distinct assemblages.

This study examines degrees of convergence versus phylogenetic niche conservatism reflected in trait-environment relationships across multiple stream fish assemblages from four continents. Specifically, we hypothesized that trait-environment relationships converge across distinct biogeographic regions as a result of a common set of environmental filters acting on functional traits. To address this hypothesis, three questions must first be answered: 1) Are there correlations between functional traits and environmental variables? 2) If significant relationships among traits and environmental features exist within biogeographic regions, then are these trait-environment relationships consistent across biogeographic regions? 3) Are these relationships a result of common ancestry or convergence in response to a common set of environmental filters acting on fish assemblages?

Methods

Data acquisition and preparation

Streams and fish assemblages were surveyed at eight study locations spanning five zoogeographic regions —Benin (Gulf of Guinea Coast, West Africa), Brazil (Amazon Basin, South America), Cambodia (Mekong Basin, Asia), Belize (Caribbean Coast, Central America), New Jersey, South Carolina and Texas (Atlantic and Gulf coasts, North America. The inclusion of different zoogeographic regions allows for comparison of distantly related lineages and testing for convergent evolution and repeated patterns in community assembly. To minimize between-location differences in habitat features, survey sites were selected based on four criteria: (1) low stream order (1-3); (2) low level of disturbance (few human impacts); (3) low gradient; and (4) similar geomorphology (meandering course with sandy substrate and presence of coarse woody structure). In each zoogeographic region, five to six wadeable streams were sampled to encompass a gradient of stream channel width: two small (< 3 m average width), two medium (3-8 m), and two large (> 8 m). Sampling took place during low-water periods when streams were wadeable and fish capture was most efficient. Because this study is intrinsically scale dependent (Smith et al., 2013), a nested sample design was used: microhabitat within stream within zoogeographic region.

For each stream, a 200-500-m channel reach was sampled in an upstream direction to obtain a representative sample of fishes from all major types of microhabitat (modified from Barbour et al., 1999; Bower and Piller, 2015; Troia et al., 2015). Microhabitat types were identified as areas with relatively consistent depth, current velocity, substrate composition, and in-channel cover. In each microhabitat, we recorded water velocity, substrate composition, and depth. Microhabitat were only sampled if the substrate composition could be categorized as sand (>90% cover), woody structure (>80% cover), aquatic macrophytes (>80% cover), leaf packs (>90% cover), root banks (banks with dense root structures, >90%), and gravel (6-25 cm diameter, >80% cover). Given the challenge of sampling fish from diverse microhabitats, various methods were employed, including: seining, cast netting, dipnetting, and backpack electrofishing. At each study site, habitat variables of water temperature (°C), dissolved oxygen (DO), pH, specific conductivity (µS cm-1), and salinity (ppt) were measured. Specimens were euthanized via anesthetic (MS222) overdose, and preserved in 10% formalin following Texas A&M University animal care protocol (IACUC 2014-0173 and 2017-0233). Only data for common species were used for data analysis, and species having relative abundance < 1% in a given survey sample were excluded.

Twenty-one morphometric traits that reflect well-documented aspects of swimming performance and habitat use were selected (Gatz, 1979; Winemiller, 1991; Supplementary Table A-1). Traditional morphometric measurements for five individuals per species were made to the nearest 0.1 mm using calipers (for rare species n = 1-4; sample sizes appear in Supplementary Table A-2). To reduce potential ontogenetic biases, only adult size classes were used for analyses (size at maturation information obtained from literature sources and FishBase, fishbase.org). Traits standardized by conversion to proportions using either standard length, body depth, body width, head length, and head depth in the denominator (Winemiller, 1991; Casatti et al., 2006).

Using a recently published time-calibrated tree, a majority-rule consensus tree was created (Rabosky et al., 2018). However, this tree did not include all species included in our study. Following Beaulieu et al., (2012), we replaced exemplar taxa (closely related taxa) to create a tree that included all of the species in our study.

Statistical methods

Three-table ordination (RQL) and fourth-corner analyses were applied to data sets for each zoogeographic region and one combined data set that included all zoogeographic regions ("global data set" hereafter; Dray et al., 2014). For each zoogeographic region and the global data set, the two methods were used to test for specific regional and overall global species-trait-environment relationships, as well as to determine possible existence of a congruent trait-environment relationships across regions. Similar species-trait-environment relationships across regions and the global data set would suggest that a common environmental filter influences these assemblages. The RQL method allows for the simultaneous analysis of three different data sets: species abundance and environmental data for sites (R), species traits (Q), and species abundance (L). This is accomplished by combining three different ordinations, (1) a Hill-Smith analysis for the R matrix because both continuous and categorical variables were used, (2) the Q matrix was created using multiple correspondence analysis, and (3) a correspondence analysis to create the L matrix, into a final ordination (Ernst et al., 2012; Dray et al., 2014). The significance of the joint structure among these matrices was tested using a two-step permutation procedure (999 permutations). Model 2 tests the null hypothesis that no relationship exists between species presence-absence data with fixed traits and their environment; model 4 tests the null hypothesis that species composition is not influence by species traits, given fixed environmental characteristics (Dray et al. 2014). If both null hypotheses are rejected, the R, Q, and L matrices are effectively linked. To correct for multiple comparisons of environmental variables, all α-values (0.05) were Bonferroni corrected so that $\alpha_{new} = \alpha/N$, where N is the number of environmental variables (Gallardo et al., 2009; Ernst et al., 2012). In addition, the α_{new} values were then square-root adjusted to account for the combination of 2 models in the fourth-corner analysis (Dray and Legendre, 2008; Ernst et al., 2012). Anguilliform species (eel-like body shape) were removed for both the RQL and fourth-corner analyses due to their extreme morphology; their inclusion produced strongly skewed gradients and assemblage ordinations that separated anguilliform fish from all other species, and the latter tightly clustered within morphospace. A forest plot with averaged niche positions for each species was created using the “forestplot” package in R to plot the average R site scores for each species, where the average R site scores were considered as the niche position of each species.

Species’ traits and niche position (average R site scores from the RQL analysis of the global data set) were tested for phylogenetic signal using Abouhief’s test (Abouheif, 1999; Münkemüller et al., 2012). Abouhief’s test is an autocorrelation index of phylogenetic proximity that does not rely on an evolutionary model (Pavoine et al., 2008). Original proximities of Abouhief's test were used in this study. In addition, Mantel tests were used to test for a correlation between phylogenetic distance and co-occurrence distance for both the regional and global data sets using the vegan package in R (Oksanen et al., 2015).

Results

Assemblage compositions

A total of 197 species was analyzed in this study, with the number of species collected in each region as follows: 57 USA, 52 Brazil, 41 Cambodia, 25 Benin, and 21 Belize. The Brazil location had the most families represented (18), followed by Benin (17), Cambodia (13), USA (10), and Belize (9) (Supplementary Table 1).

Global species-trait-habitat relationship

Significant associations among the trait, microhabitat, and species presence-absence data sets were revealed by the global RQL permutation test ($p < 0.001$ for models 2 and 4), demonstrating strong, significant relationships between microhabitats and trait data across all regions and the potential existence of a global pattern of species-trait-environment relationship at the assemblage level. Within all regions, model 2 was rejected, which suggests that species distributions were influenced by environmental conditions. Model 4 was rejected for all regions except Belize and marginally for Cambodia, which suggests that the traits influenced species composition in given habitat for stream fish assemblages in Belize ($p = 0.16$), Benin ($p = 0.031$), Brazil ($p = 0.028$), Cambodia ($p = 0.069$), and the USA ($p < 0.001$).

The first axis of the global RQL indicated a gradient of water velocity and microhabitat structure, with unstructured, high-velocity habitats loading negatively, and low-velocity microhabitats with roots along the banks, aquatic vegetation, and, to a lesser extent wood, loading positively (Figure 1). RQL axis 2 mainly divided deep from shallow microhabitats as well as microhabitats that had leaves or aquatic vegetation as substrate (Figure 1).

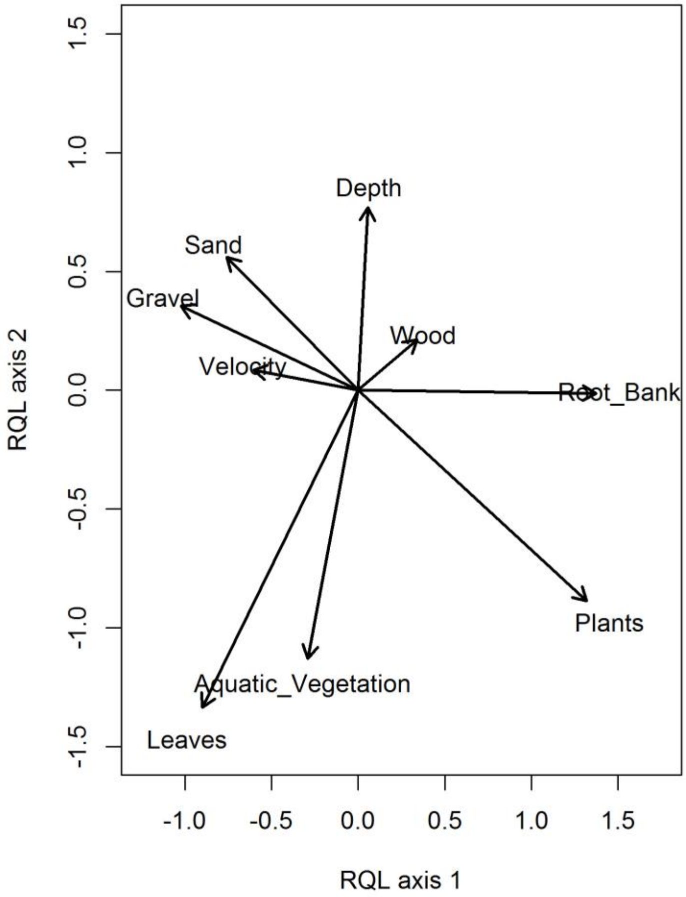

Figure 1: The ordination of the habitat variable along RQL axes 1 and 2.

Inter-regional species-trait-habitat relationships

Using the multivariate fourth-corner analysis, one trait was found to have the same or similar relationship with microhabitat variables across all regions: body width and root bank (Figure 2). Root banks (banks with dense root structures) and aquatic vegetation were the variables with most significant relationships with fish assemblage traits, such as body depth, dorsal fin length, body width, head length, and anal fin height. In general, traits associated with water velocity had negative relationships, whereas positive relationships were observed among the variables aquatic vegetation, wood, and root bank for most traits (Figure 2). Sandy habitats tended to have a negative association with morphological traits (Figure 2). Two traits showed congruent habitat-traits relationships for four out of the five regions: dorsal fin length with root bank as well as body width with sand (Figure 2). Including all rare species, produced similar results (Supplementary Figure A-2).

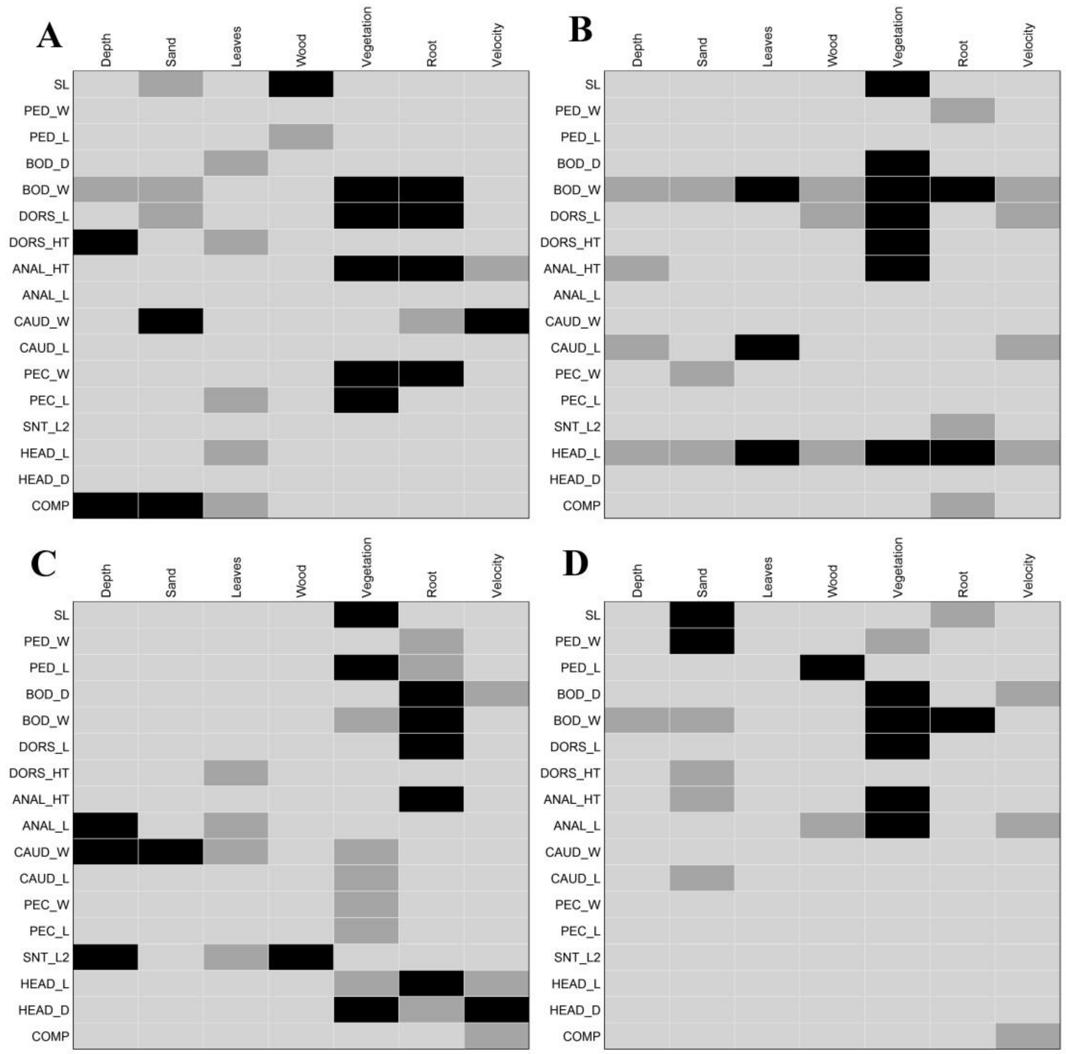

Figure 2: The results of the fourth-corner analyses for each region and the global dataset: A) Belize, B) Benin, C) Brazil, D) Cambodia, E) USA, and F) Global dataset. Black represent a positive relationship (Pearson's correlation) between mcirohabitat variable and trait, dark grey denotes a negative relationship, and light grey represents non-significant relationships.

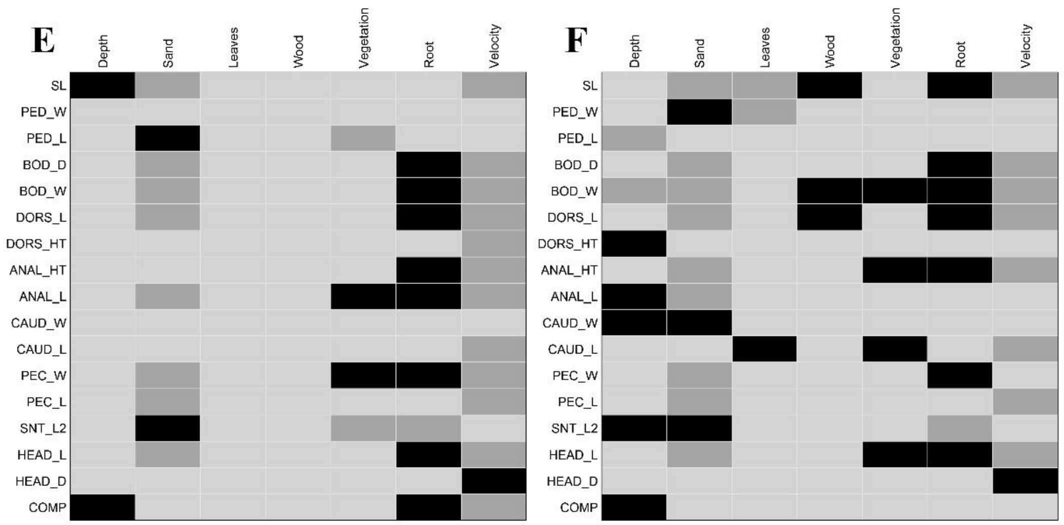

Figure 2 Continued.

Plots of habitat variables and traits reveal several consistent patterns (Figures 3, 4, and 5; Supplementary Figures 2-6). Fish with deep-bodies, long dorsal fins, and long anal fins were largely absent in microhabitats with relatively high water velocity (Figure 3A and 5). Fish with intermediate anal fin height, head length, pectoral fin length, pectoral fin width, and pelvic fin length were found in high-velocity microhabitats (Figure 3C-F). Fishes collected from low-velocity habitats displayed greater interspecific variation for most traits (Figure 3A-F). This was also shown using a linear models, wherein strong negative relationships between mean trait variance for every 0.05 units of water velocity and median water velocity per unit were found for body depth ($R^2 = 0.70$, $p < 0.001$), head length ($R^2 = 0.74$, $p = 0.001$), anal fin height ($R^2 = 0.75$, $p = 0.002$), anal fin length ($R^2 = 0.92$, $p < 0.001$), caudal fin length ($R^2 = 0.72$, $p = 0.005$), pectoral fin length ($R^2 = 0.51$, $p = 0.013$), and pelvic fin length ($R^2 = 0.61$, $p = 0.004$). A greater range of traits was also found for species occupying structurally complex microhabitats compared to species residing in areas with no structural complexity (Figure 4). Similar trait-habitat patterns where found in each region for body depth, head length, anal fin height, pectoral fin length, and pelvic fin length, where trait variance reduced with increasing water velocity (Figure 5, Supplementary Figures 2-6). A strong negative relationships between mean trait variance for every 0.05 units of water velocity and median water velocity per unit was found for body depth in each region: **A**) Belize (R^2 = 0.17, p = 0.150); **B**) Benin (R^2 = 0.59, p = 0.001); **C**) Brazil (R^2 = 0.64, p = 0.006); **D**) Cambodia (R^2 = 0.57, p = 0.005); **E**) USA (R^2 = 0.63, p = 0.002); and **F**) global data set (R^2 = 0.93, $p < 0.001$) (Figure 5).

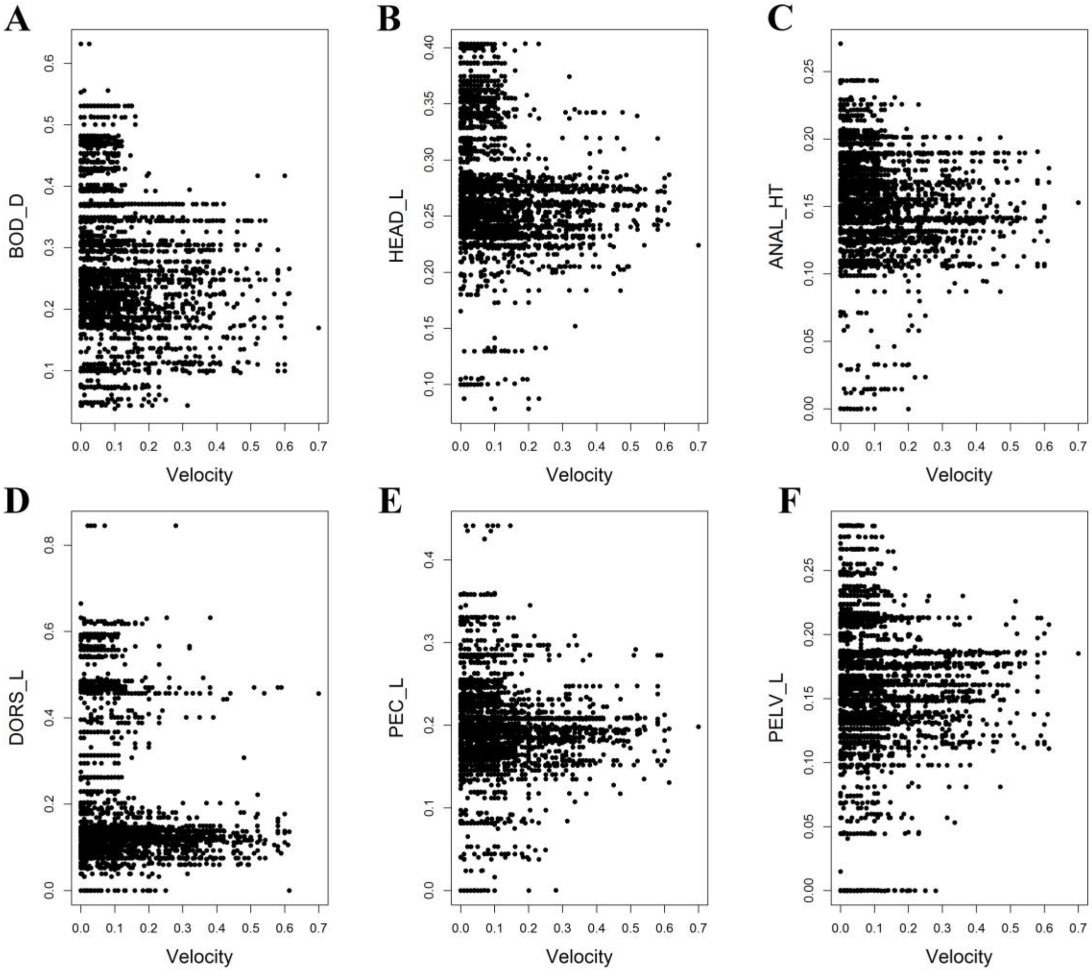

Figure 3: Scatter plots mean species trait value for each individual collected against water velocity (m s^{-1}): (A) body depth, (B) head length, (C) anal fin height, (D) dorsal length, (E) pectoral fin length, and (F) pelvic fin length.

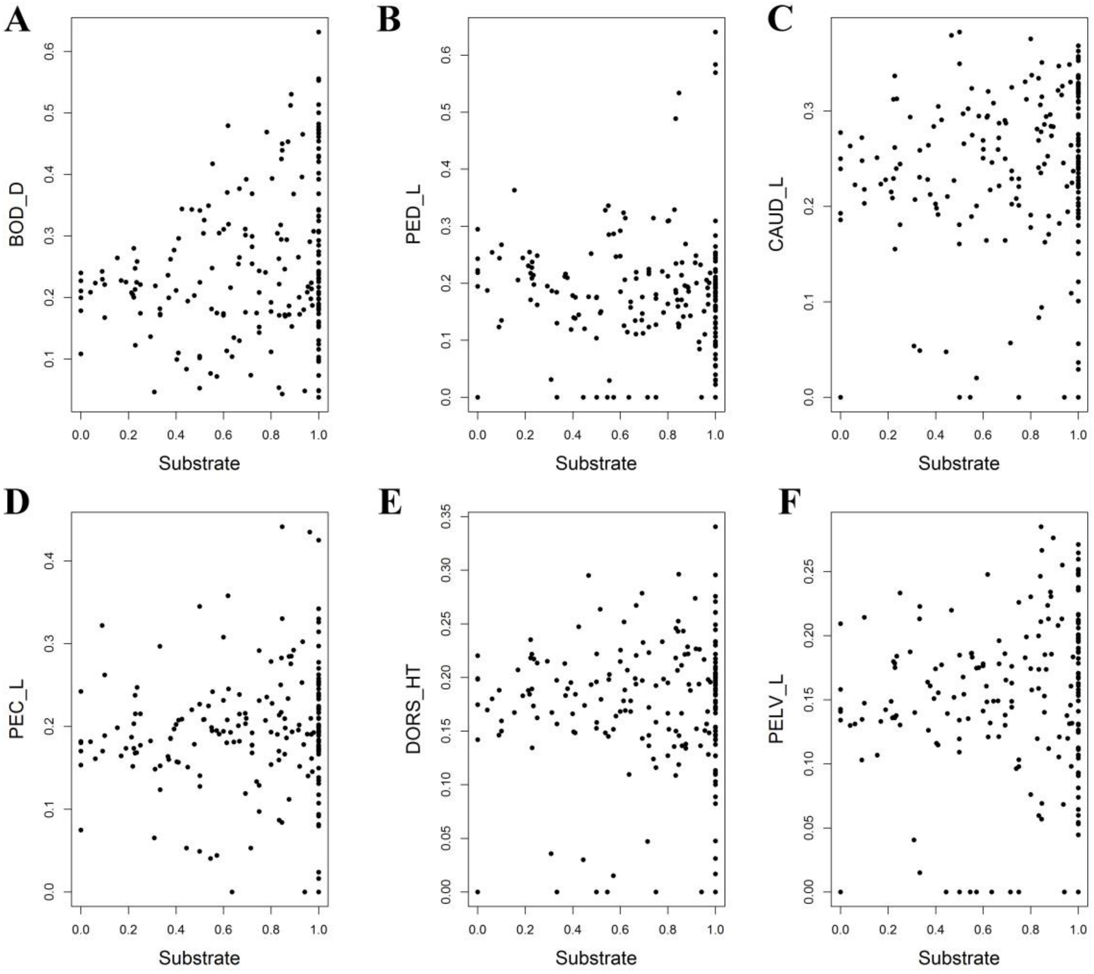

Figure 4: Scatter plots of the mean trait values against the proportion of individuals collected in structured microhabitats weighted by species abundance on the x-axis (Substrate) for all species: (A) body depth, (B) caudal peduncle length, (C) caudal fin length, (D) pectoral fin length, (E) dorsal fin length, and (F) pelvic fin length.

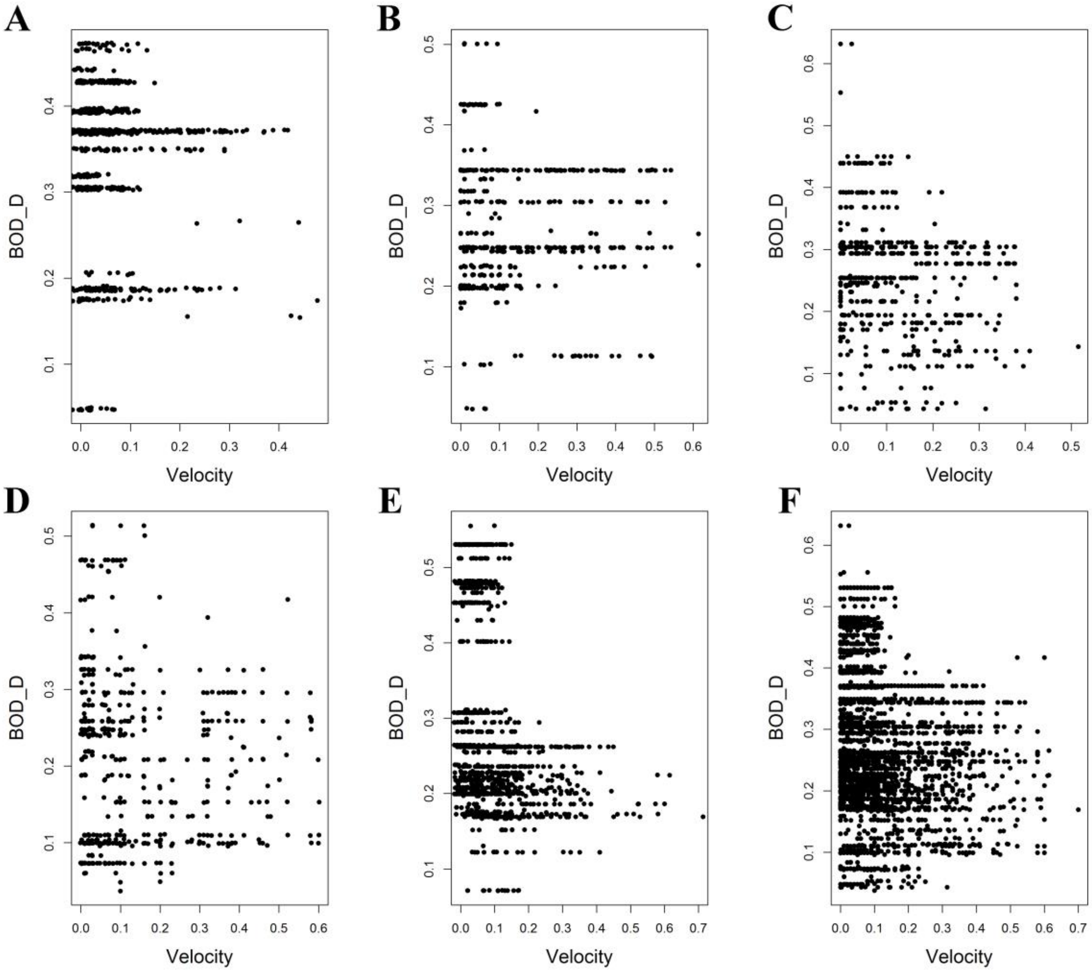

Figure 5: Scatter plots of mean body depth against water velocity (m s^{-1}) for each region and all individuals.

Habitat niche breath

High interspecific overlap in positions along microhabitat gradients as defined by RLQ analysis of the global data set was common within and among regions. Species were distributed more or less evenly along a gradient rather than clustered into regional groupings (Figure 6). This suggests high similarity of microhabitat characteristics among streams of the five regions (i.e., environmental conditions of study systems were well matched). A group of species from USA streams loaded along the negative end of the gradient, being mostly from the same genus (*Lepomis*). Relatively few species from Cambodia were collected from structurally complex microhabitats with low water velocity. In contrast, Benin and Brazil fishes were infrequently collected from habitats with high water velocities and lacking structural complexity. In addition, a limited number of Belize fishes were collected in microhabitats that loaded in the intermediate segment of the dominant habitat gradient (Figure 6).

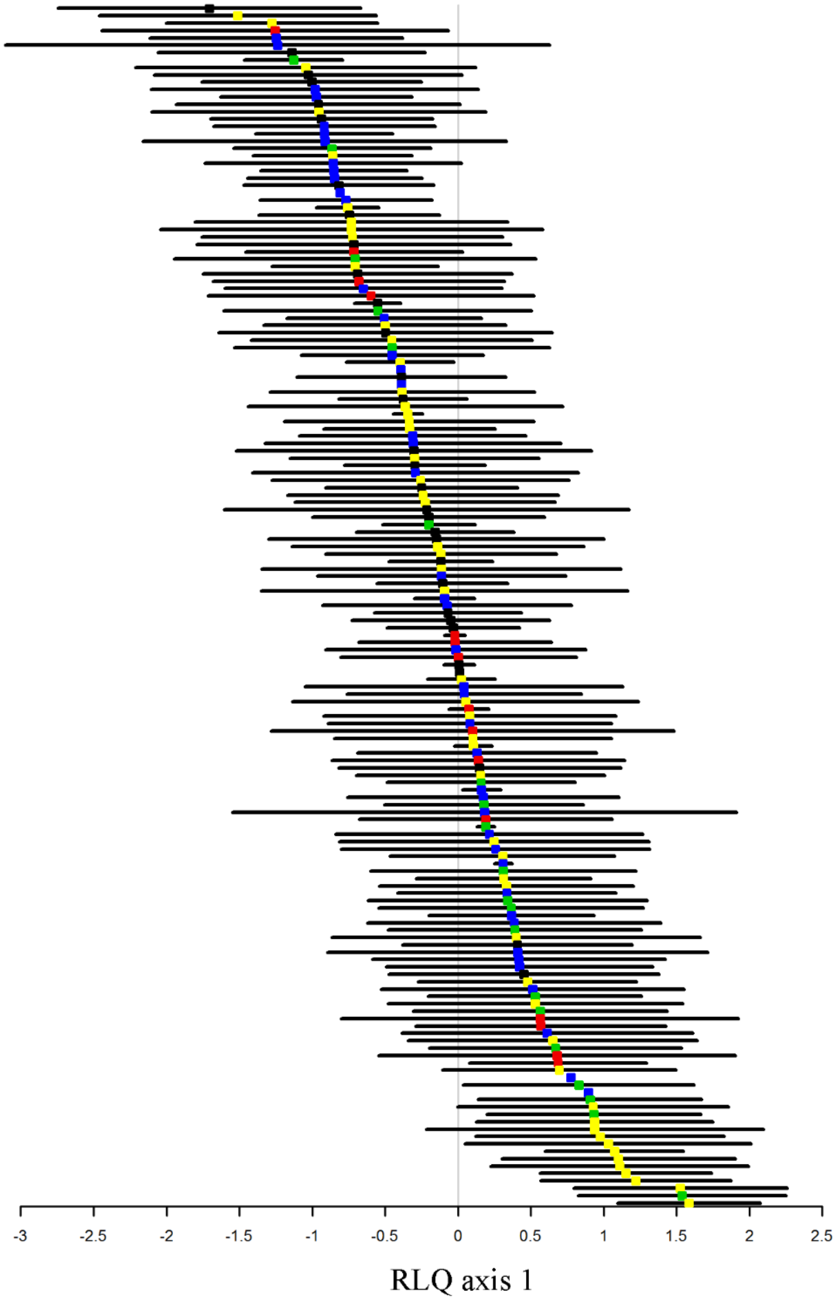

Figure 6: First axis of the global RQL representing the habitat niche position (mean) and breadth (standard deviation). Each bar represents one species, and color indicates country: Benin (red), Belize (green), Brazil (blue), Cambodia (black), and USA (yellow). Positive scores are associated with low water velocity microhabitats with root bank, plants, and wood substrate, whereas negative scores are related to high flow microhabitats with sand or gravel substrates.

Phylogenetic relationships

None of the regional assemblages had a statistically significant correlation between phylogenetic distance and co-occurrence distance (Mantel test, $p > 0.05$), suggesting related species did not co-occur more than expected at random. However, phylogenetic distance and co-occurrence distance for the global data set were found to be smaller than expected at random ($p < 0.001$), confirming that each region was phylogenetically distinct.

A high prevalence of strong phylogenetic signal, indicating that closely related species have more similar traits, was found for all traits across all regions, with the exception of Benin. Phylogenetic signal varied among regions, ranging from all traits exhibiting phylogenetic signal in North American species, to only 7 traits in West African species (Supplementary Table A-3). Strong phylogenetic signal was also found for species niche positions (Abouhief's number = 0.94, $p = 0.001$).

Discussion

This study revealed congruent patterns of trait-environment relationships across distinct zoogeographic regions that apparently derive from consistent sets of environmental filters acting on functional traits. This provides support for the idea that habitat templates structure trait distributions within stream fish assemblages. Even though fourth-corner analysis did not reveal convergent trait-environment relationships across every region, trait-environment plots indicated the existence of congruent environmental filters across all zoogeographic regions for several traits (Figure 5; Supplementary Figures A-2-6). In some cases, a strong phylogenetic signal implied that phylogenetic niche conservatism played a significant role in determining trait-environment relationships.

Within-region, trait-environment relationships

We first tested for trait-environment relationships within biogeographic regions, finding strong trait-environment relationships for each biogeographic region using RLQ and fourth corner methods. Local environmental conditions clearly played a role in shaping the traits of stream fish assemblages within each biogeographic region, which supports the habitat template theory (Southwood, 1977; Townsend and Hildrew, 1994). This implies that neutral assembly, by itself, does not apply to these fish assemblages, even though dispersal and other processes may often have stochastic aspects (Hubbell, 2001). Instead, the interaction between microhabitat variables and species traits were involved in structuring local assemblages. In general, structurally complex microhabitats had positive relationships with certain traits, whereby species with larger trait values tended to occupy structurally complex microhabitats. Deep-bodied fish, such as centrarchids and cichlids, tended to occupy structurally complex microhabitats, which likely caused the positive relationship between microhabitat complexity and several traits, such as body depth and dorsal fin length. Gibbose (deep-body) shapes facilitates maneuverability in horizontal and vertical dimensions, which is advantageous near structurally complex microhabitats, such as submerged logs and sticks, aquatic vegetation, or root tangles along stream banks (Keast and Webb, 1966; Webb, 1984;

Helfman et al., 2009). Body depth, body width, head length, and the length and height of unpaired medial fins (Figure 3) generally had negative relationships with water velocity. A possible explanation for this negative relationship is discussed below.

Across-regions, trait-environment relationships

The second question addresses the consistency of trait-environment relationships across all zoogeographic regions. Using fourth corner analyses, only one of the documented trait-environment relationships was entirely consistent across all regions. However, we expected more consistent trait-environment relationships. For instance, a strong negative relationship should exist between body depth and water velocity due to the high energy costs associated with maintaining position in fast water given the hydraulic drag exerted on a large body surface area (Webb, 1984, 1988). However, fourth-corner analysis did not reveal a significant body depth-flow relationship for Belize or Benin, and this may be due to low statistical power, owing to the relatively small numbers of species collected from streams in these regions. This result also could have been influenced by the small sample sizes for fishes collected from microhabitats with high water velocities in these regions, and the non-linear relationship observed between water velocity and many morphological traits (Figure 3).

Some consistent trait-environment patterns were identified across all regions, suggesting similar filters acting on species traits (Figure 3 and 4; Supplementary Figures 2-6). For example, fishes with greater body depth were absent from habitats with high water velocities, and only fishes with slender or fusiform body shapes occupied these habitats (Figure 3). A similar pattern has been described by other studies (Willis et al., 2005; Oliveira et al., 2010; Bower and Piller, 2015). In small, low-gradient streams, many deep-bodied fishes are restricted from occupying areas with high water velocities due to hydraulic drag and the high energetic costs of maintaining position (Webb, 1984, 1988). In microhabitats with low water velocities, this source of selection on body form is relaxed, and species with diverse body shapes often coexist. This pattern of reduced trait diversity in microhabitats with fast-flowing water was found in every region (Supplementary Figure A-2-6). This widespread pattern suggests that water velocity acts as a universal filter that selects for traits in the same manner across zoogeographic regions. Instream structure also seems to be a universal environmental filter structuring fish assemblages. Trait diversity was greater for fishes inhabiting microhabitats with more structural complexity; body width, anal fin, caudal fin, dorsal fin, and pectoral fin all had greater variation among fishes occupying structurally complex microhabitats. Structurally complex microhabitats may contain more abundant or higher quality food resources and provide shelter for avoidance of predators and harsh environmental conditions, such as high water velocity (Kovalenko et al., 2012). Thus, the loss of instream structures, such as large woody debris, generally reduces fish functional diversity (Mouillot et al., 2013; Kovalenko et al., 2012; Emslie et al., 2014; Ceneviva-Bastos et al., 2017). Many human environmental impacts tend to reduce the structural complexity of stream habitats, resulting in the decline or elimination of ecological specialists (Brejão et al., 2017) and lower functional trait diversity (Leitão et al., 2017). No apparent patterns were evident between traits and water depth, suggesting that depth was not a strong filter for traits examined in this study. However, it should be noted that streams selected for this study were small and wadeable, with limited variation in depth.

Several other factors could explain the relatively limited inter-regional similarity obtained for trait-environment relationships. First, the lack of congruent trait-environment relationships between regions suggests that idiosyncratic selective pressures may have prevented convergent trait-environment relationships. Although sites were selected to minimize environmental differences, the observed trait patterns may reflect unique environmental conditions in certain streams or regions. In that case, assemblage trait distributions might be influenced more strongly by unique environmental filters than by one or a few universal filters. A similar pattern was obtained from an inter-continental study of tropical anurans (Ernst et al., 2012). Regionally unique trait-environment relationships would imply that associations between traits and environmental features are either unpredictable or else influenced by other factors that vary in space and/or time. In this case, assemblage function structure could only be studied and predicted based on regional or perhaps even local species assemblages, and the link between traits and environmental variables should not be assumed to be universal. Another explanation for the lack of globally consistent trait-environment relationships is the potential influence of species-specific behaviors; for example, when an organism selects particular microhabitats during certain stages of its life cycle (Ross and Brenneman, 2001; Bower and Pillar, 2015). Some fishes, such as the North American minnow *Cyprinella lutrensis*, move into habitats with faster flows during breeding (Ross and Brenneman, 2001). In some cases, human environmental impacts that degrade streams and natural assemblage structure might have reduced our ability to detect convergent trait-environment relationships. Some of our Cambodian streams were subject to fishing pressure and watershed alterations that probably affected fish assemblage structure. Relatively large fishes known to inhabit small streams of the region (e.g., snakeheads (Channidae), catfishes (Clariidae), climbing perch (Anabantidae), and leaffish (Pristolepidae)) were rare or absent in our samples. Snakeheads and clariid catfishes have elongate bodies, and the climbing perch and leaffish have gibbose body shapes. Furthermore, our assemblage and habitat surveys represent snapshots in time. All stream surveys were conducted under base-flow conditions, and temporal variation in habitat conditions and local assemblage composition was not evaluated. Moreover, regional influences on assemblage structure were not accounted for in this study, and these can affect the manner in which local process influence assemblage patterns (Ricklefs, 1987).

In our study, continental faunas were well separated phylogenetically, and only one convergent trait-environmental relationships was detected by fourth-corner analysis. These results were not entirely unexpected. Studies of convergence across regional assemblages comprised of species from divergent lineages and deep evolutionary time often find limited convergence and a strong influence of phylogenetic constraint (Schoener, 2009). The strong phylogenetic signal in niche position and assemblage functional trait distributions in our study implies that phylogenetic constraints or even phylogenetic niche conservatism could have influenced assemblage trait distributions (Wiens et al., 2010; Ernst et al., 2012), whereby closely related species have more similar traits and niches than distantly related taxa. Species functional traits and habitat niche positions were to some degree constrained by phylogeny. However, Peixoto et al., (2017) found that the degree of phylogenetic signal in bats varied depending on the extent of phylogenetic inclusiveness. In our study, strong phylogenetic signal in niche position and traits was found when all species were included in the analysis, but tests for phylogenetic niche conservatism within a family or order level may produce different results (Peixoto et al., 2017). Despite the strong influence of evolutionary history on assemblage trait patterns, a high proportion of fishes were found to be convergent with at least one other species (Unpublished manuscript). For example, *Melanocharacidium dispilomma* (order Characiformes) and *Etheostoma thalassinum* (Perciformes) had similar traits and niches. Other examples of species converging on similar traits and niches were *Laubuka caeruleostigmat* (Cypriniformes) and *Carnegiella strigata* (Characiformes) as well as *Umbra pygmaea* (Esociformes) and *Erythrinus erythrinus* (Characiformes). Clearly, both convergent evolution and phylogenetic constraint both influenced assemblage trait distributions in our dataset.

Moving forward

Our study focused on traits associated with fish locomotion and microhabitat use, but additional niche dimensions, such as diet, life history, defense and metabolism, would further our understanding of community assembly (Laughlin and Messier, 2015; Winemiller et al., 2015). Presently, natural history data are lacking for many freshwater fishes, especially in the tropics and including some of the species involved in this study. Such data are essential, not only for achieving a more complete understanding of community assembly (Winemiller et al., 2015; Able, 2016), but also for natural resource management (Able, 2016). In addition, new methods to integrate phylogenetic influences on trait-environmental relationships are needed to improve inferences about niche convergence and phylogenetic niche conservatism. As new methods are combined with large-scale data sets for traits and environmental variables, more inclusive and detailed studies will elucidate mechanisms that create assemblage structure at various scales of time and space.

Our findings support the idea that environmental conditions of local habitats influence trait patterns of stream fish assemblages in a consistent manner worldwide. Water velocity and structural complexity appear to function as universal environmental filters that produce similar assemblage trait distributions in streams across multiple zoogeographic regions. This implies that some environmental filters may have consistent effects on local community assembly, knowledge of which would enhance our ability to predict outcomes from human interventions, including environmental degradation and actions aimed at restoration.

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CHAPTER III

WIDESPREAD CONVERGENCE IN STREAM FISHES

Introduction

Convergent evolution is the evolution of similar phenotypes in divergent lineages, a phenomenon that may arise via equivalent or different developmental pathways (Arendt and Reznick, 2008; Wake, Wake and Specht, 2011). Some of the more remarkable examples of convergent evolution occur when similar functional trait patterns are observed among species from different regions with distinct evolutionary histories. Examples of convergence include animals adapted to subterranean habitats (Trontelj et al., 2012), desert lizards (Melville et al. 2006), island lizards (Mahler et al., 2013), and freshwater fishes (Winemiller, 1991; Winemiller et al., 1995). These and other examples of convergence among assemblages occupying habitats with similar environmental conditions suggest that convergent evolution arises from deterministic processes rather than developmental, evolutionary, or ecological constraints or random processes (Melville et al., 2006; Conway Morris, 2010; Morinaga and Bergmann, 2017). Yet, few studies have rigorously tested for convergence over large geographic and evolutionary scales (e.g. Wiens et al., 2006; Moen et al., 2016). Instead, studies often restrict comparisons to two or three regions (e.g., Melville et al., 2006) while focusing on only a single genus or family (e.g., Morinaga and Bergmann, 2017; Serb et al., 2017; Zelditch et al., 2017). Early studies of convergence among species assemblages were constrained by a paucity of robust phylogenies (e.g., Winemiller, 1991; Winemiller et al., 1995), but larger and more robust phylogenies and methods to create "supertrees" are now available to support analysis of convergence (e.g., Rabosky et al., 2018). Here we test for convergence of teleost fishes from similar microhabitats of streams within five major zoogeographic regions.

Evolutionary convergence is thought to be common, if not ubiquitous, throughout the tree of life, and occurs at all biological levels from DNA sequences to communities (Conway Morris, 2003; Losos, 2011; McGhee, 2011; Winemiller et al., 2015), yet the means to assess convergence are not always straightforward, and inferences about mechanisms that generate convergence are often vague. Convergent taxa are rarely perfect replicas; instead, they have varying degrees of phenotypic similarity involving functional traits inferred to be associated with various niche dimensions. Convergent evolution is often taken as evidence of adaptation to similar selective pressures, implying that certain aspects of evolution are deterministic and potentially repeatable (Losos et al., 1998; Conway Morris, 2010; Mahler et al., 2013). However, convergence can also result from developmental or functional constraints that limit phenotypic variation, inevitably leading to the appearance or reappearance of similar phenotypes among multiple lineages (Losos, 2011; Frédérich et al., 2012; Agrawal, 2017). Adaptation due to selective pressures and constraints are not necessarily mutually exclusive, but together can produce convergent forms (Frédérich et al., 2012; Agrawal, 2017; Morinaga and Bergmann, 2017). Alternatively, convergence might simply result from random acquisition of similar phenotypes in divergent lineages (Gould, 1990; Stayton, 2008). Efforts to reconstruct the evolutionary sequence that resulted in convergence is even more complicated for species-rich regions with complex biogeographical histories, because traits adaptive for a given set of conditions might persist long after the lineage has evolved in response to novel conditions in a different time or place.

The interaction between a trait and function can be complex, further complicating interpretations of convergence. For example, more than one phenotype or trait configuration may perform a given ecological function, a pattern called the many-to-one relationship (Hulsey and Wainwright, 2002; Wainwright et al., 2005; Collar et al., 2014). This could result in the independent evolution of species with divergent traits that have similar functions along a given niche dimension (Zelditch et al., 2016). Alternatively, a single trait may have multiple functions, for example, allowing the organism to exploit multiple resources as their relative availabilities fluctuate (Zelditch et al., 2016). The multidimensionality of ecology and functions may lead to a many-to-many relationship between traits and functions, and multidimensionality itself may reduce the probability of convergence (Slayton et al., 2008).

A long-standing evolutionary concept is the idea of adaptive landscapes, whereby a species' fitness increases during evolution toward an adaptive peak defined by a multivariate phenotypic surface. The breadth and height of the adaptive peak can be determined by the strength of constraints, where strong ecological and functional constraints would correspond with narrow tall peaks. In contrast, weak or no selective pressure would result in a broad peak or several shallow peaks that are weakly separated reflecting weak selection for a single phenotype or suite of phenotypes. This begs the question – in habitats with stronger environmental constraints would the degree of convergent evolution be greater? If this were the case, it would suggest that convergent evolution is deterministic and potentially predictable (Trontelj et al., 2012). Like any organism, stream fishes are subject to multiple selective pressures. However, stream hydrology plays a powerful role in shaping fish ecology and evolution (Townsend and Hildrew, 1994; Poff and Allan, 1995; Mims and Olden, 2012; Bower et al., 2018). At a more local scale, water velocity can influence stream fish ecology and evolution (Lamouroux et al., 2002; Bower and Pillar, 2015; Haas et al., 2015; Lujan and Conway, 2015), and therefore function as a strong environmental filter (Willis et al. 2005; Bower and Winemiller unpublished). For example, deep-bodied fish generally do not perform well in microhabitats with rapid water velocity due to the high energetic cost of maintaining position against strong hydraulic drag (Webb, 1988; Bower and Piller, 2015). Stream substrates also influence species ecology and evolution (Kovalenko et al., 2012). Habitats with structurally complex substrates can provide refuge from predators and adverse environmental conditions (Bartholomew et al., 2000; Tokeshi and Arakaki, 2011), as well as provide greater resource and niche diversity than non-structured substrates (Willis et al., 2005; Kovalenko et al., 2012), potentially increasing the number of species and functional diversity (Richardson et al., 2017; Leitão et al., 2018). Conversely, habitats with uniform, simple substrates tend to be associated with less functional diversity (Willis et al., 2005). Here, we hypothesize that natural selection in response to abiotic features of stream microhabitats has resulted in evolution of similar suites of functional traits among independent lineages.

This study assesses the prevalence of convergent evolution in teleost fishes from similar microhabitats within small, low-gradient streams across five zoogeographic regions. Specifically, we test the following predictions: 1) fishes occupying similar microhabitats have convergent phenotypes across all zoogeographic regions; 2) species from habitat categories with high water velocity or uniform, simple substrates will exhibit a greater degree of convergence and lower functional richness; and 3) species from habitat categories with structurally complex substrates and low water velocity will have relatively weak convergence and higher functional richness.

Methods

Data acquisition and preparation

Fishes were surveyed in low-gradient streams of similar size and environmental conditions. An attempt was made to match streams according to: (1) low stream order (ranging from 1 to 3), (2) similar geomorphology and substrate (i.e. sand with patches of leaf litter and wood), (3) low gradient, (4) similar riparian features, and (5) low anthropogenic disturbance to the stream and local watershed. Five distinct zoogeographic regions were chosen to provide an opportunity to test for convergent evolution within habitat types across different regional assemblages. Four to seven streams were sampled in each region during low-water periods when the streams were wadeable, fish per-unit-area densities were highest, and fish capture was most efficient. The zoogeographic regions sampled were: West Africa (Benin), Central America

(Belize), South America (Brazil), North America (United States of America: New Jersey, South Carolina, Texas), and Southeast Asia (Cambodia).

Teleost fishes were collected from every type of microhabitat encountered within a 200-500-m stream reach that was surveyed while moving in an upstream direction (modified from Barbour et al., 1999; Bower and Piller, 2015). Microhabitats were designated and sampled based on consistency of depth, current velocity, substrate composition, submerged wood, and features at the stream margin. Microhabitat were only sampled if substrate composition could be categorized as sand (>90% cover), woody structure (>80% cover), aquatic macrophytes (>80% cover), leaf packs (>90% cover), and gravel (6-25 cm diameter, >80% cover). Water velocity, substrate composition, and depth were recorded in each microhabitat. Several methods were employed to capture fish because of the challenge of sampling diverse habitats, including: seining, dipnetting, and backpack electrofishing. Habitat variables of water temperature (°C), dissolved oxygen (DO, mg l^{-1}), pH, specific conductivity (µS cm^{-1}), and salinity (ppt) were measured at each site. Specimens were anesthetized via anesthetic (MS222) overdose and preserved in 10% formalin following Texas A&M University animal care protocol (IACUC 2014-0173 and 2017-0233).

Twenty-five morphometric features that reflect body shape and other functional traits that affect how fishes feed and use habitats were measured (Gatz 1979; Winemiller 1991; Supplementary Table A-1). The traits for five specimens of each species (for rare species n = 1-4; sample sizes appear in Supplementary Table A-2) were measured to the nearest 0.1 mm using calipers. In addition, species were grouped into life history categories based on the literature. To reduce intraspecific morphological variation associated with ontogeny, only adult size classes were analyzed. To eliminate the influence of body size, traits were standardized using proportions of linear measurement with standard length, body depth, body width, head length, and head depth in the denominator (Winemiller, 1991; Casatti et al., 2006). Averages were computed for each morphological trait and species, and two datasets were compiled. An ‘all traits dataset’ included traits inferred to influence performance for habitat, trophic, and life history dimensions, and a ‘habitat trait dataset’ only included traits inferred to influence swimming performance and microhabitat use (Gatz, 1979; Winemiller, 1991).

A time-calibrated tree was used from a previous study (Rabosky et al. 2018). However, this tree did not include all species included in our study. Following Beaulieu et al., (2012), we replaced exemplar taxa (closely related taxa) to create a tree with species included in our study.

Statistical methods

To reduce data dimensions and ordinate species within trait space, a principal coordinates analysis (PCOA) was performed using the ‘all-traits’ dataset and Gowers distance as well as a principal components analysis (PCA) (based on an eigen analysis of the correlation matrix) using the ‘habitat’ dataset. The data was scaled prior to PCA and PCOA. PC axes with eigenvalues greater than 1 were extracted for use in further analyses following the KG rule for PCA (Guttman 1954; Kaiser 1960). Anguilliform species (eel-like body shape) were removed due to their extreme morphology; their inclusion produced strongly skewed gradients and assemblage ordinations that separated anguilliform fish from all other species, and the latter tightly clustered within morphospace.

To test the first prediction, species were divided into seven microhabitat clusters: top-water species in microhabitats with low water velocities and varying amounts of instream structure (TOP-LVVS), mid-water species in microhabitats with high water velocities and low instream structure (MID-HVLS), mid-water species in microhabitats with low water velocity and low instream structure (MID-LVLS), mid-water species in microhabitats with low water velocity and high instream structure (MID-LVHS), benthic species in microhabitats with high water velocity and low instream structure (BEN-HVLS), benthic species in microhabitats with high water velocity and high instream structure (BEN-HVHS), and benthic species in microhabitats with low water velocity and varying amounts of instream structure (BEN-LVVS). These groupings were defined by clustering species based on microhabitat association, while being sufficiently broad to include species from multiple regions. To create the clusters, we used a three-table ordination (RQL analysis) to determine the microhabitat preference for each species (following Ernst et al., 2012; Dray et al., 2014). The first two dimensions of R site scores (microhabitat preference) and positions in water column (benthic, mid-water, or surface) were used in a hierarchical cluster analysis to classify species into microhabitat clusters. Ward's method was used for the cluster analysis.

To address the second and third predictions, species were categorized by habitat gradients that independently evaluated water velocity and structural complexity preferences. For each species, we calculated the weighted mean of water velocity weighted by abundance, as well as the proportion of individuals captured from locations with structured substrates weighted by abundance. Species were then arbitrarily grouped into low (0-0.1 m/sec), medium (0.1-0.2 m/sec), and high (>0.2 m/sec) water velocity categories. Species were independently divided by substrate preference: low association with structured substrates (proportion < 0.33), medium association with structured substrates (proportion 0.33-0.67), and high association with structured substrates (proportion > 0.67).

Functional richness (FRic) was calculated as a minimum convex hull area that included all species (Villéger et al., 2008) using the extracted PCA axes for each microhabitat, water velocity, and substrate complexity categories. The "geometry" package was used to calculate convex hull area (Barber et al., 2012).

Phylogenetic analyses

To examine trait convergence within each microhabitat, water velocity, and substrate complexity category, a tanglegram was created to visualize morphological similarity of groupings relative to phylogenetic relationships following Zelditch et al. (2017). A tanglegram pairs two branching diagrams, in this case, a phylogenetic tree and a phenogram created from hierarchical clustering analyses of the PCA or PCOA axes using Ward's method (Zelditch et al., 2017). For each species that occurs in both diagrams, a line is drawn that connect its positions. Convergence is demonstrated by morphological similarity of phylogenetically divergent lineages. These convergent taxa were then analyzed with the 'C_1 metric' described below. The tanglegram was created using the "cophylo" function in the phytools package (Revell, 2017).

The degree of convergence for each microhabitat, water velocity, and substrate complexity category was calculated using a recently developed convergence metric (Stayton, 2015). This method requires identifying convergent species *a priori*, which was done using the tanglegram. The C_1 metric characterizes the inverse of the proportional morphological distance between pairs of extant taxa (D_{tip}) and the maximum morphological distance between their ancestors (D_{max}), giving the reduction in morphological divergence ($C_1 = 1-D_{tip}/D_{max}$; Stayton, 2015), where 1 indicates complete convergence and morphological similarity. It is important to note that the C_1 values are sensitive to the species included in the dataset. For example, the inclusion of related but morphologically divergent species in the clades of interest will greatly inflate the resulting C_1 value because of the large increase in D_{max}. In this case, the D_{tip} would not be reduced by convergence; rather, including the related but morphologically divergent species would increase the C_1 value purely by increasing D_{max}. The degree of convergence was not tested below the genus level. To test if these metrics were significantly different from random, the observed morphological data are compared to datasets that are simulated along the phylogeny using Brownian motion (Stayton, 2015).

Species' traits and niche position (average R site scores from RQL) were tested for phylogenetic signal. Phylogenetic signal was quantified using Abouhief's test (Abouheif, 1999), an autocorrelation index of phylogenetic proximities that does not rely on an evolutionary model (Pavoine et al., 2008). Abouhief's test is an effective method for estimating phylogenetic signal that is not computationally demanding (Münkemüller et al., 2012). The original proximities of the Abouhief's test were used in this study.

Results

To test for convergence among teleost fishes within similar microhabitats, 197 species representing 16 different orders from each region were analyzed: 57 North American species, 52 South American species, 41 Southeast Asian species, 25 West African species, and 21 Central American species. The South American sites had the most families represented (19), followed by West Africa (17), Southeast Asia (13), North America (10), and Central America (9) (Supplementary Table A-1). Assemblage trait space was estimated using two different methods: PCOA using the 'all-traits dataset', and PCA using the 'habitat trait dataset'. The overall space was obtained from the first 12 axes from PCOA, which accounted for 78.6% of total trait variation (Figure 7; Supplementary Table B-2). Seven PCA axes modeled the trait space based on the 'habitat trait dataset' and accounted for 76.4% of total trait variation (Figure 8; Supplementary Table B-3).

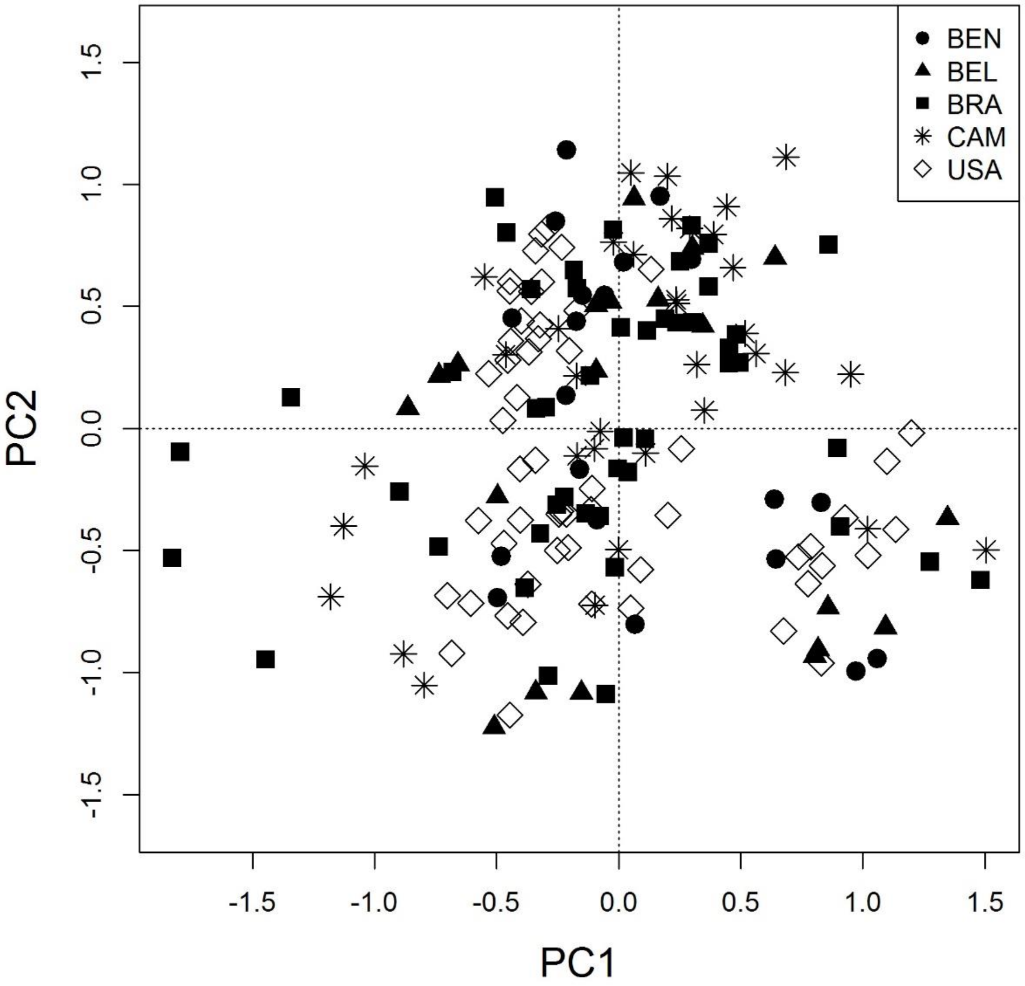

Figure 7: A plot of the first two axes from a PCA of the habitat dataset.

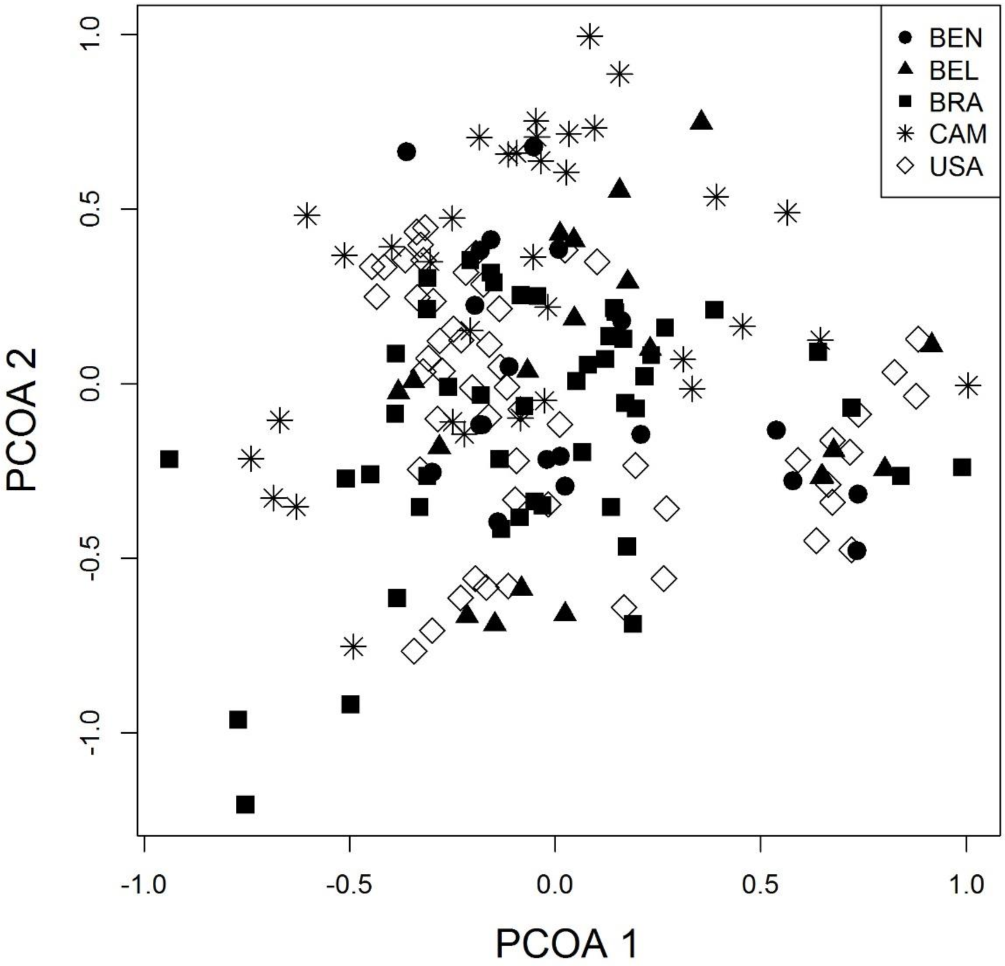

Figure 8: A plot of the first two axes from a PCOA of the all trait dataset.

The tanglegram based on the ‘habitat trait dataset’ showed many possible cases of convergence within microhabitat clusters (Figure 9), with 70 species (36% of all species) being convergent with at least one other species using only traits associated with habitat use. Within the microhabitat cluster of TOP-LVVS, three groupings of convergent species were identified. The first group consisted of three species: *Fundulus notatus*, *Nannostomus trifasciatus*, and *Copella nattereri* (Average $C_1 = 0.763$). *Pyrrhulina semifasciata, Procatopus nototaenia,* and *Gambusia luma* comprised the second group (Average $C_1 = 0.709$), and the third group was comprised of *Carnegiella strigata, Gnathocharax steindachneri*, *Laubuka caeruleostigmata*, and *Parachela sp.* (Average $C_1 = 0.520$). None of the 19 species associated with the MID-HVLS or MID-LVLS microhabitats exhibited strong convergence.

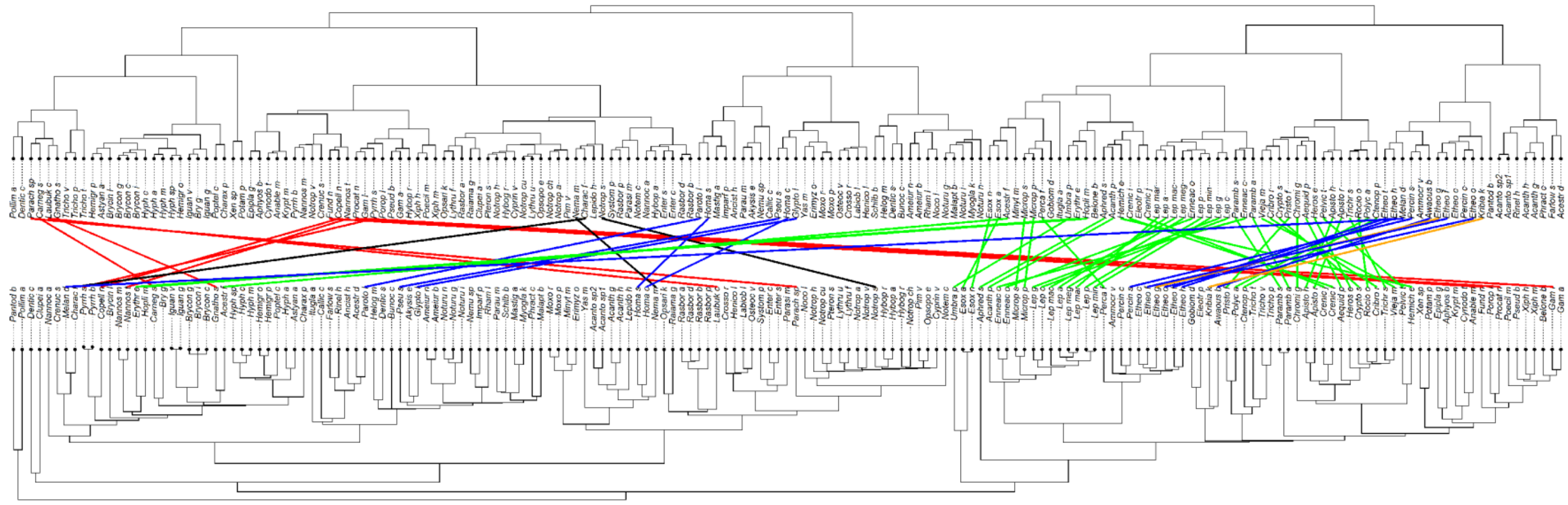

Figure 9: A tanglegram of all species depicting possibly convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis using the “habitat trait dataset” (includes only habitat associated traits) is on the right. The lines connect each species’ position on the phylogeny and phenogram. Microhabitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), and TOP-LVVS (**red** lines).

Two major subsets of convergent species associated with the MID-LVHS microhabitat were identified: a group of predatory fishes and a group of largely invertivorous fishes with relatively deep bodies. The first group contained *Acantharchus pomotis, Acestrorhynchus falcatus, Aphredoderus sayanus, Crenicichla inpa, Crenicichla johanna*, *Erythrinus erythrinus, Esox americanus, Esox niger, Hoplias malabaricus, Hemichromis elongatus, Micropterus punctulatus, Micropterus salmoides, Perca flavescens*, and *Umbra pygmaea* (Average $C_1 = 0.405$). Within this group, 4 species pairs were not convergent (Supplementary Table B-4). Widespread convergence was found in the second group of relatively deep bodied fish: *Aequidens pallidus, Apistogramma hippolytae, Apistogramma regani, Chromidotilapia guntheri, Cribroheros robertsoni, Cryptoheros spilurus, Ctenopoma petherici, Enneacanthus chaetodon, Enneacanthus obesus, Heros efasciatus, Lepomis auritus, Lepomis cyanellus, Lepomis gulosus, Lepomis macrochirus, Lepomis marginatus, Lepomis megalotis, Lepomis miniatus, Lepomis punctatus, Parambassis apogonoides, Parambassis siamensis, Pelvicachromis taeniatus, Polycentropsis abbreviata, Pristolepis fasciata, Rocio octofasciata, Trichromis salvini,* and *Vieja melanura* (Average $C_1 = 0.399$). Within this group, only 34 out of the 289 pairwise comparisons of C_1 values were not found to be significant (Supplementary Table B-4).

Within the BEN-HVLS microhabitat cluster, three taxa, *Nemacheilus masyae, Characidium fasciatum* and *Notropis sabinae*, were strongly convergent (Average $C_1 = 0.690$). The BEN-HVHS microhabitat cluster contained three different groups. The first group consisted of *Homaloptera confuzona, Pseudomystus siamensis,* and *Glyptothorax* *lampris* (Average $C_1 = 0.601$). *Homaloptera smithi* and *Parotocinclus longirostris* formed the second group (Average $C_1 = 0.628$) and the third group was formed by *Awaous banana, Etheostoma fusiforme, Etheostoma histrio, Etheostoma olmstedi, Etheostoma thalassinum, Melanocharacidium dispilomma,* and *Percina sciera* (Average $C_1 = 0.563$). Two species in the BEN-LVVS microhabitat cluster, *Etheostoma gracile* and *Kribia kribensis,* were convergent ($C_1 = 0.521$).

Another tanglegram based on the 'all-traits dataset' identified 57 possible convergent species within the microhabitat cluster (Supplementary Table B-5). Two convergent groups were found within the microhabitat cluster of MID-LVHS. The first group included 24 deep-bodied species: *Aequidens pallidus*, *Apistogramma hippolytae, Apistogramma regani, Chromidotilapia guntheri, Cribroheros robertsoni, Cryptoheros spilurus, Ctenopoma petherici, Enneacanthus chaetodon, Enneacanthus obesus, Heros efasciatus, Lepomis auritus, Lepomis cyanellus, Lepomis gulosus, Lepomis macrochirus, Lepomis marginatus, Lepomis megalotis, Lepomis miniatus, Lepomis punctatus, Pelvicachromis taeniatus, Polycentropsis abbreviata, Pristolepis fasciata, Rocio octofasciata, Trichromis salvini,* and *Vieja melanura* (Average $C_1 = 0.279$). The second group of predatory species, including *Acestrorhynchus falcatus, Crenicichla inpa, Crenicichla johanna, Erythrinus erythrinus, Esox americanus, Esox niger, Hoplias malabaricus, Micropterus punctulatus, Micropterus salmoides, Perca flavescens,* and *Umbra pygmaea* (Average $C_1 = 0.389$). Seven taxa were convergent in the BEN-HVHS cluster (Average $C_1 = 0.411$) including*, Etheostoma fusiforme, Etheostoma histrio, Etheostoma olmstedi, Etheostoma thalassinum, Melanocharacidium dispilomma,* *Percina crassa*, and *Percina sciera*. Two distinct groups were contained within the TOP-LVVS cluster. The first group included *Aphyosemion bitaeniatum, Copella nattereri, Epiplatys grahami, Fundulus notatus, Nannostomus marginatus, Nannostomus trifasciatus, Pyrrhulina brevis,* and *Pyrrhulina semifasciata* (0.482). The second group, consisting of of *Carnegiella strigata, Gnathocharax steindachneri, Laubuka caeruleostigmata,* and *Parachela sp*., did not have any significant pairwise comparisons. The BEN-HVLS microhabitat cluster also had two distinct groups: *Characidium fasciatum* and *Nannocharax ansorgii* formed one group (C_1 = 0.589), and *Nemacheilus masyae* and *Notropis sabinae* formed another (C_1 = 0.678).

Two tanglegrams based on the 'habitat trait dataset' revealed convergent species within the water velocity and substrate complexity categories (Supplementary Figure B-2 and 3). A total of 45 out of 108 species (41%) were found to be convergent with at least one other species in the low water velocity category; however, removing species from the same genus reduced this number to 39 species (38%). The average C_1 value for this category was 0.399 and FRic was equal to 36.08 (Figure 10). None of the 60 species from the medium water velocity category were convergent (FRic = 47.80, Figure 10).

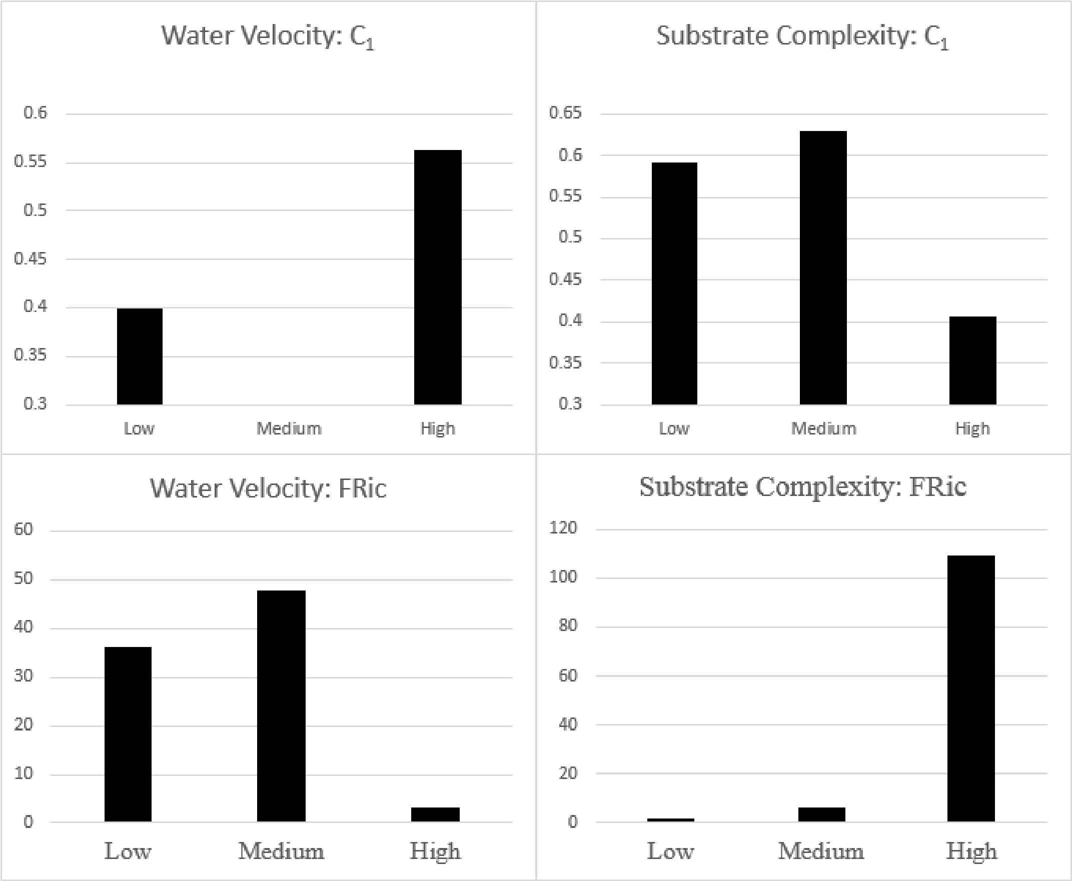

Figure 10: The C_1 and FRic values for low, medium, and high water velocity and substrate complexity.

Table 1: The results of Abouhief's test for trait phylogenetic signals. Bolded Abouhief's numbers represent significance.

Trait	**Brazil**	**Belize**	**Benin**	**Cambodia**	**USA**	**Global**
SL	0.159	**0.219**	0.053	0.070	**0.455**	**0.342**
HEAD_L	**0.385**	**0.462**	**0.329**	**0.611**	**0.821**	**0.648**
HEAD_D	**0.428**	**0.461**	-0.017	**0.371**	**0.361**	**0.404**
GAPE	**0.341**	**0.413**	**0.281**	**0.179**	**0.553**	**0.446**
MOUTH_W	**0.150**	**0.428**	0.060	**0.303**	**0.634**	**0.439**
MOUTH_P	**0.517**	**0.443**	**0.299**	**0.656**	**0.568**	**0.645**
EYE_POS	**0.391**	**0.533**	0.194	**0.531**	**0.505**	**0.498**
EYE_D	**0.537**	**0.597**	**0.506**	**0.308**	**0.595**	**0.602**
SNT_L2	**0.365**	**0.458**	**0.325**	**0.332**	**0.449**	**0.488**
SNT_PR2	**0.724**	**0.599**	0.089	**0.649**	**0.459**	**0.570**
BOD_D	**0.521**	**0.483**	0.144	**0.474**	**0.814**	**0.674**
BOD_W	0.056	**0.397**	0.117	**0.383**	**0.621**	**0.379**
PED_W	0.056	**0.527**	0.175	**0.436**	**0.420**	**0.419**
PED_L	**0.536**	**0.709**	-0.059	**0.654**	**0.516**	**0.630**
PED_D	**0.361**	**0.659**	0.066	**0.363**	**0.581**	**0.485**
DORS_L	**0.805**	**0.687**	**0.545**	**0.448**	**0.901**	**0.851**
DORS_HT	**0.317**	**0.416**	0.111	**0.263**	**0.439**	**0.394**
ANAL_L	**0.518**	**0.602**	-0.078	**0.709**	**0.639**	**0.608**
ANAL_HT	**0.382**	**0.267**	**0.383**	**0.291**	**0.512**	**0.424**
CAUD_W	**0.639**	**0.429**	**0.341**	**0.472**	**0.521**	**0.587**
CAUD_L	0.159	**0.324**	**0.415**	**0.478**	**0.502**	**0.450**
PEC_W	**0.231**	**0.445**	0.159	0.134	**0.570**	**0.286**
PEC_L	0.091	**0.299**	**0.219**	**0.230**	**0.635**	**0.278**
PELV_W	0.119	**0.387**	0.175	0.126	**0.461**	**0.333**
PELV_L	**0.263**	**0.567**	**0.389**	0.172	**0.705**	**0.514**
GUT_L	**0.147**	**0.347**	0.150	**0.626**	**0.182**	**0.429**
RAKER_L	**0.316**	**0.292**	-0.013	0.204	**0.379**	**0.346**
TOO_S	**0.700**	**0.264**	0.233	**0.648**	**0.931**	**0.823**
Life History	**0.508**	**0.355**	**0.360**	**0.572**	**0.744**	**0.637**

Thirteen species out of 26 (50%) from the high flow velocity category were convergent. After removing species from the same genus, nine species were retained in the dataset (39%) and had an average C_1 value of 0.563 and FRic of 3.37 (Figure 10). Fifty-two species out of 123 (42%) were convergent in the high structural complexity category (Average C_1 = 0.407, FRic = 109.13, Figure 10). Eleven out of 41 species (27%) were convergent in the medium structural complexity category (Average C_1 = 0.630, Fric = 6.31, Figure 10). Within the category of little to no structural complexity, only 5 out of 30 species (16%) were convergent (Average C_1 = 0. 592, FRic = 1.66, Figure 10).

Strong phylogenetic signal was observed for all traits (25 total) when analyses were performed on species datasets for Belize, USA, and all regions combined (Table 1). Phylogenetic signal was identified for 12 traits in the Benin dataset, 21 traits in the Brazil dataset, and 24 traits in the Cambodia dataset (Table 1).

Discussion

We found a high prevalence of convergence among stream fishes occupying similar microhabitats in streams from five zoogeographic regions. Congruent with our first prediction, species occupying similar microhabitats (with the exception of MID-HVLS & MID-LVLS) had convergent traits associated with swimming performance and habitat use as well as traits associated with feeding behavior and life history strategies, suggesting that adaptation to environmental conditions resulted in repeated patterns of evolution along multiple niche dimensions. Supporting our second and third predictions, fishes in the high water velocity category and those within the little or no structural complexity category generally occupied a reduced morphological space and had higher convergence values (Figure 10). Thus, it appears that high water velocity and low structural complexity exert strong selection on trait distributions in stream fish assemblages.

Ecomorphological convergence

Convergence among TOP-LVVS species was found based on analyses of the ‘all-trait dataset’ and the ‘habitat-trait dataset’. All of these species have superior-oriented mouths, a trait often associated with surface feeding (Helfman et al., 2009). Some surface feeders, such as *Fundulus notatus*, *Nannostomus trifasciatus, Pyrrhulina semifasciata, Procatopus nototaeniam, Copella nattereri,* and *Gambusia luma*, have elongate bodies with unpaired medial fins positioned posteriorly. This body shape and fin arrangement are well suited for burst swimming, but not for prolonged movement in fast water, which may explain their prevalence in low water velocity microhabitats (Keast and Webb, 1966; Webb, 1984; Webb, 1988). Another group of top-water species, *Carnegiella strigata, Gnathocharax steindachneri, Laubuka caeruleostigmata,* and *Parachela sp.*, was characterized by a relatively deep body, superior mouth orientation, and large pectoral fins. The large, wing-like pectoral fins of these fishes are used to propel the fish upward through the water column, which facilitates a rapid burst to the surface to capture of floating food items as well as escape from predators by leaping into the air (Eaton et al., 1977; Saidel et al., 2004).

Analysis of the ‘all-trait dataset’ and ‘habitat-trait dataset’ revealed convergence within two groups among species associated with the MID-LVHS microhabitat. The first group consisted of deep-bodied species that tend to have a terminal mouth and relatively large anal, dorsal, and pectoral fins. A laterally compressed, deep body allows for efficient lateral movement with a narrow turning radius (Videler, 2012), but increases hydraulic drag on the body surface which reduces the velocity of burst swimming and efficiency of sustained unidirectional swimming (Webb, 1984, 1988). Large dorsal and pectoral fins enhance deceleration as well as lateral maneuvers, such as yawing (Lauder and Drucker, 2004). Fishes with these traits are optimized for living in highly structured habitats with low water velocity wherein maneuverability is important for foraging and escape. Other studies also have reported remarkable convergence in deep-bodied fishes, such as between Centrarchidae and Cichlidae (Montaña and Winemiller, 2013). In contrast, a second group within the MID-LVHS cluster consisted of predatory fishes that tend to have torpedo-shaped bodies and posteriorly positioned unpaired median fins that enhance swimming in rapid bursts. However, these traits compromise the ability to make precise lateral movements in a small radius (Webb, 1988).

Species in the BEN-HVHS microhabitat cluster shared a number of morphological features, such as a dorso-ventrally compressed body, inferior mouth position, and relatively large pectoral fins. A dorso-ventrally compressed body was strongly associated with benthic fishes occupying microhabitats with fast flowing water. This hydrodynamic body shape reduces hydraulic drag and lessens the energetic costs of maintaining position in fast water (Webb, 1984, 1988). Benthic fishes, such as darters (North American Percidae), can use their large pectoral fins to create negative lift, forcing them against the substrate to prevent slippage downstream in habitats with fast flowing water (Page and Swofford, 1984; Lujan and Conway, 2015). However, some species produce relatively weak negative lift despite having large pectoral fins (Carlson and Lauder, 2011). One odd case of convergence was between *Etheostoma gracile* (North American percid that had riffle dwelling ancestors) and *Kribia kribensis* (African eleotrid that had estuarine dwelling ancestors). Both species have characteristics common in benthic fishes that occupy microhabitats with high water velocity, yet they were captured from areas with low water velocity. This convergent pair is of particular interest because behavior may be influencing habitat choice more than morphological specialization. For example, behavior may be more important in determining prey exploitation than morphology for an intertidal fish assemblage (Grossman, 1986). Similarly, *E. gracile* and *K. kribensis* may select low water velocity habitats even though they retain morphological traits adapted for holding position in fast water. It is important to note that these species were only convergent based on analysis of the ‘habitat-trait dataset’, and were not convergent when all traits were analyzed, apparently due to life history differences.

No convergent taxa were found within either the MID-HVLS or MID-LVLS microhabitats, which is likely because most of the species in these clusters belonged to one family, Cyprinidae. Convergent evolution can be limited by various kinds of genetic, physiological, and mechanical constraints that can facilitate phylogenetic niche conservatism, whereby lineages tend to retain ancestral niches and phenotypes (Prinzing et al., 2001; Brändle et al., 2002; Entling et al., 2007; Wiens et al., 2010; Losos, 2011; Ernst et al., 2012; Moen et al., 2015). Genetic and developmental pathways may become increasingly canalized over time, which also would constrain the potential for convergent evolution. This may be particularly true for lineages that have evolved specialized niches (Schoener, 2009; Wiens et al., 2010). Conversely, a sufficiently long period of evolution may allow divergent lineages to overcome phylogenetic and developmental constraints and converge in response to similar environmental conditions (Cody and Mooney, 1978; Melville et al., 2006; Losos, 2010). Evolutionary constraints leading to niche conservatism as well as convergence resulting from adaptation to similar environments can occur to varying degrees, and oftentimes both can be recognized when comparing assemblage trait distributions (Cooper et al., 2011; Moen et al., 2013).

Within the certain microhabitat clusters, multiple convergent groups were observed (Figure 8 and Supplementary Figure B-2). This suggests the existence of more than one viable niche (adaptive peak) exists within these microhabitats, and also is consistent with the idea of many-to-one mapping of form and function (Wainwright et al., 2005). In addition to the extensive convergence seen in this study, the influence of phylogenetic history was also evident from the strong phylogenetic signal in traits and the morphological clustering of related species, even within convergent groups (Figure 8 and Supplementary Figure B-2).

Convergence between zoogeographic regions was common, and relatively little convergence was observed within assemblages of the same region (Supplementary Figures B-5-9). This finding was not unexpected. Within zoogeographic regions, convergence between sympatric taxa should be rare, because niches are more likely to be occupied by species already possessing adaptive traits when drawn from the regional species pool during local community assembly. In contrast, evolutionary independent lineages in different regions may evolve similar traits in response to similar selective environments over long time periods, thereby contributing to the diversity of species pools in their respective regions.

Convergence along habitat gradient categories

To address our second and third hypotheses, we assessed convergence along habitat gradients, independently focusing on categories of water velocity and structural complexity. Species occupying microhabitats with high water velocity revealed greater convergence and a smaller functional trait space when compared to species associated with slow flowing water. This suggests that water velocity is a strong environmental filter that restricts the performance of species with certain traits. Hydraulic drag on the body and the high energetic costs of maintaining position in habitats with fast flowing water appear to exclude most deep-bodied fishes from occupying these habitats (Webb, 1984, 1988). Consequently, morphological variation in these habitats was low and convergence was prevalent. In microhabitats with low flow velocities, this source of selection is relaxed which permits coexistence of species with diverse morphologies and a larger assemblage morphospace.

Fishes from structurally complex microhabitats also displayed lower degrees of convergence (lower average C1 values) and greater functional richness, a finding similar to those from other studies (Willis et al., 2005, Montaña et al., 2014). Structurally complex habitats generally support more species and greater functional diversity (Gorman and Karr, 1978; MacArthur and MacArthur, 1961, Willis et al., 2005, Montaña et al., 2014), presumably because these habitats tend to support more abundant or higher quality food resources and provide refuge from predators or harsh environmental conditions (Kovalenko et al., 2012). Higher species richness in structurally complex habitats also could be associated with aspect diversity, another dimension of functional diversity (Rand, 1967; Ricklefs, 2009). Although low C_1 values were found, on average, for species pairs in structurally complex or low water velocity categories, a few of the convergent species pairs in these habitats had high C_1 values (Supplemental Table B-4). Structurally complex microhabitats with low water velocity should have greater availability of niches and weaker environmental filtering, which should support species packing, niche diversification and the evolution of specialized niches (Poff and Allan, 1995). Ecological specialists have provided some of the best examples of convergence (Harmon et al., 2005; Mahler et al., 2013; Moen et al., 2013; Blom et al., 2016).

Although results supported our second and third hypotheses, inferences may have been weakened by an interaction between water velocity and substrate. For example, a fish can avoid the force of flowing water by occupying hydraulic refuges within the laminar boundary layer along the substrate surface or behind logs and other solid structures (Carlson and Lauder, 2011). However, the inverse relationship of water velocity to convergence values and FRic as well as the positive relationship of substrate complexity to convergence values and FRic still held when finer microhabitat categories were compared (e.g. BEN-HVHS and BEN-HVLS). Many microhabitat clusters with low water velocity and high substrate complexity tended to have larger FRic and small C_1 values, further supporting hypotheses two and three.

Conclusions

Studies of evolutionary convergence have the potential to improve predictions about how species and assemblages will respond to a changing biosphere. The prevalent convergence found in this study suggests non-random processes have a strong influence on both fish evolution and local community assembly in streams. Further exploration of convergence could facilitate development of models capable of forecasting changes in assemblage functional composition in response to anthropogenic habitat alterations. For example, our findings suggest that a reduction of instream substrate structure, a likely consequence of deforestation of riparian habitats, would reduce functional diversity of fish assemblages. Ecological restoration and management of invasive species also rely on our ability to understand factors that influence the functional structure of species assemblages. Research is needed to determine whether convergence is common and predictable among fishes in other habitats and regions, not to mention other taxa. In addition, further research in molecular ecology and evolutionary developmental biology (evo-devo) could prove particularly fruitful for understanding genetic mechanisms behind the widespread convergence observed in freshwater teleosts. Convergent traits could evolve due to mutations in similar developmental pathways, such as the armor plate patterning of threespine sticklebacks (Colosimo et al., 2005; Stern, 2013), or have genetically disparate origins, such as the neofunctionalization of gene duplications resulting in antifreeze glycoproteins of Antarctic notothenioid fish and Arctic cod (Chen et al., 1997; Roelants et al., 2010). While studies using molecular and evo-devo approaches could elucidate mechanisms that produce convergent traits, ecological investigations, such as the one presented here, are needed to better understand the role of environmental factors in species and assemblage convergence.

The present study revealed extensive convergence among fishes from similar microhabitats in low-gradient streams. Environmental factors at the microhabitat scale, hydraulics especially, influence the functional diversity of local assemblages at the habitat scale and result in convergence at the inter-continental scale. Following an adaptive landscape framework, strong selective pressures produce tall, narrow peaks wherein the range of morphological possibilities is limited and the likelihood of convergence is greatest. In contrast, weak selective pressure would produce broad, low peaks with greater functional richness and a lower likelihood of convergence. Our results match these expectations with regard to the apparent influence of water velocity and substrate complexity on convergence and functional diversity of stream fishes. Other abiotic environmental factors that potentially could be strong sources of selection include dissolved oxygen concentration (e.g. aquatic hypoxia selecting for accessory respiratory adaptations), pH, and salinity. The prevalence of convergence among stream fishes implies that predictable deterministic mechanisms play a strong role not only in evolution, but also during local community assembly.

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CHAPTER IV

GLOBAL TRENDS IN FUNCTIONAL AND PHYLOGENETIC STRUCTURE OF STREAM FISH ASSEMBLAGES

Introduction

Ecologists have long sought to understand the mechanisms that account for local community assembly, species coexistence, and functional diversity. Despite the growing need to predict community responses to environmental change, mechanisms underlying community assembly remain poorly understood (Mouillot et al., 2007; Pavoine and Bonsall, 2011; Weiher et al., 2011). Two niche-based processes, environmental filtering and limiting similarity, are generally thought to play important roles in structuring communities (MacArthur and Levins, 1967; Weiher and Keddy, 1995; Chase and Myers, 2011; Perronne et al., 2017). Many studies have provided evidence of environmental filtering, the process whereby local environmental conditions prevent the successful establishment of certain species in a particular habitat (e.g., Mouillot et al., 2007; Weiher et al., 2011; Dimitriadis et al., 2012; Mouchet et al., 2013; Troia and Gido, 2015; Córdova-Tapia et al., 2018). Others supported limiting similarity, the avoidance of competitive exclusion within a given habitat through niche partitioning (e.g,, Weiher and Keddy, 1995; Ingram and Shurin, 2009; Montaña et al., 2014). To improve our ability to predict biodiversity responses to environmental change, research is needed to reveal consistent features of assemblage structure and mechanisms of community assembly in response to environmental variation.

The *stress dominance hypothesis* predicts that functional trait diversity will be reduced as environmental stress and stabilizing selection increase; whereas, interspecific trait variation is expected to be greater in less stressful environments (Weiher and Keddy, 1995; Swenson et al., 2007; Coyle et al., 2014; Ramm et al., 2018). To date, only a few studies have tested the stress dominance hypothesis, and support has been inconsistent (Coyle et al., 2014; Perronne et al., 2017; Ramm et al., 2018). Stream fishes provide an excellent model system to test this hypothesis. Environmental filters structure stream fish assemblages and can act over multiple spatial and temporal scales (Poff and Allan, 1995; Poff, 1997; Hoeinghaus et al., 2007). For stream fishes, high water velocity is a strong environmental stressor that influences their ecology and evolution (Lamouroux et al., 2002; Willis et al., 2005; Bower and Pillar, 2015; Haas et al., 2015; Lujan and Conway, 2015) because hydraulic drag associated with fast moving water exerts a high energetic cost (Webb, 1988). Substrate characteristics in streams also affect fish ecology in multiple ways (Kovalenko et al., 2012). Structurally complex substrates can provide refuge from adverse environmental conditions, such as hydraulic drag or predation (Bartholomew et al., 2000; Tokeshi and Arakaki, 2011). Streams with unstructured substrates tend to have fish assemblages with lower functional trait diversity (Kovalenko et al., 2012; Bower and Winemiller, unpublished).

Community assembly processes are expected to change along spatial hierarchies (Levin, 1992; Oberdoff et al., 1995; Poff, 1997; Smith et al., 2013; Blanchet at al., 2014). At broad spatial scales (regional to global), abiotic filters should have the greatest influence on community structure, with processes such as speciation, dispersal, and extinction, together with abiotic environmental factors, having strong effects. At local scales, community assembly and population persistence are heavily influenced by both abiotic environmental variation and biotic factors such as productivity and species interactions (Brooker et al., 2009; Algar et al., 2011; Weiher et al., 2011). Community assembly processes may vary according to levels of environmental stress (Weiher and Keddy, 1995; Swenson et al., 2007; Coyle et al. 2014; Ramm et al., 2018). For example, squamate assemblages of from arid regions of Africa displayed characteristics consistent with environmental filtering to a greater degree than those from wet tropical regions (Ramm et al., 2018). Ascertaining how assemblage structure changes along environmental gradients at different spatial scales can reveal how alternative processes influence community assembly.

Despite intense interest in community assembly processes, mechanisms and rules that apply across different systems have not been proposed. This lack of fundamental understanding may derive from three possibilities (McGill et al., 2006; HilleRisLambers et al., 2012). First, much of the research on functional diversity patterns has been focused on plants and microbes, with relatively few studies on animals (Trisos et al., 2014). Thus, our understanding of community assembly processes has largely been based on organisms with limited mobility. Second, investigations of functional diversity patterns across large spatial scales are rare, especially for vertebrates in aquatic systems (Heino et al., 2013; Troia et al., 2015). For example, functional diversity studies of fish assemblages often focus on only one zoogeographic region, preventing the comparison of phylogenetically distinct assemblages. Studies across large geographic scales are essential for identifying general patterns of ecology and community assembly (Coyle et al., 2014; Ramm et al., 2018). Third, discrepancies in methods of data collection and analysis complicate comparisons based on metanalysis of functional traits and phylogenetic diversity. Simultaneous analysis of phylogenetic and trait patterns is essential to determine the relationships between the two, and for inferences regarding community assembly (Troia and Gido, 2015; Gerhold et al., 2015; Ramm et al., 2018). Here I use a consistent methodology to reveal patterns of dispersion and infer community assembly processes along environmental gradients in multiple zoogeographic regions.

Trait-based and phylogenetic methods have been increasingly used to disentangle the influence of niche-based and neutral processes (Mouillot et al., 2007; Swenson, 2013; Violle et al., 2014). Species assemblages influenced by environmental filtering are expected to have trait distributions that are narrower, or under-dispersed, than expected at random, because only those species with traits suited for the environment can establish and persist (Weiher and Keddy, 1995; Cornwell and Ackerly, 2009). Alternatively, competition and limiting similarity should result in an assemblage trait distribution that is over-dispersed compared to random (Brown and Wilson, 1956; MacArthur and Levins, 1967; Weiher and Keddy, 1995). In some circumstances, interspecific competition could yield functional trait under-dispersion, such as when plants have similar heights due to competition for sunlight (Mayfield and Levine, 2010). When studies combine traits associated with different niche dimensions into a single analysis, independent effects of separate dimensions may be obscured, resulting in erroneous conclusion that neutral mechanisms play the dominant role in community assembly (Kraft et al., 2007; Weiher et al., 2011). For example, Trisos et al. (2014) found that datasets representing multiple niche axes had low power for detecting community assembly processes, but single niche axes were better able to detect the signals of environmental filtering and limiting similarity in bird territories. Therefore, interpreting patterns of over- and under-dispersion is challenging and requires considerable system-specific knowledge to inform study design and statistical analysis (Mayfield and Levine, 2010).

In this study I investigate the functional and phylogenetic structure of stream fishes along environmental gradients in five zoogeographic regions. My first objective was to evaluate the similarity of functional and phylogenetic dispersion patterns across regions at microhabitat and stream-reach scales. My second objective was to test the relationship between environmental gradients and metrics of functional trait and phylogenetic diversity. I hypothesized that functional diversity metrics would decline with increasing water velocity but increase with water depth and substrate complexity.

Methods

Data acquisition and preparation

Streams fish assemblages were surveyed from five zoogeographic regions on four continents – Belize, Benin, Brazil, Cambodia, and United States of America (New Jersey, South Carolina, and Texas; Figure 1). The inclusion of different zoogeographic regions allows for comparison of distantly related lineages and the testing of general, repeated patterns in community assembly processes. Streams within coastal plains and inland floodplains were chosen in an attempt to minimize differences in habitat features: (1) stream size; (2) low level of disturbance (few anthropogenic impacts); (3) low gradient; and (4) geomorphology (meandering course with sandy substrate). At each region, five to seven wadeable streams were sampled based on gradients of stream channel width: small (< 3 m), medium (3-8 m), and large (> 8 m). Collections were done under base-flow conditions when streams were wadeable and fish capture was most efficient. Because of the scale dependency in this study (Smith et al., 2013), a nested sample design was used: microhabitat stream reach, and zoogeographic region.

Within each region, stream reaches between 200-500 m were sampled in an upstream direction to obtain representative samples of fishes from major types of microhabitat (modified from Barbour et al., 1999; Bower and Piller, 2015; Troia et al., 2015). Microhabitat types were areas of relatively homogeneous depth, current velocity, substrate composition, and in-channel cover. In each microhabitat where fish were collected, I recorded water velocity, substrate composition, and depth. Microhabitats were sampled only if they fit one of these substrate categorizes: sand (>90% cover), woody structure (>80% cover), aquatic macrophytes (>80% cover), leaf packs (>80% cover), root banks (banks with dense root structures, >90%), and gravel (6-25 cm diameter, >80% cover). Given the challenge of sampling fish from diverse habitats, various methods were employed, including: seining, cast netting, dipnetting, and backpack electrofishing. At each study site, water temperature (°C), dissolved oxygen (DO), pH, specific conductivity (µS cm-1), and salinity (ppt) were measured. Specimens were euthanized via anesthetic (MS222) overdose, and preserved in 10% formalin following Texas A&M University animal care protocol (IACUC 2014-0173 and 2017-0233).

Thirty morphometric traits that affect food acquisition and locomotion were measured for 5 individuals per species (for rare species n = 1-4; samples sizes found in Supplementary Table C-1) to the nearest 0.1 mm using calipers (Gatz, 1979; Winemiller, 1991; Supplementary Table C-1). To reduce potential ontogenetic biases, only adult size classes were used for all analyses. Traits were standardized converting them to proportions based on standard length, body depth, body width, head length, and head depth (Winemiller, 1991; Casatti et al., 2006). Each species was assigned to a life history category based on information from the literature (Supplementary Table A-1).

A majority-rule consensus tree was constructed from the time-calibrated tree of Rabosky et al. (2018). Because some species in our study were not included in this tree, we followed the protocol of Beaulieu et al. (2012) and inserted these species in place of closely related taxa to create a tree that included all species in our study.

Indices and statistical methods

Analysis of diverse traits can provide an integrated assessment of assemblage structure functional (Violle et al., 2007). However, if contrasting assemblage processes act on different niche dimensions, opposing trait patterns could mask each other and produce a neutral pattern of trait dispersion (Swenson and Enquist, 2009; Trisos et al., 2014). Analysis of traits that are clearly associated with a given niche dimension may facilitate inference of niche-based assembly processes (Trisos et al., 2014). Therefore, three sets of functional traits were analyzed: 1) traits associated with habitat use (habitat traits), 2) traits associated with food acquisition (diet traits), and 3) both of these trait sets combined with life history categories (combined-traits). Three standard indices were used to determine functional diversity for each trait grouping: Rao's quadratic entropy (RaoQ), functional richness (FRic), and mean nearest neighbor distance (MNND). These indexes are recommended as robust measures of trait over-dispersion (NMMD and RaoQ) and under-dispersion (FRic and RaoQ; Aiba et al., 2013; Botta-Dukát and Czúcz, 2016). The dbFD function from the FD package was used to calculate RaoQ and FRic multi-trait metrics (Laliberté et al., 2014). The *picante* package in R was used to calculate the MNND metric (Kembel et al., 2010). Because the number of trait axes must be less than the number of species in each sample point, only the first two axes of the principal coordinates analysis (PCOA) were used in the dbFD function. Anguilliform species (eel-like body shape) were removed before calculating all diversity metrics due to their extreme morphology; their inclusion produced strongly skewed gradients and assemblage ordinations that separated anguilliform fish from all other species, and the latter tightly clustered within morphospace.

Two recommended null models were used to test if the observed dispersion indexes differ from random. Null models differ in their ability to discern assemblage processes and a family of null models should be used to identify different assemblage processes (Chalmandrier et al., 2013; Götzenberger et al., 2016). Here we use the independent-swap and taxon-label null models to test for community assembly processes (Gotelli, 2000; Götzenberger et al., 2016; Fitzgerald et al., 2017). The independent-swap model randomizes species abundance matrix while preserving the species richness and species occurrence at sites and is thought to be more appropriate for short-term data (Gotelli, 2000). The taxon-label model shuffles trait values among species without constraint and has been commonly used in community assembly studies (Cornwell and Ackerly, 2009; Lavender et al., 2016). These models were run using the RandomizeMatrix and taxaShuffle functions in the *picante* package in R (Kembel et al., 2010).

Local assemblages and regional species pools were defined at two spatial scales: (1) microhabitats as local assemblages with the corresponding stream reach as the regional species pool, and (2) stream reaches as local assemblages with the collective list of species collected from streams of the corresponding region as the regional species pool. For each FD metric, null model and location, the standard effect size (SES) was calculated as $(\text{mean}_{\text{observed}} - \text{mean}_{\text{simulated}})/\text{SD}_{\text{simulated}}$. SES values greater than 0 signify trait over-dispersion patterns, whereas SES values less than 0 demonstrate trait clustering patterns. The observed value was determined to be significantly different from random when the observed FD index value ranked higher than 950th or lower than 50th when compared to the ranked null FD index values (p value = observed rank / runs + 1).

To assess the phylogenetic structure of fish assemblages, the net relatedness index (NRI) and nearest taxon index (NTI) were used (Webb et al., 2002; Brunbjerg et al., 2014). NRI and NTI were calculated as

$$((r_{\text{obs}} - r_{\text{null}}) / \text{SD}_{\text{null}}) * -1,$$

wherein r is the mean pairwise distance (MPD) when calculating NRI, and r is the mean nearest taxon distance (MNTD) when calculating NTI. The null models for r_{null} were created by randomly swapped the tips of the phylogeny 999 times while weighting by species abundance using the taxa-labels null model in the R package picante (Kembel et al., 2010). Negative values of NRI and NTI indicate phylogenetic over-dispersion, with co-occurring species being less closely related than expected at random, and positive values showing phylogenetic clustering, whereby co-occurring species are more closely related than expected at random. Both NRI and NTI were calculated for fish assemblages at the microhabitat scale with the matching stream reaches as the regional species pool and stream reaches scale with the corresponding region as the regional species pool. Random intercept linear mixed models and general linear mixed models with a gamma distribution were used to test the correlation between habitat variables and FRic, NMMD, RaoQ, MPD, and MNTD values. Model type was selected based the how well the data fit the model assumptions. In these models, functional diversity metrics were the dependent variable, with water velocity, water depth, and substrate complexity as independent variables and region and sampling site as random factors. Habitat variables and functional metrics were log-transformed. The "Anova" function from the *car* package in R was used to test if each habitat variable significantly influenced the model.

Results

Overall, 230 fish species were collected and analyzed: 21– Belize, 53– Brazil, 26– Benin, 67– Cambodia, and 63– USA. The Cambodia region had the most families represented (20), followed by Brazil (19), Benin (17), USA (12), and Belize (9) (Supplementary Table A-1). The average species per microhabitat for each region was as follows: Cambodia region 5.21 species, Benin 3.27, Belize 3.06, USA 2.90, and Brazil 2.88.

Patterns of functional diversity at the microhabitat scale

Habitat traits dataset

Evidence for both over- and under-dispersion of traits associated with habitat use was found at the local scale, with microhabitat units defining local species assemblages, and the corresponding stream reach representing the regional species pool (Figures 11-12). Based on results from the FRic metric and both null models, low percentages of under- and over-dispersion at the local scale were detected for assemblages in all regions, with exception of the Brazil region that had a high percent of trait under-dispersed based on the taxon-label model (Figures 11-12). Again, little over-dispersion was identified for any region using MNND or either null model (Figures 11-12). However, 8-14 % of the local assemblages were significantly under-dispersed for all regions using the independent-swap null model and MNND metric. Using the taxon-label null model and MNND metric, a comparatively high number of local assemblages had traits that were under-dispersed in the Benin, Brazil, Cambodia, and USA regions (Figure 11). Relatively little over-dispersion of traits associated with habitat use was detected at the local scale for regions using the RaoQ metric and both null models (Figures 11-12). For the RaoQ metric and both null models, the percentage of trait under-dispersed local assemblages was moderate to high, ranging from 14% to 52% (Figures 11-12).

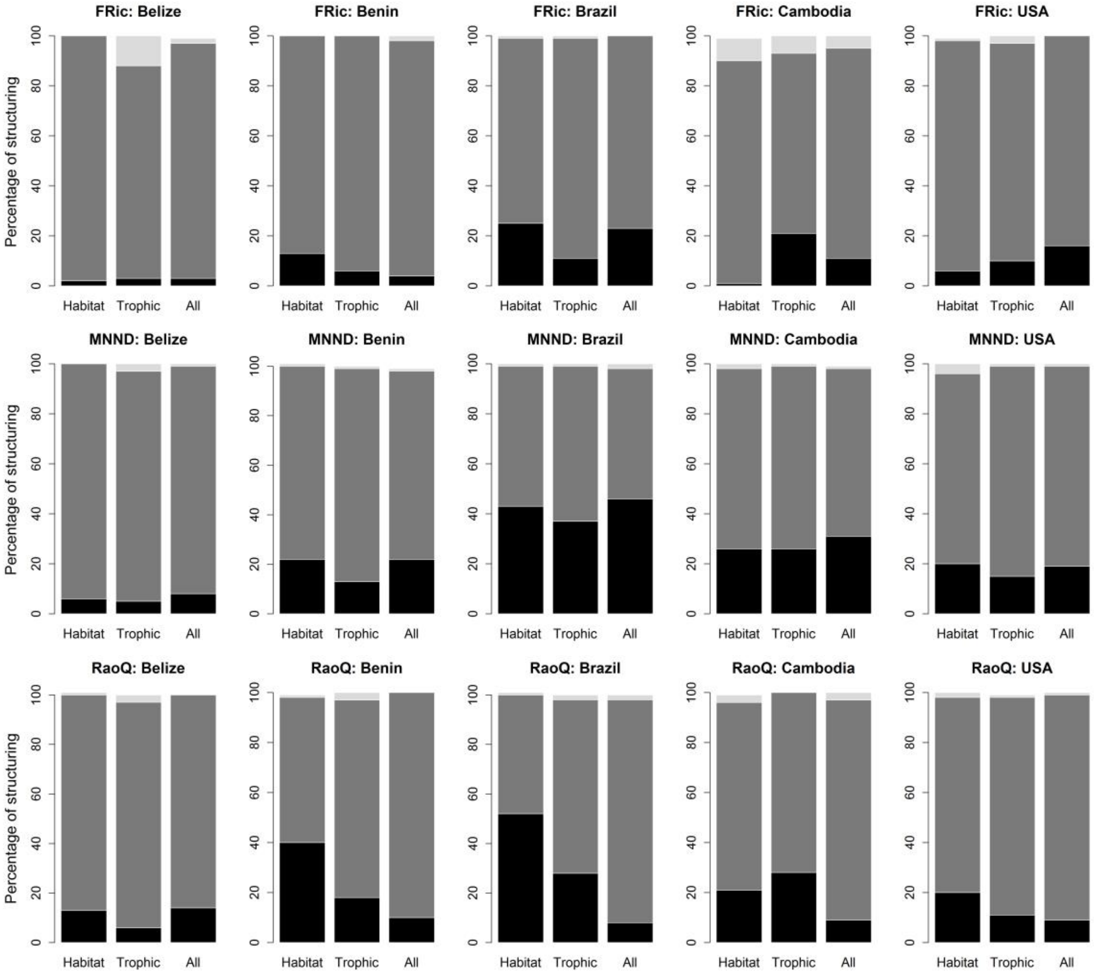


Figure 11: Functional traits diversity for each region based on taxon-label model and all three metrics: FRic, MNND, and RaoQ. Proportions of significantly over-dispersed (light gray), under-dispersed (black), and randomly (dark gray) structured local assemblages at the microhabitat scale using the corresponding stream reach as the regional species pool.

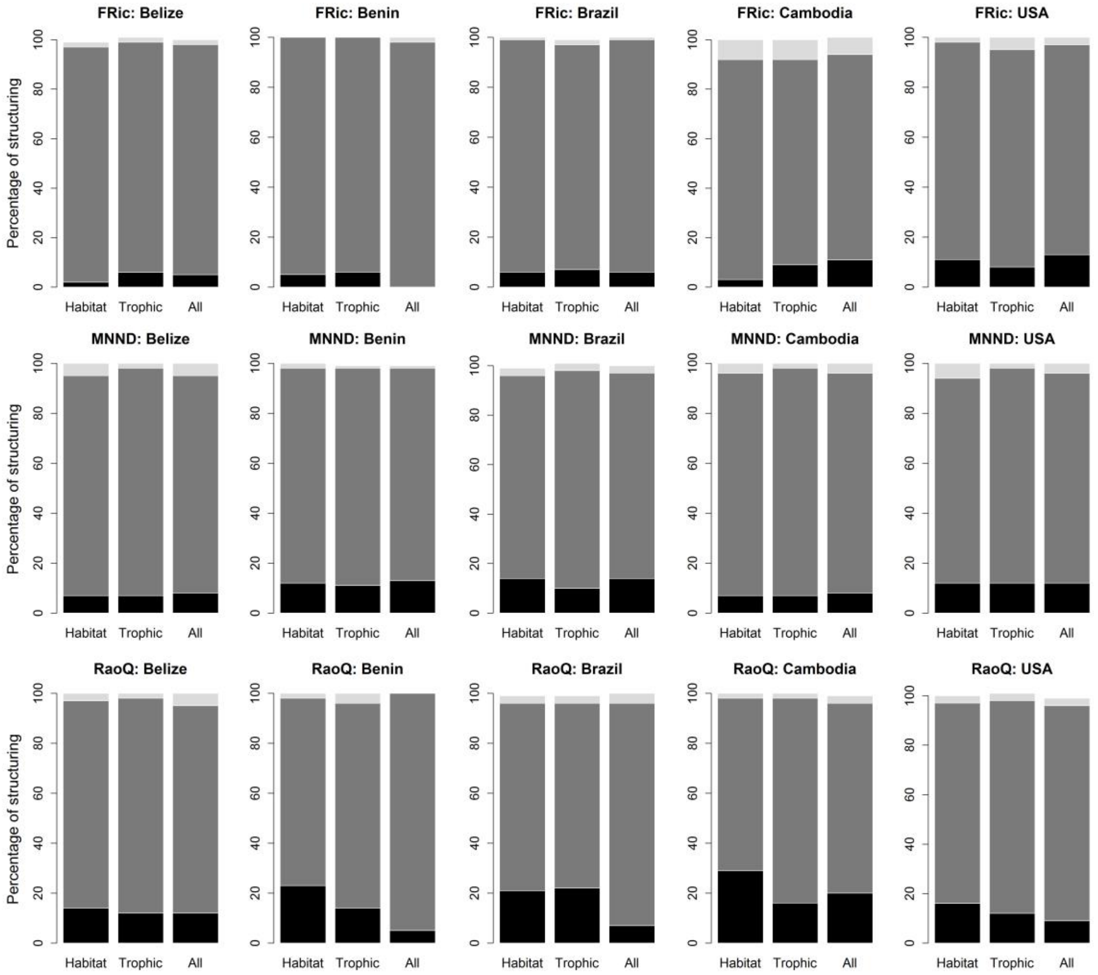


Figure 12: Functional traits diversity for each region based on independent-swap model and all three metrics: FRic, MNND, and RaoQ. Proportions of significantly over-dispersed (light gray), under-dispersed (black), and randomly (dark gray) structured local assemblages at the microhabitat scale using the corresponding stream reach as the regional species pool.

Diet traits dataset

Using traits associated with feeding ability, significant over- and under-dispersion was identified for assemblages at the local scale for all regions. Based on results from the FRic metric and independent-swap null model, similar percentages of local assemblages were found to be over- and under-dispersion (0-9%) (Figures 12). In contrast, a high percentage of local assemblages were identified as under-dispersed for the Cambodia region using the taxon-label null model (Figure 11). The FRic metric and taxon-label null model showed assemblages in Belize and Cambodia to have the highest percentage of significantly over-dispersed local sites. Using the MNND and RaoQ metrics, less than 5% of local sites were identified as significantly over-dispersed using either null model (Figures 1-2). A relatively large number of local assemblages in Brazil and Cambodia were under-dispersed based on results from the taxon-label null model and MNND metric (Figure 11). Under-dispersion of local assemblages ranged from 12% to 22% using the RaoQ metric and independent-swap null model. Under the taxon-label null model, the Benin, Brazil, and Cambodia regions had high percentages of local assemblages revealing under-dispersion for the RaoQ metric (Figure 11).

Combined-traits dataset

Significant over- and under-dispersion of traits in local assemblages was found for all regions using the combined-traits dataset at the local scale. Cambodian assemblages had highest trait over-dispersion for FRic using both null models, whereas little to no over-dispersion was detected for the other regions (Figures 11-12). Using the independent-swap null model and FRic metric, between 0-13% of local assemblages of each region had traits that were significantly under-dispersed. However, assemblages in Brazil, Cambodia, and USA showed evidence of trait under-dispersion based on the taxon-label null model and FRic metric, with 23%, 11%, and 16% of local sites under-dispersed, respectively (Figure 11). For the RaoQ metric and taxon-label null model, 8-

14% of the local assemblages were under-dispersed in all regions (Figure 11). Analysis using the independent-swap null model and RaoQ metric resulted in Cambodia having a higher percentage of local assemblages under-dispersed (Figure 12). Using RaoQ metric and both null models, relatively little over-dispersion (0-5%) was detected for all regions at the local scale. Similar percentages of over-dispersion (1-5%) were obtained for all regions using MNND metric and both null models (Figures 11-12). Eight to fourteen percent of the local assemblages were under-dispersed for all regions using the MNND metric and independent-swap null model. However, Brazil, Benin, Cambodia and the USA also had high percentages of local assemblages under-dispersed when analyses were based on the MNND metric and taxon-label null model (Figure 11).

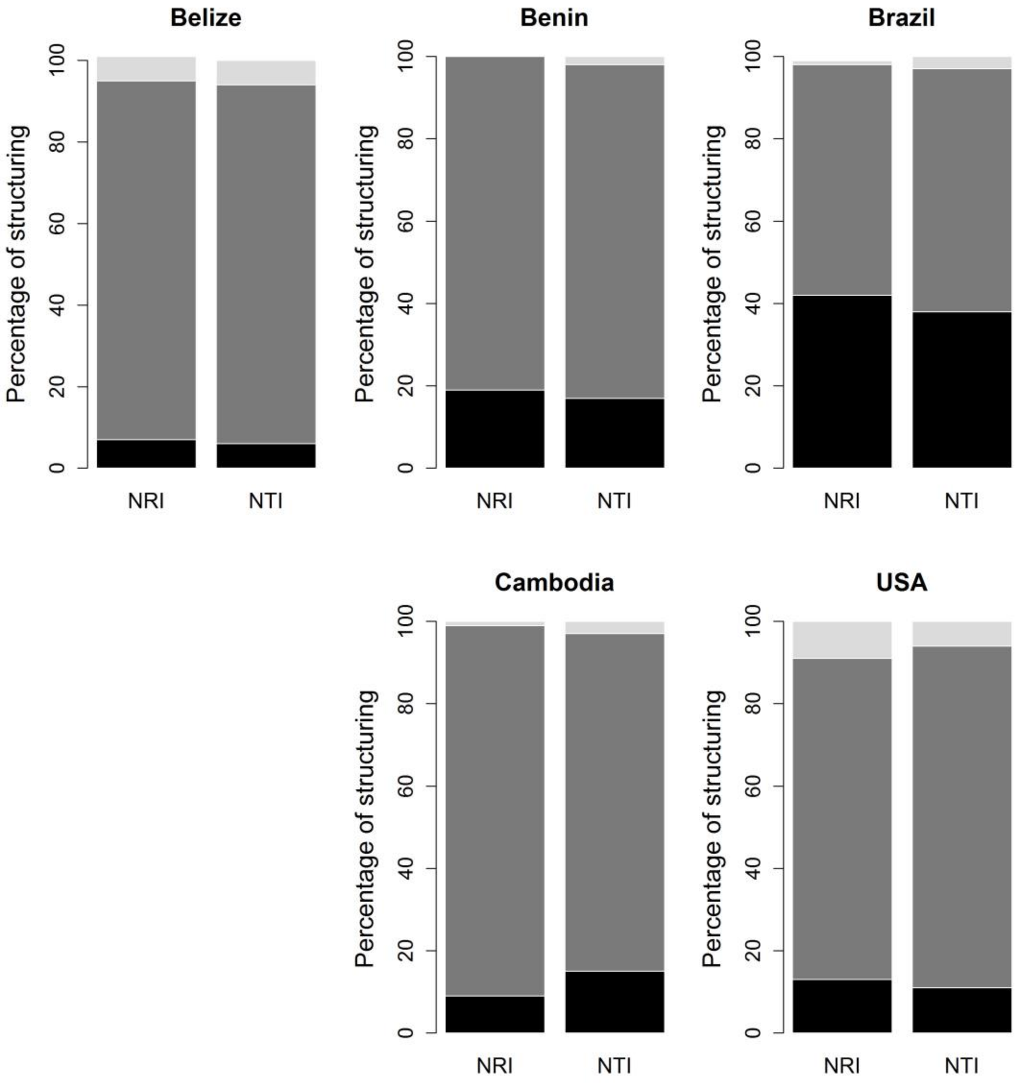
Patterns of functional diversity at the stream reach scale

When stream reach was used to define local species assemblages, there were more instances of under-dispersion than over-dispersion across all regions (Supplementary Tables C-1-3). Assemblages in Belize showed significant under-dispersion across all functional trait metrics. However, using the diet trait data set and RaoQ metric, two instances of over-dispersion were observed using the MNND metric and independent-swap null model, and five instances of over-dispersion were detected (Supplementary Tables C-2). For both the Benin and Brazil regions, sites were found to be under-dispersed for all functional diversity metrics, with RaoQ showing the most under-dispersion (Supplementary Tables C-1-3). A single instance of over-dispersion was found for both Benin and Brazil when the analysis was for the combined-traits dataset using the taxon-label null model and FRic metric (Supplementary Tables C-1).

Under-dispersion was observed in Cambodia stream-reach assemblages based on analysis of the combined-traits dataset for all functional diversity metrics and null models (Supplementary Tables C-1-3); the only exception being the RaoQ metric analyzed with the taxon-label null model. For USA assemblages, under-dispersion only resulted from analyses using the RaoQ metric (Supplementary Tables C-1-3).

Phylogenetic dispersion of local assemblages at the microhabitat scale

With local assemblages defined at the scale of the stream reach, Brazilian fish assemblages tended be more phylogenetically related than expected by chance, with 38% and 42% of local assemblages being under-dispersed for NTI and NRI metrics of phylogenetic distance (Figure 13). Between 9-19% local assemblages (reach scale) in each of the other four regions were under-dispersed at the microhabitat scale with the stream reach as the regional species pool using both metrics of phylogenetic distance (Figure 13). Belize and USA regions had highest percentages of phylogenetic over-dispersion, between 6-9% for both metrics (Figure 13). In the other regions phylogenetic over-dispersion was found for less than 3% of local species pools based on either metric.



Figures 13: Phylogenetic diversity for each region based on taxon-label model and both metrics: NTI and NRI. Proportions of significantly over-dispersed (light gray), under-dispersed (black), and randomly (dark gray) structured local assemblages at the microhabitat scale using the corresponding stream reach as the regional species pool.

Phylogenetic dispersion of local assemblages at the reach scale

None of the Brazilian assemblages at the reach scale were found to be significantly over- or under-dispersed when the analysis was based on NRI or NTI. For Belize and Cambodia, none of the local assemblages at the reach scale revealed significant phylogenetic over- or under-dispersion based on either metric of phylogenetic distance. Benin and USA each had one instance of significant under-dispersion based on analysis with the NRI. In addition, one stream reach in the Benin region was found to be phylogenetically under-dispersed using the NTI. Significant over-dispersion was observed for two USA assemblages based on NRI, and one USA assemblage based NTI.

Diversity patterns along environmental gradients

Water velocity, depth, and substrate complexity were correlated with the functional diversity metrics for the habitat-use and combined-traits datasets (Figure 14). For traits associated with habitat use, the FRic metric was negatively correlated with habitat variables. However, the FRic metric was found to have a positive relationship with water depth when using the combined-traits dataset (Figure 15). For the habitat-use and combined-traits datasets, substrate was shown to have a positive relationship based on either the MNND or RaoQ metric (Figure 1). A marginally significant negative relationship was found between water velocity and MNTD (Slope -0.337, p value = 0.073), and no significant relationship was detected between the MPD and any habitat variable.

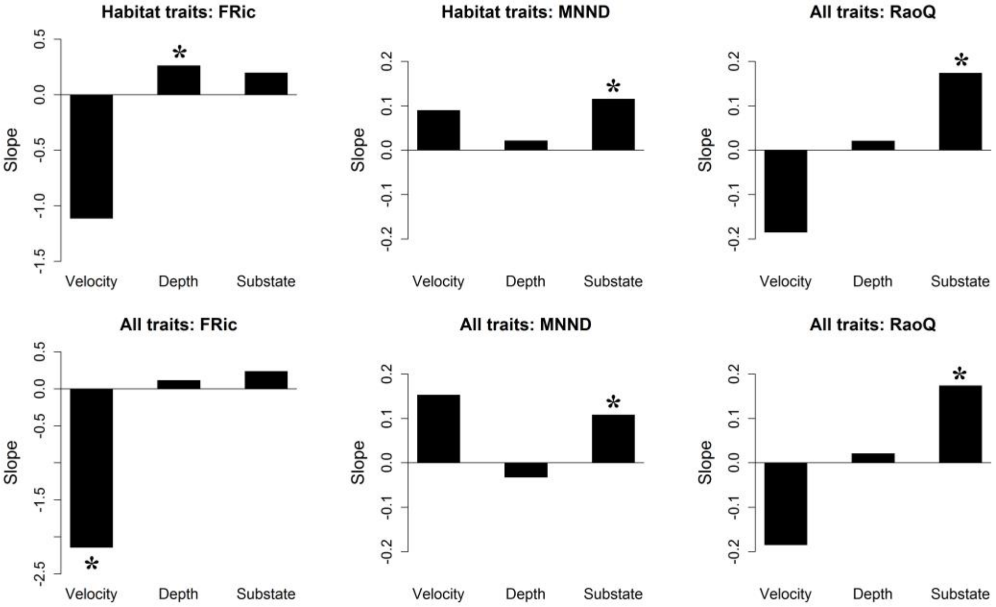


Figure 14: The slopes from the mixed models testing for a relationship between habitat variables (water velocity, water depth, and substrate complexity) and functional traits metrics (FRic, MNND, and RaoQ) using habitat traits, diet traits, and combined-traits datasets. Asterisk denotes significance (p value < 0.05).

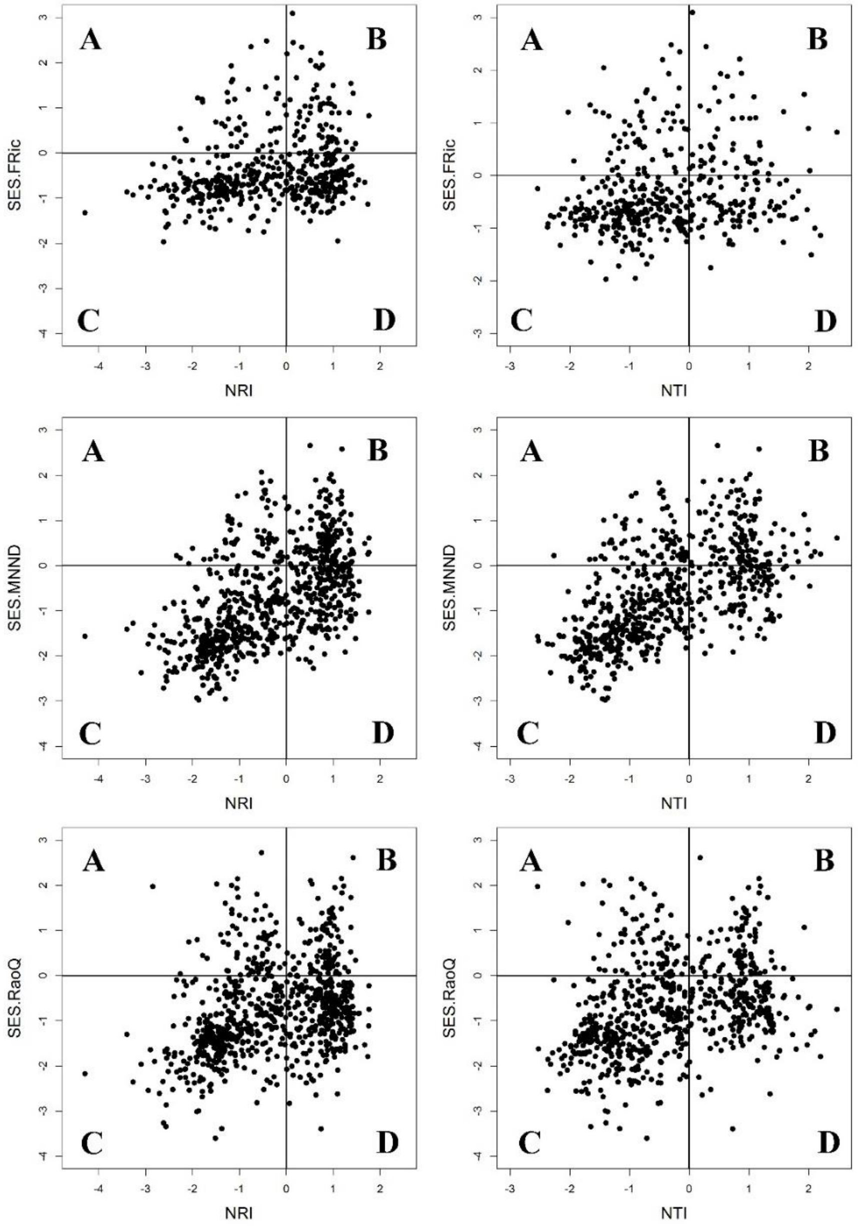


Figure 15: Standardized effect size (SES) for FRic, MNND, or RaoQ plotted against NTI or NRI based on the taxon-label model and taxon-label null model. Lines divide plot into quadrats. Quadrat A suggests morphological divergence and niche segregation of related species; B) morphological divergence and niche segregation of unrelated species; C) morphological under-dispersion of related species due to stabilizing selection or niche conservatism; D) morphological convergence of unrelated species reflecting habitat filtering of convergent forms.

Discussion

The results from this study suggest that environmental filtering and, to a lesser extent, species interactions structure fish assemblages in small, low-gradient streams in five zoogeographic regions. Habitat-use, trophic, and combined-traits datasets showed more instances of under-dispersion than over-dispersion regardless of spatial scale and regional species pool. These results generally support the paradigm that environmental filtering has a greater influence on fish assemblage structure than limiting similarity (Mouillot et al., 2007; Troia and Gido, 2015; Córdova-Tapia et al., 2018). In addition, we found reduced functional diversity in microhabitats with increased environmental stressors, such as high-water velocity, shallow water depth, and homogeneous substrates lacking structural complexity, which lends support for the stress dominance hypothesis (Weiher and Keddy, 1995; Swenson et al., 2007; Coyle et al., 2014; Ramm et al., 2018).

Phylogenetic diversity patterns

Defining spatial scale and sampling grain size is critical for understanding how community assembly processes influence species co-occurrence (Weiher et al., 2011; Trisos et al., 2014). Some studies have suggested that analysis at finer spatial resolution shifts the dominate community assembly process from environmental filtering to limiting similarity (Weiher and Keddy, 1995; Vamosi et al., 2009; Weiher et al., 2011; Gotzenberger et al., 2012; Montaña et al., 2014). However, our study does not find a shift from under-dispersion of traits at the reach scale to over-dispersion of traits at the microhabitat scale. Instead, under-dispersion was common at both spatial scales and consistent across zoogeographic regions (Figures 11-12; Supplementary Tables C-1-3).

This suggests that environmental filtering is relatively more important than limiting similarity for fishes in small streams. However, the magnitude of trait dispersion patterns depended on the functional metric, null model, and types of traits in the dataset. In our study, Brazil and Cambodia revealed strongest patterns of trait under-dispersion. This pattern may be due to the high functional diversity of stream fishes in these regions, which might increase the likelihood of producing significant under-dispersion. The amount of trait variation from a regional species pool that is assembled into local assemblage likely will be proportionally small when the regional species pool has high functional diversity. Environmental filtering has been reported as important process for structuring fish assemblages in small streams (Hoeinghaus et al., 2007; Bower et al., 2015; Pease et al., 2015; Terra et al., 2016; Rodrigues-Filho et al., 2017; Córdova-Tapia et al., 2018). The results presented here along with previous studies strongly suggests that environmental filtering is a universally important community assemblage process, structuring stream fish assemblages across multiple geographic locations and spatial scales.

In this study, the limited evidence of over-dispersion suggests that interspecific competition and other species interactions play a minor role in structuring stream fish assemblages. The low incidence of over-dispersion at the local scale was unexpected for tropical fishes that have much higher functional trait diversity compared to temperate fishes (Winemiller, 1990; Schemske et al., 2009; Montaña et al., 2014). The large percentage of over-dispersion was observed for assemblages in Cambodia and Benin. This over-dispersion was related to trophic traits for both Cambodia and Belize, suggesting competition in resource acquisition (Trisos et al., 2014). Over-dispersion was also detected for habitat and combined-traits datasets in Cambodia region which may be due to interspecific partitioning of microhabitats. However, Cambodian assemblages generally had more species per microhabitat than the other regions, thus increasing the potential for interspecific interactions. Slightly larger streams were sampled in Cambodia, which could have contributed to more species per microhabitat. The size of the microhabitats (areas of relatively homogeneous depth, current velocity, substrate composition, and in-channel cover) within a stream tended to increase with stream size. The average species per microhabitat was about three for the other regions, with many microhabitats having more than five species; yet, evidence for over-dispersion at the microhabitat scale was very limited. The low number of species per microhabitat may have also contributed to the high percentage of non-significant dispersion values. However, this is unlikely because there was no significant relationship between p values for trait dispersion and number of species in each microhabitat. A possible explanation is that competitive exclusion of traits associated with resource acquisition only occurs when resources are limiting. In small stream frequent hydrologic disturbances may reduce fish populations below carry capacity (Harvey, 1978, 1987; Resh, 1988; Poff and Allan, 1995) and produce stochastic dynamics (Chase, 2007).

The likelihood of detecting competitive exclusion may be strongly affected by the regional species pool selected (Swenson et al., 2006; Troia and Gido, 2015). Local species pools, a subset of the regional species pool, would inevitably be less functional diverse than the regional species pool, especially if environmental filtering is acting on the local species pool. In this case, over-dispersion may not be identified because the local species pool is already under-dispersed relative to the regional species pool, even if niche segregation is occurring in this local species pool. However, detection of niche segregation based on relatively small morphological differences would be more likely if the regional species pool restricted to a narrow taxonomic group, a single guild, or functionally redundant group (Chesson, 2000; Swenson et al., 2006; Montaña et al., 2014). In addition, these species would have similar habitat requirements so that environmental filtering does not strongly restrict the functional diversity of local assemblages. Our regional species pools were phylogeneticly diverse spanning several orders with little taxonomic or functional redundancy, possibly reducing the likelihood of detecting over-dispersion (Supplementary Table A-1).

Although, significant over- or under-dispersion was found for various microhabitats, a majority of the trait dispersions values were not different from random, implying stochastic factors or opposing assembly mechanisms influenced stream fish assemblages and their trait dispersion patterns. Contrasting assemblage mechanisms may mask each other producing a net neutral pattern of trait dispersion (Swenson and Enquist, 2009; Trisos et al., 2014). I attempted to deal with this issue by grouping traits according to relevant niche dimensions, certain traits may have a one-to-many relationship of form and function (Hulsey and Wainwright, 2002). For example, the sucker like mouth of armored catfish (Loricariidae) is used to scrape algae and detritus off substrate surfaces but can also be used fix themselves to substrates, minimizing the effects of strong currents (Pagotto at a., 2011). In this case, mouth traits could be associated with both diet and habitat. This issue will likely become more difficult to deal with as phylogenetic and functional diversity of a study assemblage broadens. In addition, the signal of niche-based processes may not be detected if traits other than the ones used in this study are influenced by these processes. The high mobility of fish may increase stochastic aspects of dispersal. Highly mobile organisms may move briefly into areas of strong competition or environmental stress, so that the assemblage patterns appear stochastic (Gomez et al., 2010; Weiher et al., 2011; Harmon-Threatt and Ackerly, 2013).

Functional diversity along environmental gradients

The stress dominance hypothesis proposes that stressful environments exclude species with suboptimal traits, resulting in local assemblages with high trait similarity (Weiher and Keddy, 1995). In stream fishes, functional diversity metrics were related to water depth, substrate complexity, and water velocity in a manner consistent with the stress dominance hypothesis. FRic was inversely associated with water velocity, suggesting that requirements for coping with hydraulic drag restricts the trait space. Several studies have found significant relationships between water flow and fish assemblage structure in streams (Lamouroux et al., 2002; Willis et al., 2005; Bower and Pillar, 2015; Haas et al., 2015). The energetic cost of occupying a microhabitat with high flow velocity restricts functional diversity (Webb, 1984, 1988). In my study, fish functional diversity increased with water depth, a finding consistent with other studies (Carvalho and Tejerina-Garro, 2015; Leitão et al., 2018). I captured fishes from water as shallow as 3 cm where many fishes would be excluded based on body size alone.

Moreover, predation threat from birds is greater in shallow habitats (Bancroft et al., 2002; Keppeler et al., 2016), further restricting fish functional diversity. In this study, functional diversity metrics were positively associated with substrate complexity. Structural complexity has been shown to reduce both abiotic and biotic stress by providing a refuge from harsh environmental conditions or predators (Kovalenko et al., 2012). Structural complexity in streams often is associated with higher species richness and functional diversity (Kovalenko et al., 2012; Mouillot et al., 2013; Emslie et al., 2014; Ceneviva-Bastos et al., 2017). My results overall indicated a dominant influence of environmental filtering and were consistent with the stress dominance hypothesis.

Conclusions

Relationships between habitat variables and functional diversity metrics indicates that environmental filtering is an important mechanism of community assembly for streams fishes in several regions of the world. Limiting similarity does not appear to exert a strong influence on the structure of stream fish assemblages at the two spatial scales of analysis employed here. However, caution is warranted when interpreting trait dispersion patterns (Mayfield and Levine, 2010). Assembly processes, such as facilitation, can also produce patterns of trait dispersion (Cavender-Bares et al., 2009). For example, benthivorous suckers (Catostomidae) can facilitate feeding success of other fishes when they dislodge benthic invertebrates from sediments (Ross and Brenneman, 2001). Mechanistic studies are needed to improve understanding of how traits affect performance and influence the structure and functions of species assemblages. This study found limited evidence of trait over-dispersion, and future research should examine traits with different functions as well as species assemblages spanning environmental gradients in space and time. Trait datasets could be compiled to examine patterns for other niche dimensions, including life history, defense, and physiology/metabolism (Winemiller, 2015). For example, Troia and Gido (2015) found that under-dispersion of life history traits increased from downstream to headwaters. My findings suggest that the environmental filtering was the most important mechanism of community assembly for fishes inhabiting small streams in five zoogeographic regions. Water velocity, water depth, and substrate complexity seem to be particularly influential in restricting fish occupation of certain microhabitats. I found a high incidence of functional under-dispersion coupled with phylogenetic under-dispersion that could reflect phylogenetic niche conservation or stabilizing selection. This study implies that relatively consistent, deterministic mechanisms and stochastic processes structure fish assemblages of small stream at locations worldwide.

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CHAPTER V

CONCLUSIONS

A mechanistic understanding of community assembly is crucial for predicting how species will respond to environmental changes. The pursuit of general ecological processes and community assembly processes has produced varying results (Simberloff, 2004; McGill et al., 2006). Recent progress in functional trait methods and theory may allow for general, predictable patterns to be found in community ecology (McGill et al., 2006; Verberk et al., 2008; Webb et al., 2010; Verberk, 2013). In addition, species assemblages in similar environments that display similar trait dispersion patterns and prevalent convergent evolution, regardless of geographic proximity or evolutionary history, would provide strong evidence for the existence of key repeated mechanisms underlying community organization. In this dissertation, I used consistent methods to test for convergent evolution, similarity of environment-trait patterns, and similarity of trait dispersion patterns across five distinct zoogeographic regions.

My first chapter tested for convergent trait-environment patterns across regional faunas in response to consistent sets of environmental filters acting on functional traits. Similar patterns of trait-environment patterns were shown across all five regions, implying common environmental filters acted on local community assembly. The congruent trait-environment patterns implied that water velocity and habitat structural complexity act as universal environmental filters. These universal filters appear to produce similar trait distributions of fish assemblages in streams across all regions.

Using the fourth-corner analysis, only the relationship between body width and root bank was found to be statistically significant across all regions. Phylogenetic signal in traits and habitat preference was also detected in this study, implying that niche conservatism also played a role in structuring assemblage trait distributions. The results from this chapter supported the habitat template theory and also suggested that common environmental filters influence the trait distributions of stream fish assemblages and did so in a consistent manner.

My first second showed prevalent convergent evolution of species occupying similar microhabitats in small streams. This high prevalence of convergent evolution suggested that fish species adapted to similar environmental conditions resulted in repeated patterns of evolution along multiple niche dimensions. In addition, this study found that species occupying microhabitats with relatively fast water velocity or little structural complexity generally had reduce morphological diversity and exhibited the highest degrees of convergence. These environmental factors appear to exert strong selection pressures on trait distributions patterns in stream fish assemblages. Together, the results from this chapter implied that the widespread convergence and filtering of fish functional traits resulted from selection of similar environmental factors at the microhabitat scale.

The third chapter addressed patterns of functional trait and phylogenetic dispersion across regions and along environmental gradients. In my study, under-dispersion was consistently more prevalent than over-dispersion in all regions regardless of null model or functional metric. Consistent with findings from the other chapters, functional metrics tended to decrease with high water velocity, shallow water depth, and non-structured substrates microhabitats. Together, these results emphasize that environmental filtering plays an important role in structure stream fish assemblages. Furthermore, I detected more instances of functional trait under-dispersion coupled with phylogenetic under-dispersion, which may reflect a signal of phylogenetic niche conservation or stabilizing selection acting on species' traits and ecology at the local scale. However, a large proportion of the trait dispersion values were no different from random. This result suggested that stochastic factors or opposing assembly mechanisms influenced stream fish assemblages and their trait dispersion patterns. Overall this chapter suggested that environmental filtering is relatively more important than limiting similarity for structuring stream fish assemblages.

Although environmental filtering appears to have influenced fish species in a similar manner at locations across the world, more detailed studies are needed to fully understand the mechanisms influencing species co-existence. In addition, this dissertation focused on traits associated with habitat use and food acquisition. Adding additional traits and niche dimensions would greatly improve our ability to detect ecological processes and the effect these processes have on fish assemblages (Winemiller et al., 2015). However, basic natural history information is sadly lacking for many species. Without this information, our ability to understand community assembly and find general patterns will be greatly limited. Furthermore, more studies are needed to understand how traits affect the performance of individuals and populations. For many fish traits, only a correlation with habitat or diet has been shown (Gatz, 1979), but the performance of these traits long environmental gradients or across evolutionary lineages is poorly documented. However, this task is daunting with the number of potential environmental factors that could influence trait performance being substantial. Moreover, species interactions can also affect community assembly and functional trait patterns, adding to the complexity of functional trait studies. One important aspect not considered in this study was intraspecific variation of functional traits. Intraspecific variation can plays a significant role in community assembly and other ecological dynamics (Jung et al., 2010), and adding intraspecific variation to a future study would likely enhance our predictions and understanding of how communities change along environmental gradients.

Using various methods to study patterns of functional trait convergence, functional trait structure and phylogenetic structure, my dissertation showed that microhabitat variables, such as water flow, depth and substrate structure, play a strong role in stream fish community assembly, acting as an environmental filter in a similar manner within all zoogeographic regions. These results imply that steam fish assemblages are structured by relatively consistent deterministic mechanisms. My study also suggests that variation in these environmental factors helps to maintain the functional diversity of fishes observed in small, low-gradient streams. Being able to predict species persistence in a given habitat based on general ecological patterns and their functional traits will enhance many biological fields. For example, forecasting the successful reintroduction of species requires discovery of predictable ecological processes and outcomes, and many plant restoration efforts have turned to functional trait-based approaches to address the issue of predictability (Funk et al., 2008; Drenovsky et al., 2012). Invasion biology attempts to predict which species will successfully invade an area, yet biologist still cannot accurately forecast the kinds of species that will become invasive in a given habitat (Thompson and Davis, 2011). Finding general trait-habitat patterns across independent systems can help improve our ability to predict which species can successful establish and invade. Another key goal in ecology is predicting species responses to habitat alteration. My study suggests that alteration of stream flow dynamics and depth through damming or channelization as well as removal of instream structure would have detrimental effects on the functional diversity of stream fishes. My dissertation research offers some predictions and insights into the possible results of such alterations, yet the full ramifications of such actions are still far from being completely understood. With an ever-increasing global human population, climate change, and habitat destruction, now more than ever do we need to be able to predict assemblage responses to anthropogenic alteration to the environment.

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APPENDIX A

SUPPORTING INFORMATION FOR

FISH ASSEMBLAGE CONVERGENCE ALONG STREAM ENVIRONMENTAL GRADIENTS: AN INTERCONTINENTAL ANALYSIS

Supplementaly table A-1: All measured traits, trait codes, and trait definitions

Trait	Transformation	Trait definition
Average Standard length	SL	Maximum standard length from the populations in this study
Head length	HEAD_L/SL	Distance from the tip of the jaw to the posterior edge of the operculum
Head depth	HEAD_D/ BOD_D	Vertical distance from dorsum to ventrum passing through the pupil
Oral gape	GAPE/ BOD_D	Vertical distance measured inside of fully open mouth at tallest point
Mouth position	MOUTH_P	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and the posterior-most vertebra (e.g. 90 representing a terminal mouth)
Eye position	EYE_POS/ HEAD_D	Vertical distance from the ventral pigmented region to the ventrum
Eye diameter	EYE_D/ HEAD_D	Vertical distance from eye margin to eye margin

Snout length	SNT_L/ HEAD_L	Distance from the posterior pigmented region of the eye to the tip of the upper jaw with mouth shut
Snout protrusion	SNT_PR/ HEAD_L	Additional distance from the posterior pigmented region to the tip of the upper jaw with mouth fully open and extended
Body depth	BOD_D/SL	Maximum vertical distance from dorsum to ventrum
Body width	BOD_W/SL	Maximum horizontal distance from side to side
Caudal peduncle length	PED_L/SL	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra
Caudal peduncle depth	PED_D/BOD_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle
Caudal peduncle width	PED_W/BOD_W	Horizontal width of the caudal peduncle at mid-length
Dorsal fin length	DORS_L/SL	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin
Dorsal fin height	DORS_HT/SL	Maximum distance from the proximal to distal margin of the dorsal fin (excluding filaments)
Anal fin length	ANAL_L/SL	Distance from the anterior proximal margin to the posterior proximal margin of the anal fin
Anal fin height	ANAL_HT/SL	Maximum distance from proximal to distal margin of the anal fin
Caudal fin depth	CAUD_D/SL	Maximum vertical distance across the fully spread caudal fin
Caudal fin length	CAUD_L/SL	Maximum distance from proximal to distal margin of the caudal fin (excluding filaments)
Pectoral fin length	PEC_L/SL	Maximum distance from proximal to distal margin of pectoral fin
Pelvic fin length	PELV_L/SL	Maximum distance from the proximal to distal margin of the pelvic fin

Gut length	GUT_L/SL	Length of gut from the beginning of the esophagus to the anus (extended without stretching)
Gill raker	RAKER	coded as 0 for absent, 1 for short, blunt, or toothlike, 2 for intermediate or long and sparse, and 3 for long and comb-like
Tooth shape	TOO_S	coded as 0 for absent, 1 for unicuspid (rasping), 2 for multicuspid (crushing), 3 for short conical (grasping), 4 for long conical (piercing), and 5 for triangular serrated (shearing)

Supplementaly table A-2: A table of species, their family, their order, location, and number of individuals caught.

Species	Family	Order	Location	Num
Acantharchus pomotis	Centrarchidae	Perciformes	USA	20
Acanthopsoides gracilis	Cobitidae	Cypriniformes	Cambodia	19
Acanthopsoides hapalias	Cobitidae	Cypriniformes	Cambodia	13
Acantopsis sp1.	Cobitidae	Cypriniformes	Cambodia	171
Acantopsis sp2.	Cobitidae	Cypriniformes	Cambodia	85
Acestridium discus	Loricariidae	Siluriformes	Brazil	7
Acestrorhynchus falcatus	Acestrorhynchidae	Characiformes	Brazil	2
Aequidens pallidus	Cichlidae	Cichlidiformes	Brazil	28
Akysis ephippifer	Akysidae	Siluriformes	Cambodia	5
Ameiurus brunneus	Ictaluridae	Siluriformes	USA	21
Ameiurus natalis	Ictaluridae	Siluriformes	USA	51
Ammocrypta vivax	Percidae	Perciformes	USA	49
Anablepsoides micropus	Rivulidae	Cyprinodontiformes	Brazil	16
Ancistrus hoplogenys	Loricariidae	Siluriformes	Brazil	4
Anguilla rostrata	Anguillidae	Anguilliformes	USA	15
Aphredoderus sayanus	Aphredoderidae	Percopsiformes	USA	117
Aphyosemion bitaeniatum	Nothobranchiidae	Cyprinodontiformes	Benin	70
Apistogramma hippolytae	Cichlidae	Cichlidiformes	Brazil	19
Apistogramma regani	Cichlidae	Cichlidiformes	Brazil	9
Astyanax aeneus	Characidae	Characiformes	Belize	709
Awaous banana	Gobiidae	Perciformes	Belize	3
Belonesox belizanus	Poeciliidae	Cyprinodontiformes	Belize	27
Brachirus harmandi	Soleidae	Pleuronectiformes	Cambodia	12
Brienomyrus brachyistius	Mormyridae	Osteoglossiformes	Benin	44
Brycinus longipinnis	Alestidae	Characiformes	Benin	439
Brycon guatemalensis	Bryconidae	Characiformes	Belize	3
Bryconops caudomaculatus	Iguanodectidae	Characiformes	Brazil	93
Bryconops giacopinii	Iguanodectidae	Characiformes	Brazil	150
Bryconops inpai	Iguanodectidae	Characiformes	Brazil	13
Bunocephalus coracoideus	Aspredinidae	Siluriformes	Brazil	2
Callichthys callichthys	Callichthyidae	Siluriformes	Brazil	3
Carnegiella strigata	Gasteropelecidae	Characiformes	Brazil	13
Characidium fasciatum	Crenuchidae	Characiformes	Brazil	39
Charax pauciradiatus	Characidae	Characiformes	Brazil	1
Chromidotilapia guntheri	Cichlidae	Cichlidiformes	Benin	46
Clupeichthys aesarnensis	Clupeidae	Clupeiformes	Cambodia	21
Copella nattereri	Lebiasinidae	Characiformes	Brazil	12

Crenicichla inpa	Cichlidae	Cichlidiformes	Brazil	5
Crenicichla johanna	Cichlidae	Cichlidiformes	Brazil	20
Crenuchus spilurus	Crenuchidae	Cichlidiformes	Brazil	2
Cribroheros robertsoni	Cichlidae	Cichlidiformes	Belize	21
Crossocheilus reticulatus	Cyprinidae	Cypriniformes	Cambodia	13
Cryptoheros spilurus	Cichlidae	Cichlidiformes	Belize	18
Ctenopoma petherici	Anabantidae	Perciformes	Cambodia	3
Cynodonichthys tenuis	Rivulidae	Cyprinodontiformes	Belize	11
Cyprinella venusta	Cyprinidae	Cypriniformes	USA	673
Denticeps clupeoides	Denticipitidae	Clupeiformes	Benin	342
Denticetopsis seducta	Cetopsidae	Siluriformes	Brazil	4
Doryichthys boaja	Syngnathidae	Syngnathiformes	Cambodia	5
Eleotris pisonis	Eleotridae	Perciformes	Belize	8
Enneacampus ansorgii	Syngnathidae	Syngnathiformes	Benin	6
Enneacanthus chaetodon	Centrarchidae	Perciformes	USA	3
Enneacanthus obesus	Centrarchidae	Perciformes	USA	23
Enteromius callipterus	Cyprininae	Cypriniformes	Benin	108
Enteromius sylvaticus	Cyprininae	Cypriniformes	Benin	4
Epiplatys grahami	Nothobranchiidae	Cyprinodontiformes	Benin	136
Erimyzon oblongus	Catostomidae	Cypriniformes	USA	20
Erythrinus erythrinus	Erythrinidae	Characiformes	Brazil	3
Esox americanus	Esocidae	Esociformes	USA	19
Esox niger	Esocidae	Esociformes	USA	9
Etheostoma chlorosoma	Percidae	Perciformes	USA	19
Etheostoma fusiforme	Percidae	Perciformes	USA	7
Etheostoma gracile	Percidae	Perciformes	USA	10
Etheostoma histrio	Percidae	Perciformes	USA	5
Etheostoma olmstedi	Percidae	Perciformes	USA	10
Etheostoma thalassinum	Percidae	Perciformes	USA	22
Farlowella schreitmuelleri	Loricariidae	Siluriformes	Brazil	13
Fundulus notatus	Fundulidae	Cyprinodontiformes	USA	200
Gambusia affinis	Poeciliidae	Cyprinodontiformes	USA	135
Gambusia luma	Poeciliidae	Cyprinodontiformes	Belize	89
Glyptothorax lampris	Sisoridae	Siluriformes	Cambodia	8
Gnathocharax steindachneri	Acestrorhynchidae	Characiformes	Brazil	2
Gobiomorus dormitor	Eleotridae	Perciformes	Belize	2
Gymnorhamphichthys rondoni	Rhamphichthyidae	Gymnotiformes	Brazil	5
Gymnotus coropinae	Gymnotidae	Gymnotiformes	Brazil	12
Gymnotus stenoleucus	Gymnotidae	Gymnotiformes	Brazil	4
Helogenes marmoratus	Cetopsidae	Siluriformes	Brazil	5

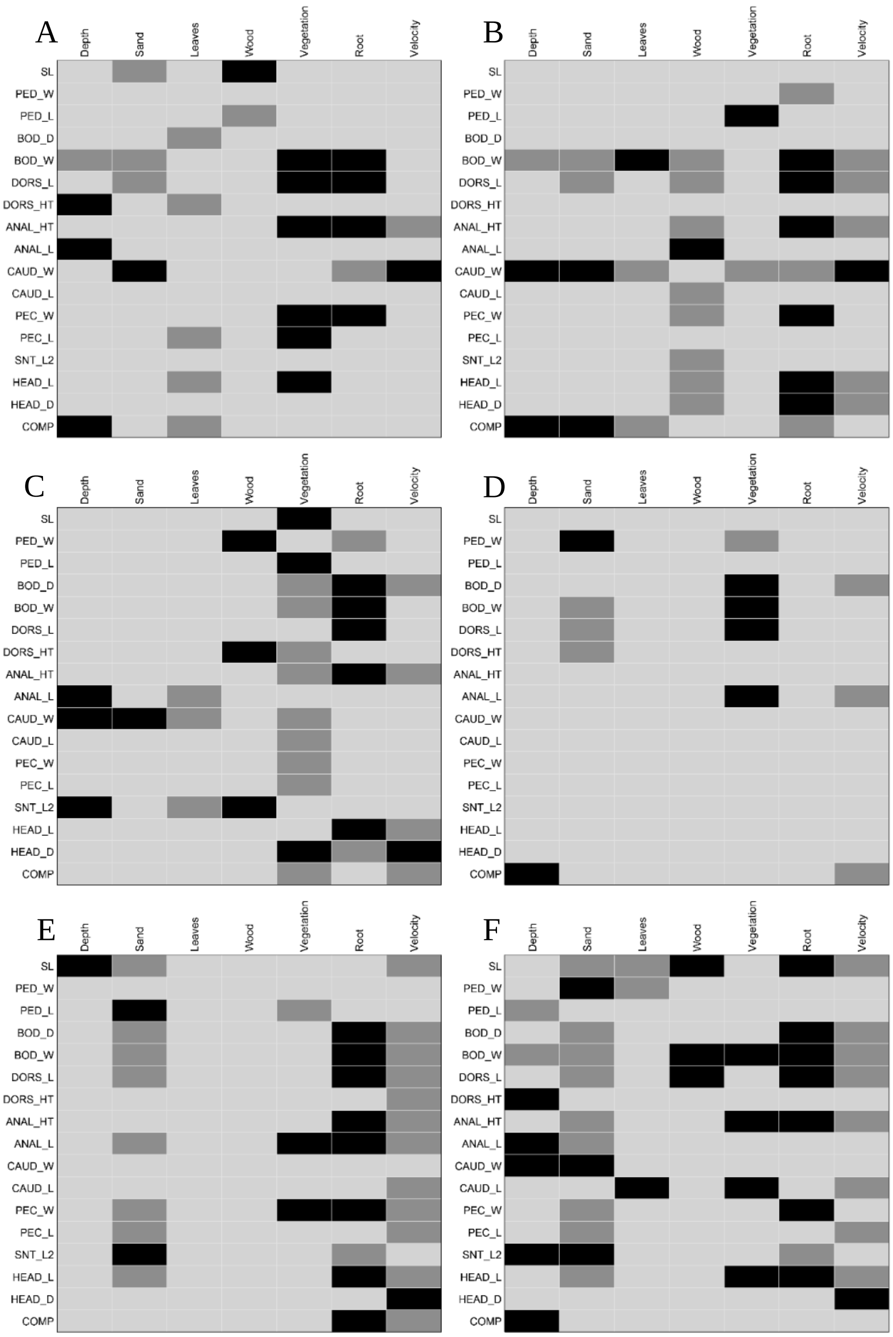
Hemichromis elongatus	Cichlidae	Cichlidiformes	Benin	5
Hemigrammus ocellifer	Characidae	Characiformes	Brazil	21
Hemigrammus pretoensis	Characidae	Characiformes	Brazil	23
Henicorhynchus lobatus	Cyprinidae	Cypriniformes	Cambodia	19
Heros efasciatus	Cichlidae	Cichlidiformes	Brazil	1
Homaloptera confuzona	Cobitidae	Cypriniformes	Cambodia	2
Homaloptera smithi	Cobitidae	Cypriniformes	Cambodia	92
Hoplias curupira	Erythrinidae	Characiformes	Brazil	5
Hoplias malabaricus	Erythrinidae	Characiformes	Brazil	5
Hybognathus regius	Cyprinidae	Cypriniformes	USA	94
Hybopsis amnis	Cyprinidae	Cypriniformes	USA	15
Hybopsis rubrifrons	Cyprinidae	Cypriniformes	USA	33
Hyphessobrycon melazonatus	Characidae	Characiformes	Brazil	165
Hyphessobrycon agulha	Characidae	Characiformes	Brazil	97
Hyphessobrycon compressus	Characidae	Characiformes	Belize	282
Hyphessobrycon sp1	Characidae	Characiformes	Brazil	193
Hypopygus hoedemani	Hypopomidae	Gymnotiformes	Brazil	2
Iguanodectes geisleri	Iguanodectidae	Characiformes	Brazil	148
Iguanodectes variatus	Iguanodectidae	Characiformes	Brazil	27
Imparfinis pristos	Heptapteridae	Siluriformes	Brazil	42
Isichthys henryi	Mormyridae	Osteoglossiformes	Benin	6
Ituglanis amazonicus	Trichomycteridae	Siluriformes	Brazil	1
Kribia kribensis	Eleotridae	Perciformes	Benin	8
Kryptolebias marmoratus	Rivulidae	Cyprinodontiformes	Belize	6
Labiobarbus lineatus	Cyprinidae	Cypriniformes	Cambodia	6
Laubuka caeruleostigmata	Cyprinidae	Cypriniformes	Cambodia	5
Lepidocephalichthys hasselti	Cobitidae	Cypriniformes	Cambodia	4
Lepomis auritus	Centrarchidae	Perciformes	USA	48
Lepomis cyanellus	Centrarchidae	Perciformes	USA	74
Lepomis gulosus	Centrarchidae	Perciformes	USA	13
Lepomis macrochirus	Centrarchidae	Perciformes	USA	50
Lepomis marginatus	Centrarchidae	Perciformes	USA	13
Lepomis megalotis	Centrarchidae	Perciformes	USA	178
Lepomis miniatus	Centrarchidae	Perciformes	USA	35
Lepomis punctatus	Centrarchidae	Perciformes	USA	14
Lythrurus fumeus	Cyprinidae	Cypriniformes	USA	11
Lythrurus umbratilis	Cyprinidae	Cypriniformes	USA	118
Macrognathus semiocellatus	Mastacembelidae	Synbranchiformes	Cambodia	12
Malapterurus beninensis	Malapteruridae	Siluriformes	Benin	3
Marcusenius senegalensis	Mormyridae	Osteoglossiformes	Benin	3

Mastacembelus favus	Mastacembelidae	Synbranchiformes	Cambodia	11
Mastiglanis asopos	Heptapteridae	Siluriformes	Brazil	6
Melanocharacidium dispilomma	Crenuchidae	Characiformes	Brazil	4
Micropterus punctulatus	Centrarchidae	Perciformes	USA	37
Micropterus salmoides	Centrarchidae	Perciformes	USA	2
Minytrema melanops	Catostomidae	Cypriniformes	USA	17
Monopterus albus	Synbranchidae	Synbranchiformes	Cambodia	3
Moxostoma poecilurum	Catostomidae	Cypriniformes	USA	16
Moxostoma rupiscartes	Catostomidae	Cypriniformes	USA	5
Myoglanis koepckei	Heptapteridae	Siluriformes	Brazil	8
Nannocharax ansorgii	Distichodontidae	Characiformes	Benin	1
Nannostomus marginatus	Lebiasinidae	Characiformes	Brazil	31
Nannostomus trifasciatus	Lebiasinidae	Characiformes	Brazil	1
Nemacheilus masyae	Cobitidae	Cypriniformes	Cambodia	14
Nemuroglanis sp	Heptapteridae	Siluriformes	Brazil	16
Nocomis leptocephalus	Cyprinidae	Cypriniformes	USA	25
Notemigonus crysoleucas	Cyprinidae	Cypriniformes	USA	11
Notropis atrocaudalis	Cyprinidae	Cypriniformes	USA	37
Notropis chlorocephalus	Cyprinidae	Cypriniformes	USA	4
Notropis cummingsae	Cyprinidae	Cypriniformes	USA	61
Notropis hudsonius	Cyprinidae	Cypriniformes	USA	132
Notropis sabinae	Cyprinidae	Cypriniformes	USA	4
Notropis volucellus	Cyprinidae	Cypriniformes	USA	90
Noturus gyrinus	Ictaluridae	Siluriformes	USA	8
Noturus insignis	Ictaluridae	Siluriformes	USA	52
Noturus nocturnus	Ictaluridae	Siluriformes	USA	20
Ophisternon aenigmaticum	Synbranchidae	Synbranchiformes	Belize	21
Opsarius koratensis	Cyprinidae	Cypriniformes	Cambodia	185
Opsopoeodus emiliae	Cyprinidae	Cypriniformes	USA	58
Osteochilus vittatus	Cyprinidae	Cypriniformes	Cambodia	14
Pangio myersi	Cobitidae	Cypriniformes	Cambodia	2
Pangio oblonga	Cobitidae	Cypriniformes	Cambodia	28
Pantodon buchholzi	Pantodontidae	Osteoglossiformes	Benin	2
Parachela sp.	Cyprinidae	Cypriniformes	Cambodia	67
Parambassis apogonoides	Ambassidae	Perciformes	Cambodia	3
Parambassis siamensis	Ambassidae	Perciformes	Cambodia	121
Parasikukia maculata	Cyprinidae	Cypriniformes	Cambodia	15
Parauchenoglanis monkei	Claroteidae	Siluriformes	Benin	39
Parotocinclus longirostris	Loricariidae	Siluriformes	Brazil	5
Pelvicachromis taeniatus	Cichlidae	Cichlidiformes	Benin	32

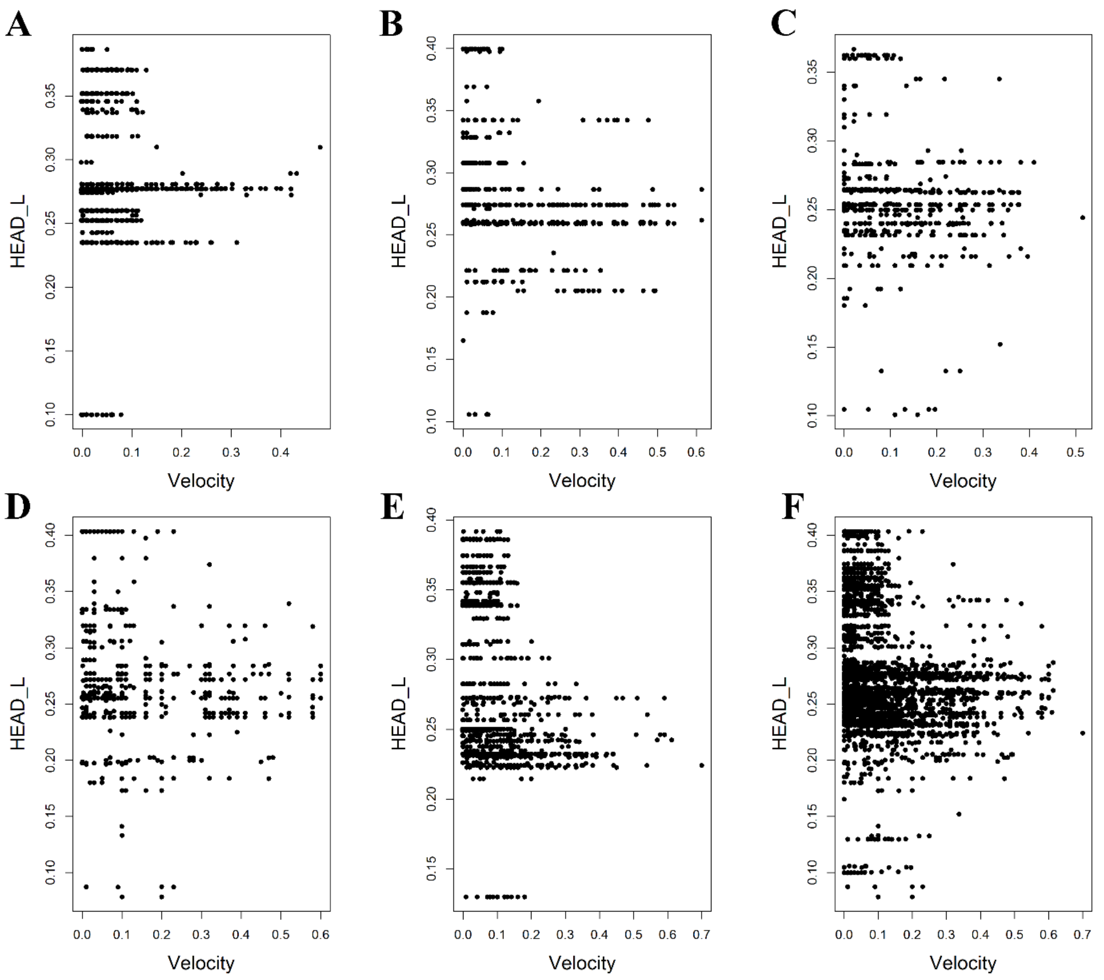
Perca flavescens	Percidae	Perciformes	USA	5
Percina crassa	Percidae	Perciformes	USA	3
Percina sciera	Percidae	Perciformes	USA	71
Phractura clauseni	Amphiliidae	Siluriformes	Benin	47
Pimephales vigilax	Cyprinidae	Cypriniformes	USA	79
Poecilia mexicana	Poeciliidae	Cyprinodontiformes	Belize	86
Pollimyrus adspersus	Mormyridae	Osteoglossiformes	Benin	17
Polycentropsis abbreviata	Nandidae	Perciformes	Benin	9
Poptella compressa	Characidae	Characiformes	Brazil	25
Poropanchax luxophthalmus	Poeciliidae	Cyprinodontiformes	Benin	720
Potamorrhaphis petersi	Belonidae	Beloniformes	Brazil	2
Pristolepis fasciata	Pristolepididae	Perciformes	Cambodia	10
Procatopus nototaenia	Poeciliidae	Cyprinodontiformes	Benin	167
Pseudomystus siamensis	Bagridae	Siluriformes	Cambodia	2
Pseudoxiphophorus bimaculatus	Poeciliidae	Cyprinodontiformes	Belize	212
Pteronotropis stonei	Cyprinidae	Cypriniformes	USA	161
Pyrrhulina brevis	Lebiasinidae	Characiformes	Brazil	23
Pyrrhulina semifasciata	Lebiasinidae	Characiformes	Brazil	3
Raiamas guttatus	Cyprinidae	Cypriniformes	Cambodia	123
Rasbora aurotaenia	Cyprinidae	Cypriniformes	Cambodia	373
Rasbora borapetensis	Cyprinidae	Cypriniformes	Cambodia	91
Rasbora dusonensis	Cyprinidae	Cypriniformes	Cambodia	436
Rasbora paviana	Cyprinidae	Cypriniformes	Cambodia	7
Rhamdia laticauda	Heptapteridae	Siluriformes	Belize	115
Rineloricaria heteroptera	Loricariidae	Siluriformes	Brazil	2
Rocio octofasciata	Cichlidae	Cichlidiformes	Belize	116
Schilbe brevianalis	Schilbeidae	Siluriformes	Benin	1
Systomus partipentazona	Cyprinidae	Cypriniformes	Cambodia	8
Trichopodus trichopterus	Osphronemidae	Perciformes	Cambodia	12
Trichopsis pumila	Osphronemidae	Perciformes	Cambodia	10
Trichopsis vittata	Osphronemidae	Perciformes	Cambodia	10
Trichromis salvini	Cichlidae	Cichlidiformes	Belize	126
Umbra pygmaea	Umbridae	Esociformes	USA	14
Vieja melanura	Cichlidae	Cichlidiformes	Belize	39
Xenentodon sp.	Belonidae	Beloniformes	Cambodia	70
Xenomystus nigri	Notopteridae	Osteoglossiformes	Benin	1
Xiphophorus hellerii	Poeciliidae	Cyprinodontiformes	Belize	181
Xiphophorus maculatus	Poeciliidae	Cyprinodontiformes	Belize	3
Yasuhikotakia morleti	Cobitidae	Cypriniformes	Cambodia	28

Supplemental Table A-3: The results of Abouhief's test for trait phylogenetic signals. Bolded Abouhief's numbers represent significance.

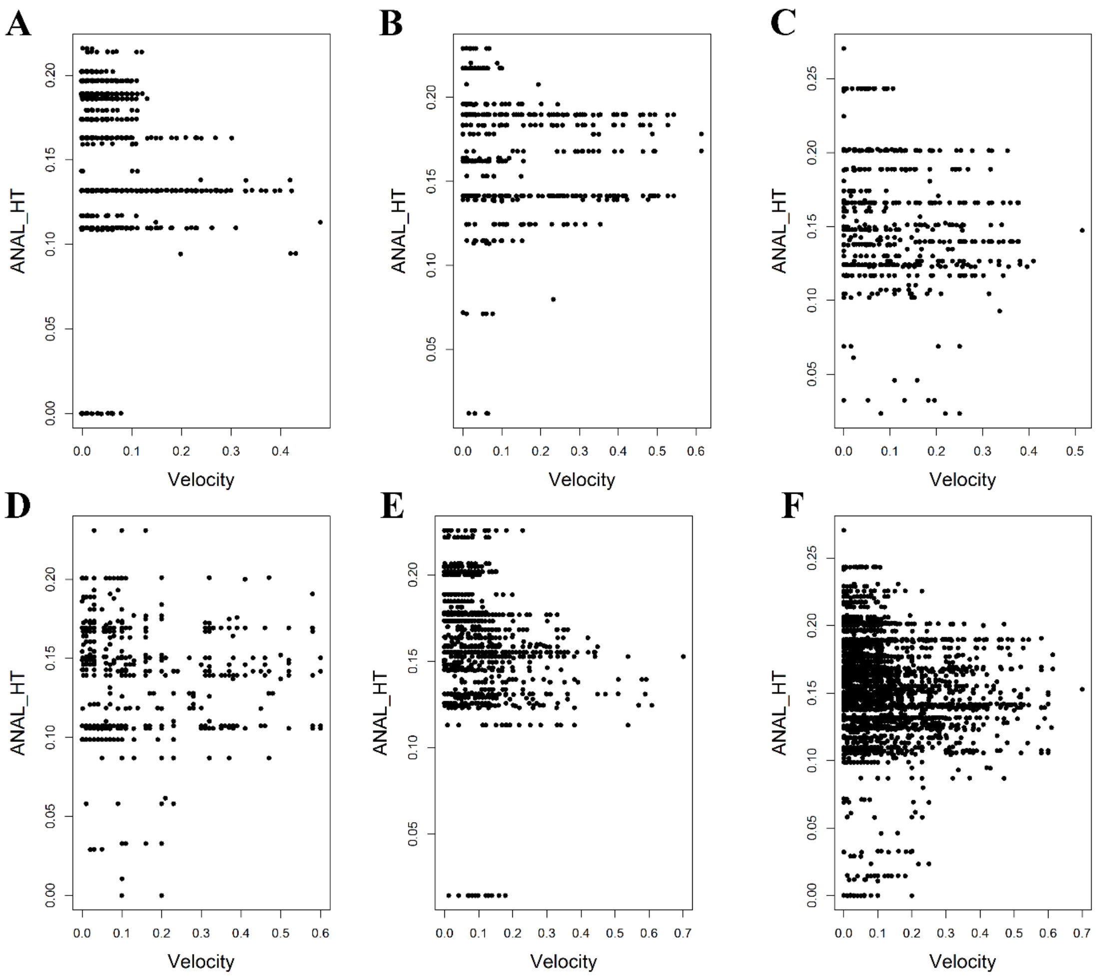
Trait	Brazil	Belize	Benin	Cambodia	USA	Global
SL	0.115	0.150	**0.239**	**0.460**	**0.453**	**0.441**
PED_W	**0.535**	**0.281**	0.079	**0.615**	**0.439**	**0.556**
PED_L	**0.650**	**0.306**	-0.037	**0.694**	**0.474**	**0.664**
BOD_D	**0.649**	**0.428**	0.016	**0.493**	**0.779**	**0.623**
BOD_W	**0.390**	**0.382**	0.155	**0.300**	**0.638**	**0.509**
DORS_L	**0.697**	**0.367**	**0.349**	**0.175**	**0.839**	**0.668**
DORS_HT	**0.718**	0.155	0.038	**0.335**	**0.497**	**0.520**
ANAL_HT	**0.570**	**0.180**	0.113	**0.302**	**0.573**	**0.555**
ANAL_L	**0.695**	**0.331**	0.215	**0.342**	**0.597**	**0.580**
CAUD_W	**0.756**	0.132	0.110	**0.438**	**0.542**	**0.575**
CAUD_L	**0.754**	0.126	0.180	**0.361**	**0.581**	**0.599**
PEC_W	**0.456**	**0.212**	0.063	**0.282**	**0.617**	**0.448**
PEC_L	**0.417**	0.131	0.087	**0.310**	**0.638**	**0.469**
SNT_L	**0.326**	**0.240**	**0.375**	**0.256**	**0.408**	**0.401**
HEAD_L	**0.431**	**0.393**	0.100	**0.368**	**0.709**	**0.562**
HEAD_D	**0.392**	**0.431**	**0.212**	**0.274**	**0.285**	**0.374**



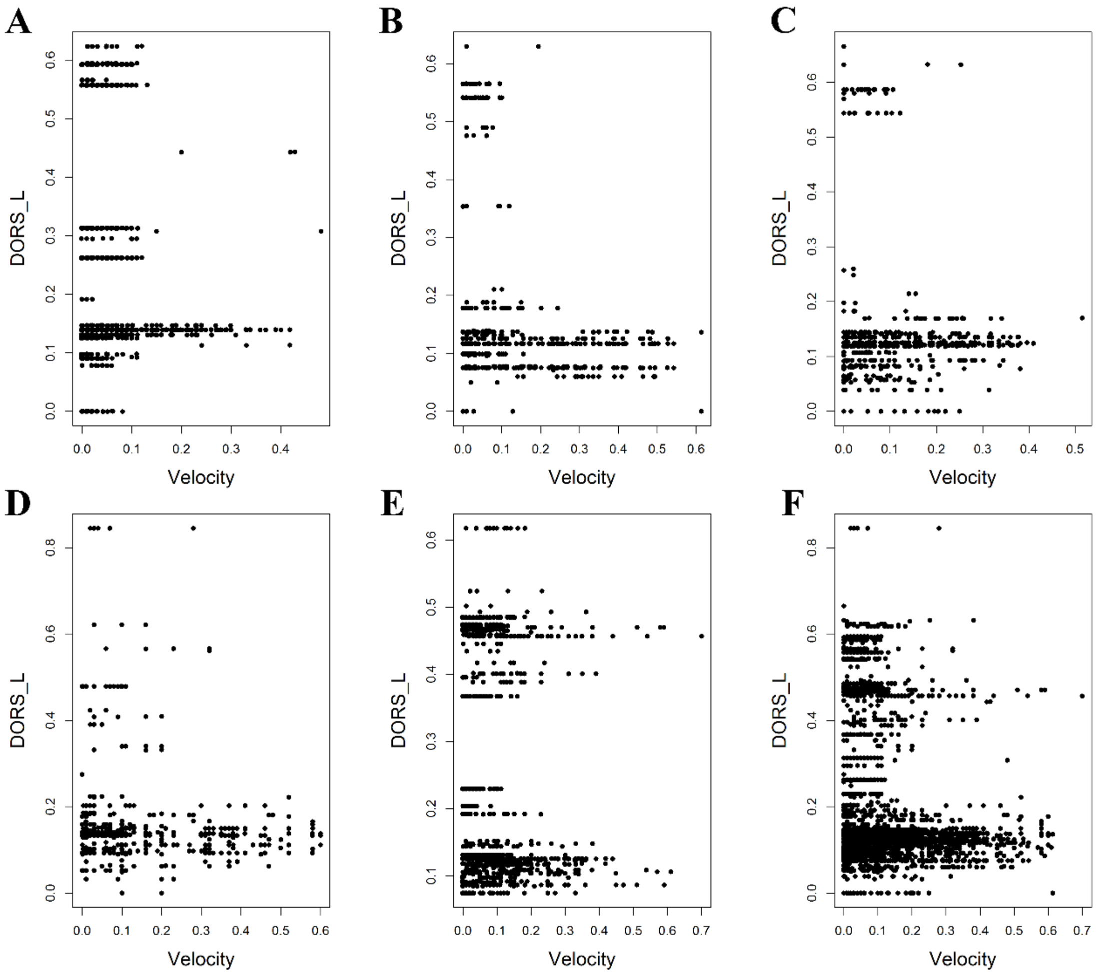
Supplementary Figure A-1: The results of the fourth-corner analyses for each region and the global dataset: A) Belize, B) Benin, C) Brazil, D) Cambodia, E) USA, and F) Global dataset. Black represent a positive relationship (Pearson's correlation) between mcirohabitat variable and trait, dark grey denotes a negative relationship, and light grey represents non-significant relationships.



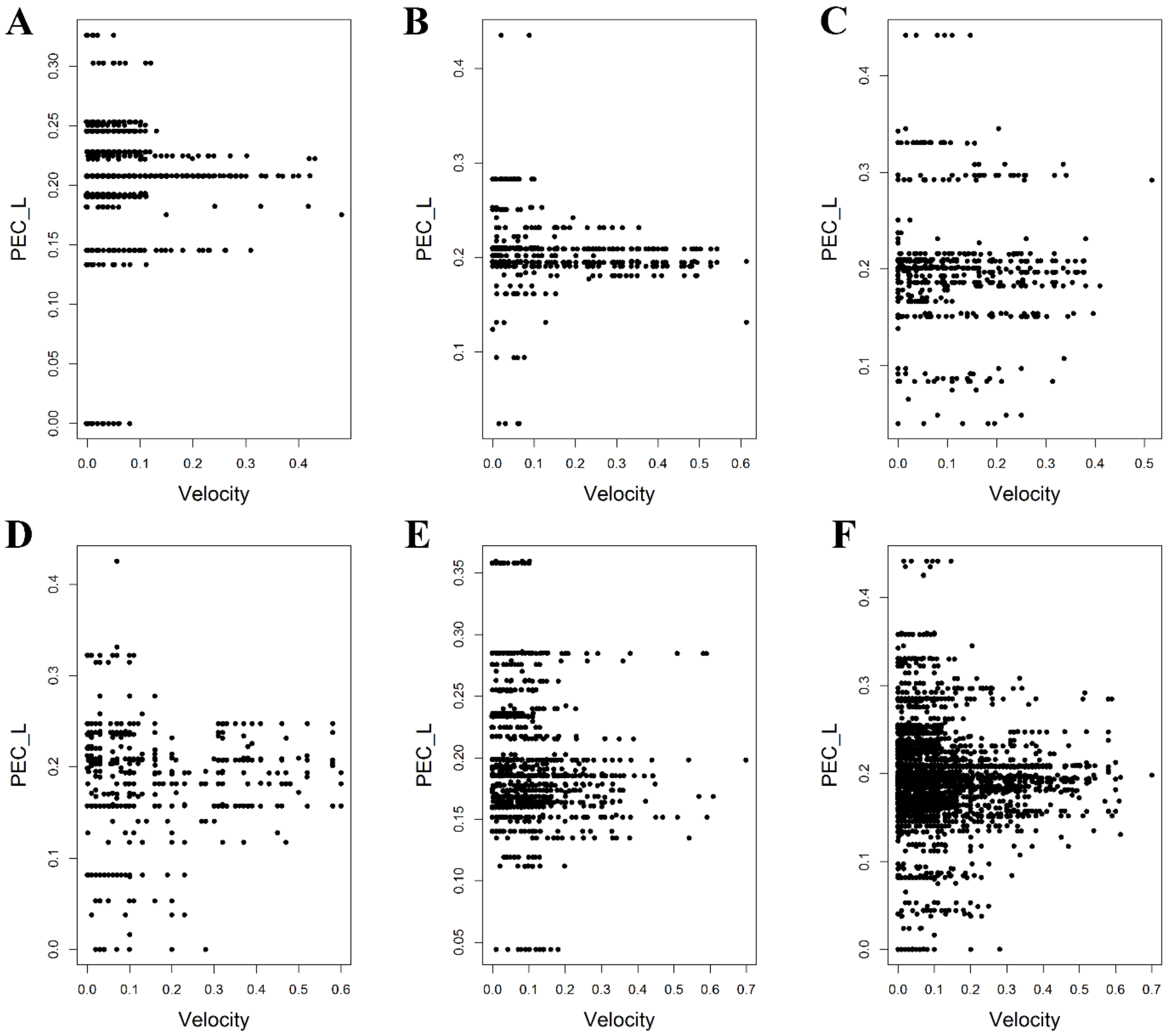
Supplementary Figure A-2: Plots water velocity (m s^{-1}) and mean head length for each region and all individuals. Linear regression of head length variance of every 0.05 units of water velocity show a relationship to median water velocity per unit for: **A**) Belize ($R^2 = 0.68$, $p = 0.006$); **B**) Benin ($R^2 = 0.71$, $p = 0.001$); **C**) Brazil ($R^2 = 0.80$, $p = 0.001$); **D**) Cambodia ($R^2 = 0.88$, $p < 0.001$); **E**) USA ($R^2 = 0.66$, $p = 0.003$); and **F**) global data set ($R^2 = 0.75$, $p < 0.001$).



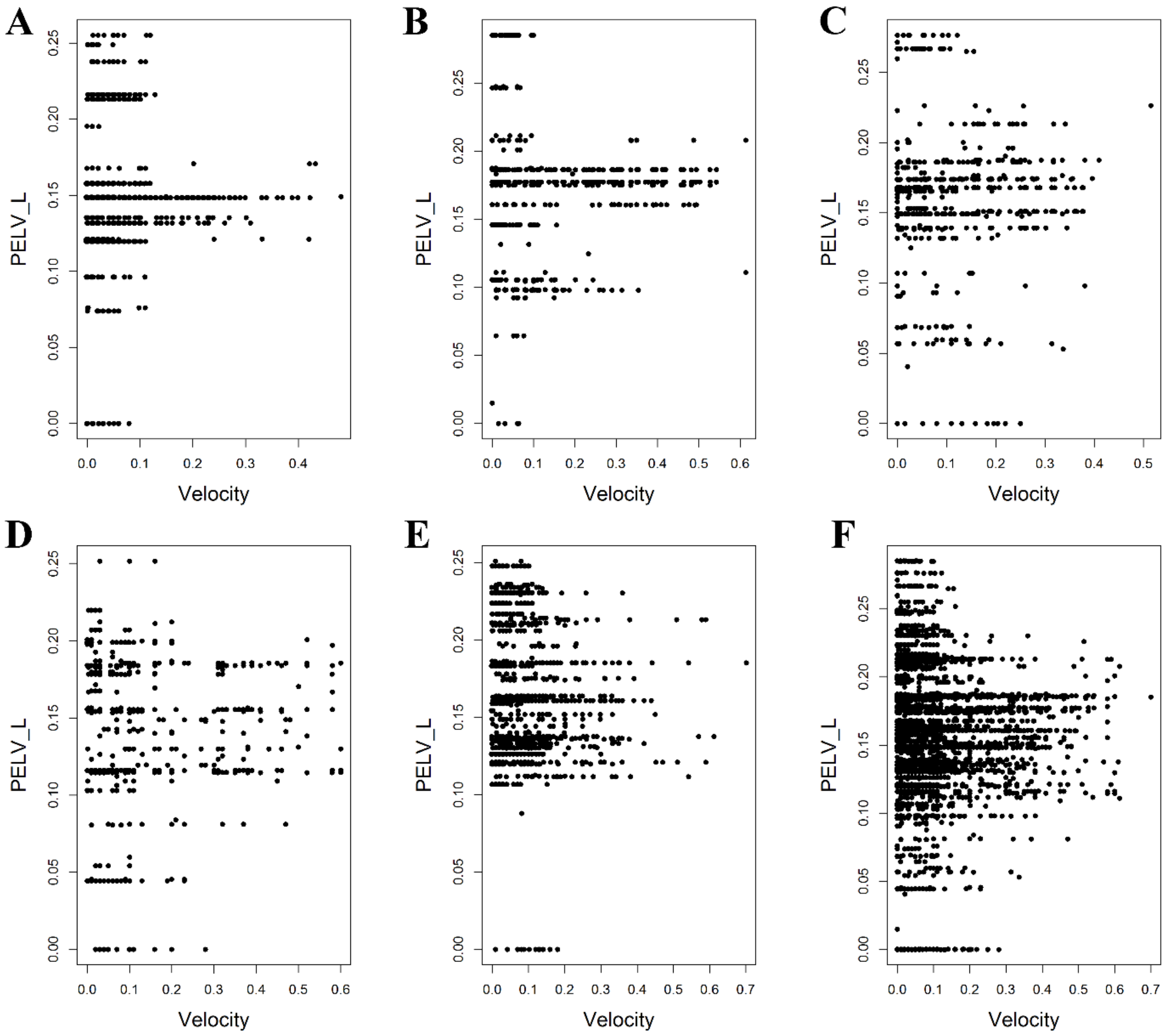
Supplementary Figure A-3: Plots water velocity (m s^{-1}) and mean anal fin height for each region and all individuals. Linear regression of anal fin length variance of every 0.05 units of water velocity show a relationship to median water velocity per unit for: **A**) Belize ($R^2 = 0.61$, $p = 0.013$); **B**) Benin ($R^2 = 0.70$, $p = 0.001$); **C**) Brazil ($R^2 = 0.98$, $p < 0.001$); **D**) Cambodia ($R^2 = 0.91$, $p < 0.001$); **E**) USA ($R^2 = 0.84$, $p < 0.001$); and **F**) global data set ($R^2 = 0.79$, $p < 0.001$).



Supplementary Figure A-4: Plots water velocity (m s^{-1}) and mean dorsal fin length for each region and all individuals. Linear regression of dorsal fin length variance of every 0.05 units of water velocity show a relationship to median water velocity per unit for: **A**) Belize ($R^2 = 0.07$, $p = 0.487$); **B**) Benin ($R^2 = 0.50$, $p = 0.015$); **C**) Brazil ($R^2 = 0.78$, $p = 0.002$); **D**) Cambodia ($R^2 = 0.94$, $p < 0.001$); **E**) USA ($R^2 = 0.39$, $p = 0.042$); and **F**) global data set ($R^2 = 0.50$, $p = 0.015$).



Supplementary Figure A-5: Plots water velocity (m s^{-1}) and mean pectoral fin length for each region and all individuals. Linear regression of pectoral fin length variance of every 0.05 units of water velocity show a relationship to median water velocity per unit for: **A**) Belize ($R^2 = 0.75$, $p = 0.003$); **B**) Benin ($R^2 = 0.17$, $p = 0.118$); **C**) Brazil ($R^2 = 0.02$, $p = 0.729$); **D**) Cambodia ($R^2 = 0.83$, $p < 0.001$); **E**) USA ($R^2 = 0.12$, $p = 0.293$); and **F**) global data set ($R^2 = 0.59$, $p = 0.006$).



Supplementary Figure A-6: Plots water velocity (m s^{-1}) and mean pelvic fin length for each region and all individuals. Linear regression of pelvic fin length variance of every 0.05 units of water velocity show a relationship to median water velocity per unit for: **A**) Belize ($R^2 = 0.56$, $p = 0.021$); **B**) Benin ($R^2 = 0.576$, $p = 0.007$); **C**) Brazil ($R^2 = 0.93$, $p < 0.001$); **D**) Cambodia ($R^2 = 0.81$, $p < 0.001$); **E**) USA ($R^2 = 0.03$, $p = 0.620$); and **F**) global data set ($R^2 = 0.61$, $p = 0.004$)

APPENDIX B

SUPPORTING INFORMATION FOR

WIDESPREAD CONVERGENCE IN STREAM FISHES

Supplementary table B-1: The PC scores, eigenvalues, proportion variance explained, and Cumulative variance explained from the PCA of the habitat traits dataset for all species.

Traits	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
PED_W	0.387	-0.539	0.849	-0.194	0.911	-0.379	0.361
PED_L	0.718	-0.166	1.041	-0.213	0.190	-0.023	0.242
PED_D	0.674	-0.035	0.550	-1.074	-0.272	0.388	-0.273
BOD_D	-1.508	-0.073	-0.299	0.006	0.321	-0.157	0.015
BOD_W	-0.754	0.654	0.286	-0.702	-0.575	-0.040	-0.661
DORS_L	-1.017	0.819	0.339	0.076	0.504	0.414	0.226
DORS_HT	-0.988	-0.720	0.337	0.569	-0.168	-0.123	-0.349
ANAL_HT	-1.250	-0.092	0.401	-0.068	0.094	0.229	-0.051
ANAL_L	-0.805	0.054	-1.263	0.133	-0.141	0.051	0.169
CAUD_W	-0.973	-0.885	-0.062	0.173	0.021	-0.733	-0.061
CAUD_L	-1.208	-0.719	0.137	-0.208	-0.427	0.142	-0.040
PEC_W	-0.981	0.311	0.251	-0.431	-0.409	-0.069	0.579
PEC_L	-1.192	-0.020	0.093	-0.065	-0.428	0.178	0.722
PELV_L	-1.193	0.158	0.898	0.158	0.133	0.211	-0.144
SNT_L2	-0.024	-0.403	0.250	1.218	-0.332	0.385	-0.225
PELV_W	-1.076	-0.021	0.682	0.006	0.242	-0.399	-0.309
EYE_POS	0.373	-1.115	-0.101	-0.292	-0.068	0.292	-0.694
EYE_D	0.138	-1.222	-0.008	0.160	0.510	0.746	0.155
HEAD_D	0.629	0.718	0.551	0.752	-0.326	0.582	0.121
HEAD_L	-0.976	0.709	-0.106	0.022	0.555	0.559	-0.439
MOUTH_P	-0.488	-0.319	-0.780	-0.641	0.632	0.552	0.059
SL	0.163	0.991	-0.243	0.332	0.672	-0.403	-0.461
Eigenvalues	6.124	2.961	2.363	1.785	1.391	1.156	1.012
Proportion variance explained	0.278	0.135	0.107	0.081	0.063	0.053	0.046
Cumulative variance explained	0.278	0.413	0.520	0.602	0.665	0.717	0.763

Supplementary table B-2: The PC scores, eigenvalues, proportion variance explained, and Cumulative variance explained from the PCOA of the all traits dataset for all species.

Traits	PCOA1	PCOA2	PCOA3	PCOA4	PCOA5	PCOA6	PCOA7
SL	-0.064	-0.304	0.097	-0.114	0.135	0.010	-0.435
HEAD_L	-0.283	-0.163	-0.028	0.123	-0.007	-0.058	0.083
HEAD_D	0.105	-0.262	0.182	0.024	-0.077	-0.362	0.213
GAPE	0.153	-0.318	-0.092	0.126	-0.184	0.053	0.027
MOUTH_W	-0.070	-0.256	-0.238	0.047	-0.215	0.281	-0.053
MOUTH_P	-0.131	0.010	-0.469	0.195	0.042	0.169	0.061
EYE_POS	0.111	0.206	-0.142	-0.107	-0.276	0.075	0.292
EYE_D	0.057	0.281	-0.267	0.053	-0.209	-0.332	0.070
SNT_L2	0.006	0.094	0.077	-0.318	-0.014	-0.441	0.320
SNT_PR2	-0.231	0.009	0.078	0.196	0.040	-0.038	-0.060
BOD_D	-0.344	0.119	-0.068	-0.100	0.077	0.094	-0.104
BOD_W	-0.182	-0.088	0.218	0.126	-0.075	0.354	0.257
PED_W	0.100	0.152	0.083	0.180	-0.122	-0.057	-0.304
PED_L	0.144	-0.010	0.192	0.158	-0.408	-0.062	-0.119
PED_D	0.164	0.011	0.077	0.468	-0.168	0.220	0.282
DORS_L	-0.285	-0.096	0.157	0.245	0.075	-0.222	-0.145
DORS_HT	-0.164	0.254	0.050	-0.200	-0.110	-0.060	0.083
ANAL_L	-0.194	-0.038	-0.306	-0.211	0.223	0.110	0.055
ANAL_HT	-0.272	0.145	0.079	0.092	-0.046	0.016	0.079
CAUD_W	-0.155	0.315	-0.080	-0.271	-0.002	0.135	-0.137
CAUD_L	-0.209	0.301	-0.042	0.008	-0.100	0.131	0.280
PEC_W	-0.192	0.052	0.111	0.108	0.023	0.160	0.017
PEC_L	-0.242	0.122	0.042	0.001	-0.060	-0.021	0.086
PELV_W	-0.221	0.168	0.230	0.045	0.011	0.033	-0.125
PELV_L	-0.265	0.109	0.252	0.171	-0.101	-0.158	0.030
GUT_L	-0.030	0.114	0.238	-0.176	-0.205	-0.045	0.047
RAKER_L	-0.067	-0.013	0.053	-0.312	-0.602	0.152	-0.219
TOO_S	-0.149	-0.177	-0.360	0.012	-0.232	-0.270	-0.080
Life History	0.226	0.287	-0.107	0.248	-0.005	-0.058	-0.276
Eigenvalues	1.205	0.646	0.464	0.351	0.266	0.239	0.195
Proportion variance explained	0.236	0.127	0.091	0.069	0.052	0.047	0.038
Cumulative variance explained	0.236	0.363	0.454	0.522	0.574	0.621	0.659

Supplementary table B-3: C_1 and p values for all convergent pairwise comparisons using the habitat traits dataset.

Species 1	Species 2	C_1	p value
Aequidens_pallidus	Apistogramma_regani	0.459024	0.001
Chromidotilapia_guntheri	Apistogramma_regani	0.48728	0.002

Cribroheros_robertsoni	Apistogramma_regani	0.489221	0.004
Cryptoheros_spilurus	Apistogramma_regani	0.448861	0.001
Ctenopoma_petherici	Apistogramma_regani	0.084041	0.235
Enneacanthus_chaetodon	Apistogramma_regani	0.233032	0.048
Enneacanthus_obesus	Apistogramma_regani	0.210563	0.085
Heros_efasciatus	Apistogramma_regani	0.265492	0.015
Lepomis_auritus	Apistogramma_regani	-0.03999	0.999
Lepomis_cyanellus	Apistogramma_regani	-0.07178	0.999
Lepomis_gulosus	Apistogramma_regani	-0.01979	0.999
Lepomis_macrochirus	Apistogramma_regani	0.051694	0.421
Lepomis_marginatus	Apistogramma_regani	0.174218	0.135
Lepomis_megalotis	Apistogramma_regani	0.13128	0.227
Lepomis_miniatus	Apistogramma_regani	0.289962	0.03
Lepomis_punctatus	Apistogramma_regani	0.409477	0.008
Parambassis_apogonoides	Apistogramma_regani	0.218244	0.047
Parambassis_siamensis	Apistogramma_regani	0.004641	0.635
Pelvicachromis_taeniatus	Apistogramma_regani	0.747285	0
Polycentropsis_abbreviata	Apistogramma_regani	0.166022	0.092
Pristolepis_fasciata	Apistogramma_regani	0.400322	0.004
Rocio_octofasciata	Apistogramma_regani	0.308685	0.017
Trichromis_salvini	Apistogramma_regani	0.498008	0.002
Vieja_melanura	Apistogramma_regani	0.332768	0.009
Aequidens_pallidus	Pelvicachromis_taeniatus	0.367897	0.003
Apistogramma_hippolytae	Pelvicachromis_taeniatus	0.872083	0
Chromidotilapia_guntheri	Pelvicachromis_taeniatus	0.482262	0.001
Cribroheros_robertsoni	Pelvicachromis_taeniatus	0.48238	0.001
Cryptoheros_spilurus	Pelvicachromis_taeniatus	0.351542	0.006
Ctenopoma_petherici	Pelvicachromis_taeniatus	0.114862	0.104
Enneacanthus_chaetodon	Pelvicachromis_taeniatus	0.247241	0.034
Enneacanthus_obesus	Pelvicachromis_taeniatus	0.304754	0.023
Heros_efasciatus	Pelvicachromis_taeniatus	0.129355	0.089
Lepomis_auritus	Pelvicachromis_taeniatus	0.161957	0.11
Lepomis_cyanellus	Pelvicachromis_taeniatus	0.153206	0.107
Lepomis_gulosus	Pelvicachromis_taeniatus	0.196017	0.079
Lepomis_macrochirus	Pelvicachromis_taeniatus	0.234144	0.058
Lepomis_marginatus	Pelvicachromis_taeniatus	0.36546	0.016
Lepomis_megalotis	Pelvicachromis_taeniatus	0.299544	0.031
Lepomis_miniatus	Pelvicachromis_taeniatus	0.349778	0.014
Lepomis_punctatus	Pelvicachromis_taeniatus	0.488027	0.002
Parambassis_apogonoides	Pelvicachromis_taeniatus	0.370466	0.003

Parambassis_siamensis	Pelvicachromis_taeniatus	0.118569	0.109
Polycentropsis_abbreviata	Pelvicachromis_taeniatus	0.23588	0.034
Pristolepis_fasciata	Pelvicachromis_taeniatus	0.427105	0.002
Rocio_octofasciata	Pelvicachromis_taeniatus	0.347862	0.009
Trichromis_salvini	Pelvicachromis_taeniatus	0.585743	0
Vieja_melanura	Pelvicachromis_taeniatus	0.492297	0.001
Aequidens_pallidus	Apistogramma_hippolytae	0.724677	0
Chromidotilapia_guntheri	Apistogramma_hippolytae	0.68073	0
Cribroheros_robertsoni	Apistogramma_hippolytae	0.752613	0
Cryptoheros_spilurus	Apistogramma_hippolytae	0.678747	0
Ctenopoma_petherici	Apistogramma_hippolytae	0.52889	0.001
Enneacanthus_chaetodon	Apistogramma_hippolytae	0.553975	0.001
Enneacanthus_obesus	Apistogramma_hippolytae	0.593741	0.001
Heros_efasciatus	Apistogramma_hippolytae	0.571545	0
Lepomis_auritus	Apistogramma_hippolytae	0.368617	0.017
Lepomis_cyanellus	Apistogramma_hippolytae	0.418044	0.005
Lepomis_gulosus	Apistogramma_hippolytae	0.452384	0.002
Lepomis_macrochirus	Apistogramma_hippolytae	0.414986	0.002
Lepomis_marginatus	Apistogramma_hippolytae	0.460904	0.008
Lepomis_megalotis	Apistogramma_hippolytae	0.505714	0
Lepomis_miniatus	Apistogramma_hippolytae	0.602986	0
Lepomis_punctatus	Apistogramma_hippolytae	0.635489	0
Parambassis_apogonoides	Apistogramma_hippolytae	0.563195	0
Parambassis_siamensis	Apistogramma_hippolytae	0.458019	0.001
Polycentropsis_abbreviata	Apistogramma_hippolytae	0.559391	0.001
Pristolepis_fasciata	Apistogramma_hippolytae	0.671035	0
Rocio_octofasciata	Apistogramma_hippolytae	0.65589	0
Trichromis_salvini	Apistogramma_hippolytae	0.730617	0
Vieja_melanura	Apistogramma_hippolytae	0.671076	0
Aequidens_pallidus	Lepomis_auritus	0.112345	0.202
Chromidotilapia_guntheri	Lepomis_auritus	0.447299	0.003
Cribroheros_robertsoni	Lepomis_auritus	0.256027	0.049
Cryptoheros_spilurus	Lepomis_auritus	0.212941	0.074
Ctenopoma_petherici	Lepomis_auritus	0.156267	0.106
Enneacanthus_chaetodon	Lepomis_auritus	0.522666	0.001
Enneacanthus_obesus	Lepomis_auritus	0.477648	0.002
Heros_efasciatus	Lepomis_auritus	0.075796	0.319
Parambassis_apogonoides	Lepomis_auritus	0.513367	0.001
Parambassis_siamensis	Lepomis_auritus	0.41195	0.003
Polycentropsis_abbreviata	Lepomis_auritus	0.247407	0.035

Pristolepis_fasciata	Lepomis_auritus	0.424947	0.006
Rocio_octofasciata	Lepomis_auritus	0.282426	0.032
Trichromis_salvini	Lepomis_auritus	0.362398	0.011
Vieja_melanura	Lepomis_auritus	0.384649	0.008
Aequidens_pallidus	Lepomis_cyanellus	-0.04319	0.999
Chromidotilapia_guntheri	Lepomis_cyanellus	0.460518	0.004
Cribroheros_robertsoni	Lepomis_cyanellus	0.178955	0.128
Cryptoheros_spilurus	Lepomis_cyanellus	0.043286	0.469
Ctenopoma_petherici	Lepomis_cyanellus	0.112565	0.147
Enneacanthus_chaetodon	Lepomis_cyanellus	0.461995	0.001
Enneacanthus_obesus	Lepomis_cyanellus	0.487129	0.001
Heros_efasciatus	Lepomis_cyanellus	-0.13083	0.999
Parambassis_apogonoides	Lepomis_cyanellus	0.27458	0.023
Parambassis_siamensis	Lepomis_cyanellus	0.253016	0.035
Polycentropsis_abbreviata	Lepomis_cyanellus	0.124184	0.151
Pristolepis_fasciata	Lepomis_cyanellus	0.465999	0.003
Rocio_octofasciata	Lepomis_cyanellus	0.284036	0.024
Trichromis_salvini	Lepomis_cyanellus	0.407889	0.005
Vieja_melanura	Lepomis_cyanellus	0.309361	0.027
Aequidens_pallidus	Lepomis_gulosus	0.008871	0.597
Chromidotilapia_guntheri	Lepomis_gulosus	0.449547	0.001
Cribroheros_robertsoni	Lepomis_gulosus	0.198936	0.095
Cryptoheros_spilurus	Lepomis_gulosus	0.076495	0.352
Ctenopoma_pethericі	Lepomis_gulosus	0.318888	0.015
Enneacanthus_chaetodon	Lepomis_gulosus	0.467632	0.001
Enneacanthus_obesus	Lepomis_gulosus	0.528415	0.002
Heros_efasciatus	Lepomis_gulosus	-0.07809	0.999
Parambassis_apogonoides	Lepomis_gulosus	0.315378	0.011
Parambassis_siamensis	Lepomis_gulosus	0.318076	0.014
Polycentropsis_abbreviata	Lepomis_gulosus	0.272867	0.028
Pristolepis_fasciata	Lepomis_gulosus	0.475821	0.008
Rocio_octofasciata	Lepomis_gulosus	0.361205	0.012
Trichromis_salvini	Lepomis_gulosus	0.45352	0.004
Vieja_melanura	Lepomis_gulosus	0.349832	0.015
Aequidens_pallidus	Lepomis_macrochirus	0.065008	0.313
Chromidotilapia_guntheri	Lepomis_macrochirus	0.419475	0.004
Cribroheros_robertsoni	Lepomis_macrochirus	0.199739	0.097
Cryptoheros_spilurus	Lepomis_macrochirus	0.20403	0.075
Ctenopoma_petherici	Lepomis_macrochirus	0.137301	0.111
Enneacanthus_chaetodon	Lepomis_macrochirus	0.701973	0

Enneacanthus_obesus	Lepomis_macrochirus	0.660979	0
Heros_efasciatus	Lepomis_macrochirus	-0.07391	0.999
Parambassis_apogonoides	Lepomis_macrochirus	0.658854	0
Parambassis_siamensis	Lepomis_macrochirus	0.620061	0
Polycentropsis_abbreviata	Lepomis_macrochirus	0.094733	0.164
Pristolepis_fasciata	Lepomis_macrochirus	0.461501	0.003
Rocio_octofasciata	Lepomis_macrochirus	0.175932	0.093
Trichromis_salvini	Lepomis_macrochirus	0.334782	0.022
Vieja_melanura	Lepomis_macrochirus	0.251798	0.054
Aequidens_pallidus	Lepomis_marginatus	0.299075	0.019
Chromidotilapia_guntheri	Lepomis_marginatus	0.550809	0
Cribroheros_robertsoni	Lepomis_marginatus	0.355101	0.012
Cryptoheros_spilurus	Lepomis_marginatus	0.33671	0.019
Ctenopoma_petherici	Lepomis_marginatus	0.295379	0.023
Enneacanthus_chaetodon	Lepomis_marginatus	0.703574	0
Enneacanthus_obesus	Lepomis_marginatus	0.696979	0
Heros_efasciatus	Lepomis_marginatus	0.192846	0.112
Parambassis_apogonoides	Lepomis_marginatus	0.612324	0
Parambassis_siamensis	Lepomis_marginatus	0.569538	0.001
Polycentropsis_abbreviata	Lepomis_marginatus	0.285926	0.025
Pristolepis_fasciata	Lepomis_marginatus	0.621138	0.001
Rocio_octofasciata	Lepomis_marginatus	0.363204	0.014
Trichromis_salvini	Lepomis_marginatus	0.384434	0.013
Vieja_melanura	Lepomis_marginatus	0.458033	0.003
Aequidens_pallidus	Lepomis_megalotis	0.259992	0.045
Chromidotilapia_guntheri	Lepomis_megalotis	0.526774	0
Cribroheros_robertsoni	Lepomis_megalotis	0.416473	0.011
Cryptoheros_spilurus	Lepomis_megalotis	0.414591	0.008
Ctenopoma_petherici	Lepomis_megalotis	0.250748	0.03
Enneacanthus_chaetodon	Lepomis_megalotis	0.709354	0
Enneacanthus_obesus	Lepomis_megalotis	0.734509	0
Heros_efasciatus	Lepomis_megalotis	0.207726	0.082
Parambassis_apogonoides	Lepomis_megalotis	0.613721	0.001
Parambassis_siamensis	Lepomis_megalotis	0.512083	0.002
Polycentropsis_abbreviata	Lepomis_megalotis	0.361958	0.012
Pristolepis_fasciata	Lepomis_megalotis	0.596767	0
Rocio_octofasciata	Lepomis_megalotis	0.413481	0.006
Trichromis_salvini	Lepomis_megalotis	0.505584	0.005
Vieja_melanura	Lepomis_megalotis	0.53196	0.001
Aequidens_pallidus	Lepomis_miniatus	0.234033	0.051

Chromidotilapia_guntheri	Lepomis_miniatus	0.403426	0.012
Cribroheros_robertsoni	Lepomis_miniatus	0.422086	0.005
Cryptoheros_spilurus	Lepomis_miniatus	0.374564	0.012
Ctenopoma_petherici	Lepomis_miniatus	0.408437	0.005
Enneacanthus_chaetodon	Lepomis_miniatus	0.656581	0
Enneacanthus_obesus	Lepomis_miniatus	0.727641	0
Heros_efasciatus	Lepomis_miniatus	0.139322	0.164
Parambassis_apogonoides	Lepomis_miniatus	0.592442	0
Parambassis_siamensis	Lepomis_miniatus	0.518587	0.001
Polycentropsis_abbreviata	Lepomis_miniatus	0.480616	0.001
Pristolepis_fasciata	Lepomis_miniatus	0.593353	0
Rocio_octofasciata	Lepomis_miniatus	0.492309	0.001
Trichromis_salvini	Lepomis_miniatus	0.602437	0
Vieja_melanura	Lepomis_miniatus	0.531373	0.002
Aequidens_pallidus	Lepomis_punctatus	0.370565	0.013
Chromidotilapia_guntheri	Lepomis_punctatus	0.490586	0.004
Cribroheros_robertsoni	Lepomis_punctatus	0.490999	0.002
Cryptoheros_spilurus	Lepomis_punctatus	0.472783	0.002
Ctenopoma_petherici	Lepomis_punctatus	0.464976	0.002
Enneacanthus_chaetodon	Lepomis_punctatus	0.773073	0
Enneacanthus_obesus	Lepomis_punctatus	0.835912	0
Heros_efasciatus	Lepomis_punctatus	0.257139	0.04
Parambassis_apogonoides	Lepomis_punctatus	0.704908	0
Parambassis_siamensis	Lepomis_punctatus	0.663693	0
Polycentropsis_abbreviata	Lepomis_punctatus	0.488562	0.001
Pristolepis_fasciata	Lepomis_punctatus	0.647101	0
Rocio_octofasciata	Lepomis_punctatus	0.518261	0.002
Trichromis_salvini	Lepomis_punctatus	0.558309	0.001
Vieja_melanura	Lepomis_punctatus	0.58954	0.001
Aequidens_pallidus	Enneacanthus_chaetodon	0.296245	0.017
Chromidotilapia_guntheri	Enneacanthus_chaetodon	0.456695	0.004
Cribroheros_robertsoni	Enneacanthus_chaetodon	0.383323	0.014
Cryptoheros_spilurus	Enneacanthus_chaetodon	0.429798	0.001
Ctenopoma_petherici	Enneacanthus_chaetodon	0.194706	0.05
Enneacanthus_obesus	Enneacanthus_chaetodon	0.679517	0
Heros_efasciatus	Enneacanthus_chaetodon	0.22438	0.06
Parambassis_apogonoides	Enneacanthus_chaetodon	0.724395	0
Parambassis_siamensis	Enneacanthus_chaetodon	0.678601	0
Polycentropsis_abbreviata	Enneacanthus_chaetodon	0.312152	0.019
Pristolepis_fasciata	Enneacanthus_chaetodon	0.637931	0

Rocio_octofasciata	Enneacanthus_chaetodon	0.338429	0.016
Trichromis_salvini	Enneacanthus_chaetodon	0.454924	0.005
Vieja_melanura	Enneacanthus_chaetodon	0.476991	0.002
Aequidens_pallidus	Enneacanthus_obesus	0.28936	0.015
Chromidotilapia_guntheri	Enneacanthus_obesus	0.445999	0.003
Cribroheros_robertsoni	Enneacanthus_obesus	0.423609	0.004
Cryptoheros_spilurus	Enneacanthus_obesus	0.437958	0.004
Ctenopoma_petherici	Enneacanthus_obesus	0.284028	0.016
Heros_efasciatus	Enneacanthus_obesus	0.163289	0.122
Parambassis_apogonoides	Enneacanthus_obesus	0.620495	0
Parambassis_siamensis	Enneacanthus_obesus	0.421426	0.003
Polycentropsis_abbreviata	Enneacanthus_obesus	0.393752	0.012
Pristolepis_fasciata	Enneacanthus_obesus	0.700785	0
Rocio_octofasciata	Enneacanthus_obesus	0.433484	0.003
Trichromis_salvini	Enneacanthus_obesus	0.547655	0.002
Vieja_melanura	Enneacanthus_obesus	0.502015	0.003
Aequidens_pallidus	Parambassis_apogonoides	0.070702	0.167
Chromidotilapia_guntheri	Parambassis_apogonoides	0.316362	0.009
Cribroheros_robertsoni	Parambassis_apogonoides	0.240373	0.026
Cryptoheros_spilurus	Parambassis_apogonoides	0.276065	0.022
Ctenopoma_petherici	Parambassis_apogonoides	0.0737	0.103
Heros_efasciatus	Parambassis_apogonoides	-0.04138	0.999
Parambassis_siamensis	Parambassis_apogonoides	0.738237	0
Polycentropsis_abbreviata	Parambassis_apogonoides	-0.06508	0.999
Pristolepis_fasciata	Parambassis_apogonoides	0.399263	0.004
Rocio_octofasciata	Parambassis_apogonoides	0.267202	0.03
Trichromis_salvini	Parambassis_apogonoides	0.399246	0.007
Vieja_melanura	Parambassis_apogonoides	0.288385	0.023
Aequidens_pallidus	Parambassis_siamensis	0.024677	0.471
Chromidotilapia_guntheri	Parambassis_siamensis	0.214279	0.029
Cribroheros_robertsoni	Parambassis_siamensis	0.186407	0.075
Cryptoheros_spilurus	Parambassis_siamensis	0.268477	0.025
Ctenopoma_petherici	Parambassis_siamensis	0.053342	0.245
Heros_efasciatus	Parambassis_siamensis	0.028956	0.422
Polycentropsis_abbreviata	Parambassis_siamensis	0.156502	0.066
Pristolepis_fasciata	Parambassis_siamensis	0.456738	0.001
Rocio_octofasciata	Parambassis_siamensis	0.162293	0.076
Trichromis_salvini	Parambassis_siamensis	0.40041	0.01
Vieja_melanura	Parambassis_siamensis	0.333941	0.016
Aequidens_pallidus	Pristolepis_fasciata	0.585743	0

Chromidotilapia_guntheri	Pristolepis_fasciata	0.551284	0.001
Cribroheros_robertsoni	Pristolepis_fasciata	0.562709	0
Cryptoheros_spilurus	Pristolepis_fasciata	0.554803	0.001
Ctenopoma_petherici	Pristolepis_fasciata	0.494221	0
Heros_efasciatus	Pristolepis_fasciata	0.432826	0.004
Polycentropsis_abbreviata	Pristolepis_fasciata	0.495518	0
Rocio_octofasciata	Pristolepis_fasciata	0.540655	0.002
Trichromis_salvini	Pristolepis_fasciata	0.540004	0.001
Vieja_melanura	Pristolepis_fasciata	0.65978	0
Aequidens_pallidus	Cryptoheros_spilurus	0.373961	0.002
Chromidotilapia_guntheri	Cryptoheros_spilurus	0.426749	0.001
Cribroheros_robertsoni	Cryptoheros_spilurus	0.670639	0
Ctenopoma_petherici	Cryptoheros_spilurus	0.1592	0.105
Heros_efasciatus	Cryptoheros_spilurus	0.383628	0.003
Polycentropsis_abbreviata	Cryptoheros_spilurus	0.339765	0.014
Rocio_octofasciata	Cryptoheros_spilurus	0.479865	0.001
Trichromis_salvini	Cryptoheros_spilurus	0.619711	0
Vieja_melanura	Cryptoheros_spilurus	0.614102	0
Aequidens_pallidus	Cribroheros_robertsoni	0.556316	0
Chromidotilapia_guntheri	Cribroheros_robertsoni	0.62225	0
Ctenopoma_petherici	Cribroheros_robertsoni	0.31631	0.011
Heros_efasciatus	Cribroheros_robertsoni	0.556965	0
Polycentropsis_abbreviata	Cribroheros_robertsoni	0.562416	0
Rocio_octofasciata	Cribroheros_robertsoni	0.66549	0
Trichromis_salvini	Cribroheros_robertsoni	0.77333	0
Vieja_melanura	Cribroheros_robertsoni	0.790208	0
Aequidens_pallidus	Heros_efasciatus	0.473986	0
Chromidotilapia_guntheri	Heros_efasciatus	0.4923	0
Ctenopoma_petherici	Heros_efasciatus	-0.07335	0.999
Polycentropsis_abbreviata	Heros_efasciatus	0.129581	0.115
Rocio_octofasciata	Heros_efasciatus	0.308614	0
Trichromis_salvini	Heros_efasciatus	0.484993	0.002
Chromidotilapia_guntheri	Aequidens_pallidus	0.634457	0
Ctenopoma_petherici	Aequidens_pallidus	-0.05751	0.999
Polycentropsis_abbreviata	Aequidens_pallidus	0.111134	0.141
Rocio_octofasciata	Aequidens_pallidus	0.35495	0.002
Trichromis_salvini	Aequidens_pallidus	0.489089	0.001
Chromidotilapia_guntheri	Rocio_octofasciata	0.439719	0.001
Ctenopoma_petherici	Rocio_octofasciata	0.514573	0.001
Polycentropsis_abbreviata	Rocio_octofasciata	0.746493	0

Trichromis_salvini	Rocio_octofasciata	0.821205	0
Ctenopoma_petherici	Chromidotilapia_guntheri	0.137445	0.07
Polycentropsis_abbreviata	Chromidotilapia_guntheri	0.337122	0.007
Trichromis_salvini	Chromidotilapia_guntheri	0.571346	0.002
Ctenopoma_petherici	Trichromis_salvini	0.599294	0
Polycentropsis_abbreviata	Trichromis_salvini	0.808035	0
Ctenopoma_petherici	Polycentropsis_abbreviata	0.55721	0
Nemacheilus_masyae	Characidium_fasciatum	0.762525	0
Notropis_sabinae	Characidium_fasciatum	0.596898	0
Notropis_sabinae	Nemacheilus_masyae	0.628937	0
Glyptothorax_lampris	Homaloptera_confuzona	0.445433	0.006
Pseudomystus_siamensis	Homaloptera_confuzona	0.69028	0
Pseudomystus_siamensis	Glyptothorax_lampris	0.287021	0.009
Awaous_banana	Etheostoma_histrio	0.724379	0
Melanocharacidium_dispilomma	Etheostoma_histrio	0.633255	0
Percina_sciera	Etheostoma_histrio	0.614111	0
Awaous_banana	Etheostoma_thalassinum	0.650724	0
Melanocharacidium_dispilomma	Etheostoma_thalassinum	0.54204	0
Percina_sciera	Etheostoma_thalassinum	0.57446	0
Awaous_banana	Melanocharacidium_dispilomma	0.549627	0.003
Etheostoma_chlorosoma	Melanocharacidium_dispilomma	0.355775	0.021
Etheostoma_fusiforme	Melanocharacidium_dispilomma	0.346655	0.021
Etheostoma_olmstedi	Melanocharacidium_dispilomma	0.537683	0
Percina_sciera	Melanocharacidium_dispilomma	0.353828	0.012
Etheostoma_chlorosoma	Awaous_banana	0.566653	0
Etheostoma_fusiforme	Awaous_banana	0.497088	0.001
Etheostoma_olmstedi	Awaous_banana	0.681855	0
Percina_sciera	Awaous_banana	0.803857	0
Etheostoma_chlorosoma	Percina_sciera	0.533693	0.001
Etheostoma_fusiforme	Percina_sciera	0.454906	0.002
Etheostoma_olmstedi	Percina_sciera	0.721312	0
Etheostoma_gracile	Kribia_kribensis	0.521207	0.001
Homaloptera_smithi	Parotocinclus_longirostris	0.643006	0.001
Acantharchus_pomotis	Acestrorhynchus_falcatus	0.167173	0.117
Aphredoderus_sayanus	Acestrorhynchus_falcatus	0.2858	0.023
Crenicichla_inpa	Acestrorhynchus_falcatus	0.195989	0.111
Erythrinus_erythrinus	Acestrorhynchus_falcatus	0.011804	0.191
Esox_americanus	Acestrorhynchus_falcatus	0.657092	0
Esox_niger	Acestrorhynchus_falcatus	0.606959	0.001
Hemichromis_elongatus	Acestrorhynchus_falcatus	0.168779	0.136

Hoplias_malabaricus	Acestrorhynchus_falcatus	0.323037	0.013
Micropterus_punctulatus	Acestrorhynchus_falcatus	0.359388	0.02
Micropterus_salmoides	Acestrorhynchus_falcatus	0.285942	0.046
Perca_flavescens	Acestrorhynchus_falcatus	0.353484	0.015
Umbra_pygmaea	Acestrorhynchus_falcatus	0.389974	0.005
Acantharchus_pomotis	Esox_niger	0.212761	0.033
Aphredoderus_sayanus	Esox_niger	0.320261	0.002
Crenicichla_inpa	Esox_niger	0.298791	0.036
Erythrinus_erythrinus	Esox_niger	0.105616	0.163
Hemichromis_elongatus	Esox_niger	0.251601	0.032
Hoplias_malabaricus	Esox_niger	0.279504	0.021
Micropterus_punctulatus	Esox_niger	0.530761	0.001
Micropterus_salmoides	Esox_niger	0.470126	0.001
Perca_flavescens	Esox_niger	0.471317	0
Umbra_pygmaea	Esox_niger	0.184219	0
Acantharchus_pomotis	Esox_americanus	0.301816	0.011
Aphredoderus_sayanus	Esox_americanus	0.356644	0.003
Crenicichla_inpa	Esox_americanus	0.424826	0.004
Erythrinus_erythrinus	Esox_americanus	0.090748	0.213
Hemichromis_elongatus	Esox_americanus	0.214457	0.049
Hoplias_malabaricus	Esox_americanus	0.465208	0.001
Micropterus_punctulatus	Esox_americanus	0.689899	0
Micropterus_salmoides	Esox_americanus	0.582768	0
Perca_flavescens	Esox_americanus	0.562664	0
Umbra_pygmaea	Esox_americanus	0.161245	0
Aphredoderus_sayanus	Acantharchus_pomotis	0.596791	0
Crenicichla_inpa	Acantharchus_pomotis	0.335734	0.018
Erythrinus_erythrinus	Acantharchus_pomotis	0.047689	0.449
Hemichromis_elongatus	Acantharchus_pomotis	0.495093	0.002
Hoplias_malabaricus	Acantharchus_pomotis	0.402754	0.007
Micropterus_punctulatus	Acantharchus_pomotis	0.291411	0.007
Micropterus_salmoides	Acantharchus_pomotis	0.23203	0.014
Perca_flavescens	Acantharchus_pomotis	0.41227	0.001
Umbra_pygmaea	Acantharchus_pomotis	0.457076	0.001
Aphredoderus_sayanus	Hemichromis_elongatus	0.463255	0.001
Crenicichla_inpa	Hemichromis_elongatus	0.50789	0.002
Erythrinus_erythrinus	Hemichromis_elongatus	0.06685	0.357
Hoplias_malabaricus	Hemichromis_elongatus	0.409915	0.008
Micropterus_punctulatus	Hemichromis_elongatus	0.231648	0.058
Micropterus_salmoides	Hemichromis_elongatus	0.192062	0.054

Perca_flavescens	Hemichromis_elongatus	0.40588	0.009
Umbra_pygmaea	Hemichromis_elongatus	0.433194	0.001
Aphredoderus_sayanus	Crenicichla_inpa	0.420504	0
Erythrinus_erythrinus	Crenicichla_inpa	0.311125	0.031
Hoplias_malabaricus	Crenicichla_inpa	0.490827	0.003
Micropterus_punctulatus	Crenicichla_inpa	0.373574	0.01
Micropterus_salmoides	Crenicichla_inpa	0.264542	0.04
Perca_flavescens	Crenicichla_inpa	0.359679	0.018
Umbra_pygmaea	Crenicichla_inpa	0.642393	0
Erythrinus_erythrinus	Aphredoderus_sayanus	0.088616	0.187
Hoplias_malabaricus	Aphredoderus_sayanus	0.597478	0
Micropterus_punctulatus	Aphredoderus_sayanus	0.519706	0
Micropterus_salmoides	Aphredoderus_sayanus	0.50393	0.001
Perca_flavescens	Aphredoderus_sayanus	0.505565	0
Umbra_pygmaea	Aphredoderus_sayanus	0.497632	0.001
Erythrinus_erythrinus	Perca_flavescens	-0.24537	0.999
Hoplias_malabaricus	Perca_flavescens	0.22979	0.061
Micropterus_punctulatus	Perca_flavescens	0.744901	0
Micropterus_salmoides	Perca_flavescens	0.765492	0
Umbra_pygmaea	Perca_flavescens	0.34827	0.007
Erythrinus_erythrinus	Micropterus_punctulatus	-0.03731	0.999
Hoplias_malabaricus	Micropterus_punctulatus	0.383183	0.01
Umbra_pygmaea	Micropterus_punctulatus	0.421246	0.004
Erythrinus_erythrinus	Micropterus_salmoides	-0.13536	0.999
Hoplias_malabaricus	Micropterus_salmoides	0.337366	0.016
Umbra_pygmaea	Micropterus_salmoides	0.366144	0.005
Erythrinus_erythrinus	Hoplias_malabaricus	0.452305	0
Umbra_pygmaea	Hoplias_malabaricus	0.593567	0
Erythrinus_erythrinus	Umbra_pygmaea	0.626073	0
Copella_nattereri	Fundulus_notatus	0.667138	0.001
Nannostomus_trifasciatus	Fundulus_notatus	0.687119	0
Nannostomus_trifasciatus	Copella_nattereri	0.661182	0
Poropanchax_luxophthalmus	Gambusia_luma	0.584911	0
Procatopus_nototaenia	Gambusia_luma	0.815258	0
Pyrrhulina_semifasciata	Gambusia_luma	0.852372	0
Procatopus_nototaenia	Poropanchax_luxophthalmus	0.114133	0.002
Pyrrhulina_semifasciata	Poropanchax_luxophthalmus	0.787271	0
Pyrrhulina_semifasciata	Procatopus_nototaenia	0.803318	0
Carnegiella_strigata	Laubuka_caeruleostigmata	0.446432	0.008
Gnathocharax_steindachneri	Laubuka_caeruleostigmata	0.671337	0

Parachela_sp.	Laubuka_caeruleostigmata	0.153385	0.052
Gnathocharax_steindachneri	Carnegiella_strigata	0.58716	0
Parachela_sp.	Carnegiella_strigata	0.531863	0
Gnathocharax_steindachneri	Parachela_sp.	0.556366	0.001

Supplementary table B-4: C_1 and p values for all convergent pairwise comparisons using the all traits dataset.

Species 1	Species 2	C_1	P value
Aequidens_pallidus	Apistogramma_regani	0.524269	0
Chromidotilapia_guntheri	Apistogramma_regani	0.459616	0
Cribroheros_robertsoni	Apistogramma_regani	0.281069	0.002
Cryptoheros_spilurus	Apistogramma_regani	0.410018	0
Ctenopoma_petherici	Apistogramma_regani	0.299039	0.003
Enneacanthus_chaetodon	Apistogramma_regani	0.182008	0.024
Enneacanthus_obesus	Apistogramma_regani	0.216121	0.021
Heros_efasciatus	Apistogramma_regani	0.092938	0.049
Lepomis_auritus	Apistogramma_regani	0.144392	0.04
Lepomis_cyanellus	Apistogramma_regani	-0.04281	0.999
Lepomis_gulosus	Apistogramma_regani	0.037245	0.317
Lepomis_macrochirus	Apistogramma_regani	0.12458	0.072
Lepomis_marginatus	Apistogramma_regani	0.186386	0.025
Lepomis_megalotis	Apistogramma_regani	0.118901	0.096
Lepomis_miniatus	Apistogramma_regani	0.34221	0.001
Lepomis_punctatus	Apistogramma_regani	0.330195	0.002
Parambassis_apogonoides	Apistogramma_regani	0.042969	0.144
Parambassis_siamensis	Apistogramma_regani	0.067997	0.136
Pelvicachromis_taeniatus	Apistogramma_regani	0.583719	0
Polycentropsis_abbreviata	Apistogramma_regani	-0.14698	0.999
Pristolepis_fasciata	Apistogramma_regani	0.447439	0
Rocio_octofasciata	Apistogramma_regani	0.273388	0.003
Trichromis_salvini	Apistogramma_regani	0.485964	0
Vieja_melanura	Apistogramma_regani	0.115919	0.044
Aequidens_pallidus	Pelvicachromis_taeniatus	0.481877	0
Apistogramma_hippolytae	Pelvicachromis_taeniatus	0.753538	0
Chromidotilapia_guntheri	Pelvicachromis_taeniatus	0.413362	0.001
Cribroheros_robertsoni	Pelvicachromis_taeniatus	0.176627	0.022
Cryptoheros_spilurus	Pelvicachromis_taeniatus	0.18831	0.012
Ctenopoma_petherici	Pelvicachromis_taeniatus	0.013852	0.129
Enneacanthus_chaetodon	Pelvicachromis_taeniatus	0.220247	0.007

Enneacanthus_obesus	Pelvicachromis_taeniatus	0.159078	0.03
Heros_efasciatus	Pelvicachromis_taeniatus	0.06794	0.074
Lepomis_auritus	Pelvicachromis_taeniatus	0.277769	0.004
Lepomis_cyanellus	Pelvicachromis_taeniatus	0.108382	0.076
Lepomis_gulosus	Pelvicachromis_taeniatus	0.175963	0.02
Lepomis_macrochirus	Pelvicachromis_taeniatus	0.272789	0.001
Lepomis_marginatus	Pelvicachromis_taeniatus	0.415321	0
Lepomis_megalotis	Pelvicachromis_taeniatus	0.343843	0.002
Lepomis_miniatus	Pelvicachromis_taeniatus	0.326235	0
Lepomis_punctatus	Pelvicachromis_taeniatus	0.344355	0.001
Parambassis_apogonoides	Pelvicachromis_taeniatus	0.000399	0.334
Parambassis_siamensis	Pelvicachromis_taeniatus	-0.06225	0.999
Polycentropsis_abbreviata	Pelvicachromis_taeniatus	-0.41154	0.999
Pristolepis_fasciata	Pelvicachromis_taeniatus	0.338897	0.002
Rocio_octofasciata	Pelvicachromis_taeniatus	0.219928	0.006
Trichromis_salvini	Pelvicachromis_taeniatus	0.437095	0
Vieja_melanura	Pelvicachromis_taeniatus	0.127301	0.033
Aequidens_pallidus	Apistogramma_hippolytae	0.666994	0
Chromidotilapia_guntheri	Apistogramma_hippolytae	0.620014	0
Cribroheros_robertsoni	Apistogramma_hippolytae	0.600466	0
Cryptoheros_spilurus	Apistogramma_hippolytae	0.632562	0
Ctenopoma_pethérici	Apistogramma_hippolytae	0.422985	0
Enneacanthus_chaetodon	Apistogramma_hippolytae	0.494198	0
Enneacanthus_obesus	Apistogramma_hippolytae	0.482113	0
Heros_efasciatus	Apistogramma_hippolytae	0.364305	0
Lepomis_auritus	Apistogramma_hippolytae	0.466764	0
Lepomis_cyanellus	Apistogramma_hippolytae	0.354008	0.001
Lepomis_gulosus	Apistogramma_hippolytae	0.379248	0.001
Lepomis_macrochirus	Apistogramma_hippolytae	0.372189	0
Lepomis_marginatus	Apistogramma_hippolytae	0.538053	0
Lepomis_megalotis	Apistogramma_hippolytae	0.524641	0
Lepomis_miniatus	Apistogramma_hippolytae	0.604268	0
Lepomis_punctatus	Apistogramma_hippolytae	0.542217	0
Parambassis_apogonoides	Apistogramma_hippolytae	0.347456	0.002
Parambassis_siamensis	Apistogramma_hippolytae	0.322194	0.002
Polycentropsis_abbreviata	Apistogramma_hippolytae	0.204579	0.012
Pristolepis_fasciata	Apistogramma_hippolytae	0.585728	0
Rocio_octofasciata	Apistogramma_hippolytae	0.594524	0
Trichromis_salvini	Apistogramma_hippolytae	0.668888	0
Vieja_melanura	Apistogramma_hippolytae	0.459696	0

Aequidens_pallidus	Lepomis_auritus	0.204553	0.02
Chromidotilapia_guntheri	Lepomis_auritus	0.403573	0
Cribroheros_robertsoni	Lepomis_auritus	0.322943	0.002
Cryptoheros_spilurus	Lepomis_auritus	0.273477	0.004
Ctenopoma_pethererici	Lepomis_auritus	0.308467	0.003
Enneacanthus_chaetodon	Lepomis_auritus	0.520142	0
Enneacanthus_obesus	Lepomis_auritus	0.571935	0
Heros_efasciatus	Lepomis_auritus	0.010502	0.475
Parambassis_apogonoides	Lepomis_auritus	0.195934	0.014
Parambassis_siamensis	Lepomis_auritus	0.095464	0.095
Polycentropsis_abbreviata	Lepomis_auritus	-0.12592	0.999
Pristolepis_fasciata	Lepomis_auritus	0.406111	0
Rocio_octofasciata	Lepomis_auritus	0.329888	0
Trichromis_salvini	Lepomis_auritus	0.424967	0.001
Vieja_melanura	Lepomis_auritus	0.330797	0.005
Aequidens_pallidus	Lepomis_cyanellus	-0.03569	0.999
Chromidotilapia_guntheri	Lepomis_cyanellus	0.343119	0.001
Cribroheros_robertsoni	Lepomis_cyanellus	0.23595	0.007
Cryptoheros_spilurus	Lepomis_cyanellus	0.00598	0.522
Ctenopoma_pethererici	Lepomis_cyanellus	0.236246	0.006
Enneacanthus_chaetodon	Lepomis_cyanellus	0.40511	0
Enneacanthus_obesus	Lepomis_cyanellus	0.522965	0
Heros_efasciatus	Lepomis_cyanellus	-0.22488	0.999
Parambassis_apogonoides	Lepomis_cyanellus	0.199764	0.01
Parambassis_siamensis	Lepomis_cyanellus	0.056659	0.212
Polycentropsis_abbreviata	Lepomis_cyanellus	-0.16908	0.999
Pristolepis_fasciata	Lepomis_cyanellus	0.364755	0
Rocio_octofasciata	Lepomis_cyanellus	0.178618	0.031
Trichromis_salvini	Lepomis_cyanellus	0.405151	0
Vieja_melanura	Lepomis_cyanellus	0.175937	0.028
Aequidens_pallidus	Lepomis_gulosus	0.079735	0.141
Chromidotilapia_guntheri	Lepomis_gulosus	0.353516	0
Cribroheros_robertsoni	Lepomis_gulosus	0.289227	0.008
Cryptoheros_spilurus	Lepomis_gulosus	0.108173	0.1
Ctenopoma_pethererici	Lepomis_gulosus	0.38097	0
Enneacanthus_chaetodon	Lepomis_gulosus	0.465941	0
Enneacanthus_obesus	Lepomis_gulosus	0.590866	0
Heros_efasciatus	Lepomis_gulosus	-0.167	0.999
Parambassis_apogonoides	Lepomis_gulosus	0.169351	0.017
Parambassis_siamensis	Lepomis_gulosus	0.118758	0.055

Polycentropsis_abbreviata	Lepomis_gulosus	-0.02692	0.999
Pristolepis_fasciata	Lepomis_gulosus	0.425938	0
Rocio_octofasciata	Lepomis_gulosus	0.249406	0.011
Trichromis_salvini	Lepomis_gulosus	0.50238	0.001
Vieja_melanura	Lepomis_gulosus	0.273241	0.005
Aequidens_pallidus	Lepomis_macrochirus	0.143766	0.044
Chromidotilapia_guntheri	Lepomis_macrochirus	0.347996	0.001
Cribroheros_robertsoni	Lepomis_macrochirus	0.189758	0.031
Cryptoheros_spilurus	Lepomis_macrochirus	0.231253	0.011
Ctenopoma_petherici	Lepomis_macrochirus	0.375108	0
Enneacanthus_chaetodon	Lepomis_macrochirus	0.722041	0
Enneacanthus_obesus	Lepomis_macrochirus	0.709985	0
Heros_efasciatus	Lepomis_macrochirus	-0.12934	0.999
Parambassis_apogonoides	Lepomis_macrochirus	0.157061	0.022
Parambassis_siamensis	Lepomis_macrochirus	0.222178	0.004
Polycentropsis_abbreviata	Lepomis_macrochirus	-0.22632	0.999
Pristolepis_fasciata	Lepomis_macrochirus	0.456531	0
Rocio_octofasciata	Lepomis_macrochirus	0.215229	0.01
Trichromis_salvini	Lepomis_macrochirus	0.453211	0
Vieja_melanura	Lepomis_macrochirus	0.193115	0.02
Aequidens_pallidus	Lepomis_marginatus	0.174265	0.035
Chromidotilapia_guntheri	Lepomis_marginatus	0.410385	0
Cribroheros_robertsoni	Lepomis_marginatus	0.175502	0.042
Cryptoheros_spilurus	Lepomis_marginatus	0.315404	0.002
Ctenopoma_petherici	Lepomis_marginatus	0.335309	0.005
Enneacanthus_chaetodon	Lepomis_marginatus	0.493561	0
Enneacanthus_obesus	Lepomis_marginatus	0.487969	0
Heros_efasciatus	Lepomis_marginatus	-0.07376	0.999
Parambassis_apogonoides	Lepomis_marginatus	0.074277	0.127
Parambassis_siamensis	Lepomis_marginatus	0.062087	0.202
Polycentropsis_abbreviata	Lepomis_marginatus	-0.20594	0.999
Pristolepis_fasciata	Lepomis_marginatus	0.423653	0
Rocio_octofasciata	Lepomis_marginatus	0.252152	0.008
Trichromis_salvini	Lepomis_marginatus	0.440552	0
Vieja_melanura	Lepomis_marginatus	0.205295	0.029
Aequidens_pallidus	Lepomis_megalotis	0.242473	0.012
Chromidotilapia_guntheri	Lepomis_megalotis	0.466279	0
Cribroheros_robertsoni	Lepomis_megalotis	0.267195	0.011
Cryptoheros_spilurus	Lepomis_megalotis	0.268335	0.009
Ctenopoma_petherici	Lepomis_megalotis	0.179358	0.022

Enneacanthus_chaetodon	Lepomis_megalotis	0.416932	0
Enneacanthus_obesus	Lepomis_megalotis	0.385243	0
Heros_efasciatus	Lepomis_megalotis	0.001258	0.615
Parambassis_apogonoides	Lepomis_megalotis	0.180428	0.016
Parambassis_siamensis	Lepomis_megalotis	-0.00476	0.999
Polycentropsis_abbreviata	Lepomis_megalotis	-0.19676	0.999
Pristolepis_fasciata	Lepomis_megalotis	0.347615	0.003
Rocio_octofasciata	Lepomis_megalotis	0.273519	0.005
Trichromis_salvini	Lepomis_megalotis	0.40734	0
Vieja_melanura	Lepomis_megalotis	0.146495	0.067
Aequidens_pallidus	Lepomis_miniatus	0.20918	0.011
Chromidotilapia_guntheri	Lepomis_miniatus	0.340256	0
Cribroheros_robertsoni	Lepomis_miniatus	0.318427	0.004
Cryptoheros_spilurus	Lepomis_miniatus	0.434368	0.001
Ctenopoma_petherici	Lepomis_miniatus	0.457128	0
Enneacanthus_chaetodon	Lepomis_miniatus	0.478202	0
Enneacanthus_obesus	Lepomis_miniatus	0.591519	0
Heros_efasciatus	Lepomis_miniatus	-0.04564	0.999
Parambassis_apogonoides	Lepomis_miniatus	0.228501	0.007
Parambassis_siamensis	Lepomis_miniatus	0.23295	0.009
Polycentropsis_abbreviata	Lepomis_miniatus	0.131932	0.049
Pristolepis_fasciata	Lepomis_miniatus	0.616163	0
Rocio_octofasciata	Lepomis_miniatus	0.419795	0
Trichromis_salvini	Lepomis_miniatus	0.589096	0
Vieja_melanura	Lepomis_miniatus	0.360571	0.001
Aequidens_pallidus	Lepomis_punctatus	0.266621	0.001
Chromidotilapia_guntheri	Lepomis_punctatus	0.320826	0.001
Cribroheros_robertsoni	Lepomis_punctatus	0.37543	0
Cryptoheros_spilurus	Lepomis_punctatus	0.411659	0
Ctenopoma_petherici	Lepomis_punctatus	0.46531	0
Enneacanthus_chaetodon	Lepomis_punctatus	0.595601	0
Enneacanthus_obesus	Lepomis_punctatus	0.739818	0
Heros_efasciatus	Lepomis_punctatus	0.035949	0.351
Parambassis_apogonoides	Lepomis_punctatus	0.286212	0
Parambassis_siamensis	Lepomis_punctatus	0.316288	0.002
Polycentropsis_abbreviata	Lepomis_punctatus	0.184949	0.018
Pristolepis_fasciata	Lepomis_punctatus	0.656294	0
Rocio_octofasciata	Lepomis_punctatus	0.411687	0
Trichromis_salvini	Lepomis_punctatus	0.508047	0
Vieja_melanura	Lepomis_punctatus	0.45353	0.001

Aequidens_pallidus	Enneacanthus_chaetodon	0.201043	0.016
Chromidotilapia_guntheri	Enneacanthus_chaetodon	0.261842	0.003
Cribroheros_robertsoni	Enneacanthus_chaetodon	0.290155	0.001
Cryptoheros_spilurus	Enneacanthus_chaetodon	0.26852	0.005
Ctenopoma_petherici	Enneacanthus_chaetodon	0.108386	0.049
Enneacanthus_obesus	Enneacanthus_chaetodon	0.667741	0
Heros_efasciatus	Enneacanthus_chaetodon	-0.06512	0.999
Parambassis_apogonoides	Enneacanthus_chaetodon	0.333103	0
Parambassis_siamensis	Enneacanthus_chaetodon	0.256637	0.005
Polycentropsis_abbreviata	Enneacanthus_chaetodon	-0.11017	0.999
Pristolepis_fasciata	Enneacanthus_chaetodon	0.48278	0
Rocio_octofasciata	Enneacanthus_chaetodon	0.181401	0.013
Trichromis_salvini	Enneacanthus_chaetodon	0.383614	0.001
Vieja_melanura	Enneacanthus_chaetodon	0.239807	0.01
Aequidens_pallidus	Enneacanthus_obesus	0.162954	0.031
Chromidotilapia_guntheri	Enneacanthus_obesus	0.314059	0
Cribroheros_robertsoni	Enneacanthus_obesus	0.341135	0.001
Cryptoheros_spilurus	Enneacanthus_obesus	0.287002	0.004
Ctenopoma_petherici	Enneacanthus_obesus	0.383017	0.001
Heros_efasciatus	Enneacanthus_obesus	-0.10475	0.999
Parambassis_apogonoides	Enneacanthus_obesus	0.356355	0.001
Parambassis_siamensis	Enneacanthus_obesus	0.31373	0.003
Polycentropsis_abbreviata	Enneacanthus_obesus	-0.00334	0.999
Pristolepis_fasciata	Enneacanthus_obesus	0.624172	0
Rocio_octofasciata	Enneacanthus_obesus	0.259002	0.005
Trichromis_salvini	Enneacanthus_obesus	0.451949	0
Vieja_melanura	Enneacanthus_obesus	0.33973	0
Aequidens_pallidus	Parambassis_apogonoides	-0.11287	0.999
Chromidotilapia_guntheri	Parambassis_apogonoides	0.026357	0.05
Cribroheros_robertsoni	Parambassis_apogonoides	0.149228	0.031
Cryptoheros_spilurus	Parambassis_apogonoides	0.025781	0.211
Ctenopoma_petherici	Parambassis_apogonoides	0.002132	0.21
Heros_efasciatus	Parambassis_apogonoides	-0.27206	0.999
Parambassis_siamensis	Parambassis_apogonoides	0.613663	0
Polycentropsis_abbreviata	Parambassis_apogonoides	0.023406	0.056
Pristolepis_fasciata	Parambassis_apogonoides	0.230928	0
Rocio_octofasciata	Parambassis_apogonoides	0.055096	0.125
Trichromis_salvini	Parambassis_apogonoides	0.396131	0
Vieja_melanura	Parambassis_apogonoides	-0.03519	0.999
Aequidens_pallidus	Parambassis_siamensis	-0.06174	0.999

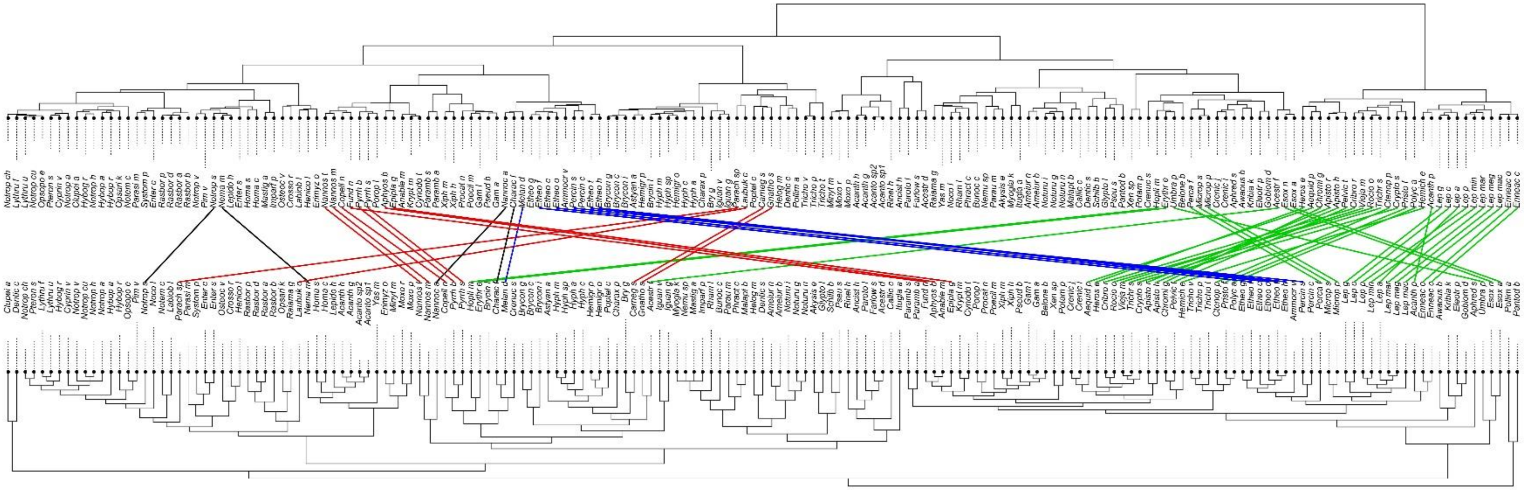
Chromidotilapia_guntheri	Parambassis_siamensis	-0.09863	0.999
Cribroheros_robertsoni	Parambassis_siamensis	0.259336	0.004
Cryptoheros_spilurus	Parambassis_siamensis	0.097829	0.087
Ctenopoma_petherici	Parambassis_siamensis	0.088444	0.033
Heros_efasciatus	Parambassis_siamensis	-0.15432	0.999
Polycentropsis_abbreviata	Parambassis_siamensis	-0.27791	0.999
Pristolepis_fasciata	Parambassis_siamensis	0.286371	0.002
Rocio_octofasciata	Parambassis_siamensis	0.128394	0.039
Trichromis_salvini	Parambassis_siamensis	0.445437	0
Vieja_melanura	Parambassis_siamensis	0.089442	0.103
Aequidens_pallidus	Pristolepis_fasciata	0.407962	0
Chromidotilapia_guntheri	Pristolepis_fasciata	0.437074	0
Cribroheros_robertsoni	Pristolepis_fasciata	0.580842	0
Cryptoheros_spilurus	Pristolepis_fasciata	0.637245	0
Ctenopoma_petherici	Pristolepis_fasciata	0.523126	0
Heros_efasciatus	Pristolepis_fasciata	0.175697	0.011
Polycentropsis_abbreviata	Pristolepis_fasciata	0.183921	0
Rocio_octofasciata	Pristolepis_fasciata	0.565979	0
Trichromis_salvini	Pristolepis_fasciata	0.644347	0
Vieja_melanura	Pristolepis_fasciata	0.568456	0
Aequidens_pallidus	Cryptoheros_spilurus	0.421861	0
Chromidotilapia_guntheri	Cryptoheros_spilurus	0.318734	0.001
Cribroheros_robertsoni	Cryptoheros_spilurus	0.357403	0
Ctenopoma_petherici	Cryptoheros_spilurus	0.452514	0
Heros_efasciatus	Cryptoheros_spilurus	0.23487	0
Polycentropsis_abbreviata	Cryptoheros_spilurus	-0.16366	0.999
Rocio_octofasciata	Cryptoheros_spilurus	0.490931	0
Trichromis_salvini	Cryptoheros_spilurus	0.655635	0
Vieja_melanura	Cryptoheros_spilurus	0.434453	0
Aequidens_pallidus	Cribroheros_robertsoni	0.448219	0
Chromidotilapia_guntheri	Cribroheros_robertsoni	0.435186	0
Ctenopoma_petherici	Cribroheros_robertsoni	0.370113	0
Heros_efasciatus	Cribroheros_robertsoni	0.307501	0.001
Polycentropsis_abbreviata	Cribroheros_robertsoni	-0.1477	0.999
Rocio_octofasciata	Cribroheros_robertsoni	0.608922	0
Trichromis_salvini	Cribroheros_robertsoni	0.674426	0
Vieja_melanura	Cribroheros_robertsoni	0.533378	0
Aequidens_pallidus	Heros_efasciatus	0.416996	0
Chromidotilapia_guntheri	Heros_efasciatus	0.106648	0.022
Ctenopoma_petherici	Heros_efasciatus	0.069763	0.108

Polycentropsis_abbreviata	Heros_efasciatus	-0.59835	0.999
Rocio_octofasciata	Heros_efasciatus	0.330997	0
Trichromis_salvini	Heros_efasciatus	0.444749	0
Chromidotilapia_guntheri	Aequidens_pallidus	0.531477	0
Ctenopoma_petherici	Aequidens_pallidus	0.049425	0.112
Polycentropsis_abbreviata	Aequidens_pallidus	-0.46034	0.999
Rocio_octofasciata	Aequidens_pallidus	0.394493	0
Trichromis_salvini	Aequidens_pallidus	0.513033	0
Chromidotilapia_guntheri	Rocio_octofasciata	0.347623	0.001
Ctenopoma_petherici	Rocio_octofasciata	0.538647	0
Polycentropsis_abbreviata	Rocio_octofasciata	-0.02536	0.999
Trichromis_salvini	Rocio_octofasciata	0.842641	0
Ctenopoma_petherici	Chromidotilapia_guntheri	0.065584	0.037
Polycentropsis_abbreviata	Chromidotilapia_guntheri	-0.138	0.999
Trichromis_salvini	Chromidotilapia_guntheri	0.525616	0
Ctenopoma_petherici	Trichromis_salvini	0.638928	0
Polycentropsis_abbreviata	Trichromis_salvini	0.299443	0.003
Ctenopoma_petherici	Polycentropsis_abbreviata	0.018868	0.031
Nemacheilus_masyae	Characidium_fasciatum	0.484819	0
Notropis_sabinae	Characidium_fasciatum	0.375903	0
Notropis_sabinae	Nemacheilus_masyae	0.679629	0
Glyptothorax_lampris	Homaloptera_confuzona	0.26189	0.002
Pseudomystus_siamensis	Homaloptera_confuzona	0.270844	0.006
Pseudomystus_siamensis	Glyptothorax_lampris	0.298432	0.001
Etheostoma_gracile	Kribia_kribensis	0.093323	0.088
Homaloptera_smithi	Parotocinclus_longirostris	0.267594	0.006
Awaous_banana	Etheostoma_histrio	0.12211	0.064
Melanocharacidium_dispilomma	Etheostoma_histrio	0.329151	0.003
Percina_sciera	Etheostoma_histrio	0.182077	0.006
Awaous_banana	Etheostoma_thalassinum	0.484628	0
Melanocharacidium_dispilomma	Etheostoma_thalassinum	0.594167	0
Percina_sciera	Etheostoma_thalassinum	0.527618	0
Awaous_banana	Melanocharacidium_dispilomma	0.192413	0.021
Etheostoma_chlorosoma	Melanocharacidium_dispilomma	0.389891	0.001
Etheostoma_fusiforme	Melanocharacidium_dispilomma	0.547504	0
Etheostoma_olmstedi	Melanocharacidium_dispilomma	0.535502	0
Percina_sciera	Melanocharacidium_dispilomma	0.223477	0.017
Etheostoma_chlorosoma	Awaous_banana	0.299265	0.003
Etheostoma_fusiforme	Awaous_banana	0.329504	0.002
Etheostoma_olmstedi	Awaous_banana	0.513274	0

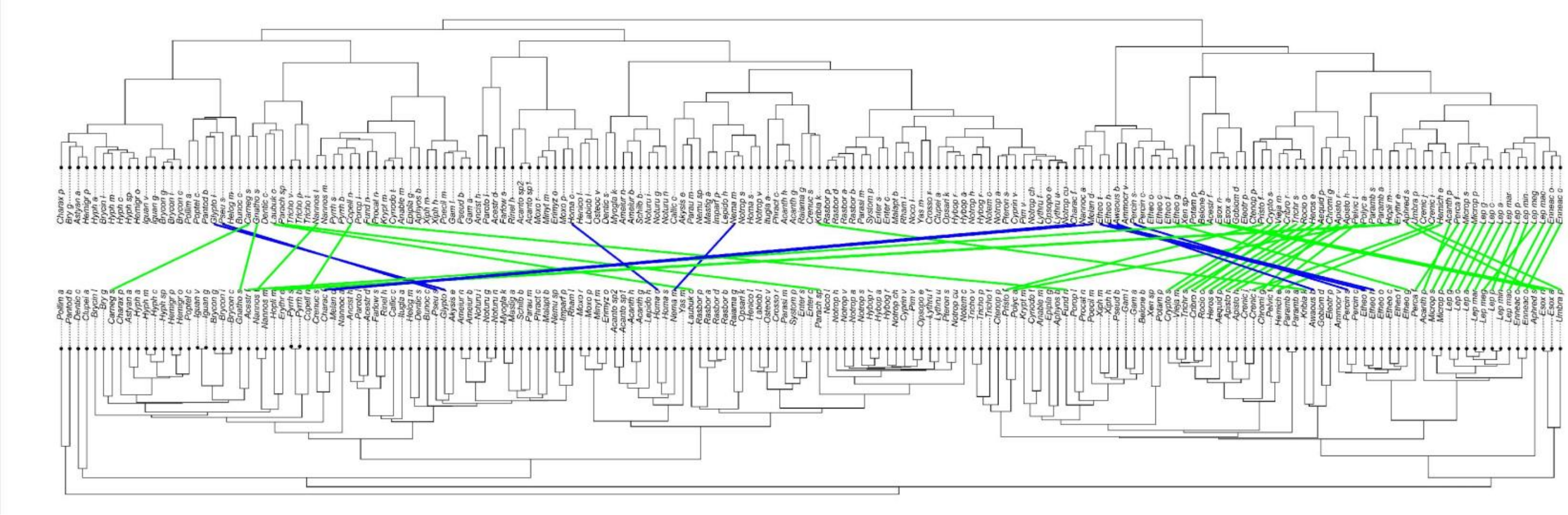
Percina_sciera	Awaous_banana	0.248128	0.008
Etheostoma_chlorosoma	Percina_sciera	0.544334	0
Etheostoma_fusiforme	Percina_sciera	0.491966	0
Etheostoma_olmstedi	Percina_sciera	0.547709	0
Aphyosemion_bitaeniatum	Fundulus_notatus	0.523192	0
Copella_nattereri	Fundulus_notatus	0.600387	0
Epiplatys_grahami	Fundulus_notatus	0.395709	0
Nannostomus_marginatus	Fundulus_notatus	0.467137	0
Nannostomus_trifasciatus	Fundulus_notatus	0.559034	0
Pyrrhulina_brevis	Fundulus_notatus	0.45943	0
Pyrrhulina_semifasciata	Fundulus_notatus	0.642937	0
Aphyosemion_bitaeniatum	Copella_nattereri	0.486379	0
Epiplatys_grahami	Copella_nattereri	0.187808	0.028
Nannostomus_marginatus	Copella_nattereri	0.452109	0
Nannostomus_trifasciatus	Copella_nattereri	0.560267	0
Pyrrhulina_brevis	Copella_nattereri	0.597162	0
Pyrrhulina_semifasciata	Copella_nattereri	0.743336	0
Aphyosemion_bitaeniatum	Nannostomus_trifasciatus	0.416683	0.002
Epiplatys_grahami	Nannostomus_trifasciatus	0.235204	0.014
Pyrrhulina_brevis	Nannostomus_trifasciatus	0.442856	0
Pyrrhulina_semifasciata	Nannostomus_trifasciatus	0.548604	0
Aphyosemion_bitaeniatum	Pyrrhulina_semifasciata	0.603959	0
Epiplatys_grahami	Pyrrhulina_semifasciata	0.615845	0
Nannostomus_marginatus	Pyrrhulina_semifasciata	0.629375	0
Epiplatys_grahami	Aphyosemion_bitaeniatum	0.650218	0
Nannostomus_marginatus	Aphyosemion_bitaeniatum	0.352408	0.001
Pyrrhulina_brevis	Aphyosemion_bitaeniatum	0.486607	0
Nannostomus_marginatus	Epiplatys_grahami	0.091812	0.147
Pyrrhulina_brevis	Epiplatys_grahami	0.269958	0.01
Pyrrhulina_brevis	Nannostomus_marginatus	0.516775	0
Carnegiella_strigata	Laubuka_caeruleostigmata	0.01505	0.249
Gnathocharax_steindachneri	Laubuka_caeruleostigmata	-0.22228	0.999
Parachela_sp.	Laubuka_caeruleostigmata	-0.06688	0.999
Gnathocharax_steindachneri	Carnegiella_strigata	0.018925	0.049
Parachela_sp.	Carnegiella_strigata	0.006772	0.34
Gnathocharax_steindachneri	Parachela_sp.	-0.1911	0.999
Acantharchus_pomotis	Acestrorhynchus_falcatus	0.23776	0.007
Aphredoderus_sayanus	Acestrorhynchus_falcatus	0.292885	0.002
Crenicichla_inpa	Acestrorhynchus_falcatus	0.530231	0
Erythrinus_erythrinus	Acestrorhynchus_falcatus	0.208202	0.005

Esox_americanus	Acestrorhynchus_falcatus	0.679292	0
Esox_niger	Acestrorhynchus_falcatus	0.652275	0
Hemichromis_elongatus	Acestrorhynchus_falcatus	0.338093	0.001
Hoplias_malabaricus	Acestrorhynchus_falcatus	0.101881	0.038
Micropterus_punctulatus	Acestrorhynchus_falcatus	0.520693	0
Micropterus_salmoides	Acestrorhynchus_falcatus	0.186135	0.029
Perca_flavescens	Acestrorhynchus_falcatus	0.07817	0.153
Umbra_pygmaea	Acestrorhynchus_falcatus	0.23333	0.008
Acantharchus_pomotis	Esox_niger	0.053974	0.174
Aphredoderus_sayanus	Esox_niger	0.207733	0.003
Crenicichla_inpa	Esox_niger	0.400201	0
Erythrinus_erythrinus	Esox_niger	0.110948	0.057
Hemichromis_elongatus	Esox_niger	0.317511	0.003
Hoplias_malabaricus	Esox_niger	0.191619	0.007
Micropterus_punctulatus	Esox_niger	0.530589	0
Micropterus_salmoides	Esox_niger	0.231789	0.003
Perca_flavescens	Esox_niger	0.130801	0.026
Umbra_pygmaea	Esox_niger	0.121376	0
Acantharchus_pomotis	Esox_americanus	0.216355	0.008
Aphredoderus_sayanus	Esox_americanus	0.119338	0.011
Crenicichla_inpa	Esox_americanus	0.527188	0
Erythrinus_erythrinus	Esox_americanus	0.153868	0.033
Hemichromis_elongatus	Esox_americanus	0.4341	0
Hoplias_malabaricus	Esox_americanus	0.179962	0.017
Micropterus_punctulatus	Esox_americanus	0.603467	0
Micropterus_salmoides	Esox_americanus	0.320607	0
Perca_flavescens	Esox_americanus	0.197369	0.008
Umbra_pygmaea	Esox_americanus	0.171943	0
Aphredoderus_sayanus	Acantharchus_pomotis	0.618553	0
Crenicichla_inpa	Acantharchus_pomotis	0.595017	0
Erythrinus_erythrinus	Acantharchus_pomotis	0.316663	0.002
Hemichromis_elongatus	Acantharchus_pomotis	0.684929	0
Hoplias_malabaricus	Acantharchus_pomotis	0.245923	0.003
Micropterus_punctulatus	Acantharchus_pomotis	0.603818	0
Micropterus_salmoides	Acantharchus_pomotis	0.538788	0
Perca_flavescens	Acantharchus_pomotis	0.344936	0
Umbra_pygmaea	Acantharchus_pomotis	0.316771	0
Aphredoderus_sayanus	Hemichromis_elongatus	0.656368	0
Crenicichla_inpa	Hemichromis_elongatus	0.729098	0
Erythrinus_erythrinus	Hemichromis_elongatus	0.308399	0.006

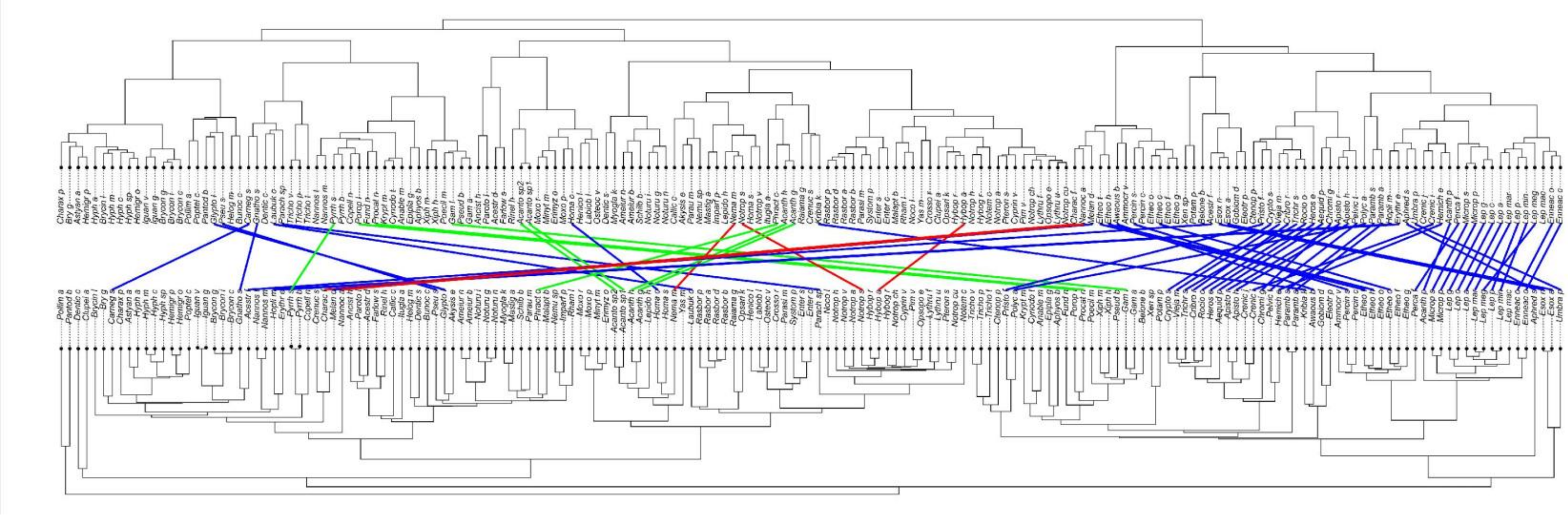
Hoplias_malabaricus	Hemichromis_elongatus	0.318403	0.006
Micropterus_punctulatus	Hemichromis_elongatus	0.650975	0
Micropterus_salmoides	Hemichromis_elongatus	0.499736	0
Perca_flavescens	Hemichromis_elongatus	0.393263	0
Umbra_pygmaea	Hemichromis_elongatus	0.297128	0.001
Aphredoderus_sayanus	Crenicichla_inpa	0.680423	0
Erythrinus_erythrinus	Crenicichla_inpa	0.455209	0
Hoplias_malabaricus	Crenicichla_inpa	0.453613	0
Micropterus_punctulatus	Crenicichla_inpa	0.651876	0
Micropterus_salmoides	Crenicichla_inpa	0.520555	0
Perca_flavescens	Crenicichla_inpa	0.43269	0
Umbra_pygmaea	Crenicichla_inpa	0.610303	0
Erythrinus_erythrinus	Aphredoderus_sayanus	0.497474	0
Hoplias_malabaricus	Aphredoderus_sayanus	0.443559	0
Micropterus_punctulatus	Aphredoderus_sayanus	0.660923	0
Micropterus_salmoides	Aphredoderus_sayanus	0.425129	0
Perca_flavescens	Aphredoderus_sayanus	0.164035	0.013
Umbra_pygmaea	Aphredoderus_sayanus	0.615584	0
Erythrinus_erythrinus	Perca_flavescens	0.132806	0.064
Hoplias_malabaricus	Perca_flavescens	-0.00343	0.999
Micropterus_punctulatus	Perca_flavescens	0.67972	0
Micropterus_salmoides	Perca_flavescens	0.510424	0
Umbra_pygmaea	Perca_flavescens	0.120652	0.043
Erythrinus_erythrinus	Micropterus_punctulatus	0.514282	0
Hoplias_malabaricus	Micropterus_punctulatus	0.593893	0
Umbra_pygmaea	Micropterus_punctulatus	0.569716	0
Erythrinus_erythrinus	Micropterus_salmoides	0.328635	0.001
Hoplias_malabaricus	Micropterus_salmoides	0.345036	0
Umbra_pygmaea	Micropterus_salmoides	0.292607	0.002
Erythrinus_erythrinus	Hoplias_malabaricus	0.568115	0
Umbra_pygmaea	Hoplias_malabaricus	0.397536	0
Erythrinus_erythrinus	Umbra_pygmaea	0.546176	0



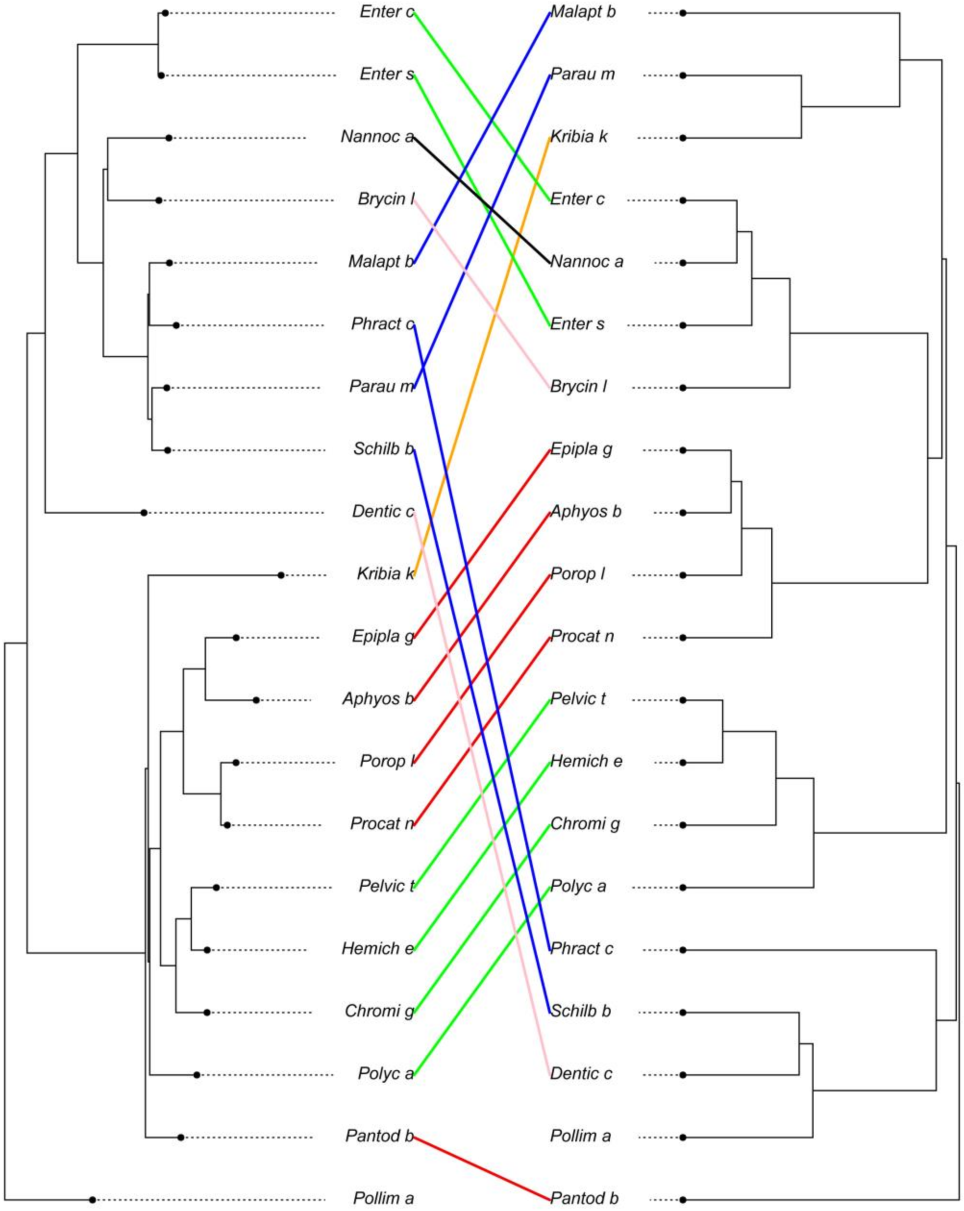
Supplementary Figure B-1: A tanglegram of all species depicting possible convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of the ‘all traits dataset’ is on the right. The lines connect each species’ position on the phylogeny and phenogram. Microhabitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), MID-LVAS (**green** lines), and TOP-LVVS (**red** lines).



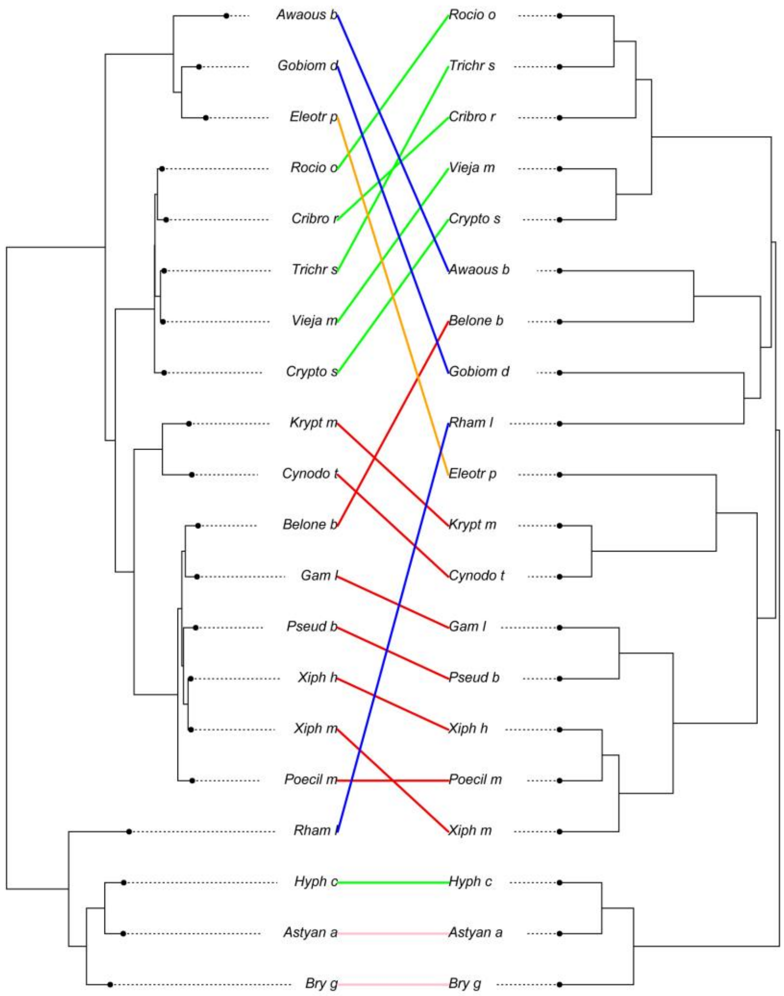
Supplementary Figure B-2: A tanglegram of all species depicting possible convergent taxa from the water velocity groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Water velocity groupings are labeled as follow: high water velocity (**blue** lines) and low water velocity (**green** lines).



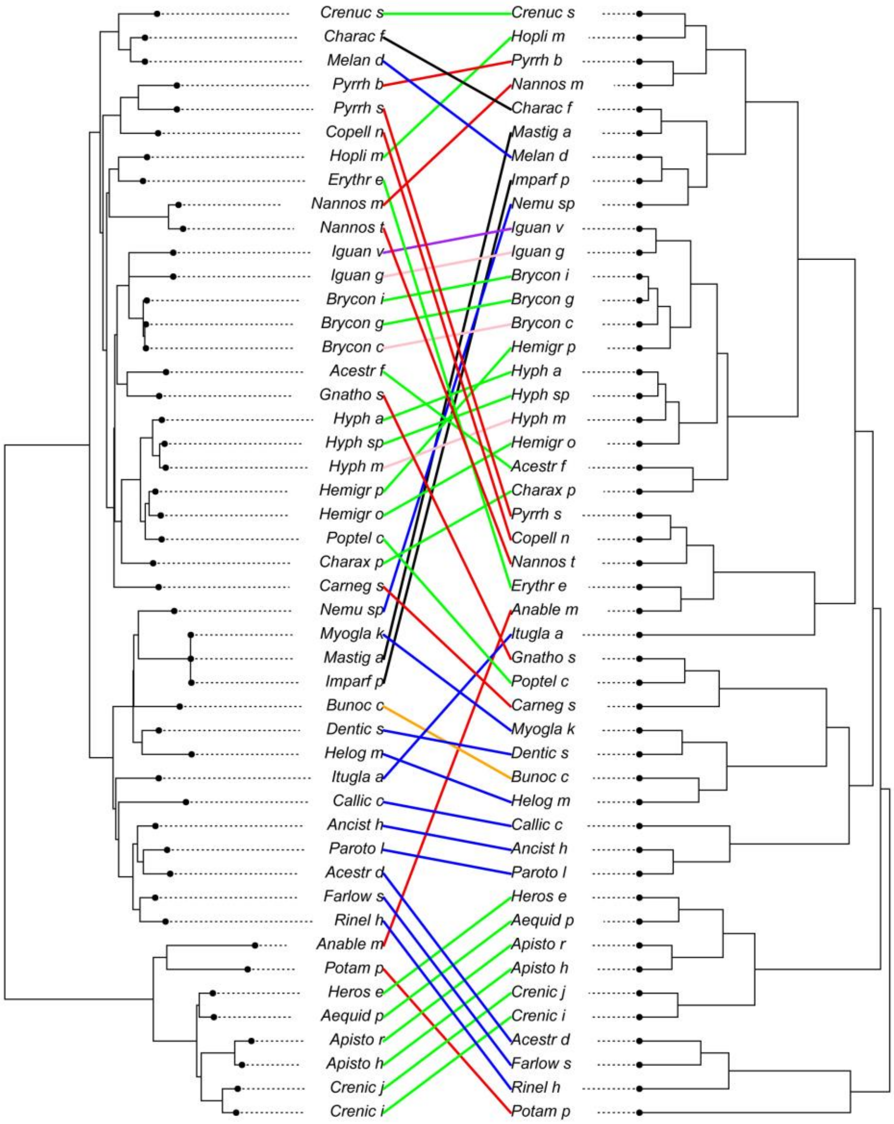
Supplementary Figure B-3: A tanglegram of all species depicting possible convergent taxa from the substrate complexity groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Substrate complexity groupings are labeled as follow: high substrate complexity (**blue** lines), medium substrate complexity (**red** lines), and low substrate complexity (**green** lines).



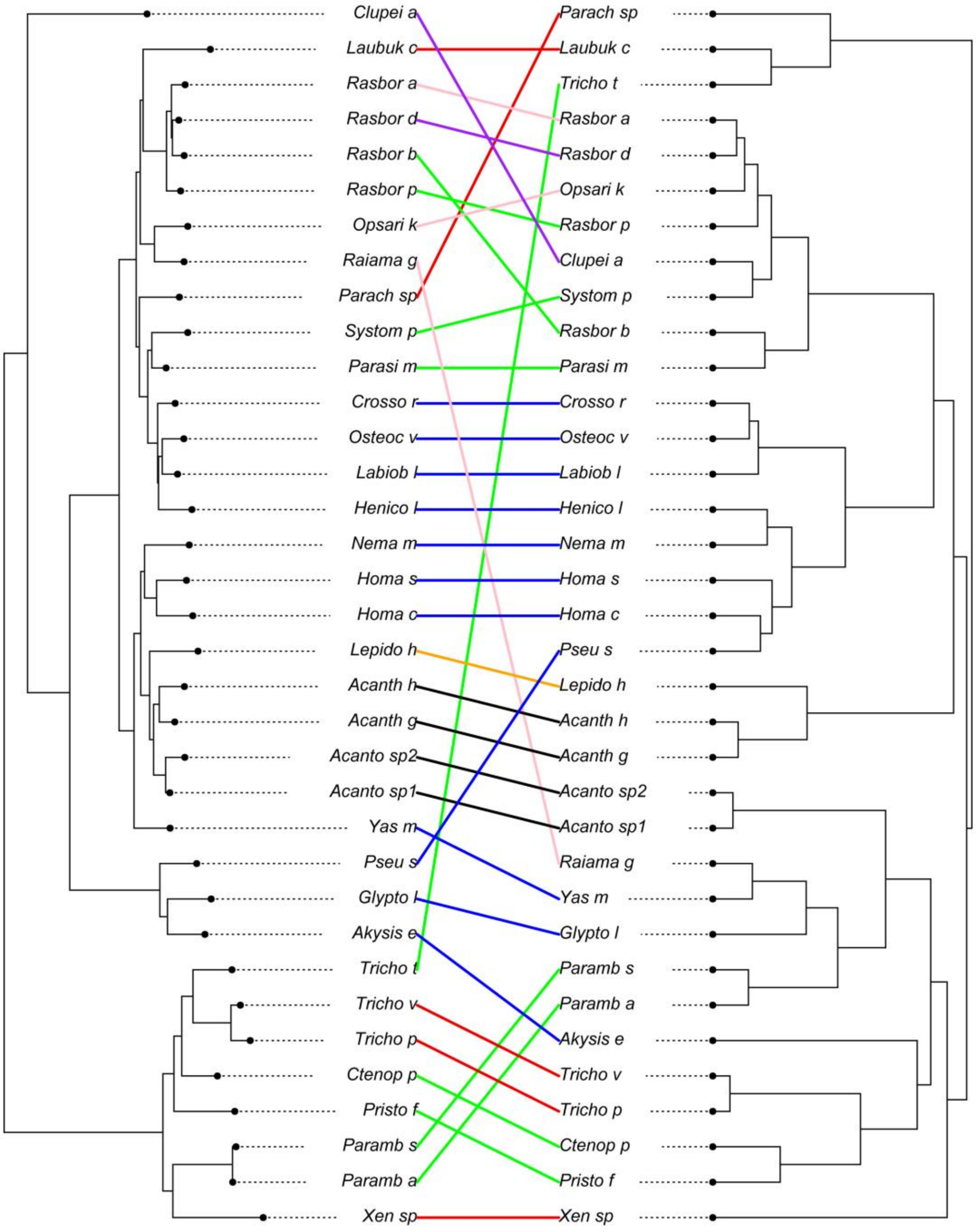
Supplementary Figure B-4: A tanglegram of species from Benin depicting possible convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Habitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), MID-HVSS (**pink** lines), MID-LVSS (**purple** lines), and TOP-LVVS (**red** lines).



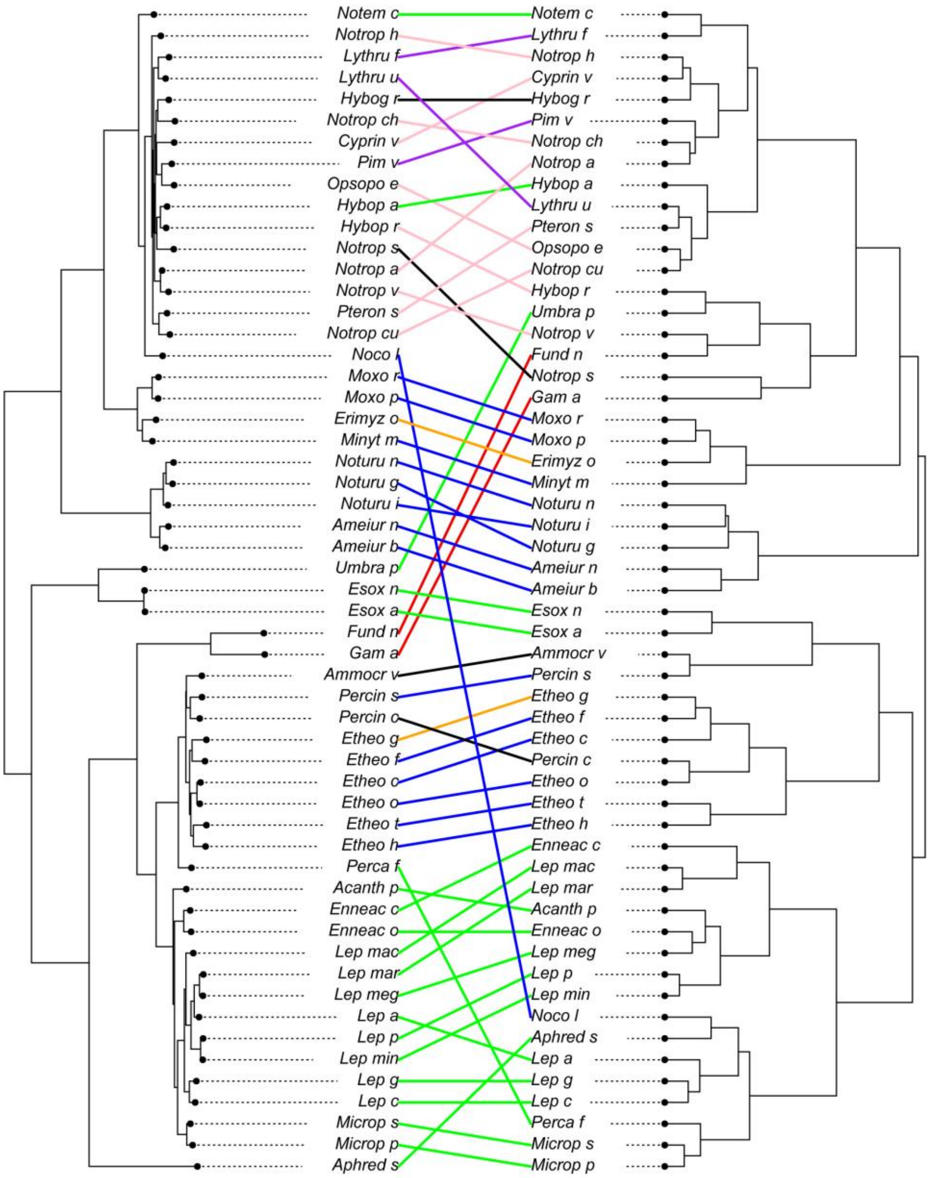
Supplementary Figure B-5: A tanglegram of species from Belize depicting possible convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Habitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), MID-HVSS (**pink** lines), MID-LVSS (**purple** lines), and TOP-LVVS (**red** lines).



Supplementary Figure B-6: A tanglegram of species from Brazil depicting only possible convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Habitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), MID-HVSS (**pink** lines), MID-LVSS (**purple** lines), and TOP-LVVS (**red** lines).



Supplementary Figure B-7: A tanglegram of species from Cambodia depicting only possible convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Habitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), MID-HVSS (**pink** lines), MID-LVSS (**purple** lines), and TOP-LVVS (**red** lines).



Supplementary Figure B-8: A tanglegram of species from USA depicting only **possible** convergent taxa of the microhabitat groupings. The phylogeny is on the left side and the phenogram from a cluster analysis of habitat associated traits on the right. The lines connect each species' position on the phylogeny and phenogram. Habitat groupings are labeled as follow: BEN-HVAS (**blue** lines), BEN-HVSS (**black** lines), BEN-LVVS (**orange** lines), MID-LVAS (**green** lines), MID-HVSS (**pink** lines), MID-LVSS (**purple** lines), and TOP-LVVS (**red** lines).

APPENDIX C

SUPPORTING INFORMATION FOR

GLOBAL TRENDS IN FUNCTIONAL AND PHYLOGENETIC STRUCTURE OF STREAM FISH ASSEMBLAGES

Supplementary table C-1: Functional traits diversity for each region based on independent-swap (*Independent*) and taxon-label (*Labels*) model and the FRic metrics. Number of stream reaches that are significantly over-dispersed, under-dispersed, and randomly structured local assemblages at the stream reaches using the corresponding stream reach as the regional species pool.

Belize						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	4	0	0	0	0
# Random	6	2	6	6	6	6
# Over-dispersed	0	0	0	0	0	0
Benin						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	0	1	1	0	0
# Random	5	5	4	4	5	4
# Over-dispersed	0	0	0	0	0	1
Brazil						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	1	1	1	1	0	0
# Random	6	6	6	6	7	6
# Over-dispersed	0	0	0	0	0	1
Cambodia						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*

Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	1	0	1	0	1	0
# Random	3	4	3	4	3	4
# Over-dispersed	0	0	0	0	0	0
USA						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	0	0	0	0	0
# Random	14	14	14	14	14	14
# Over-dispersed	0	0	0	0	0	0

Supplementary table C-2: Functional traits diversity for each region based on independent-swap (*Independent*) and taxon-label (*Labels*) model and the MNND metrics. Number of stream reaches that are significantly over-dispersed, under-dispersed, and randomly structured local assemblages at the stream reaches using the corresponding stream reach as the regional species pool.

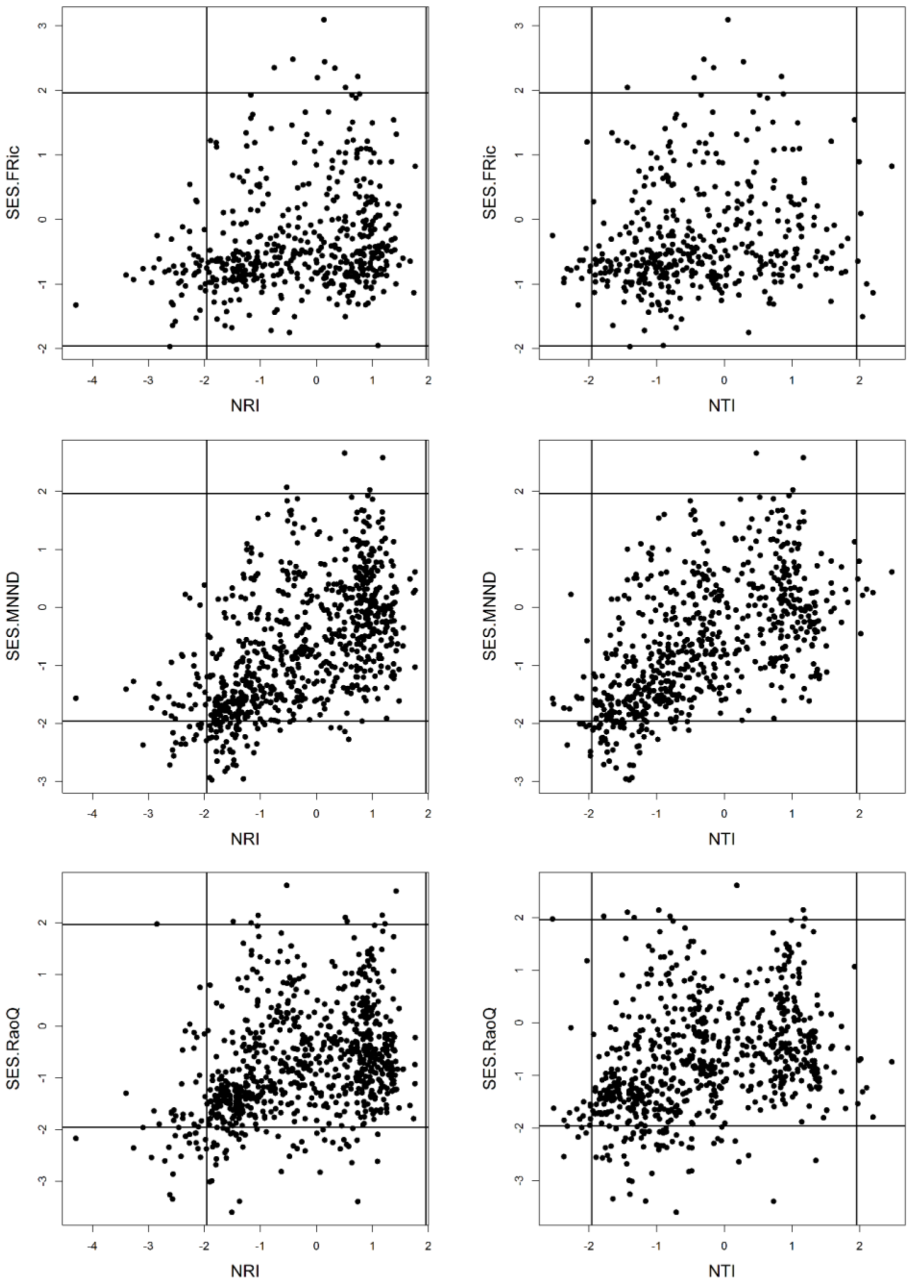
Belize						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	2	0	2	1	3
# Random	5	4	6	4	4	3
# Over-dispersed	1	0	0	0	1	0
Benin						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	2	0	0	1	1
# Random	5	3	5	5	4	4
# Over-dispersed	0	0	0	0	0	0
Brazil						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*

# Under-dispersed	0	5	1	4	0	4
# Random	7	2	6	3	7	3
# Over-dispersed	0	0	0	0	0	0
Cambodia						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	1	0	1	0	1
# Random	4	3	4	2	4	3
# Over-dispersed	0	0	0	0	0	0
USA						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	0	0	0	0	0	0
# Random	14	14	14	14	14	14
# Over-dispersed	0	0	0	0	0	0

Supplementary table C-3: Functional traits diversity for each region based on independent-swap (*Independent*) and taxon-label (*Labels*) model and the RaoQ metrics. Number of stream reaches that are significantly over-dispersed, under-dispersed, and randomly structured local assemblages at the stream reaches using the corresponding stream reach as the regional species pool.

Belize						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	5	6	2	0	5	5
# Random	1	0	4	3	1	1
# Over-dispersed	0	0	2	3	0	0
Benin						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	5	5	5	4	5	4

# Random	0	0	0	1	0	1
# Over-dispersed	0	0	0	0	0	0
Brazil						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	5	6	3	3	2	3
# Random	2	1	4	4	5	4
# Over-dispersed	0	0	0	0	0	0
Cambodia						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	2	1	2	2	2	0
# Random	2	3	2	2	2	3
# Over-dispersed	0	0	0	0	0	1
USA						
Model	*Independent*	*Labels*	*Independent*	*Labels*	*Independent*	*Labels*
Traits	*Habitat*	*Habitat*	*Trophic*	*Trophic*	*All*	*All*
# Under-dispersed	5	5	2	4	4	2
# Random	9	9	12	10	10	12
# Over-dispersed	0	0	0	0	0	0



Supplementary Figure C-1: Plots of standardized effect size (SES) for FRic, MNND, and RaoQ against NRI and NTI. Following Silva and Brandão 2014, lines mark SES values of positive and negative 1.96, SES values that were over-dispersed (>1.96) and under-dispersed (<1.96).