

Seasonal changes in the assembly mechanisms structuring tropical fish communities

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Abstract. Despite growing interest in trait-based approaches to community assembly, little attention has been given to seasonal variation in trait distribution patterns. Mobile animals can rapidly mediate influences of environmental factors and species interactions through dispersal, suggesting that the relative importance of different assembly mechanisms can vary over short time scales. This study analyzes seasonal changes in functional trait distributions of tropical fishes in the Xingu River, a major tributary of the Amazon with large predictable temporal variation in hydrologic conditions and species density. Comparison of observed functional diversity revealed that species within wet-season assemblages were more functionally similar than those in dry-season assemblages. Further, species within wet-season assemblages were more similar than random expectations based on null model predictions. Higher functional richness within dry season communities is consistent with increased niche complementarity during the period when fish densities are highest and biotic interactions should be stronger; however, null model tests suggest that stochastic factors or a combination of assembly mechanisms influence dry-season assemblages. These results demonstrate that the relative influence of community assembly mechanisms can vary seasonally in response to changing abiotic conditions, and suggest that studies attempting to infer a single dominant mechanism from functional patterns may overlook important aspects of the assembly process. During the prolonged flood pulse of the wet season, expanded habitat and lower densities of aquatic organisms likely reduce the influence of competition and predation. This temporal shift in the influence of different assembly mechanisms, rather than any single mechanism, may play a large role in maintaining the structure and diversity of tropical rivers and perhaps other dynamic and biodiverse systems.

Key words: Amazon Basin; diversity; functional trait; null model; temporal; Xingu River.

INTRODUCTION

Community ecologists now recognize that multiple assembly mechanisms can operate simultaneously (Cavender-Bares et al. 2004, Spasojevic and Suding 2012) and have focused recently on how the relative influence of mechanisms change with spatial scale and spatial variation in environmental conditions. For example, environmental filtering (inferred from clustering of functional traits) appears to be the dominant mechanism structuring plant communities at the regional scale, whereas biotic interactions (inferred from dispersion of functional traits) have been shown to operate at finer scales (Weiher et al. 2011, Gotzenberger et al. 2012). Some studies of mobile animals have observed the opposite pattern, finding evidence for environmental filtering at small spatial grains and evidence of interspecific competition at larger grain

sizes (Gotelli et al. 2010, Trisos et al. 2014). In temperate fish communities, environmental filtering was found to dominate across three spatial scales, though the types of traits driving functional similarity changed along a gradient of stream order (Troia and Gido 2015).

Considerably less attention has been given to how functional patterns and inferred assembly mechanisms vary temporally, despite wide recognition that ecological communities are highly influenced by temporal changes in environmental conditions (Junk et al. 1989, Walther et al. 2002, Houlahan et al. 2007). Most studies exploring temporal patterns of community assembly mechanisms analyze interannual changes. Purschke et al. (2013) found that the relative importance of environmental filtering in plant communities decreased throughout a 270-yr successional chronosequence, in which different-aged patches were assumed to represent a temporal sequence of change. Through the use of permanent plots analyzed over 44 yr, it was recently shown that decreases in phylogenetic and functional clustering in late successional stages result from colonization dynamics rather than the loss of closely

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related species (Li et al. 2015). In addition to variation in biotic factors, interannual fluctuations in precipitation rates have been shown to result in changes in the distribution of specific leaf area (Dwyer et al. 2014). Alternatively, interannual patterns of assembly of both plants and animals in experimental ponds changed very little over a 4-yr period (Chase 2010). This focus on interannual changes in functional assembly partially reflects the large number of studies conducted on organisms with limited mobility over short time periods.

The mechanisms structuring the assembly of highly mobile animal species may vary over much finer temporal scales. Animals can rapidly mediate competitive interactions through dispersal, suggesting that even over short temporal scales unrelated to successional stage, assembly mechanisms can vary in response to ontogenetic shifts in dispersal abilities, seasonal migrations, or intraannual changes in habitat availability. For example, the phylogenetic dispersion and functional richness of euglossine bee communities have been shown to change seasonally in response to rainfall patterns (Ramirez et al. 2015). In tropical fish communities, temporal dynamics of colonization have been shown to change on the order of weeks, and vary according to stages of the hydrologic cycle (Arrington et al. 2005, Arrington and Winemiller 2006). On the other hand, tropical estuarine fish communities showed no clear temporal changes in trait distribution patterns, with environmental filtering appearing to dominate throughout the year (Mouchet et al. 2013). The magnitude and predictability of temporal environmental changes are known to influence the distribution of life history strategies in local assemblages, population stability, food web structure, and ecosystem productivity (Power et al. 2008, Sabo et al. 2010, Mims and Olden 2012, Jardine et al. 2015), and therefore should also affect community assembly dynamics.

Because they have large and predictable variation in hydrological discharge, tropical rivers are excellent model systems to reveal the importance of temporal variation when inferring assembly mechanisms from functional diversity patterns. The ecology of large tropical rivers is strongly influenced by predictable hydrologic cycles and associated changes in available habitat and resources (Lowe-McConnell 1987, Junk et al. 1989, Chapman and Chapman 1993, Correa and Winemiller 2014). During the annual flood pulse, increased volume and connectivity of aquatic habitat and high dispersal result in reduced densities of aquatic organisms relative to base-flow conditions during the dry season. These regular fluctuations in species density should strongly influence temporal patterns of biotic and abiotic factors affecting community structure, with biotic interactions playing a greater role during low-water conditions (Zaret and Rand 1971, Arrington and Winemiller 2006). For example, the relative strength of top-down control of basal resources has been shown to shift with seasonal changes in hydrology, with stronger top-down effects during the low-water period (Winemiller et al. 2014).

To assess intraannual changes in community assembly mechanisms, we investigated functional trait patterns of tropical fish communities in the lower Xingu River, Brazil, during dry and wet seasons. Specifically, we addressed two questions: 1) are wet-season assemblages more functionally similar than dry-season assemblages, and 2) are trait distributions of dry- and wet-season assemblages significantly different from patterns derived from random assembly. Due to increased potential for biotic interactions during the low-water period, trait distributions of dry-season assemblages should be relatively dispersed and more evenly spaced compared to wet-season assemblages. Previous studies of functional assembly of fishes have found a dominant pattern of trait underdispersion, suggesting that fish assemblages are generally structured by environmental filtering (Mason et al. 2007, Mouillot et al. 2007, Troia and Gido 2015); however, dry-season assemblages of perciform fishes in tropical and temperate rivers appear to be primarily structured by biotic interactions (Montaña et al. 2014). Therefore, temporal changes were expected to manifest as a shift from trait underdispersion during the wet season to random patterns during the dry season, with the latter resulting from stochastic colonization during the preceding falling-water period (Arrington et al. 2005) and/or the combined effects of abiotic and biotic filters canceling out (Swenson and Enquist 2009).

Metrics associated with single niche axes have been shown to have a higher power of detecting complex patterns of competition and habitat filtering (Trisos et al. 2014). We therefore separately examined two sets of traits related to different niche dimensions: habitat use and trophic strategy (Winemiller et al. 2015). Due to the selective pressure of high water velocities for convergence in body shape (Lamouroux et al. 2002, Lujan and Conway 2015) and prevalence of trophic niche partitioning in fishes of tropical rivers (e.g., Lujan et al. 2012, Montaña et al. 2014), we hypothesized that fish assemblages would be underdispersed in traits related to habitat use, while traits related to trophic strategy would reveal overdispersion or even spacing.

METHODS

Data collection

Fish surveys were conducted along a 400-km stretch of the lower Xingu River, the largest clear water tributary to the Amazon River (Fig. 1A). This section of the river includes a 130-km complex of rapids and anastomosing channels over bedrock, known as the Volta Grande, which contains exceptionally high fish species richness and a variety of taxa specialized for life in high-velocity rapids (Fig. 1B). The hydrologic regime is strongly seasonal, with mean daily discharge recorded near the city of Altamira between 1976–2005 ranging from 1,222 m³/s during the low-water period to 19,331 m³/s during the high-water period (HidroWeb 2015). Water levels are

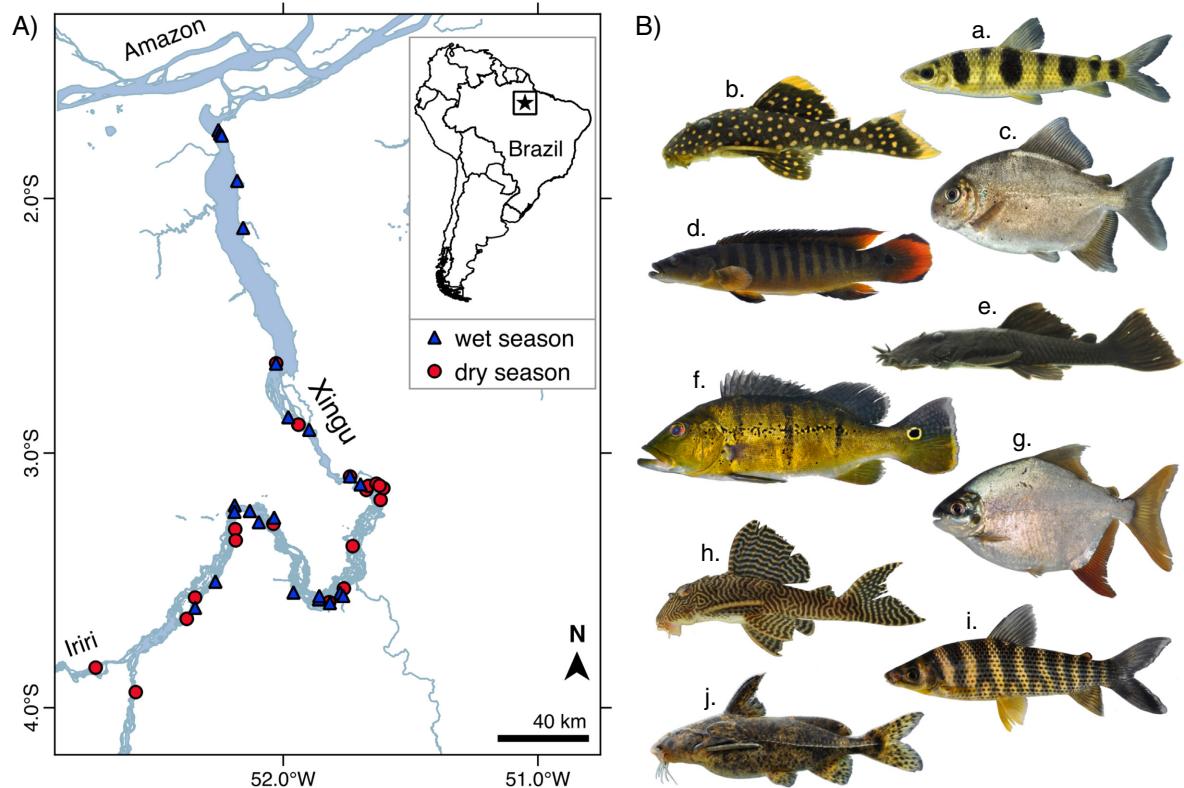


FIG. 1 Study system, showing (A) map with survey locations and (B) several representative species. Survey locations are 100-m² reaches separated by at least 1 km. Species shown are: (a) *Leporinus maculatus* (Anostomidae), (b) *Baryancistrus xanthellus* (Loricariidae), (c) *Ossubtus xinguense* (Serrasalminidae), (d) *Crenicichla* sp. (Cichlidae), (e) *Ancistrus ramunculus* (Loricariidae), (f) *Cichla melaniae* (Cichlidae), (g) *Tometes kranponhah* (Serrasalminidae), (h) *Hypancistrus* sp. (Loricariidae), (i) *Leporinus* aff. *fasciatus* (Anostomidae), and (j) *Rhinodoras* sp. (Doradidae).

lowest during September–October, when the river is composed of numerous shallow, braided channels with swift rocky rapids, and highest during March and April, when a 5-m rise in water level forms a broad singular channel that inundates a relatively confined zone of riparian forest (Zuanon 1999, Sabaj Pérez 2015).

Fishes were collected by cast net and by hand while diving/snorkeling with the help of local fishermen, providing a unique opportunity for standardized sampling methods between dry- and wet-season main-channel habitats. Surveys targeted shallow rapids and deep, swift water over rocky substrates, with each sampling site receiving 60–80 minutes of fishing effort over an area of roughly 100 m². This technique primarily targets benthic species and those that hide in crevices, though rapids-dwelling species that swim within the water column also were consistently sampled. A total of 148 species was collected from 20 sites during the 2013 dry season and 23 sites during the 2014 wet season (Fig. 1A). Although attempts were made to sample the same locations in both seasons, the dangers of surveying rapids during high water resulted in many sites being unpaired. Assemblage taxonomic structure was quite similar among sites within major reaches; therefore, variation in site placement should not bias seasonal analyses. In addition, β -diversity

measured as Whittaker's β_w was similar between seasons (analysis of multivariate homogeneity of group dispersions; $F_{(1,21)} = 0.23$; $P = 0.64$), indicating that spatial variation should not confound results.

Functional traits were measured for 41 of the most common rheophilic species, representing 9 families (Appendix S1: Table S1). Species pools varied slightly between seasons, resulting in 38 species accounting for 77% of abundance in dry season samples and 25 species accounting for 66% of abundance in wet season samples. Functional traits were divided into trait categories reflecting two fundamental niche dimensions *sensu* Winemiller et al. (2015). Nineteen morphological traits related to habitat use and swimming ability, such as body depth, fin dimensions, and eye position (hereafter “Habitat”) and 23 morphological traits related to feeding behavior and diet, such as mouth width, gut length, and tooth shape (hereafter “Trophic”), were measured on 3–6 adult individuals per species. Traits were selected based on the strength of their inferred relationships with habitat use and feeding ecology (e.g., Gatz 1979, Winemiller 1991); full descriptions of trait measurements are available in Appendix S2: Table S1. Length-based measurements were expressed relative to standard length, body depth, or head length/depth as appropriate and averaged for each species

(Winemiller 1991). Species mean trait values were log, nth root, or inverse transformed to improve normality (see Appendix S2: Table S1), and Principal Components Analysis (PCA) was performed on standardized data for the combined species pools from both seasons to visualize niche trade offs within each trait category.

Data analysis

To compare seasonal changes in community assembly, we first compared observed functional diversity between dry- and wet-season assemblages. Five functional diversity metrics were selected based on their power to distinguish assembly patterns (Mouchet et al. 2010, Aiba et al. 2013). Mean Nearest Neighbor distance (MNN) estimates how close species are in functional trait space, Standard Deviation of Nearest Neighbor distance (SDNN) estimates how evenly species are spaced, Functional Richness (FRic) was measured as the convex hull and estimates overall niche volume, Functional Dispersion (FDis) was calculated as mean distance to centroid and estimates position relative to the center of niche space, and Functional Evenness (FEve) was measured as evenness of branches of a minimum spanning tree.

PCA was applied to the standardized data for habitat and trophic traits in each season separately. Species scores on the first two PC axes (explaining 63–66% of total morphological variation) were used to compute functional diversity measures based on species presence/absence per site in each season. FRic, FDis, and FEve were calculated using the package FD (Laliberté et al. 2014) and nearest neighbor distances were calculated using the fast nearest neighbor algorithm (Beygelzimer et al. 2013) in R version 3.2.2 for OS X (R Core Team 2015). Observed functional diversity was only compared using the 21 species present in both seasons to control for variation in species richness; however, results were identical when all species were included. Functional diversity metrics for dry- and wet-season assemblages were compared using a Fligner-Killeen Test of Homogeneity of Variances and a Wilcoxon Rank Sum Test.

Functional diversity of local assemblages in each season was also compared to two null models based on species presence/absence, where the regional species pool was the 400-km stretch of river and local sites were 100 m² reaches. Both null models maintain observed species occurrence frequencies, but vary in how species richness among sites is treated. In the “uniform-fixed” model, species randomly colonized local sites with equal probability so that richness per site varies, but each site has the same average richness (Gotelli 2000). The “fixed-fixed” null model preserves observed differences in species richness between sites. By constraining both richness among sites and species occurrence frequency, the fixed-fixed model effectively tests for the impacts of species interactions and is widely used in community assembly studies. However, this model assumes nearly complete lists of species from well-defined habitat patches (e.g.,

long-term censuses of islands), an assumption that is rarely met by short-term ecological censuses based on standardized surveys. Gotelli (2000) argued that the uniform-fixed model might be more appropriate for short-term data. Therefore, we present results based on both null models for comparison. Simulations were run 1,000 times and the five functional diversity metrics described above were calculated for each community. The fixed-fixed model used the matrix-swap algorithm of Gotelli (2000) with a 1,000 step burn-in and 500 step thinning parameter, implemented via the function `RandomizeMatrix` in the package `picante` (Kembel et al. 2010). Standard Effect Size (SES) was calculated as $(\text{mean}_{\text{observed}} - \text{mean}_{\text{simulated}}) / \text{SD}_{\text{simulated}}$ for each functional diversity metric, null model, and season. Significant dispersion from random assembly was assessed using a two-sided Wilcoxon Signed Rank Test of SES values. Results were compared qualitatively between seasons.

RESULTS

The dominant pattern within functional niche space of fish assemblages from the lower Xingu River was the separation of species in the family Loricariidae from the remaining eight families in both the habitat and trophic dimensions (Fig. 2). The PCA of habitat traits (Fig. 2A) described a primary gradient (PC1) contrasting wide-bodied benthic species with large fins and eyes positioned high on the head against narrow-bodied species with relatively smaller fins and eyes positioned lower on the head. PC2 described a gradient from small, deep-bodied species to more elongate, shallow-bodied species that accounted for variation within the two major groups. Within the trophic dimension (Fig. 2B), PC1 described a gradient of species with long gut lengths, long gill rakers, and flat or rounded teeth typical of primary consumers and detritivores to species with shorter gut lengths, shorter gill rakers, and sharp-pointed teeth typical of carnivorous species. PC2 contrasted species with large oral gapes and numerous fine teeth with species having smaller mouths and fewer, more robust teeth. Species richness was highest for Loricariidae (20 spp.), which displayed a large amount of variation in both habitat and trophic niches compared to the other individual families. Several families, including Cichlidae, Anostomidae, and Characidae, revealed greater variation in habitat traits relative to trophic traits.

Observed functional diversity was significantly different between seasons, with similar temporal changes observed for both habitat and trophic traits (Fig. 3). Traits of wet-season assemblages were significantly clustered compared to dry-season communities based on MNN and FDis. In addition, FRic displayed significantly lower variance in wet-season assemblages. The evenness of trait distributions displayed a pattern opposite of that predicted, with wet-season samples being more evenly spaced (i.e., lower SDNN) than dry-season samples. FEve was not significantly different between seasons ($W = 174$, $P = 0.089$; not shown in Fig. 3).

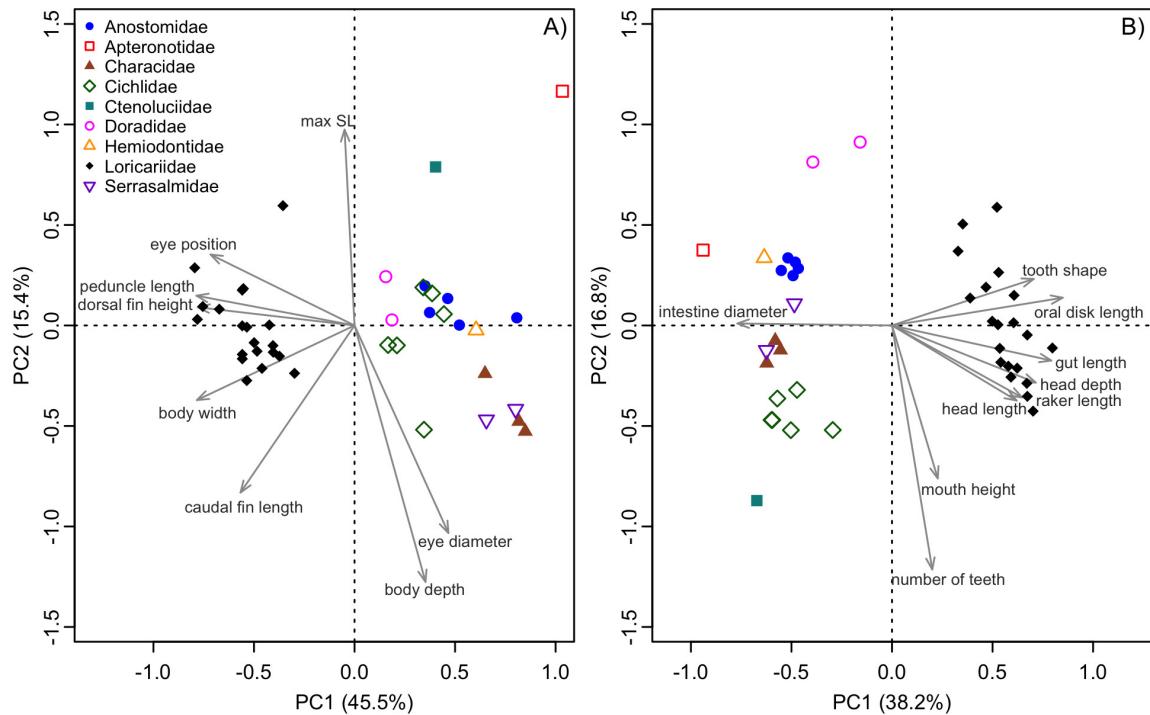


FIG. 2 Plot of Principal Components Analysis (PCA) based on functional traits of combined species pools from local assemblages sampled during dry and wet seasons. PCA was run separately on standardized data for traits related to (A) habitat use and (B) trophic ecology. Only traits with the highest factor loadings on PC1 and PC2 are shown for clarity; a full list of traits used is provided in Appendix S2: Table S1.

While results of null model comparisons differed slightly depending on the particular metric and null model used, wet-season assemblages tended to show more evidence of trait underdispersion than dry-season assemblages (Table 1). Dry- and wet-season assemblages both displayed strong evidence of being more tightly packed than random based on MNN, though results were marginally nonsignificant ($P = 0.056$) based on the fixed-fixed model for habitat traits in the wet season. However, only wet-season assemblages showed clear evidence of occupying a significantly smaller niche volume based on FRic. Wet season assemblages were significantly underdispersed in both habitat and trophic traits based on FRic for both null models, while only trophic FRic based on the uniform-fixed model revealed significant underdispersion in dry-season assemblages. Evidence for trait distributions being more evenly spaced than random was observed only for SDNN within the habitat dimension; however, the two null models differed in which season they detected significant differences. FDis and FEve were not significantly different from random expectations for either niche dimension or null model. No evidence for trait overdispersion was found.

DISCUSSION

Differences in functional diversity between wet- and dry-season fish assemblages support the hypothesis that

the relative strengths of biotic and abiotic mechanisms of community assembly can vary over the course of the annual hydrologic cycle. Direct comparison of functional diversity between seasons indicated that wet-season assemblages contained species that were more functionally similar than those in dry-season assemblages (Fig. 3). In addition, comparison with null models revealed that wet-season assemblages were significantly more similar than expected at random (Table 1), consistent with the idea that tropical fish assemblages in the wet season are highly structured by environmental filtering as they disperse and select habitats within expansive flooded areas. Higher values of MNN and FDis during the dry season suggest that local assemblages were composed of complementary resource acquisition and habitat use strategies during a time when densities of aquatic organisms and, therefore, potential for competition were greatest. Null model results based on SDNN of habitat traits found some evidence consistent with an influence of limiting similarity during the dry season (Table 1). Wet-season assemblages also showed even spacing of habitat traits under the fixed-fixed model, though this should be interpreted with caution due to unmet model assumptions (see *Methods*).

In addition to evidence for limiting similarity, functional patterns observed in dry-season assemblages also suggest an increased influence of stochastic factors relative to wet-season assemblages. The increased variance

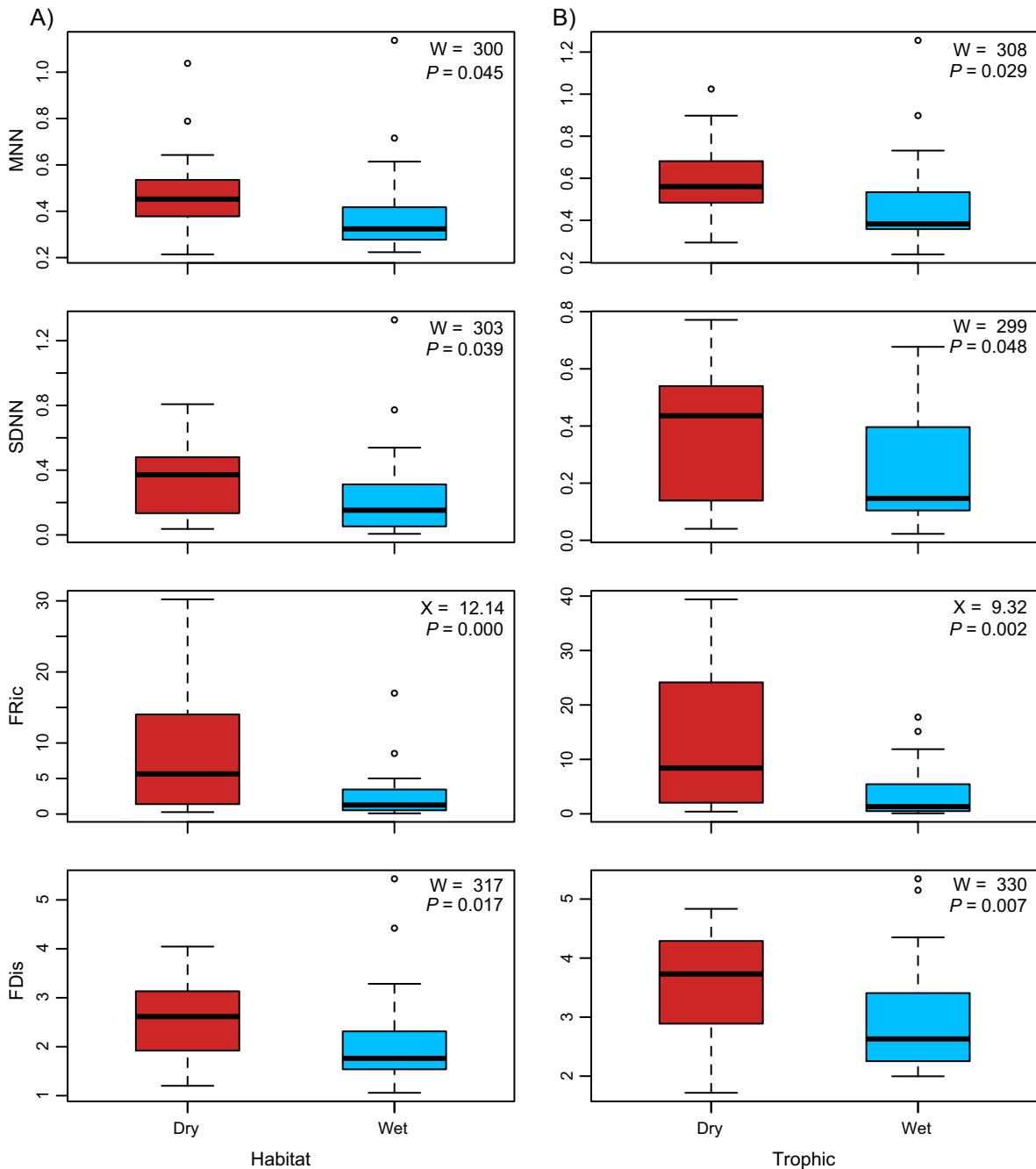


FIG. 3 Comparison of observed functional diversity of local fish assemblages during dry and wet seasons based on traits related to habitat use (A) and trophic strategy (B). Functional diversity metrics refer to mean nearest neighbor distance (MNN), standard deviation of nearest neighbor distance (SDNN), functional richness as convex hull volume (FRic), and functional dispersion as mean distance to centroid (FDis). Functional evenness was not significantly different between seasons and is not shown here. Test statistics refer to Fligner-Killeen Test of Homogeneity of Variances (W) and Wilcoxon Rank Sum Test (X).

in FRic during the dry season and nonsignificant null model results for most metrics are consistent with an influence of random colonization. Previous work on community assembly in tropical rivers has shown that initial patterns of patch colonization during the falling-water period are largely random, with increasingly

deterministic patterns revealed over time (Arrington et al. 2005). Stochastic colonization early in the dry season could lead to priority or mass effects, resulting in spatial variation in which assembly mechanism appears to dominate (Leibold et al. 2004, Allen et al. 2011). Results from experimental pond communities have

TABLE 1. Results of two-sided Wilcoxon Signed Rank test of Standard Effect Sizes (SES) based on two null modeling approaches for each trait category. Median SES, test statistic, and *P* value are given. Significant results are presented in bold italics. Negative/positive SES values represent under/over dispersion of trait distribution compared to random expectation.

Diversity index	Habitat		Trophic	
	Uniform-fixed	Fixed-fixed	Uniform-fixed	Fixed-fixed
Dry season				
MNN	<i>-0.635</i> <i>V = 50</i> <i>P = 0.039</i>	<i>-0.586</i> <i>V = 48</i> <i>P = 0.032</i>	<i>-0.393</i> <i>V = 39</i> <i>P = 0.012</i>	<i>-0.180</i> <i>V = 42</i> <i>P = 0.017</i>
SDNN	<i>-0.560</i> <i>V = 51</i> <i>P = 0.044</i>	-0.553 <i>V = 57</i> <i>P = 0.076</i>	0.085 <i>V = 87</i> <i>P = 0.522</i>	0.096 <i>V = 98</i> <i>P = 0.812</i>
FRic	-0.138 <i>V = 95</i> <i>P = 0.729</i>	-0.482 <i>V = 64</i> <i>P = 0.133</i>	<i>-0.363</i> <i>V = 13</i> <i>P = 0.000</i>	-0.215 <i>V = 72</i> <i>P = 0.230</i>
FDis	0.097 <i>V = 85</i> <i>P = 0.475</i>	-0.022 <i>V = 83</i> <i>P = 0.430</i>	-0.328 <i>V = 75</i> <i>P = 0.277</i>	-0.202 <i>V = 84</i> <i>P = 0.452</i>
FEve	0.152 <i>V = 130</i> <i>P = 0.368</i>	0.285 <i>V = 131</i> <i>P = 0.349</i>	-0.046 <i>V = 119</i> <i>P = 0.622</i>	-0.102 <i>V = 102</i> <i>P = 0.927</i>
Wet season				
MNN	<i>-0.440</i> <i>V = 56</i> <i>P = 0.011</i>	-0.529 <i>V = 75</i> <i>P = 0.056</i>	<i>-0.576</i> <i>V = 63</i> <i>P = 0.021</i>	<i>-0.613</i> <i>V = 69</i> <i>P = 0.035</i>
SDNN	-0.476 <i>V = 81</i> <i>P = 0.086</i>	<i>-0.495</i> <i>V = 70</i> <i>P = 0.039</i>	-0.663 <i>V = 107</i> <i>P = 0.360</i>	-0.692 <i>V = 99</i> <i>P = 0.247</i>
FRic	<i>-0.424</i> <i>V = 65</i> <i>P = 0.025</i>	<i>-0.376</i> <i>V = 72</i> <i>P = 0.045</i>	<i>-0.611</i> <i>V = 65</i> <i>P = 0.025</i>	<i>-0.440</i> <i>V = 30</i> <i>P = 0.000</i>
FDis	-0.371 <i>V = 93</i> <i>P = 0.179</i>	-0.629 <i>V = 92</i> <i>P = 0.170</i>	-0.472 <i>V = 104</i> <i>P = 0.314</i>	-0.493 <i>V = 92</i> <i>P = 0.170</i>
FEve	0.259 <i>V = 181</i> <i>P = 0.200</i>	0.314 <i>V = 183</i> <i>P = 0.179</i>	0.141 <i>V = 168</i> <i>P = 0.376</i>	0.111 <i>V = 157</i> <i>P = 0.580</i>

Notes: MNN, mean nearest neighbor distance; SDNN, standard deviation of nearest neighbor distance; FRic, functional richness measured as convex hull volume; FDis, functional dispersion measured as mean distance to centroid; FEve, functional evenness measured as the evenness of branches of a minimum spanning tree.

demonstrated that increased productivity can lead to increased influence of stochastic processes and priority effects due to differential colonization (Chase 2010). Aquatic primary productivity is known to increase during dry season conditions in the main channel of clear-water tropical rivers (Cotner et al. 2006), suggesting that this same mechanism may also drive the increased stochastic patterns observed. Alternatively, the simultaneous influence of opposing assembly mechanisms can result in random patterns of trait dispersion even when the assembly process is highly deterministic (Weiher et al. 2011, Spasojevic and Suding 2012).

Higher variance of FRic and greater SDNN observed for dry season assemblages did not match predictions, but can be explained by seasonal turnover in the species pool and changes in occurrence frequencies. Specifically,

higher variance in FRic was associated with a greater range in local species richness among dry-season samples (3–17 spp.) compared to wet-season samples (3–9 spp.). In addition, this turnover resulted in changes in the functional space occupied between seasons. While the majority of species in the family Loricariidae are present in collections from both seasons, several other families had more species with higher occurrence frequencies in dry-season samples, with the families Anostomidae and Serrasalminidae only present in dry-season collections. The Loricariidae occupy a distinct region of morphological trait space (Fig. 2), resulting in two distinct functional groups inhabiting Xingu rapids. The higher number of species occupying the non-loricariid functional group within local assemblages during the dry season yielded greater variance in trait spacing.

Differences in statistical results from the two null models may also be explained by seasonal shifts in functional spaces occupied within local assemblages. Because the uniform-fixed model effectively compares observed assemblages against a simulated average, it was more sensitive to additional species occupying the periphery of local assemblage morphological space during the dry season. SES SDNN was a particularly sensitive metric, with the two null models revealing opposite seasonal patterns for habitat-associated traits. Given the short duration of each survey and unpaired design, the uniform-fixed model should provide a more appropriate test of these data (Gotelli 2000), and would further support predictions for SDNN. While this model does not control for variation between sites, similarity of habitat and assemblage structure (β_w) across sites suggest that changes reflect real temporal differences in the average assemblage. These differences highlight the importance of carefully selecting functional traits, associated diversity metrics, and null models for statistical inference. Explicitly discussing model assumptions and potential data limitations may aid interpretation of results, as well as comparisons across studies.

Because the current study focused on main-channel habitats, seasonal turnover in the species pool was likely influenced by interspecific differences in lateral migrations into floodplain habitats during the high-water period. Although some loriciariids have local dispersal associated with ontogeny, lateral migrations onto floodplains are rare (Fernandes 1997, Lucas and Baras 2001). Indeed, 17 out of 19 loriciariid species analyzed were captured during both seasons, suggesting that many of these species are highly sedentary in rocky habitats within the main channel. The absence of two species of the family Serrasalmidae (*Ossubtus xinguense* and *Tometes kranponhah*) from wet-season samples is consistent with the migratory behavior of related species known to use flooded forests as feeding and nursery grounds during the high-water period (Lucas and Baras 2001, Correa et al. 2007). Similarly, the absence of anostomids from wet season samples is consistent with seasonal movements described for these fishes (Fernandes 1997, Lucas and Baras 2001, Makrakis et al. 2012). Differences in sampling efficiency between seasons also could have influenced patterns of species turnover. High turbidity during the wet season reduces visibility, which could have affected divers' ability to capture fishes swimming within the water column. Many of the species found in the water column of high velocity rapids (e.g., anostomids) were captured with cast nets, which are less efficient during the high-water period. Nonetheless, analyses performed using only species of Loriciariidae, which have a consistent sampling efficiency as evidenced by low seasonal turnover, produced identical temporal patterns in trait distributions. This suggests that seasonal changes reflect real differences in the strength of assembly mechanisms rather than sampling bias.

Despite strong selection for convergent body morphology in rapids-dwelling species, Xingu fishes have

slight differences that allow species to exploit structurally complex and heterogeneous microhabitats within rocky substrates. The even spacing of habitat traits and underdispersion of trophic traits reflect adaptations to exploit similar resources in a variety of microhabitats. Although PCA revealed large variation in trophic traits, species existing on the periphery of this space were relatively rare and had little influence on functional diversity patterns. Species with the highest occurrence frequencies (e.g., *Baryancistrus xanthellus*, *Spectracanthicus punctatissimus*, *S. zuanoni*, *Ancistrus ranunculus*) all have similar jaw and gut morphologies that facilitate feeding on benthic algae and detritus. However, these same species display large variation in body depth, with strongly dorso-ventrally compressed species, such as *A. ranunculus*, able to occupy narrow spaces between rocks that deeper-bodied species cannot access (Fig. 1B). Whereas previous studies have hypothesized that periphyton grazers and detritivores may partition trophic niches based on stoichiometric differences (Hall 2004, Lujan et al. 2012), our results imply that microhabitat partitioning is more influential in facilitating coexistence of diverse benthivorous fishes in the Xingu River. Large interspecific variation in body shape associated with habitat use is also displayed among fishes occupying other trophic positions. For example, insectivorous and carnivorous species of the family Cichlidae vary greatly in relative body depth (Fig. 1B), a trait that strongly influences performance in relation to flow velocity and substrate complexity.

While structural complexity should facilitate species co-occurrence at the local scale, seasonal relaxation of competition and predation within expanded aquatic habitat during the high-water period may play a major role in maintaining high fish diversity over a larger scale. Increased inputs of terrestrial resources during the wet season together with decreased species density should enhance fitness via greater surplus energy for growth, reproduction, and migration. It has been suggested that the predictable, gradual increase in water level during the annual flood pulse of tropical rivers should result in competitive release among fishes (Zaret and Rand 1971, Junk et al. 1989), a hypothesis consistent with findings from our study and others (e.g., Correa and Winemiller 2014). Our results stress the importance of evaluating temporal changes in functional patterns when attempting to infer assembly mechanisms. Data collected over a restricted time period would be unlikely to shed light on the interplay of multiple factors influencing communities of rivers and other dynamic ecosystems.

The degree of predictability and magnitude of environmental change will affect the relevant temporal scale, as well as our ability to infer mechanisms from patterns. Communities experiencing high magnitude changes (i.e., stress inducing) may display little temporal variation in assembly mechanisms after environmental change. For example, experimentally induced drought in pond

mesocosms increased the influence of environmental filtering for 2 yr after the perturbation (Chase 2007). Shallow floodplain depressions that experience hypoxic conditions during the dry season show little interannual variation in fish species composition, despite high colonization potential during the annual flood period (Chapman and Chapman 1993). In communities experiencing unpredictable environmental fluctuations, such as the flashy hydrologic regimes of high-gradient streams, assembly mechanisms may fluctuate so rapidly that dynamics appear largely stochastic throughout the year. Additionally, temporal variation may remain highly dependent on spatial scale, and studies integrating both temporal and spatial variation in functional trait patterns are needed to explore this potential interaction.

Several authors have cast doubt on the assumption that functional trait clustering reflects environmental filters and trait dispersion indicates a strong influence from biotic interactions (HilleRisLambers et al. 2012, Herben and Goldberg 2014). Indeed, many fishes use floodplain habitats for both resource acquisition and refuge from predation (Winemiller and Jepsen 1998). Therefore, the significant underdispersion observed in wet-season assemblages could arise not only from habitat filtering based on resource availability, but also spatial variation in predation vulnerability. This emphasizes the need to consider temporal dynamics when attempting to infer assembly processes. While trait distributions in either season could reflect multiple assembly mechanisms, the greater interspecific trait similarity observed in wet-season assemblages is consistent with predictions based on seasonal changes in species density and resource availability.

While many studies have used functional traits to infer the dominant mechanisms structuring communities, few have considered the strong potential for mechanisms, and therefore functional patterns, to change seasonally. Using tropical fishes inhabiting rapids as a model, we demonstrated that functional assemblage structure varies between hydrologic seasons. This variation reveals the interplay of multiple assembly mechanisms and suggests that studies analyzing functional patterns from a single season may overlook key aspects of the assembly process. Temporally shifting influences of multiple assembly mechanisms, rather than any specific mechanism, may play a large role in structuring high diversity systems, such as tropical rivers.

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