

High intraspecific variability in morphology and diet in tropical stream fish communities

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Abstract

Functional diversity of fish communities has been measured according to (a) interspecific variability, assuming that intraspecific variability is negligible, or (b) morphological differences, as good descriptors of complex functions, such as diet. These two assumptions have been scarcely tested on the individual level, especially in species-rich tropical ecosystems. Here, we adapted intraspecific specialisation (*ISpe*) and intraspecific originality indices (*IOri*) to assess complementary components of intraspecific variability. Next, we applied these indices to evaluate the intra- and interspecific variability of morphological and diet traits in two contrasting Brazilian stream-dwelling fish assemblages (rainforest and savannah). We also compared correlations between morphology and diet at the individual and species level to test whether accounting for intraspecific variability increases the predictability of diet due to morphological differences. Significant contributions of intraspecific variability to differences between fish were revealed for morphology and diet. Intraspecific variability in the diet was higher than that in morphology in both assemblages. The *ISpe* was positively correlated to *IOri* in the diet of both ecosystems. The morphological–dietary relationships were significant but weak at both individual and species levels. Our findings highlight the importance of measuring individual variability and accounting for complementary components of the intraspecific variability (*ISpe* and *IOri*). Importantly, we showed that the variability in morphology does not predict diet variability at both intra- and interspecific levels. Thus, high intraspecific variability in morphology and diet challenges the use of functional traits measured at the species level to describe the functional diversity of different fish assemblages.

KEYWORDS

community ecology, functional traits, originality, rainforest stream, savannah stream, specialisation

1 | INTRODUCTION

Biological characteristics of organisms reflect the resource use and habitat requirements of the species (Lavorel & Garnier, 2002) and are shaped by environmental conditions and biotic interactions (Violle et al., 2012). Understanding how the variability of these

characteristics influences the multi-faceted biodiversity at different organisation levels has been one of the most important issues in community ecology.

In general, the functional diversity of assemblages is often computed based on trait values at the species level after averaging values among individuals (e.g. Buisson, Grenouillet, Villéger, Canal, &

Laffaille, 2013; Carvalho & Tejerina-Garro, 2015; Teresa, Casatti, & Cianciaruso, 2015) under the assumption that intraspecific variability is lower than interspecific variability (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017). However, intraspecific variability has been increasingly accounted in community ecological research during the last decade (see Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Nakazawa, 2017), and there is a growing consensus it could not be negligible as it is important for the ecosystem functioning (Albert et al., 2012; de Bello et al., 2011; Violle et al., 2012). Many of these studies were led on plants, as studies on animal communities regarding intraspecific variability are less frequent. Despite that, population-level studies on many taxa have reported that individuals can strongly differ in ecological aspects, such as diet, morphology and elemental composition (Boily & Magnan, 2002; El-Sabaawi et al., 2012; Zhao, Villéger, Lek, & Cucherousset, 2014), as a response to different resource use, competitive ability or anti-predator tactics (Bolnick et al., 2011). Most studies on intraspecific variability evaluated differences among individuals from different populations from an evolutionary perspective (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2010; Svanbäck & Bolnick, 2007) or compared intraspecific variability among less than ten co-occurring species (e.g. Cachera, Ernande, Villanueva, & Lefebvre, 2017).

Intra- and interspecific variability are both affected by environmental conditions (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). The response of intraspecific variability to environmental gradients has been scarcely explored regarding animal taxa, especially fish communities that often experienced a marked gradient of conditions (Blanck & Lamouroux, 2007; Brandl & Bellwood, 2014; Erös, Heino, Schmera, & Rask, 2009; Goldstein & Meador, 2004; Matthews, Marchinko, Bolnick, & Mazumder, 2010). For example, different physical structures, such as the substratum, the intensity of water flow and the quantity of allochthonous and autochthonous organic matter, provide different available resources to be exploited by fish (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). Fish individuals show high plasticity concerning morphology and diet habits (Svanbäck & Persson, 2004; Ward, Webster, & Hart, 2006) to cope with diverse resources and variable abiotic conditions (Goulding, Carvalho, & Ferreira, 1988). For example, ecological attributes of fish, such as habitat use, feeding habitats, morphology and life-history traits, can vary along the gradient of the same tropical stream, with a different functional organisation in upstream and downstream sites (Lobón-Cerviá, Mazzoni, & Rezende, 2016; Manna, Rezende, & Mazzoni, 2012; Teresa & Casatti, 2012). Thus, the magnitude of intraspecific variability compared to interspecific variability needs to be assessed under different abiotic conditions (McGill, Enquist, Weiher, & Westboy, 2006).

Diet is a key feature of fish niche that depends on both environmental conditions and fish ecology. It determines trophic interactions between species and their impacts on ecosystem functioning (Berg & Ellers, 2010; Tullos, Penrose, Jennings, & Cope, 2009; Villéger et al., 2017). Although resource use has received more considerable attention at the level of interspecific variation, variability in

the use of resources can also occur within species (de Bello et al., 2011; Violle et al., 2012; Zhao et al., 2014). Some species exhibit a marked ontogenetic variability, with individuals from different age classes feeding on various sources (Wolff, Abilhoa, Rios, & Donatti, 2009; Zhao et al., 2014). Intraspecific variability in the diet could also be high within an age class, with individuals using different predation strategies (Bolnick et al., 2011; Zhao et al., 2014). Besides, as assessing diet composition of fish species (based on the analysis of stomach content or stable isotope concentration in tissues) is a demanding task, morphology has been suggested as a proxy for diet, under the assumption that morphological constraints determine diet (Pouilly, Lino, Bretenoux, & Rosales, 2003; Sibbing & Nagelkerke, 2001; Ward-Campbell, Beamish, & Kongchaiya, 2005). However, some studies performed at the species level reported weak morphological-dietary correlation (Albouy et al., 2011; Brandl, Robbins, & Bellwood, 2015; Ibañez et al., 2007). Such low predictability of diet based on morphological attributes could be increased through accounting for the individual variability of both morphology and diet.

Intraspecific variability is a multifaceted concept (Figure 1) that should be investigated beyond accounting for variance of attributes within species. Here, we adapted the functional specialisation (*FSpe*) and functional originality (*FOri*) indices, proposed by Mouillot et al. (2013), for measuring variability between species in an assemblage. We extended them into design indices for measuring intraspecific specialisation (*ISpe*) and intraspecific originality (*IOri*) of individuals within a species. Next, we applied these complementary indices to investigate the respective magnitude of intra- and interspecific variability in both morphology and diet, considering two fish assemblages from Brazilian rainforest and savannah biomes.

2 | MATERIALS AND METHODS

2.1 | Data collection

Fishes were sampled in two Brazilian streams (see Supporting Information Figure S1), with contrasting environmental conditions and microhabitat structure. The rainforest stream (southeastern Brazil, 22°26'47"S and 42°45'74"W) is located in the state of Rio de Janeiro. It is within a fourth-order drainage basin, surrounded by rainforest vegetation. The savannah stream (northeastern Brazil, 03°49'08"S and 39°19'57"W) is located in the state of Ceará. It is also a fourth-order drainage basin but surrounded by savannah vegetation. The rainforest stream is wider than the savannah stream (maximum width of 13 meters vs. 8 m) and deeper (maximum depth of 1.5 vs. 0.8 m). Both streams show differences in the structure of surrounding terrestrial vegetation and aquatic habitats, such as the mesohabitat, stream substratum, stream width, stream depth and water velocity (Manna, Rezende, & Mazzoni, 2017). The rainforest stream was formed by three types of mesohabitat, whereas the savannah stream was characterised by pools and runs (riffles were absent). The rainforest stream also had the highest density, regarding surrounding terrestrial

vegetation but the lowest amount of aquatic vegetation cover. The savannah stream was characterised by the presence of abundant macrophytes. The two streams studied also showed an entirely distinct fish species composition.

Fish sampling was conducted in June, July and October 2012 at the rainforest stream and in April, May and September 2012 at the savannah stream. During the sampling period, rainfall varied from 26.2 to 71.1 mm in the rainforest, and from 4.7 to 60.5 mm in the savannah. As these rainfall values are low in both biomes, the study was performed during dry months in both stream sites. In each site, a 200-meter-long stretch was delimited using two dragnets (mesh size 5 mm). We used a backpack portable electrofishing device in all sites (Mazzoni, Frenerich-Verani, & Caramaschi, 2000) to catch individual fish through successive removals, following the Zippin method (Zippin, 1958). We achieved the premises of constant electrofishing effort and capturability expected by the Zippin method in all sites. Fishes were anaesthetised in a solution of 0.4 ml of eugenol, 3.6 ml of methanol and 1L of distilled water, and subsequently fixed in formalin 10%. After 7 days, all fish specimens were preserved in ethanol 70% and stored separated by species.

2.2 | Ecomorphological trait measurements and diet assessment

Fifteen morphological measures and the wet body mass were recorded for each individual fish of every species collected, following Villéger, Miranda, Hernandez, and Mouillot (2010). These measurements led to the estimation of 13 ecomorphological traits to describe food acquisition and locomotion, by quantifying the size and shape of mouth, body and fins (Albouy et al., 2011; Mason, Lanoiselée, Mouillot, Wilson, & Argillier, 2008; Mouchet, Villéger, Mason, & Mouillot, 2010; Pouilly et al., 2003; Sibbing & Nagelkerke, 2001; Villéger et al., 2010) (for more details see Supporting Information Table S1 and Figure S2).

Stomach contents were preserved in 70% ethanol, and food items were identified under a stereomicroscope and an optical microscope to the lowest feasible taxonomic level according to the literature (Bicudo & Bicudo, 1970; Mugnai, Nessimian, & Baptista, 2010; Passos, Nessimian, & Junior, 2007; Pes, Hamada, & Nessimian, 2005; Salles, Da-Silva, Serrão, & Francischetti, 2004; Triplehorn & Johnson, 2005). Food items were grouped into seven broad categories: fish,

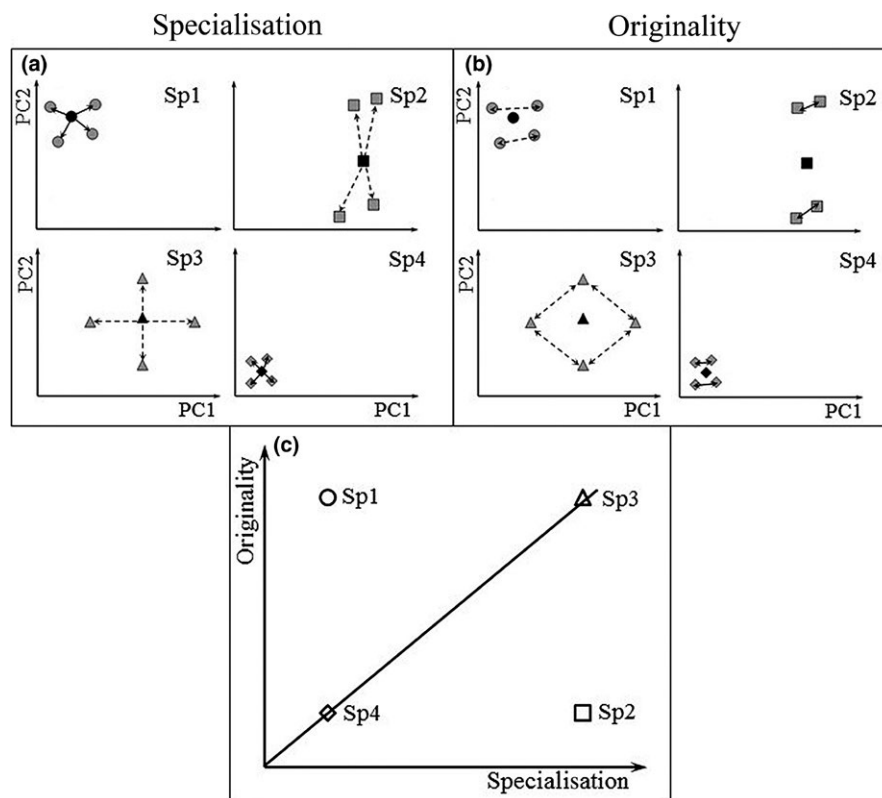


FIGURE 1 Illustration of specialisation and originality indices to assess components of intraspecific variability. Four hypothetical species (circles—Sp1, squares—Sp2, triangles—Sp3 and diamonds—Sp4) with four individuals each (grey filling) are represented in a multidimensional space, built based on attributes of all individuals (only two axes and one panel per species for graphical commodity). The average hypothetical individual of each species is represented by the black symbol. Specialisation of each of the four species is illustrated in panel (a): high values (Sp2 and Sp3) indicate that individuals are on average far from the average individual (dashed arrows), whereas low values (Sp1 and Sp4) indicate that the individuals are similar (continuous arrows). Originality is illustrated in panel (b): low values (Sp2 and Sp4) indicate that all individuals have at least one individual with similar characteristics (continuous arrows), high values (Sp1 and Sp3) indicate that each individual has unique features (dashed arrows). In this example, the four species have contrasting intraspecific specialisation and originality (c)

filamentous algae, periphyton, vegetal debris, aquatic invertebrates, terrestrial invertebrates and detritus (the classification of food items was adapted from Teresa et al., 2015). These categories based on ecological characteristics of prey reflect ecological strategies of predators and, consequently, do not account for intraspecific variation in fish preference within each category (e.g. a preference for some invertebrate species). The relative abundance of each food category was measured as the relative stomach volume occupied by the corresponding diet items in each fish (Hyslop, 1980). The volume of microscopic items, such as algae, periphyton and detritus, was estimated with a Sedgewick-Rafter counting camera (SRcc) under an optical microscope following Mazzoni, Rezende, and Manna (2010).

Data on species with at least five individuals were used in all analyses. The number of individuals per species was lower in the diet analysis because some individuals for which morphological traits were measured had empty stomachs. Individuals from all size classes were analysed to explore intraspecific variability. We included ontogenetic (juveniles and adults) and sex (female and male) variations in the analyses to express intraspecific variability, instead of just individual variations. *Parauchenipterus galeatus*, a species from the savannah assemblage, which showed only adults individuals, was removed from the analysis to avoid a possible interference in intraspecific variability.

2.3 | Assessing intra- and interspecific variability

The intraspecific variability (i.e. differences among individuals within species) and the interspecific variability (i.e. differences between species) were assessed through the same method, regarding both morphology and diet in the two assemblages. We scaled each morphological trait to a null mean and a standard deviation of 1 to give them the same weight, and, then, we computed Euclidean distances between individuals. The relative abundance of food items in the diet was used to calculate Bray-Curtis distance between all individuals. Next, we built two multidimensional spaces summarising differences in morphology (or diet) between all individuals from the two assemblages, using Principal Coordinates Analysis (PCoA) computed on Euclidean distance for morphology and Bray-Curtis distance matrices for diet, respectively. The first four axes of each PCoA provided a mean squared-deviation index (mSD; Maire, Grenouillet, Brosse, & Villéger, 2015) lower than 0.01, which proved the good quality of these four-dimensional spaces for representing species morphological and dietary dissimilarities.

The importance of variability in morphology and diet between assemblages was tested with a permutational multivariate analysis of variance (PERMANOVA), with 999 permutations, using dissimilarities among species in their respective distance matrices. Thus, one PERMANOVA was applied for morphology and another one for diet. To test for differences between intraspecific and interspecific variability, an analysis of variance (ANOVA) was performed (Cai et al., 2016; Classen, Steffan-Dewenter, Kindeketa, & Peters, 2017), which used the position of individuals on each of the four PCoA axes (Buisson et al., 2013). A separate ANOVA was applied to each

assemblage (one for the rainforest and another one for the savannah) and each group of traits (one for morphology and another one for diet). The F -statistic ratio (i.e. between-group variance/within-group variance) compiled from these ANOVAs was used to compare the relative importance of intraspecific variability between assemblages and between morphology and diet. High F values indicate a significant effect of interspecific variability, whereas low F values indicate a strong effect of intraspecific variability. To assess the relative magnitude of intra- and interspecific variability in morphology and diet in the two assemblages studied, we decomposed them into intra- and interspecific effects of a mean sum of squares computed on the position of individuals on each PCoA axis, following de Bello et al. (2011).

To go further than assessing intraspecific variability as the variance of individual features, we decomposed the intraspecific variability into two complementary facets (Figure 1). Therefore, we adapted the functional specialisation ($FSpe$) and functional originality ($FOri$) indices developed for measuring the variability of species trait values (Buisson et al., 2013; Mouillot et al., 2013). Thus, intraspecific specialisation ($ISpe$) was computed as the average distance of traits (of morphology and diet) to the hypothetical individual average in the multidimensional space per species (Figure 1a). The $ISpe$ is similar to the common definition of variability, that is, deviation from the mean. The $ISpe$ reaches its minimum value when all individuals are identical, and it increases when individuals tend to be dissimilar (i.e. low redundancy). However, a high $ISpe$ could be paired with either a few different groups made of similar individuals or individuals bearing unique features (i.e. original). Therefore, we also measured intraspecific originality ($IOri$) of each species as the average distance to the nearest-neighbour in the multidimensional space (Figure 1b). The $IOri$ reaches its minimum value when the species is represented by pairs of identical individuals and it increases when some individuals are different from all others. $ISpe$ and $IOri$ indices were computed for each species, regarding morphology and diet, respectively, through the use of the position of individuals in the corresponding four-dimensional spaces. The advantage of these indices is that they can be used to compare facets of intraspecific variability on several species simultaneously, contrary to indices developed for studying single species (e.g. Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002).

To check whether the sample size influenced estimates of intraspecific variability, we ran the Spearman correlation test between the number of individuals, for which morphology or diet was assessed, and $ISpe$ and $IOri$ values. In addition, the relationship between these two indices was also tested for both morphology and diet in each assemblage, with the Spearman correlation test. The $ISpe$ and $IOri$ of species from the rainforest and savannah assemblages were compared with the non-parametric Wilcoxon test to test whether intraspecific variability differs between fish assemblages from contrasting biomes.

Finally, we tested whether the correlation between morphological features and diet was affected by their respective intraspecific variability. For this, we performed the Mantel correlation test on Euclidean distances between individuals in the morphological and

dietary four-dimensional PCoA spaces to evaluate the relationship between morphology and diet based on individual data in each assemblage. To test how disregarding intraspecific variability affects the link between morphology and diet, we ran the same analysis using the average position of species (interspecific variability) in the four-dimension space.

All analyses were performed in the R statistical and programming environment (R 3.1.0., R Development Core Team 2014), with the “vegan” (Dixon, 2003), “ade4” (Dray & Dufour, 2007) and “ape” (Paradis, Claude, & Strimmer, 2004) packages.

3 | RESULTS

We collected 306 individuals in the rainforest stream, of four orders, eight families, and 15 species and 231 individuals in the savannah stream, of four orders, eight families and 13 species (see Supporting Information Table S2 for the full list of species). On average, the rainforest assemblage showed 20 individuals per species for morphological traits ($SD = 11.5$) and diet composition ($SD = 10.6$). The savannah assemblage showed 18 individuals per species ($SD = 13.9$) for morphological traits and 14 individuals per species ($SD = 11.1$) for diet composition. Individuals from different sizes were captured in all species, except for *Parauchenipterus galeatus* from the savannah assemblage, which was represented only by adults (Table 1).

3.1 | Intraspecific versus interspecific variability in morphology and diet

The PERMANOVA revealed significant differences between the two assemblages in both morphological (Pseudo- $F = 15.99$; $p < 0.001$) and diet variability (Pseudo- $F = 12.08$; $p < 0.001$). The ANOVA revealed significant intra- and interspecific variability in both morphology and diet of the two assemblages (see Supporting Information Figures S3 and S4 for details of the intraspecific variation on the two-first PCoA axes). Lower F values in the diet of both assemblages revealed a higher level of intraspecific variability in the diet than in morphology (Table 2).

Analysis of trait variance, based on the decomposition of the mean sum of squares, revealed that the ratio between intra- and interspecific variability was lower for morphology than diet in both assemblages (Figure 2, Supporting Information Figures S5 and S6). Intraspecific variability contributed to 17.02% and 20.00% of the total variability in fish morphology for rainforest and savannah assemblages, respectively. Intraspecific variability contributed to 39.35% and 45.54% of the total variability in the fish diet for rainforest and savannah assemblages, respectively (Figure 2).

3.2 | $ISpe$ and $IOri$ of diet and morphology in the two fish assemblages

Intraspecific specialisation ($ISpe$) and $IOri$ values of morphology in the rainforest assemblage (mean \pm $SD = 0.20 \pm 0.08$; 0.12 ± 0.03 ,

respectively) were lower than in the savannah ($ISpe = 0.26 \pm 0.14$; $IOri = 0.16 \pm 0.16$), although these differences were not significant (Wilcoxon test, $p > 0.001$). For diet, $ISpe$ values averaged 0.49 ($SD = 0.30$) in the rainforest and 0.40 ($SD = 0.32$) in the savannah, whereas the average of $IOri$ was 0.17 ($SD = 0.13$) in the rainforest and 0.14 ($SD = 0.16$) in the savannah, with no significant differences between assemblages (Wilcoxon test, $p > 0.001$; details for each species in Supporting Information Table S3). $ISpe$ and $IOri$ values for both morphology and diet were weakly correlated to the number of individuals sampled (absolute value of Spearman's $\rho < 0.4$, Supporting Information Figure S7).

Intraspecific originality ($IOri$) and $ISpe$ values for morphological traits were weakly correlated in the rainforest assemblage ($\rho = 0.23$; $p = 0.3966$, Figure 3a) but strongly correlated in the savannah assemblage ($\rho = 0.61$; $p = 0.0285$, Figure 3b). Correlations between $IOri$ and $ISpe$ values of diet were strong in both assemblages studied (rainforest: $\rho = 0.68$; $p = 0.0053$ and savannah: $\rho = 0.89$; $p < 0.0001$, Figure 3c,d, respectively).

3.3 | Effect of the intraspecific variability on the correlation between morphology and diet

Correlations between morphological dissimilarity and diet dissimilarity among individuals were significant but weak in both ecosystems (rainforest - $r = 0.305$; savannah - $r = 0.349$, Figure 4a,b, respectively). Correlations between morphology and diet dissimilarities measured at the species level were higher in both ecosystems, with the highest value found in the savannah assemblage (rainforest - $r = 0.331$; savannah - $r = 0.645$, Figure 4c,d, respectively).

4 | DISCUSSION

Intraspecific variability contributed to more than 20% of the total variability in the diet and morphology among all fishes. The intraspecific variability found was higher in the diet than morphology in the two assemblages, which highlights the different use of trophic resources by individuals. Species with high dietary intraspecific variability can be linked with specific morphological traits, which enables the use of a wide variety of food resources (Vrede et al., 2011; Zhao et al., 2014), in addition to high plasticity and ontogenetic changes (Brandl & Bellwood, 2014; Guo et al., 2014). Moreover, these features can influence the variation within and among species and are related to changes during fish development across morphological, physiological, and behavioural characteristics (Amundsen et al., 2003; Bonato & Fialho, 2014). Intraspecific variability was slightly higher in the savannah stream, which could be related to a higher heterogeneity in microhabitat and resource availability (Manna et al., 2017) and could favour the coexistence of individuals with more contrasting diets and morphologies. These results highlight the importance of intraspecific variability as an essential process for species coexistence, as variability can occur in stream assemblages with entirely different environmental characteristics.

TABLE 1 Body size distribution (maximum, minimum, mean and standard deviation values) and number of analysed individuals on each size class and group of traits for each species in the two studied assemblages

	Body size range (mm)				Number of individuals				Dietary analyses
	Maximum	Minimum	Mean	Standard deviation	Juveniles	Adults	Morphological analyses		
Rainforest									
<i>Astyanax janeiroensis</i>	92.45	58.12	82.56	12.60	1	5	6	3	
<i>Astyanax taeniatus</i>	106.88	67.14	85.72	12.59	6	11	17	16	
<i>Astyanax hastatus</i>	63.9	51.08	57.36	3.37	4	17	21	21	
<i>Bryconamericus microcephalus</i>	50.73	32.12	41.84	5.25	9	14	23	23	
<i>Mimagoniastes microlepis</i>	48.21	13.56	29.92	8.46	17	27	44	44	
<i>Schizolecis guntheri</i>	47.62	28.93	38.05	5.07	5	12	17	17	
<i>Trichomycterus gr. zonatus</i>	54.79	27.49	42.02	9.58	3	5	8	8	
<i>Gymnotus pantherinus</i>	221.43	112.59	176.10	33.19	1	9	10	7	
<i>Ancistrus multispinis</i>	78.50	27.59	47.24	21.16	6	3	9	9	
<i>Acentronichthysleptos</i>	77.43	28.60	57.22	13.42	8	11	19	16	
<i>Scleromystax barbatus</i>	65.39	24.37	49.59	10.95	4	16	20	17	
<i>Rineloricaria sp.</i>	146.99	61.44	100.73	22.92	8	16	24	23	
<i>Phalloceros harpagos</i>	27.68	15.3	19.03	3.14	5	13	18	18	
<i>Characidium vidali</i>	62.22	24.17	44.46	9.20	13	30	43	39	
<i>Pimelodella lateristriga</i>	106.61	27.32	71.18	21.43	15	14	29	23	
Savannah									
<i>Parauchenipterus galeatus</i>	166.10	140.60	150.59	7.30	0	10	-	-	
<i>Prochilodus brevis</i>	219.00	61.02	106.95	50.25	5	6	11	8	
<i>Leporinus piau</i>	228.00	72.82	138.50	49.31	1	5	6	5	
<i>Hypostomus jaguribensis</i>	150.17	16.73	99.29	57.01	2	3	5	5	
<i>Compsura heterura</i>	27.52	17.58	23.90	2.33	13	41	54	46	
<i>Serrapinus piaba</i>	32.09	23.68	28.02	1.94	5	20	25	16	
<i>Astyanax fasciatus</i>	72.54	32.57	46.38	9.35	9	14	23	19	
<i>Astyanax bimaculatus</i>	68.50	20.09	43.01	14.81	3	7	10	10	
<i>Hoplias malabaricus</i>	272.00	1791	56.25	65.08	14	2	16	12	
<i>Poecilia vivipara</i>	32.29	15.96	23.72	4.62	16	20	36	20	
<i>Poecilia reticulata</i>	20.33	11.70	14.26	2.91	5	4	9	8	
<i>Cichlasoma orientale</i>	70.58	12.58	44.71	23.50	6	8	14	11	
<i>Crenicichla menezesi</i>	95.18	24.69	38.94	20.76	9	6	15	14	

TABLE 2 Results of ANOVA testing intraspecific versus interspecific variability on the four PCoA axes for morphological and dietary traits in the two studied assemblages

	Rainforest				Savannah			
	Morphology		Diet		Morphology		Diet	
	F	p value	F	p value	F	p value	F	p value
Axis 1	78.94	<0.001	43.17	<0.001	69.27	<0.001	19.32	<0.001
Axis 2	83.83	<0.001	46.62	<0.001	124.7	<0.001	9.62	<0.001
Axis 3	226.1	<0.001	7.92	<0.001	59.28	<0.001	22.05	<0.001
Axis 4	66.48	<0.001	25.07	<0.001	44.21	<0.001	13.79	<0.001

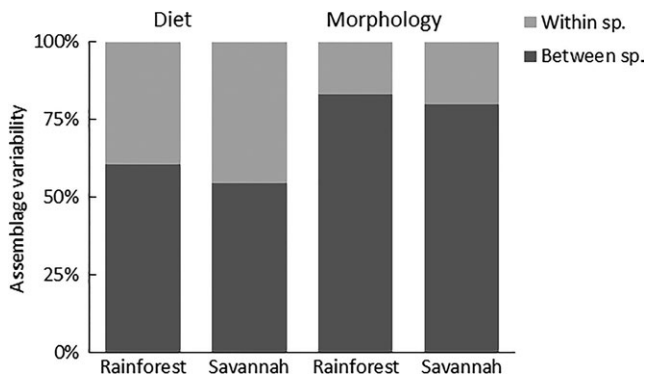


FIGURE 2 Partitioning of intra- and interspecific variability (light gray and dark gray elements, respectively) on morphology and diet in the two different assemblages. The values are expressed as a mean proportion of trait variance of the first four PCoA axes computed on morphological or diet dissimilarity

Species with high values of *ISpe* gather individuals that use a wide range of resources into different functional entities (Villéger et al., 2017), whereas a high *IOri* indicates that individuals into these entities are varying on ecological features (Buisson et al., 2013; Mouillot et al., 2013). For example, groups of individuals can feed on different resources, revealing ontogenetic or sexual variation (i.e. high *ISpe*), whereas assemblages with high values of *IOri* are represented by individuals within these groups feeding on different preys. In this sense, given the complementarity between *ISpe* and *IOri*, the differences between values of the two indices indicate the use of *IOri* as a relevant framework to assess the intraspecific variability of morphology and diet. A high *IOri* indicates differences between pairs of individuals and, consequently, unique particularities of some individuals could be revealed. For example, individuals of two Siluriformes species, one from each assemblage (*Trichomycterus gr. zonatus* and *Hypostomus jaguribensis*), were on average more original than specialist. This pattern of high *IOri* between pairs of individuals reveals that the high intraspecific variability is coupled to a high level of uniqueness of individuals.

For instance, some species have a high morphological *ISpe* and a low *IOri* because intraspecific variability occurs between and within functional entities (e.g. sex and age class). Such species were present in both rainforest (*Phalloceros harpagos*, *Rineloricaria* sp. and *Gymnotus pantherinus*) and savannah assemblages (*Prochilodus brevis*, *Poecilia reticulata* and *Poecilia vivipara*). They were represented by

individuals of different life stages and sexes, whereas closely related species showed sexual dimorphism or ontogenetic morphological changes (Bisazza & Pilastro, 1997; Galindo-Villegas & Sosa-Lima, 2002; Leal, Junqueira, & Pompeu, 2011; Py-Daniel & Fernandes, 2005). As an opposite example, *Hypostomus jaguribensis* from the savannah assemblage, showed high *ISpe* and *IOri* values in morphology. This result means that individuals are unique with no morphological redundancy between them. Functionally unique species can perform key functions for the maintenance of biotic assemblages, directly affecting some ecosystem functions (Córdova-Tapia & Zambrano, 2016; Scherer-Lorenzen, 2005). Considering the complementarity of *ISpe* and *IOri* and the importance of intraspecific variability as an essential process for community assembly structuring, we believe that the use of these two indices can help researchers to detect intraspecific variability in many assemblages, as it has been described in populations but not in communities.

Regarding diet, most species showed high *ISpe* and *IOri* (see Figure 3c,d). However, feeding habits are more plastic than morphology. Thus, individuals are more prone to change feeding habits, which results in high intraspecific variability (Buisson et al., 2013). Two Poeciliidae species, one from each assemblage (*Phalloceros harpagos* and *Poecilia vivipara*) and two Loricariidae species, also one from each assemblage (*Rineloricaria* sp. and *Hypostomus jaguribensis*) were represented by individuals with high values of both intraspecific indices. Dietary versatility is a striking aspect of neotropical fishes and most species can change from one food item to another whenever the trophic resource availability oscillates (Guo et al., 2014; Manna et al., 2012). Furthermore, this versatility is paired with intraspecific variability in the diet that can be driven by differences in body size, for example, larger sized individuals consume larger prey more efficiently (Weise, Harvey, & Costa, 2010).

On the other hand, some species exhibited low *ISpe* and *IOri* values, testifying for their narrow diet (i.e. not variable among individuals). Such examples were found at several trophic levels; detritivores (*Prochilodus brevis*), invertivores, such as *Compsura heterura* (savannah assemblage), *Gymnotus pantherinus* and *Trichomycterus gr. zonatus* (rainforest assemblage) and carnivores/piscivores (*Crenicichla menezesi*). Although Characidae species are opportunistic and generalist feeders (Lobón-Cerviá & Bennemann, 2000; Manna et al., 2012), *C. heterura* consumed exclusively aquatic invertebrates, which could be related to an association between invertebrates and aquatic macrophytes that provides feeding microhabitats to this fish species

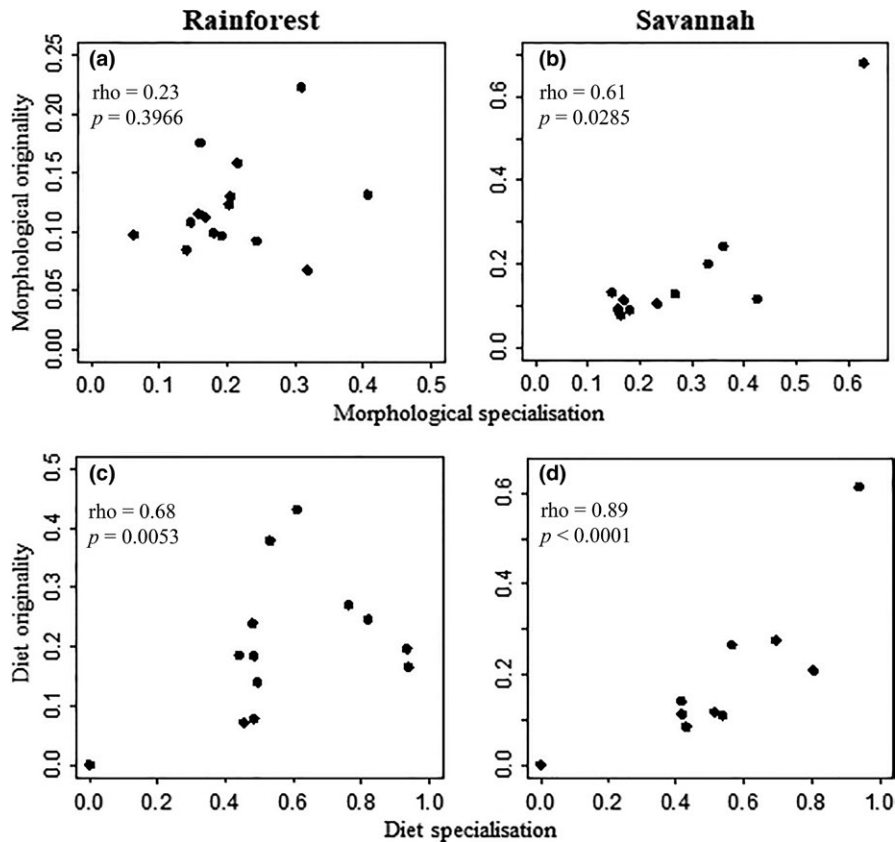


FIGURE 3 Correlations between morphological specialisation and originality (a and b), and diet specialisation and originality (c and d) for the two fish assemblages from rainforest and savannah ecosystems. The rho value is Spearman's correlation coefficient with associated p -values

(Manna et al., 2017). *Crenicichla* species are considered ambush predators that are commonly hidden in marginal vegetation and quickly attack their prey (mostly aquatic invertebrates and small fishes; Brejão, Gerhard, & Zuanon, 2013). Thus, the consumption of a specific dietary item can be influenced by abiotic conditions, such as microhabitat heterogeneity (Quirino, Carniatto, Guglielmetti, & Fugi, 2017), and resources availability (Evangelista, Boiche, Lecerf, & Cucherousset, 2014). However, fish diet was assessed based on gut content, which could exacerbate the level of inter-individual variability. Future studies should confirm our results by the use of approaches describing average diet through time (e.g. using stable isotopes).

Morphological variability was not strongly correlated with diet dissimilarity between species (interspecific variability) in the two assemblages studied ($r < 0.7$). Besides, correlation coefficients were lower than those reported in previous studies, such as Ibañez et al. (2007), regarding relationships between diet and morphology in 30 fish species from tropical forest streams of the Bolivian Amazon (0.953 and 0.757 on the two-first axis of the Redundancy Analysis). These results suggest that the morphological constraints (e.g. oral gape size and shape), which determine patterns of resource use, are not strict enough to explain feeding habits of fishes that change their choice of prey resources according to biotic or abiotic conditions. Thus, the morphological and diet variability were weakly correlated due to versatile dietary behaviour among species with similar morphology (Boyle & Horn, 2006; Labropoulou & Eleftheriou, 1997) and a trophic convergence between species with different morphologies (Norton & Brainerd, 1993).

Although there is a weak correlation between morphology and diet dissimilarities, the novelty of the present study is that accounting for intraspecific variability considering both diet and morphology did not improve the correlation. Fish species in Neotropical streams have high plasticity and versatility in their diet (Lowe-McConnell, 1987; Svanbäck & Persson, 2004) and even species with specialist morphology are not necessarily associated with specialised diets (Bellwood, Wainwright, Fulton, & Hoey, 2006). This versatility allows individuals with similar morphology to have different diets. For example, closely related species can feed on different resources (Ross, 1986) and change according to environmental characteristics (Lobón-Cerviá et al., 2016; Quirino et al., 2017; Vrede et al., 2011). In our study, the dietary-morphological correlation is higher in the savannah than in the rainforest assemblage. Hence, the two systems show different availability of aquatic vegetation with higher diversity in the savannah stream, which enhances heterogeneity in feeding microhabitats. As a result, the morphology explained better the diet in the savannah assemblage. As streams with high physical heterogeneity host species with unique morphological adaptations (Manna et al., 2017), the morphological and diet plasticity can be influenced by environmental variability (Bellwood et al., 2006; Hegrenes, 2001).

In conclusion, the present study offers a framework to assess two complementary components of intraspecific variability, namely intraspecific specialisation (*ISpe*) and intraspecific originality (*I Ori*), and reports high levels of these two components in two species-rich

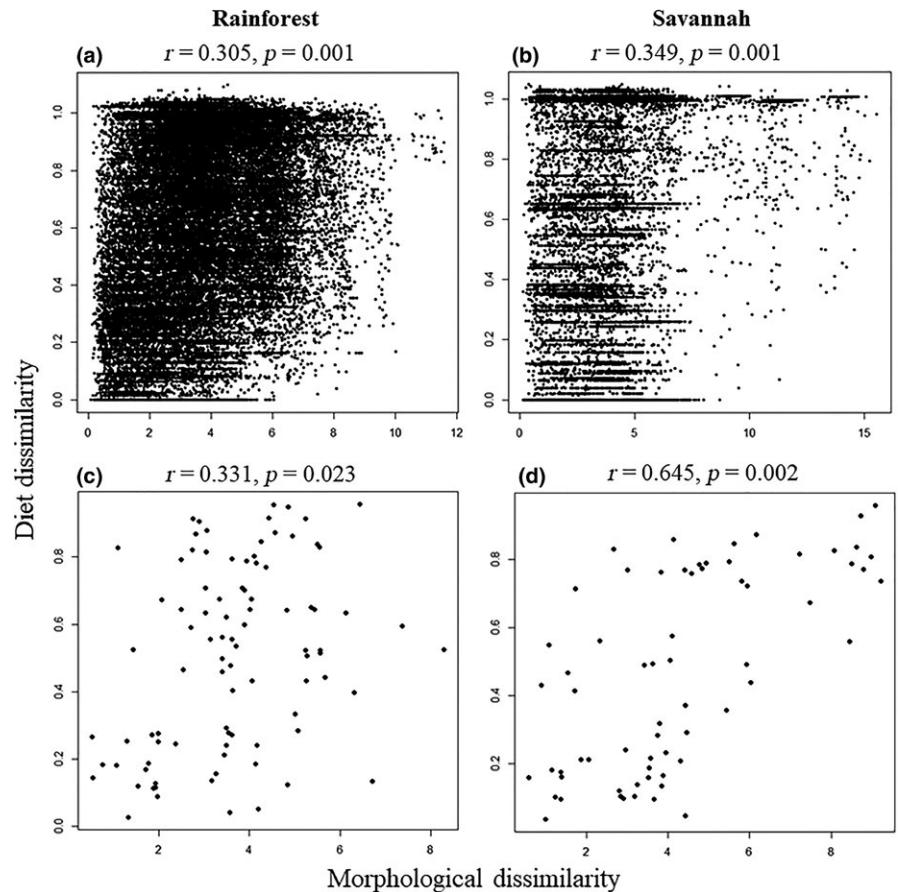


FIGURE 4 Correlation between dissimilarity in fish morphology and fish diet for the rainforest and savannah ecosystem. Top panels show correlation computed on individuals data (a and b), that is, the Euclidean distance between individuals on the first four axes of PCoA led to morphological features and diet composition, respectively. Bottom panels show results computed on average position of species on PCoA axes (c and d). Values of Mantel's correlation test are provided at the top of each panel

freshwater fish assemblages, highlighting the importance of measuring individual differences in empirical ecological studies. Our results also show that integrating intraspecific variability is necessary to further ecological analyses measuring functional diversity. The considerable variability of morphological traits and diet within species challenges the use of mean values of functional traits to describe functional diversity in different environments. Besides, it is important to consider the feeding habits of the individuals as morphological features did not explain the choice of prey resources in these fish species. From an applied perspective, we propose that species mean traits should be replaced by populations mean traits when intraspecific variability is high to accurately quantify the link between the functional trait variation and environmental conditions or ecosystem processes.

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SUPPORTING INFORMATION

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