Habitat use, trophic, and occurrence patterns of *Inpaichthys kerri* and *Hyphessobrycon vilmae* (Pisces: Characidae) in Amazonian streams

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Fish ecomorphology and diet can help us to understand species response to impacts and coexistence patterns. Thus, we developed a comparative analysis of ecomorphology and diet of *Inpaichthys kerri* and *Hyphessobrycon vilmae* and tested for environmental variables that explain their abundance in headwater streams. We sampled streams from the Aripuanã River basin, Mato Grosso State, Brazil. We sampled environmental variables following a standardized protocol and used 30 and 80 individuals from each species to obtain ecomorphological attributes and feeding index, respectively. To identify environmental variables that influence species abundance, we developed generalized additive mixed models. *Inpaichthys kerri* presented broader and deeper caudal peduncles, more dorsal eyes, and larger fins, besides the lower consumption of aquatic insects, algae, and detritus when compared to *H. vilmae*. *Inpaichthys kerri* was more abundant in fast waters with little amounts of marginal grasses, conditions associated with more forested streams, while *H. vilmae* was more abundant in streams with more abundant marginal grasses from pasture. Deforestation in the Aripuanã basin threatens the persistence of *I. kerri*, since its optimal environmental conditions tend to be replaced by *H. vilmae* optimal conditions. Natural history helps us to understand species occurrence and represents a substantial contribution for more effective conservation measures.

Keywords: Deforestation, Diet, Ecomorphology, Marginal grasses, Species coexistence.

Ecomorfologia e dieta dos peixes nos ajudam a entender a resposta das espécies aos impactos e padrões de coexistência. Nós desenvolvemos uma análise comparativa da ecomorfologia e dieta de *Inpaichthys kerri* e *Hyphessobrycon vilmae* e testamos quais variáveis ambientais explicam suas abundâncias em riachos. Nós amostramos riachos da bacia do rio Aripuanã, Mato Grosso, Brasil. Amostramos variáveis ambientais seguindo protocolo padronizado e usamos 30 e 80 indivíduos de cada espécie para obter os atributos ecomorfológicos e a dieta, respectivamente. Para identificar as variáveis ambientais que influenciam a abundância, nós desenvolvemos Modelos Mistos Aditivos Generalizados. *Inpaichthys kerri* apresentou pedúnculos caudais mais largos e compridos, olhos mais dorsais e nadadeiras mais largas, assim como menor consumo de insetos aquáticos, algas e detritos comparado à *H. vilmae*. *Inpaichthys kerri* foi mais abundante em águas rápidas e com menos gramíneas marginais (riachos mais florestados), enquanto *H. vilmae* foi mais abundante em riachos com mais gramíneas (pastagem). O desmatamento no Aripuanã ameaça a persistência de *I. kerri* porque pode substituir as condições ambientais ótimas para essa espécie pelas condições de *H. vilmae*. A história natural das espécies auxilia no entendimento dos padrões de ocorrência e representa importante contribuição para medidas conservacionistas mais efetivas.

Palavras-chave: Coexistência de espécies, Desmatamento, Dieta, Ecomorfologia, Gramíneas marginais.

INTRODUCTION

Headwater streams are small and open ecosystems highly interconnected to the terrestrial environment (Allan, 2004). The land cover at catchment and riparian corridor scales can drive physical habitat structure, water quality (Heartsill-Scalley, Aide, 2003; Fernandes *et al*., 2013; Tanaka *et al*., 2016), and food items availability to the stream biota (Sweeney, 1992; Carvalho *et al*., 2017; Manoel, Uieda, 2018). Native forests provide allochthonous structures, like roots, leaves, and trunks that create different stream habitats and increase the supply of terrestrial food items, mainly insects and seeds, for stream fishes, for stream fishes (Lo *et al*., 2020). However, anthropic-driven shifts in the land cover (*e.g*., deforestation followed by pasture/agriculture development) have homogenized physical habitat conditions by the loss of meso and microhabitats associated with forests (Walrath *et al*., 2016; Zeni *et al*., 2019) and the invasion of exotic grasses (Zeni *et al*., 2019). Moreover, agriculture expansion over Tropical Rainforest biomes (*e.g*., Amazon) has changed the energetic balance in streams by altering resource availability, since it shifts predominant resources from allochthonous (*e.g*., terrestrial insects and plants) to autochthonous (*e.g*., aquatic insects and algae) (Zeni, Casatti, 2014).

These changes caused by human activities have the potential to influence several aspects related to the occurrence and persistence of fish assemblages, such as habitat use and trophic ecology (Chua *et al*., 2020). In fact, Chua *et al*. (2020) found that morphological traits can mediate fish occurrence in streams under deforestation, since fish with superior mouths and small body mass were associated with marginal grasses and

reduced wood debris. According to these authors, fishes with such morphological traits are more successful in the use of trophic resources (*e.g.*, drifted insects) and habitats in oil palm streams. Thus, ecomorphology, that studies the relationship between body shape and patterns of habitats use and foraging behavior by fishes, represents an important tool to understand patterns and process in fish ecology and conservation (Bourke *et al.*, 1997; Peres-Neto, 1999; Oliveira *et al.*, 2010; Feilich, López-Fernández, 2019). For example, depressed and elongated body with large pectoral fins, as in Loricariidae, facilitates the occupancy of bottom habitats with high water velocity (*e.g.*, riffles) because these characteristics can deflect most of the dragging forces present in the high current (Casatti, Castro, 2006; Oliveira *et al.*, 2010). In a scenario of deforestation followed by the loss of riffles due to siltation, species with these morphological features will probably be locally extinct.

Besides ecomorphology, land use (Ferreira *et al.*, 2012) and instream habitat changes (Zeni, Casatti, 2014), trophic aspects can trophic aspects can also be driven by be driven by species interactions (Barros *et al.*, 2017). For instance, Barros *et al.* (2017) showed that individuals of *Hyphessobrycon* aff. *melazonatus* Durbin, 1908 have trophic plasticity and change their diet when in the presence of other small characids. According to these authors, this is a vital mechanism to weaken deleterious species interaction that, ultimately, promotes species coexistence. Although tropical stream fishes occupy almost the entire spectrum of trophic niches that can occur in aquatic communities (Winemiller *et al.*, 2008) probably mediated by their general morphology (Abelha *et al.*, 2001), species coexistence, occurrence, and abundance can be determined by resource partitioning that minimizes interspecific competition (Silva *et al.*, 2016).

For closely related species, niche segregation (Bouton *et al.*, 1997) and adjustments to different environmental conditions (Manna *et al.*, 2012) can facilitate species coexistence. In the Neotropical region, this issue has been studied mostly for loricariids (*e.g.*, Manna *et al.*, 2012; Leitão *et al.*, 2015; Abilhoa *et al.*, 2016), a group that generally shows conservative morphology and similar ecological requirements. For characids, by contrast, morphology and ecology correlate to a lesser extent (for examples of morpho-ecological convergence see Casatti, Castro, 2006; Mazzoni *et al.*, 2010) and coexistence mechanisms remain little known. Several authors consider resource abundance, feeding plasticity, and differential habitat use as primary explanations for characid species coexistence (Ceneviva-Bastos *et al.*, 2010; Manna *et al.*, 2012; Moraes *et al.*, 2013). Despite being the most abundant family in Neotropical streams (together with Loricariidae) (Lowe-McConnell, 1999), characids members still pose unanswered questions regarding morphology and dietary relationships.

A morphologically similar pair of characids is represented by the so-called "tetras" *Inpaichthys kerri* (Gery, Junk, 1977) and *Hyphessobrycon vilmae* (Géry, 1966) (Fig. 1), from meridional Amazon headwater streams, where their relative abundances differ according to the stream conditions (Casatti *et al.*, 2020). In the present study, we developed a comparative analysis of ecomorphology and diet of *I. kerri* and *H. vilmae* and tested for environmental variables that can explain the abundance of these species in the set of streams where they occur. Considering that morphology resemblance would predict similar ecological requirements between closely related species (see Feilich, López-Fernández, 2019), we predict that *I. kerri* and *H. vilmae* would show similar habitat use and trophic patterns. However, because there is a limit to the similarity that

allows species coexistence (MacArthur, Levins, 1967), we may expect that each species will have their abundance maximized in different environmental conditions if high trophic and ecomorphological niche resemblance are observed.

MATERIAL AND METHODS

Study area and target species. We developed the study in the Aripuanã River basin, north of Mato Grosso State, Brazil. The Aripuanã River belongs to the Amazonian basin in the "Madeira Brazilian Shield" ecoregion, which has high richness and endemism of fish species (WWF, TNC, 2015). The region is in the deforestation arc, where the native forests are being replaced by pasture since the 1980's, with higher intensity occurring after the year 2000 (Casatti *et al.*, 2020). In this basin, we sampled 30 streams reaches (80 meters length) in independent catchments (Fig. 2) during the dry period in the region, in July and August 2017. Samples were done in the dry season because of the access to the streams and the low water volume, which guarantees a standardized sampling of the target species.

Inpaichthys kerri is a small fish characterized by the presence of an incomplete lateral line and a caudal fin without scales. It is a monotypic genus, characterized by having a superior mouth, more posterior dorsal fin, and relatively deep caudal peduncle (Fig. 1A).

FIGURE 1 | Lateral view of **A.** *Inpaichthys kerri*, 34 mm SL; and **B.** *Hyphessobrycon vilmae*, 32 mm SL. Photos: A. R. Manzotti.

Inpaichthys kerri is endemic from Aripuanã River basin and inhabits relatively fast waters (Géry, Junk, 1977). *Hyphessobryon vilmae* is also a small fish with a relatively elongated body, dorsal fin in the middle portion of the body, and small pectoral fins not reaching the insertion of the pelvic fins (Géry, 1966) (Fig. 1B). There is no information on the
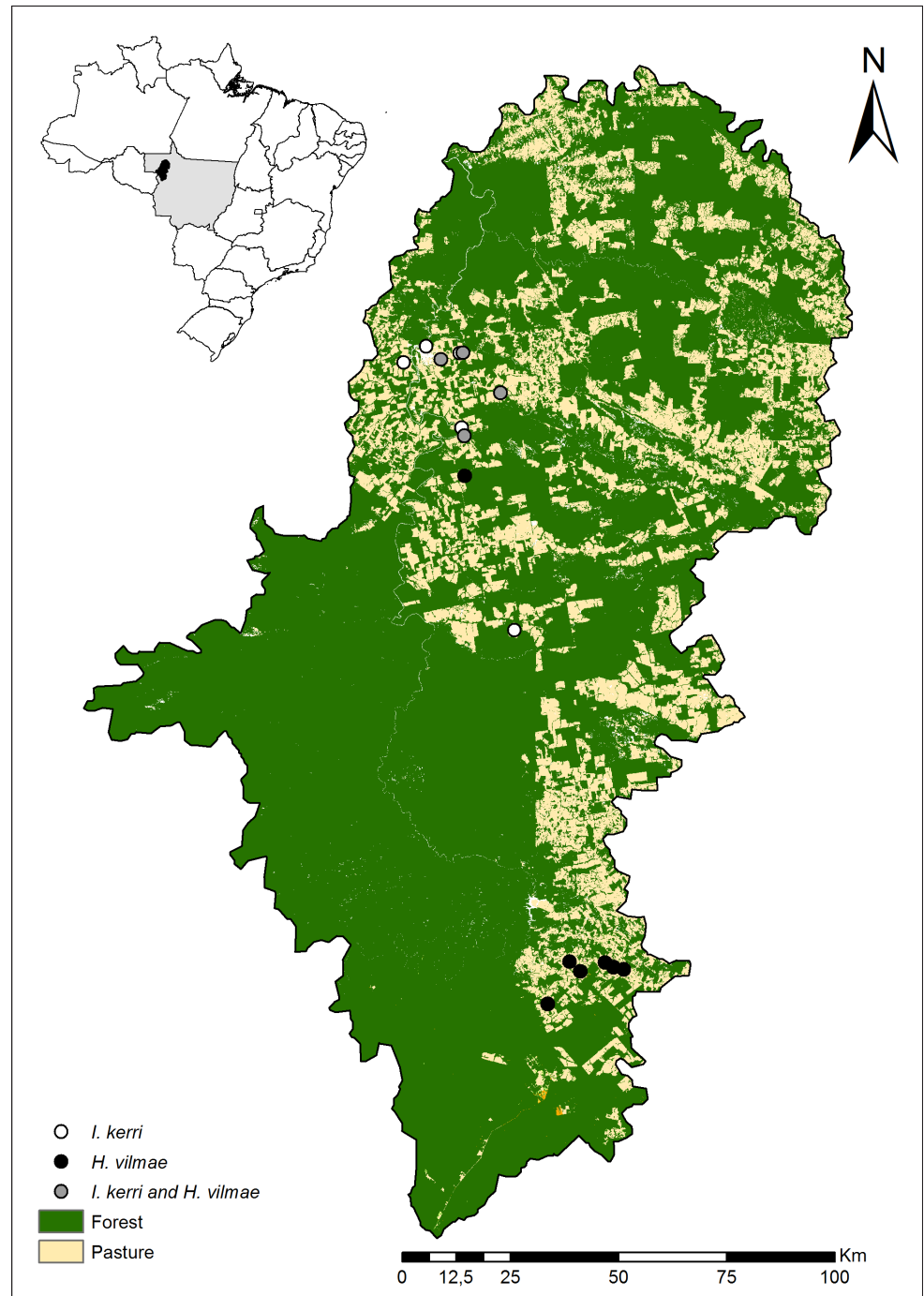
FIGURE 2 | Location of the sampled streams in the Aripuanã River basin, Mato Grosso State, Brazil. White circles represent streams with *Inpaichthys kerri*, black circles represent streams with *Hyphessobrycon vilmae*, and gray circles represent streams with both species.

habitat use or other ecological aspects of this species, but it belongs to the *Hyphessobrycon heterorhabdus* group (Fernando R. Carvalho, 2019, pers. comm.), in which the species uses marginal habitats while foraging items drifted by the current (Brejão *et al.*, 2013).

Field sampling. We used upstream and downstream block nets and sampled fish species with a hand seine (2 mm mesh) and a dip net (2 mm mesh) for one hour by two collectors. We anesthetized collected fishes with eugenol (Lucena *et al.*, 2013), fixed them with formaldehyde (10%), and after 72 h, transferred them to alcohol (70%). All specimens are deposited in the fish collection of the Departamento de Zoologia e Botânica – Universidade Estadual Paulista, São José do Rio Preto, SP, Brazil - DZSJRP (voucher numbers presented in the Tab. 1).

We used a standardized protocol to obtain physical and chemical variables. We measured chemical variables related to water quality (temperature, conductivity, dissolved oxygen, and pH) with a multiparameter probe (YSI 556 MPS). We took one measure in the downstream section for each stream reach before the fish sampling. We visually estimated substrate composition (% of consolidated and unconsolidated particles), trunks (%), marginal grasses (%), and shrubs and trees (%) in a 10 m stripe of the riparian buffer both in both stream margins. Moreover, we obtained average depth, width, and water velocity (flowmeter) by measuring these variables at several points along different mesohabitats in the stream reach. We also calculated the physical habitat index (PHI, based on Casatti *et al.*, 2006) that measures the physical habitat integrity based on stream physical attributes (hydrological, structural, and riparian characteristics). High PHI values indicate streams with high habitat diversity and stability, while low values indicate streams with some degree of habitat homogenization and instability (Casatti *et al.*, 2006). We standardized all our environmental variables (average = 1 and standard deviation = 0) and conducted a principal component analysis (PCA) to select the most important ones based on the highest eigenvalues (Legendre, Legendre, 1998). Based on this selection, we used PHI, dissolved oxygen, water velocity, % of marginal grasses, and % of trees in the riparian buffer for further analysis (Tab. 1).

Ecomorphological patterns. We selected 30 adult individuals from *I. kerri* and *H. vilmae* with similar standard length and well-preserved fins from all the streams they occurred. We followed Oliveira *et al.* (2010) to obtain 31 morphometric measures and calculated 22 ecomorphological attributes as shown in the Tab. **S1**. We obtained lengths, widths, and heights with digital calipers. For specimens smaller than five centimeters, we obtained measurements in a stereomicroscope 4 Zeiss, SteREO Discovery V12, with the help of AxioVision/Zeiss image software. To evaluate the multicollinearity of ecomorphological attributes, we used the Draftsman Plot function in the Primer 6 & Permanova+ (Clarke, Gorley, 2012). Most of the correlations were low, only three of them were superior to |0.80| as shown in the Tab. **S2**. Despite Legendre, Legendre (1998) considered |0.80| as a high correlation, we decided to keep these ecomorphological attributes in the analysis, since we were trying to identify the morphological differences between the species and these attributes perform different functions. After that, we ran a principal component analysis (PCA) with a Pearson correlation (from –1 to +1) to evaluate differences in the use of the ecomorphological space between *I. kerri* and *H. vilmae*. To test for differences in the ecomorphological patterns of *I. kerri* and *H.*

TABLE 1 | Abundance (N) and voucher number in the DZSJRP collection of *Inpaichthys kerri* and *Hyphessobrycon vilmae*, regional and local environmental variables in the sampled streams. FO = proportion of forest in the watershed; PAS = proportion of pasture in the watershed; PHI = physical habitat index; DO = dissolved oxygen (mg/l); Cur = water current (m/s); Gra = % of marginal grasses in the banks; Trees = % of the riparian buffer covered by trees.

Streams	*I. kerri*		*H. vilmae*		Regional variables		Local variables				
	N	DZSJRP	N	DZSJRP	FO	PAS	PHI	DO	Cur	Gra	Trees
S1	11	21482	0		0.35	0.64	152	7.40	0.06	0.00	23.75
S3	17	21506	0		0.06	0.93	116	8.74	0.06	0.00	33.75
S4	8	21519	0		0.22	0.77	23	7.68	0.07	31.25	5.00
S6	42	21566	6	21569	0.26	0.73	123	8.48	0.13	17.50	27.50
S12	21	21701	2	21707	0.57	0.42	114	7.40	0.05	0.00	28.13
S15	69	21740	8	21741	0.58	0.41	102	8.16	0.09	0.00	28.13
S16	45	21760	0		0.33	0.66	49	7.34	0.17	70.00	1.88
S17	19	21783	15	21781	0.73	0.26	140	9.54	0.13	0.00	49.38
S18	5	21815	0		0.33	0.66	145	8.77	0.09	0.00	28.75
S21	9		0		0.65	0.34	148	7.60	0.06	0.00	41.25
S22	0		39	21851	0.03	0.96	99	8.29	0.06	47.50	2.50
S23	0		14	21859	0.00	0.99	112	5.69	0.07	1.88	29.38
S25	0		10	21877	0.32	0.67	73	9.95	0.17	37.50	5.00
S27	0		3	21902	0.07	0.92	146	9.41	0.05	0.00	21.88
S28	0		13	21915	0.54	0.45	161	10.13	0.17	0.00	37.50
S30	0		30	21943	0.43	0.56	109	10.18	0.13	19.38	18.75

vilmae, we ran an analysis of similarity (ANOSIM) with normalized (square root) data and Euclidean index, followed by the SIMPER analysis to obtain the percentage of dissimilarity, in the Primer 6 & Permanova+ (Clarke, Gorley, 2012).

Trophic patterns. For the trophic analysis, we selected specimens from streams where more than five adult individuals were sampled. Thus, stomach contents of 80 adult specimens of *I. kerri* and 80 of *H. vilmae* were used to describe the diet of these two species. We identified the food items based on the lowest possible level of taxonomic classification. Due to the high degree of fragmentation and digestion, we were unable to identify the food items in levels lower than order. To evaluate if the number of analyzed stomachs were able to sum up the most of the food items variation, we run an ICE (Incidence-based Coverage Estimator) and Jackniffe 1 (based on the number of items that are present only in one stomach) in the EstimateS 9.1 software (Colwell, 2013). The sample completeness was calculated considering the number of items observed (NO) by the number of items estimated (NE) multiplied by 100 (NO/NE*100) (Marques *et al.*, 2019). We obtained the frequency of occurrence (FO) for each food item, based on the number of times that each item appeared in the stomachs divided by the number of analyzed stomachs (Hyslop, 1980). We also obtained the volume (V), based on the visually estimated volume occupied by the item considering the volume total of the stomach (Zeni, Casatti, 2014). With the values of FO and V, we calculated an adapted feeding index (IAi) from Kawakami, Vazzoler (1980) for each

species. After that, we calculated the trophic niche breadth following the Levins index (Levins, 1968) standardized as proposed by Hurlbert (1978). To calculate trophic niche overlap between the species, we used the Bray-Curtis similarity index in Primer 6 & Permanova+ software (Clarke, Gorley, 2012).

To test for differences in the diet of *I. kerri* and *H. vilmae*, we ran an analysis of similarity (ANOSIM) with normalized (square root) data and Bray-Curtis index in the Primer 6 & Permanova+ (Clarke, Gorley, 2012). The SIMPER analysis was applied to verify the items that contribute most to the observed differences between the species. Finally, in the same software, we used non-parametric multivariate form of Mantel test called RELATE routine to test if environmental variables influenced the species diet. For these analyses, items were grouped into the following categories: algae (filamentous and diatoms algae), aquatic insects (immature obtained and into the Coleoptera, Diptera, Ephemeroptera, Hemiptera, Lepidoptera, Megaloptera, Odonata, Plecoptera, and Trichoptera), aquatic invertebrates (Acari, Bivalve, Cladocera, Copepoda, Decapoda, Nematoda, Oligochaeta, and Ostracoda), periphyton, superior plants (roots, seeds, and leaves of plants), terrestrial insects (Coleoptera, Isoptera, Diptera, and Hymenoptera), terrestrial invertebrates (Acari and Araneae), animal fragment (animal fragment that was impossible to determine the origin), and detritus (particulate organic matter).

Occurrence patterns. To identify the environmental variables that influence *I. kerri* and *H. vilmae* occurrence and abundance, we developed generalized additive mixed models (GAMMs). Despite species samples did not include clustering effects, we used these models because they allow incorporating spatial autocorrelation and detecting nonlinear relationships between explanatory and response variables. Thus, *I. kerri* and *H. vilmae* abundances (response variables) were modeled against the environmental factors (explanatory variables: PHI, dissolved oxygen, water velocity, % of marginal grasses in the banks, and % of the riparian buffer area covered by trees) considering five structures of spatial correlation: exponential, gaussian, linear, rational, and spherical (Zuur *et al*., 2009), and poisson distribution. We selected the best-fitted model based on the significant p-values ($p < 0.05$) for all variables that composed the model, posteriorly on the lowest AIC values (*Akaike Information Criterion*) (Akaike, 1974), and also on the variance of the residual. To run the GAMMs, we used "mgcv" version 1.8-16 (Wood, 2017) and "nlme" packages in the R 3.2.2 environment (R Development Core Team, 2011).

RESULTS

The first two PCA axes from the ecomorphological data explained 45.6% of the variation in the species morphological patterns. The first axis highlighted the interspecific variation by separating *I. kerri* and *H. vilmae*, while the second one showed the intraspecific variation (Fig. 3). *Inpaichthys kerri* seems to have higher intraspecific morphological variation. Moreover, *I. kerri* showed higher and wider caudal peduncles, more dorsally located eyes, and larger dorsal, pectoral, anal, and caudal fin areas compared to *H. vilmae* (Tab. 2, Fig. 3). Both species had distinct ecomorphological patterns (ANOSIM R = 0.695; p-value = 0.0001) with an average dissimilarity of 56.6%.
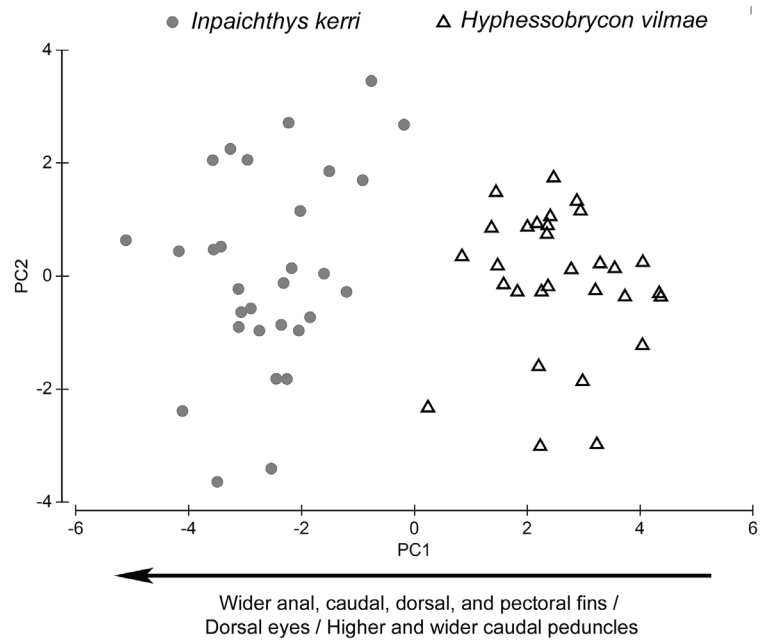
FIGURE 3 | Biplot resulting from the principal component analysis (PCA) from ecomorphological data, showing the position of 30 individuals of *Inpaichthys kerri* and 30 of *Hyphessobrycon vilmae* in the ecomorphological space, represented by the two first axis (PC1 and PC2) and analyzed from 22 ecomorphological attributes. Arrow indicates the variation of the most important attributes (see Tab. 2).

TABLE 2 | Abbreviation and Pearson correlation values obtained for each ecomorphological attributes in the two first axis (PC1 and PC2) of the principal component analysis (PCA). Values > 0.7 are in bold because they explained the most the ecomorphological pattern for both species.

Attributes	Abbreviation	PC1	PC2
Compression index	CI	-0.5634	-0.6594
Depression index	DI	-0.3312	0.0921
Relative length of caudal peduncle	RLPd	0.2803	0.0302
Relative height of caudal peduncle	RHPd	**-0.7362**	-0.1768
Relative width of caudal peduncle	RWPd	**-0.7204**	-0.4430
Relative length of head	RLHd	0.3483	-0.3538
Relative height of head	RHHd	0.4631	-0.4793
Relative width of head	RWHd	-0.3080	-0.6859
Relative width of mouth	RWM	0.6566	-0.2583
Relative height of mouth	RHM	-0.3859	-0.6522
Protrusion index	PI	-0.2876	0.2627
Eye position	EP	**-0.8219**	0.2136
Relative area of eye	RAE	-0.5529	0.2621
Relative area of dorsal fin	RAD	**-0.8981**	0.0516
Relative area of caudal fin	RAC	**-0.8991**	0.0483
Relative aspect of caudal fin	ARC	-0.6228	0.0777
Relative area of anal fin	RAA	**-0.8711**	0.1011
Relative aspect of anal fin	ARA	-0.2092	0.0066
Relative area of pectoral fin	RAPt	**-0.8044**	0.0348
Relative aspect of pectoral fin	ARPt	0.2998	-0.0002
Relative area of pelvic fin	RAPv	-0.4408	0.3101
Relative aspect of pelvic fin	ARPv	0.6057	0.0613

We recorded 30 food items for *I. kerri* and 24 for *H. vilmae* with estimation and completeness values that indicate acceptable sampling effort in reporting fish diet (*I. kerri* ICE = 33 items, completeness = 91% / Jackknife 1 = 35, completeness = 86%; *H. vilmae* ICE = 25, completeness = 96% / Jackknife 1 = 27, completeness = 89%). Both species consumed mainly aquatic insects (IAi > 0.80) (Tab. 3), but *H. vilmae* showed higher dominance of this item. Despite the similar consumption of aquatic insects, *I. kerri* had broader niche breadth (β = 0.40) than *H. vilmae* (β = 0.23), with 55% of niche overlap. We did not find any relationship between species diet and environmental

TABLE 3 | Alimentary importance index (IAi) of feeding items grouped into categories, and correlations (Rho) derived from RELATE routine between environmental variables and species' diets.

Feeding categories	*I. kerri*	*H. vilmae*
Algae	0.00999	0.04529
Aquatic insects	0.83977	0.90505
Aquatic invertebrates	0.00234	0.00122
Periphyton	0.00000	0.00095
Superior plants	0.00573	0.01798
Terrestrial insects	0.12967	0.00098
Terrestrial invertebrates	0.00499	0.00002
Unidentified animal fragments	0.00561	0.00000
Detritus	0.00189	0.02848
Rho	-0.187	-0.150
p-value	0.7128	0.7072

TABLE 4 | Average alimentary importance index (IAi), average dissimilarity between groups ± standard deviation, contribution (%), and cumulative contribution (%) of most important feeding items (listed in order of contribution) to the dissimilarity between *Inpaichthys kerri* and *Hyphessobrycon vilmae* in streams from the Aripuanã River basin (Mato Grosso State, Brazil).

Feeding items	*I. kerri* IAi	*H. vilmae* IAi	Average dissimilarity	Contribution	Cumulative contribution
Unidentified fragments	22.32	56.41	32.52 ± 1.23	39.23	39.23
Aquatic Chironomidae larvae	5.91	6.60	6.27 ± 0.65	7.57	46.8
Terrestrial Hymenoptera	10.93	0.13	5.84 ± 0.43	7.04	53.84
Filamentous algae	0.06	8.26	5.76 ± 0.44	6.96	60.8
Animal fragments	2.73	4.69	4.94 ± 0.35	5.97	66.77
Terretrial insect fragments	7.40	1.23	4.89 ± 0.39	5.90	72.66
Aquatic Diptera larvae	2.94	2.63	3.06 ± 0.32	3.69	76.35
Detritus	1.37	2.41	2.25 ± 0.27	2.72	79.07
Diatomaceae	0	2.66	1.67 ± 0.22	2.02	81.09
Terrestrial Diptera	2.59	0.44	1.65 ± 0.22	1.99	83.08
Terrestrial Lepidoptera	2.11	0.38	1.47 ± 0.23	1.78	84.85
Tecamoeba	2.44	0	1.34 ± 0.17	1.62	86.47
Periphyton	2.26	0.24	1.34 ± 0.18	1.62	88.09
Aquatic Ephemeroptera	0.74	1.35	1.32 ± 0.26	1.60	89.69
Terrestrial Isoptera	0.56	1.43	1.3 ± 0.20	1.57	91.26

variables (Tab. 3). Despite that, both species had distinct trophic patterns (ANOSIM R = 0.166; p-value = 0.0001) with an average dissimilarity of 79.7%. The consumption of aquatic insect fragments, Chironomidae, filamentous algae, terrestrial Hymenoptera and terrestrial insect fragments contributed the most to this dissimilarity (Tab. 4).

Inpaichthys kerri and *H. vilmae* abundances responded to different environmental conditions (Fig. 4), both without a significant spatial autocorrelation (as shown in the Fig. **S3** and Fig. **S4**, respectively; and as shown in the Tab. **S5** and Tab. **S6**, respectively). The optimal environment for *I. kerri* (*i.e.*, maximum abundance) is established in conditions with high water velocity, dissolved oxygen ranging from 7 to 9 mg/l, and low proportion of marginal grasses (GAMM; Adj. R^2 = 0.91; p < 0.05) as shown in the Tab. **S5**. For *H. vilmae* optimal conditions were on streams with high PHI, a high
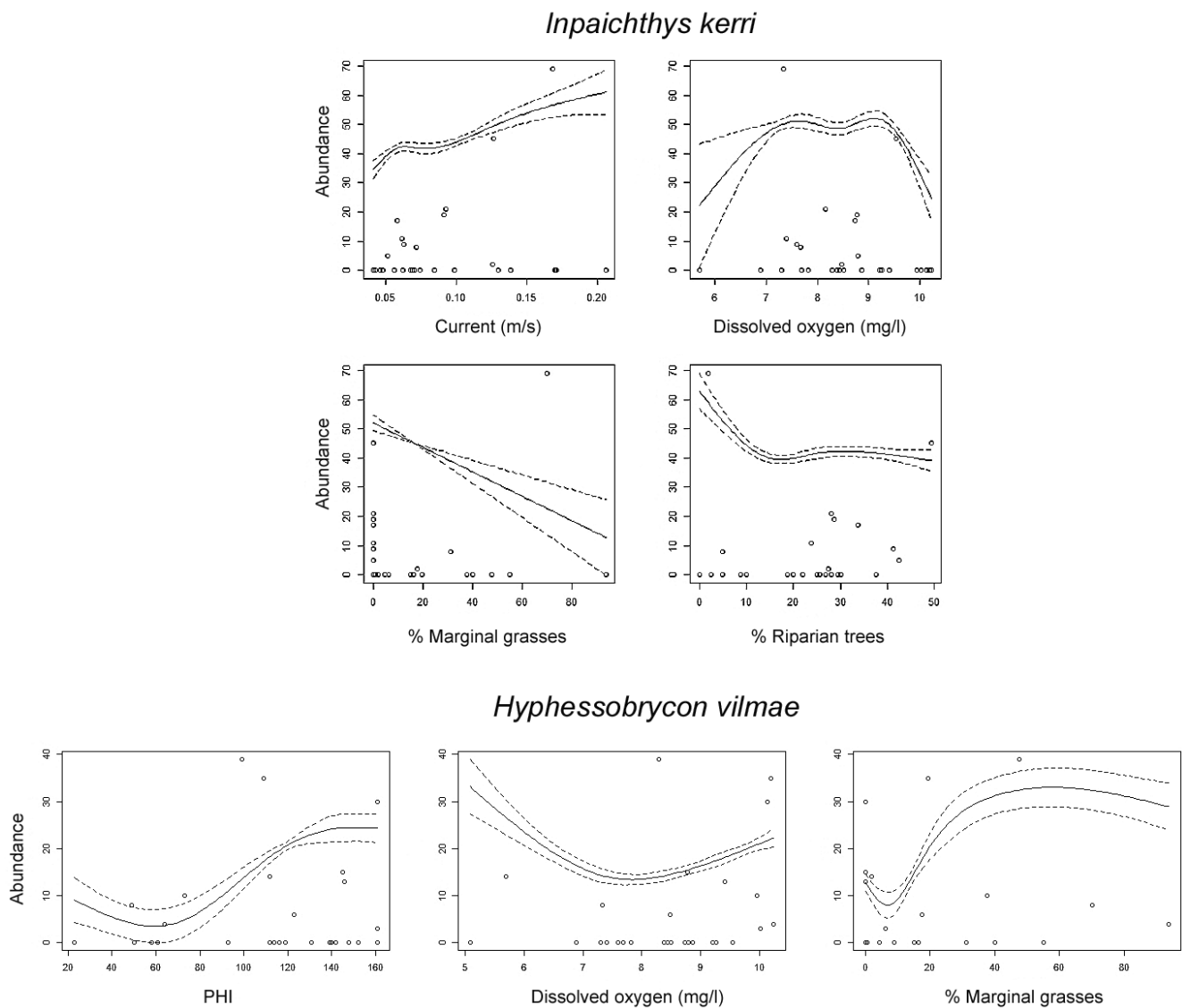
FIGURE 4 | Relationships obtained from generalized additive mixed models (GAMM) among the environmental variables and *Inpaichthys kerri* (**A**) and *Hyhessobrycon vilmae* (**B**) abundance.

proportion of marginal grasses, and dissolved oxygen concentrations higher than 9 mg/l (GAMM; Adj. R^2 = 0.80; p < 0.05) as shown in the Tab. **S6**.

DISCUSSION

Despite the overall morphological resemblance between *I. kerri* and *H. vilmae*, and contrary to our former predictions, ecomorphological and trophic patterns were different. *Inpaichthys kerri* has a broader and deeper caudal peduncle, more dorsal eyes, and larger dorsal, caudal, pectoral, and anal fin areas when compared to *H. vilmae*. Despite the similar consumption of aquatic insects and 55% of niche overlap, species showed different trophic patterns, with *I. kerri* feeding upon a lower proportion of aquatic insects, filamentous algae, and detritus and a higher proportion of terrestrial insects when compared to *H. vilmae*. Following the ecomorphological and trophic patterns, *I. kerri* and *H. vilmae* abundances were maximized in different environmental conditions.

Large dorsal, caudal, pectoral, and anal fins in *I. kerri* allow a better capacity of stabilization in deflections (Gosline, 1971), acceleration (Balon *et al*., 1986) and maneuverability potential (Watson, Balon, 1984; Wilga, Lauder, 1999). Moreover, more dorsal eyes lead to a better ability to detect items drifted by the current in streams (Pouilly *et al*., 2003). These morphological features improve the natatorial ability, which probably increase the success of *I. kerri* feeding strategy. This species exploits stream margins and invests in drift-feeding (*i.e.*, to consume items carried by the current) in the center of the channel, where water velocity and the probability of finding drifted items are higher. Accordingly, the optimal environmental conditions for *I. kerri* encompass fast waters and banks covered by low amounts of marginal grasses. Such conditions refer to more preserved and forested streams. Forests, notably those in the streamside buffers, help to trap inorganic sediments (see Sweeney, Newbold, 2014, and authors cited therein), and consequently, avoid riffles to be buried by fine sediments (Rabeni, Smale, 1995; Barbour *et al*., 1999). Indeed, when compared to *H. vilmae*, *I. kerri* occurrence was associated with streams located within more forested conditions (see Tab. 1).

Despite the ecomorphological differences, *H. vilmae* also occupies stream margins. However, with a lower natatorial ability compared to *I. kerri*, it is possible that *H. vilmae* invests less in the drift-feeding strategy and forages by picking food items close to the marginal vegetation. The abundance of *H. vilmae* was high in streams characterized by having copious amounts of marginal grasses, which is commonly associated with the conversion of native forests to pasture in many regions (Zeni *et al*., 2019). The removal of the native forest, especially in the riparian area, reduces canopy shading and increases solar radiation, which together contribute to the invasion of exotic grasses from adjacent pasture (Bunn *et al*., 1997; Evangelista *et al*., 2017).

The fact that differences in abundance between species were explained by specific stream conditions suggests that, at some level, environmental filtering is modulating the coexistence of these species. When co-occurring, which happened in four streams, one species was more abundant than the other one (see Tab. 1). Thus, environmental conditions contribute to determining which of these species may exhibit higher performance. Another way in which environmental conditions can modulate species

performance is through resource availability. Aquatic insects are equally crucial for both species; however, filamentous algae were more important to *H. vilmae* and terrestrial insects to *I. kerri*, which indicates their occurrences are related to more altered (pasture in the catchment and grasses in the stream margins) and more preserved (forests in the catchment and in the streamside buffer) streams, respectively (Fig. 5).

Both species can be associated with a more generalist trophic pattern (Baldasso *et al.*, 2019). A detailed analysis of the consumed items, however, revealed that *I. kerri* preyed on a higher volume of immature Trichoptera than *H. vilmae*. Trichopterans

FIGURE 5 | General view of streams where *Inpaichthys kerri* (**A**) and *Hyphessobrycon vilmae* (**B**) individuals were collected in the Aripuanã River basin, Mato Grosso State, Brazil.

are relatively sensitive to environmental degradation (Pereira *et al*., 2012), being more frequent and abundant in streams associated with native forests (Nessimian *et al*., 2008). By contrast, pasture dominance can be associated with a more significant development of filamentous algae, which is favored by high light intensities and high nutrient concentrations (Vázquez *et al*., 2011). Zeni, Casatti (2014) reported that the consumption of insects (especially Diptera) and algae can be associated with the presence of marginal grasses in altered streams, such as observed for *H. vilmae*. This finer observation of the trophic spectrum can reinforce the role of environmental conditions by mediating species coexistence by influencing the availability of fish feeding resources.

Therefore, morphology, trophic features and environment interact to determine *I. kerri* and *H. vilmae* abundances in streams of the Aripuanã River basin. *Inpaichthys kerri* occurred in streams with high water velocity (*e.g*., riffles) and preserved margins (*i.e*., without grasses) and fed mainly on aquatic insects, especially Trichoptera and terrestrial insects obtained through a drift-feeding strategy, maximized by its larger fin areas. On the other hand, *H. vilmae* occurred mainly in streams with high proportion of marginal grasses and preyed almost entirely on aquatic insects, probably from these grasses. The environmental features that maximize *I. kerri* abundances are probably associated with more forested catchments and riparian areas that can prevent grasses proliferation (Evangelista *et al*., 2017; Zeni *et al*., 2019), while *H. vilmae* abundance is maximized in streams with high degree of forest conversion to pasture. In this context, we can argue that the deforestation in the Aripuanã basin could be a sharp threat to the persistence of *I. kerri* through time, since the optimal environmental conditions that sustain this species tend to be gradually replaced by the optimal conditions of *H. vilmae*. This prediction is especially alarming because *I. kerri* is an endemic species that can be locally extinct if deforestation keeps increasing, and the occurrence of this species may be restricted to conservation units and indigenous lands of the region. Thus, the natural history information obtained in this study can help understanding species function in the ecosystems they occur, and it can also represent essential contributions for more effective conservation measures.

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Jaquelini O. Zeni: Data curation, Formal analysis, Investigation, Methodology, Supervision, Writing–original draft, Writing–review & editing.

Luisa Martins Sensato–Azevedo: Data curation, Investigation.

Eduardo Fernando dos Santos: Methodology, Formal analysis, Writing–review & editing.

Gabriel Lourenço Brejão: Data curation, Writing–review & editing.

Lilian Casatti: Methodology, Formal analysis, Writing–review & editing.

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The authors declare no competing interests.

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