



Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish

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Abstract The aim of this study was to test the hypothesis that a widespread non-native fish species in Brazil displays opportunistic feeding behavior and changes its diet according to environmental conditions. We compared the diet, feeding selectivity, carbon assimilation, trophic niche, and trophic level of *Knodus moenkhausii* (a small non-native characid fish species of Upper Paraná River) in streams surrounded by natural riparian vegetation (natural cover streams) and in streams impacted by pasture. We analyzed

stomach contents and stable isotopes (carbon and nitrogen), simultaneously. Overall, insects were the most common food items (> 65%). In natural cover streams, *K. moenkhausii* showed higher selectivity among aquatic macroinvertebrates consumed, while in pasture streams, they fed on the most abundant groups. The proportion of feeding groups assimilated by *K. moenkhausii* and the proportion of primary sources consumed by each feeding group of macroinvertebrates also varied between natural cover and pasture streams, as indicated by stable isotopes. In natural cover streams, fine and coarse particulate organic matter accounted for approximately 80% of *K. moenkhausii*'s diet, while in pasture streams, algae and periphyton also contributed greatly. As a result, *K. moenkhausii* occupied a higher trophic level and

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exhibited a broader niche width in pasture streams. We conclude that *K. moenkhausii* presents feeding selectivity with capacity to alter the trophic niche depending on environmental conditions. Such opportunism could be one of the reasons underpinning the abundance and wide distribution of this invasive species.

Keywords *Knodus moenkhausii* · Trophic level · Trophic niche · Pasture · Streams

Introduction

The introduction of non-native species is a major threat to both aquatic and terrestrial ecosystems (Chapin et al. 2000; Richardson 2011) and a major driver of species loss worldwide (Simberloff et al. 2013; Bellard et al. 2016). Within aquatic ecosystems, freshwaters tend to be the most vulnerable to invasion (Tricarico et al. 2016) and have been extensively altered by invasive species (Ricciardi and MacIsaac 2011). Biotic homogenization, or the replacement of specific native species by generalist non-native species in space and time (McKinney and Lockwood 1999; Tabarelli et al. 2012), results in freshwater systems with lower diversity at both regional and global scales (Rahel 2002; Drake and Lodge 2004). The introduction of non-native species is often related to anthropic actions and can occur accidentally or intentionally, through agriculture, recreation, biological control, fish stocks, aquaculture, sport fishing, and river transposition, among other routes (Welcomme 1988; Courtenay and Williams 1992; Lever 1998).

The potential establishment of non-native species in new geographic locations is closely related to environmental quality (e.g., Herborg et al. 2007; Kilroy et al. 2008; Kulhanek et al. 2011) and may be related to disturbance (Hobbs and Huenneke 1992; Minchinton 2002; Marchetti et al. 2004a). Land-use changes such as the conversion of natural habitats to pastures and croplands constitute a key factor disturbing natural terrestrial and aquatic environments. For instance, the establishment of pastures can increase autochthony in aquatic environments (e.g., Carvalho et al. 2015; De Carvalho et al. 2017), which may facilitate biological invasions due to changes in resource availability (Davis et al. 2000).

In addition to changes in resource availability, habitat alteration facilitates the success of non-native species by reducing native competitors and predators and increasing habitat homogenization that benefits opportunistic invaders (Scott and Helfman 2001; Scott 2006; Johnson et al. 2008). Other characteristics that increase the invasive potential of a non-native species are high reproductive rates, long life spans, long-distance dispersal, high physiological tolerance, generalist habit, and high trophic plasticity (Kolar and Lodge 2001; Marchetti et al. 2004b; Funk 2008; Barrett 2011).

Feeding strategies and trophic plasticity can be evaluated by comparing trophic webs and a species' niche breadth between environments that experience different levels of disturbance. In particular, combining stomach content analyses with whole-body stable isotopes (e.g., carbon and nitrogen) can yield robust and accurate information. Stomach content analysis provides detailed taxonomic information about the food items consumed and is one of the most common techniques used to evaluate fish feeding habits (e.g., Hyslop 1980; Lima-Junior and Goitein 2001; Buckland et al. 2017). However, stomach content analyses are limited in that they only inform a single point in time (Cortés 1997), and the relative assimilation of some resources is poorly quantified, such as detritus (Keough et al. 1998). Complementary approaches, such as whole-body analysis of stable isotopes, provide an integrated assessment of carbon and nitrogen sources an organism assimilates over time. These analyses have often been used in conjunction to assess the importance of different food items in the diet of fishes and other organisms (e.g., Polito et al. 2011; Carassou et al. 2017).

The objective of this study was to evaluate whether a non-native species displays an opportunistic feeding behavior and exhibits dietary shifts according to environmental conditions. We evaluated the diet and feeding selectivity (through stomach content analysis) and the food sources assimilated, trophic level and trophic niche occupied (through stable isotopes analysis) of *Knodus moenkhausii* (Eigenmann and Kennedy 1903). To assess whether the invasive species shows trophic plasticity between environments with different levels of disturbance, we compared the diet of fish in streams surrounded by riparian vegetation (natural cover streams) and streams surrounded by pasture (an activity responsible for 71% of deforestation in South America, FAO 2016). We

expected different types of resources would be available in streams with different land uses, with a high influence of autochthonous resources in pasture streams and allochthonous resources from riparian forest in natural cover streams. Consequently, the differences in resource availability would have cascading effects on abundance and diversity of aquatic macroinvertebrates leading to changes in *K. moenkhausii* feeding habits. We tested two hypotheses: (1) As a generalist, *K. moenkhausii* feeds on the most abundant food items available and (2) variation in local resource availability will result in changes in *K. moenkhausii* trophic niche.

Methods

Study area and land-use classification

This study was conducted in six second- and third-order streams (Strahler 1957) located in the sub-basin of the Paranaíba River, southeastern Brazil (Fig. 1,

Table 1). The Paranaíba River Basin is the second largest hydrographic unit of the Paraná Basin, encompassing 25.4% of its area (222.8 km²). Most of the Paranaíba River Basin is in the Cerrado (neotropical savanna), the second largest Brazilian biome, but much of this area has already been deforested (Strassburg et al. 2017). The hydrological regime of the rivers in this basin is governed by rains from October to March (annual average precipitation 1200 mm) and with episodic rainfall in the remaining months of the year (CBH Paranaíba 2012).

Six streams located in the states of Goiás and Minas Gerais were selected according to the different predominant types of land use and local assessment of the physical habitat of each stream. The length of the section sampled in each stream was 150 m. Each stream was sampled once in the dry season, in September 2012.

The land use surrounding the sampled streams was evaluated according to the oriented mapping method described in Lima et al. (2010), in eight multispectral RapidEye images of September and October of 2011,

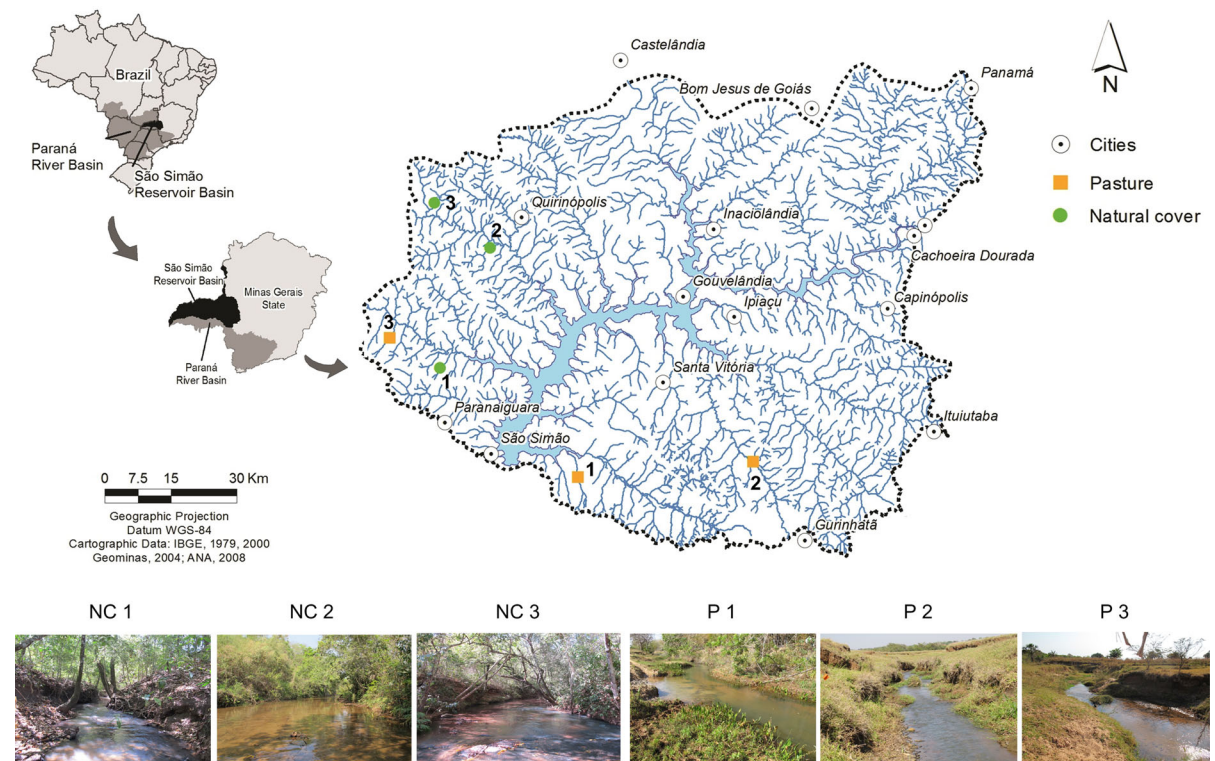


Fig. 1 Location and characterization (by photographs) of the six second- and third-order streams located in the sub-basin of the Paranaíba River sampled in September 2012. NC1, NC2 and NC3 = natural cover streams and P1, P2 and P3 = pasture streams

Table 1 Land use (calculated in a 150-m-radius buffer and a 50-m upstream buffer) and physical characteristics of the six second- and third-order streams located in the sub-basin of the Paranaíba River sampled in September 2012

Streams	Geographic coordinates	Alt. (m)	Characteristics of streams			Land use (150-m-radius buffer/50 m upstream buffer)				Environmental variables				
			Order (Strahler)	Mean depth (m)	Mean width (m)	Mean area (m ²)	Natural vegetation (%)	Pasture (%)	Others (%)	Riparian woody cover (%)	Fine subst. (%)	Leaf banks (%)	Algae (%)	
Natural cover	1	18°47'19.49"S 50°39'40.86"W	482	2 ^a	0.2	3.42	0.68	53.14/58.93	0/0	46.86/41.07	153.41	0	17.00	0
	2	18°30'56.82"S 50°31'51.62"W	434	3 ^a	0.19	7.29	1.36	39.13/29.73	57.87/0	3.00/70.27	74.55	0	14.00	< 1
	3	18°24'20.08"S 50°39'49.89"W	509	3 ^a	0.19	7.35	1.43	50.86/39.57	49.14/0	0/60.43	170.57	0	18.00	0
Pasture	1	19°03'03.40"S 50°20'06.81"W	425	3 ^a	0.64	3.49	2.25	8.57/52.19	62.35/3.71	29.08/44.10	12.50	41.89	2.00	21.81
	2	19°01'38.55"S 49°54'32.40"W	461	3 ^a	0.13	2	0.25	0/33.25	97.69/47.83	2.31/18.92	0	20.95	0	13.86
	3	18°42'59.17"S 50°46'52.77"W	479	2 ^a	0.17	4.8	0.82	16.41/57.78	65.35/25.05	18.24/17.16	32.50	1.90	2.00	< 1

Alt altitude, *Riparian woody cover* sum of riparian canopy cover, riparian mid-layer and riparian ground layer, *subst.* substrate

with five spectral bands. The percentage cover of natural vegetation and pasture was determined for the six study streams in a 150-m-radius buffer around the upstream limit of the sampled stretch. Orthorectified and atmospherically corrected images were obtained through a partnership between the Federal University of Lavras (UFLA) and the Ministry of Environment (MMA). Acquisition errors, clouds, and shadows were removed in the preprocessing phase (Coppin et al. 2004), which also included visual evaluation of image registration. To validate the classification results, we generated an array of errors measuring the global and kappa accuracy (Shanmugam et al. 2006). The mapping resulted in a high kappa and global accuracy with values from 96% and 98%, respectively. To assess the representativeness of the vegetation that is interacting with the stream channel, we also assessed the percentage cover of natural vegetation and pasture within a buffer of 50 m upstream of each site by interpreting a combination of high-resolution satellite images (0.6–5 m spatial resolution, Google Earth data, Google 2010) and Landsat multispectral satellite images (R4G3B2 false color band combination).

Physical habitat at the site scale was characterized using the US EPA field methods (Lazorchak et al. 1998; Peck et al. 2006). At each site, we characterized the physical habitat by channel hydromorphological variables (depth, width, and area); substrate (% of fine substrate—smaller than 16 mm); riparian woody cover (sum of riparian canopy cover, riparian mid-layer and riparian ground layer) and in-stream habitat variables (% of algae and leaf banks). All site variables were calculated according to Kaufmann et al. (1999), who described concepts and analytical procedures for calculating metrics based on data generated from the physical habitat field protocols. These variables were assessed because they consistently reflected the effects of different land uses on physical habitat features related to resource availability (Table 1).

Three streams were located in pasture-dominated areas, and three reference streams were surrounded by natural riparian cover (Fig. 1). The pasture streams were surrounded by a buffer zone containing more than 62% pasture, lacked riparian vegetation (or had only sparse trees), and stream beds were dominated by the prevalence of fine substrate and algae. Natural vegetation, as well as other land uses, occurred upstream of the study reaches (Table 1). The natural cover streams were located in sites surrounded by

more than 39% of natural vegetation and were characterized by the presence of riparian forest, few fine substrates, and a higher amount of leaf banks than algae on the stream bed. Although other land uses, especially agriculture, occurred upstream of the natural cover sites, these streams were not influenced by pastures (Table 1).

Characteristics of the invasive fish species and sampling methods

The Upper Paraná is the second largest basin in Brazil and has approximately 310 described fish species, over 20% of which are non-native (Langeani et al. 2007). *Knodus moenkhausii* is noteworthy among the non-native species mentioned. It is a small characid, originally described based on specimens collected in the drainage of the Paraguay River basin and its presence in the Upper Paraná has uncertain origins (Langeani et al. 2007). This species has been consistently registered in the Upper Paraná in high densities (Casatti et al. 2009; Teresa and Casatti 2013; Fagundes et al. 2015). Due to its remarkable abundance and frequency in the Upper Paraná basin, *K. moenkhausii*'s habitat use, feeding preferences and reproductive biology have been widely studied (Appendix S1). However, its hypothesized opportunistic feeding behavior and trophic plasticity have not been explored in the context of different land uses.

Individuals of *K. moenkhausii* were collected using hand nets (80 cm in diameter, 1 mm mesh) and trawls (3 m long, 5 mm mesh). A total of 336 individuals were sampled in the six streams (259 in natural cover streams and 77 in pastures). The average total lengths were similar in natural cover (3.93 ± 0.60 cm) and pasture streams (3.32 ± 0.69 cm). A total of 35 adult individuals (18 sampled in natural cover streams and 17 in pasture streams) was selected for stable isotope analysis and was processed whole (except the digestive track) due to the small size of the sampled individuals. For the stable isotope analysis, the collected fish were immediately killed and stored on ice for further processing in the laboratory.

Sixty-five adult specimens of *K. moenkhausii* (35 collected in natural cover streams and 30 in pastures) had their stomachs removed and their contents analyzed using a stereomicroscope. Individuals selected for evaluation of stomach contents were anesthetized with eugenol and subsequently fixed in

formaldehyde 10% to reduce the chance of rapid digestion of any food item.

For isotopic analysis, fish samples were lyophilized for 24 h and ground to a fine and homogeneous powder using a mortar and pestle and stored in *Eppendorf* tubes. Approximately 2–5 mg of dry animal tissue was used. The individuals used for stomach content analysis were preserved in 70% alcohol until they were processed in the laboratory. Voucher specimens of *K. moenkhausii* were deposited in the Ichthyological Collection of the Federal University of Lavras, under the catalogue number CI-UFLA 0839.

Collection and processing of resources

Samples of basal resources and benthic macroinvertebrates were collected in situ, five samples of each resource per stream. Basal resources consisted of filamentous algae, periphyton (or biofilm), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), leaves from the riparian vegetation, and grasses. The filamentous algae samples were manually collected, stored in plastic bottles, and immediately frozen. Periphyton was sampled by scraping and washing rocks with distilled water, and then, the collected materials were stored in plastic bottles. The FPOM samples were collected from sediment deposits by revolving the sediment and passing the suspended material through a phytoplankton net (45 µm mesh). After collection, both periphyton and FPOM samples were immediately frozen to preserve the material. In the laboratory, samples were vacuum-filtered through 45-micron Millipore glass fiber filters previously calcined. The CPOM was randomly collected from leaf litter deposits in the streams, and samples of vegetation (riparian forest and grasses) were collected at different points outside the streams. All leaves were packed in paper bags and stored in plant presses until processing in the laboratory.

Benthic macroinvertebrates were collected using a D-frame kick net (30 cm aperture, 500 µm mesh). To obtain the abundance of benthic macroinvertebrates in each stream, eleven subsample units (0.09 m² each) were taken per site following a systematic zigzag pattern along a segment of 150 m, covering all different substrates and habitats, generating one composite sample for each site and totaling an area

of 1 m² (Castro et al. 2017) (see Appendix S2 to access data of benthic macroinvertebrates abundance). To obtain individuals for isotopic analysis, we carried out an additional collection, following the same procedures described above. The individuals designated for isotopic analysis were immediately frozen and stored in plastic bottles. In the laboratory, the collected organisms were washed in distilled water, taxonomically identified (Merritt et al. 2008; Mugnai et al. 2010; Hamada et al. 2014) and classified into main orders and functional feeding groups (predators, scrapers, shredders, gathering-collectors and filtering-collectors) based on the literature (Cummins et al. 2005; Tomanova et al. 2006; Ramírez and Gutiérrez-Fonseca 2014) (Appendix S3).

In the laboratory, all samples of resources (basal resources and benthic macroinvertebrates) were dried at 60° for 48 h prior to homogenization using mortar and pestle and storage in *Eppendorf* tubes. Approximately 2–5 mg of dry animal tissue was selected for isotopic analysis, while approximately 5–10 mg was required for the basal resources samples.

Isotopic analysis

Stable isotopes for carbon and nitrogen were analyzed at the Center for Nuclear Energy in Agriculture (CENA) at the University of São Paulo. To determine the isotopic ratio, a mass spectrometer system in the continuous-flow (CF-IRMS) mode was used with a Carlo Erba elemental analyzer (CHN 1110) coupled to a Delta Plus mass spectrometer (Thermo Scientific). The results are expressed as the difference of international reference standards, in the delta notation (δ) in parts per mil (‰), and calculated using the following formula:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

where X is ¹³C or ¹⁵N and R represents the isotopic ratio ¹³C/¹²C or ¹⁵N/¹⁴N (Barrie and Prosser 1996).

Stomach content analysis

Food items were weighed (0.001 g accuracy/wet weight) and identified under stereomicroscope to the lowest feasible taxonomic unit according to macroinvertebrate identification guides (Costa et al. 2006; Mugnai et al. 2010). To characterize the diet of *K.*

moenkhausii, we used the feeding index (IA) proposed by Kawakami and Vazzoler (1980), combining the frequency of occurrence (F_i = number of times the item i occurred divided by the total number of stomachs with food) and the relative weight (P_i = sum of the weight of the item i divided by the sum of the weight of all items) of each item:

$$IA_i = (F_i P_i) / \sum F_i P_i$$

where IA_i = feeding index of item i ; F_i = frequency of occurrence of item i , and P_i = weight of the item i .

Data analysis

We addressed the hypothesis that *K. moenkhausii* feeds on the most abundant food items by using aquatic macroinvertebrates (the most common item in stomach contents) as a proxy. A simple linear regression was performed to evaluate whether *K. moenkhausii* feeds on the most abundant aquatic macroinvertebrates in both natural cover and pasture streams. This analysis was performed to determine whether the frequency of Coleoptera, Diptera, Hemiptera, Ephemeroptera, and Trichoptera in *K. moenkhausii* stomach contents was proportional to their natural abundances in the streams based on the quantitative samplings.

Differences in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) signatures of *K. moenkhausii* between pasture and natural cover areas were tested using a generalized linear mixed model (GLMM) that assumed a normal distribution for variation in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). In order to avoid pseudoreplication, each fish was nested to the respective stream. The streams were considered as a random factor, while land use was included as a fixed effect. Analyses were conducted in the software R v3.2.2 (R Core Team 2017), using the package *lme4* (Bates et al. 2015) for the GLMMs.

Source contributions to *K. moenkhausii* diet were estimated for both natural cover and pasture streams based on stable isotope data analyzed through Bayesian stable isotope mixing models (Moore and Semmens 2008; Parnell et al. 2010), using the MixSIAR package in R (Stock and Semmens 2016a). Markov chain Monte Carlo sampling was implemented with the following parameters: number of chains = 3; chain length = 100,000; burn in = 50,000; thin = 50 and model 4 (Residual×Process) error structure (Stock and Semmens 2016b).

Diagnostic tests (Gelman–Rubin, Heidelberger–Welch and Geweke) and trace plots were examined for model convergence. Individuals of *K. moenkhausii* were considered consumers and the basal resources (algae, riparian vegetation, grasses and periphyton), and the five feeding groups of benthic macroinvertebrates (predators, shredders, gathering-collectors, filtering-collectors and scrapers) were considered food resources. From this, the partition analysis was developed in two steps. The first step considered the items observed on stomach contents of *K. moenkhausii*, that is, vegetal remains (fragments of riparian vegetation leaves and grasses) and macroinvertebrates separated into feeding groups. In this step, we chose to use the riparian vegetation and the grasses as resources, as they also represent the isotopic signature of terrestrial insects observed in stomach contents. Algae and periphyton were not observed in the stomachs of *K. moenkhausii* and therefore were not considered in this step. The second step evaluated the proportion of basal resources (CPOM, FPOM, algae and periphyton) consumed by each feeding group of macroinvertebrates separately to investigate the resources assimilated indirectly by *K. moenkhausii*. The fractionation values used for fish and for macroinvertebrates were $0.5 \pm 0.13\text{‰}$ for C and $2.3 \pm 0.18\text{‰}$ for N because it is an enrichment appropriate for detritivores or omnivores that consume mixtures of plant material and microbial or animal material (McCutchan et al. 2003).

After the two steps, it was possible to calculate the contribution of primary sources to the isotopic composition of *K. moenkhausii* in streams with different degrees of conservation. To do so, we multiplied the proportion of each resource consumed by *K. moenkhausii* (results of step 1) by the proportion of each primary resource consumed by each feeding groups of macroinvertebrates separately (results of step 2).

The isotopic niches of *K. moenkhausii* in both categories of land use (natural cover and pasture) were quantified based on total area (TA) and standard ellipse areas (SEA and SEAc—expressed in ‰^2) through use of the Stable Isotope Bayesian Ellipses package in R (SIBER, Jackson et al. 2011). The standard ellipse area (SEA) represents the core isotopic niche space, and it is a proxy of the richness and evenness of resources consumed by the population (Bearhop et al. 2004). A small sample size correction (indicated by the subscript letter “c”) was applied to

SEA to increase the accuracy of the comparisons, enabling the comparison of niches of populations with different sample sizes.

The trophic position (TP) of *K. moenkhausii* in both categories of land use was estimated through the trophic position model proposed by Vander Zanden et al. (1997): $TP = [(^{15}N_{fish} - ^{15}N_{resources}) \div 2.3] + 1$, where $^{15}N_{fish}$ = ^{15}N values of each individual of *K. moenkhausii*, $^{15}N_{resources}$ = mean values of ^{15}N of basal resources, 2.3 represents the fractionation per trophic level (McCutchan et al. 2003), and 1 is the position of producers within the food chain. The ^{15}N of basal resources was assessed multiplying the percentage of total contribution of each basal resource (calculated in the partition analysis) by its mean ^{15}N values in each category of land use. The trophic position was calculated for each individual of *K. moenkhausii*. A *t* test was performed to determine whether there was variation in the trophic levels occupied by *K. moenkhausii* in the different land-use categories.

Results

Aquatic and terrestrial insects (also considering insect remains) were the primary food items consumed by *K. moenkhausii* in natural cover (77%) and in streams influenced by pastures (67%) (Table 2). Detritus was

the second most commonly consumed item in pasture-influenced streams (26%), and in natural cover streams it represented 11% as well as plant remains. In pastures, plant remains constituted only 6% of the feeding of *K. moenkhausii* (Table 2).

There was a variation among the proportion of each order of insects consumed by *K. moenkhausii*. In natural cover streams, the most commonly consumed groups were Coleoptera (19%) and terrestrial insects of the order Hymenoptera (16%). In pastures, the most consumed groups were Diptera (15%), Trichoptera (3%), Ephemeroptera (2%) and terrestrial insects of the order Hymenoptera (2%) (Table 2). However, the frequency of occurrence of macroinvertebrates in the stomachs of *K. moenkhausii* did not reflect the abundance of each order in the substrate sampled in natural cover streams ($R^2 = 0.09$; $t = -0.53$; $p = 0.63$) (Fig. 2a). By contrast, *K. moenkhausii* in pasture streams fed on aquatic macroinvertebrates that were most abundant ($R^2 = 0.87$; $t = 4.58$; $p = 0.02$) (Fig. 2b).

The isotopic composition of *K. moenkhausii* varied between streams in different land uses for both carbon ($t = 4.29$; $p = 0.041$) and nitrogen ($t = 4.58$; $p = 0.031$). Stable isotope values of ^{13}C were more enriched in natural cover streams (-28.11 to -22.65%) than in pasture-influenced streams (-34.09 to -24.10%). In contrast, values of ^{15}N were more enriched in pasture-influenced streams

Table 2 Feeding index (IA), frequency of occurrence (*F*) and relative weight (*P*) of each food item found in the stomachs of *Knodus moenkhausii* in natural cover streams and streams influenced by pasture

Item	Natural cover			Pasture		
	AI	<i>F</i>	<i>P</i>	AI	<i>F</i>	<i>P</i>
Coleoptera ^{SH, CO, SC, PR}	0.19	0.27	0.26	0.01	0.09	0.06
Hymenoptera (terrestrial)	0.16	0.27	0.23	0.02	0.11	0.06
Diptera ^{FI, CO, SC, SH, PR}	0.00	0.10	0.00	0.15	0.31	0.17
Hemiptera ^{PR}	0.00	0.13	0.01	0.00	0.03	0.00
Ephemeroptera ^{FI, CO, SC}	0.00	0.03	0.02	0.02	0.09	0.07
Trichoptera ^{FI, SH, CO, SC, PR}	0.00	0.07	0.00	0.03	0.14	0.07
Insects remains	0.41	0.63	0.24	0.44	0.49	0.31
Plant remains	0.11	0.33	0.12	0.06	0.34	0.06
Detritus	0.11	0.50	0.08	0.26	0.54	0.17
Sediment	0.01	0.10	0.03	0.01	0.06	0.03

Aquatic macroinvertebrates possible feeding groups according to Cummins et al. (2005), Tomanova et al. (2006), Ramírez and Gutiérrez-Fonseca (2014): *PR* predator, *SH* shredder, *FI* filtering-collector, *CO* gathering-collector and *SC* scraper

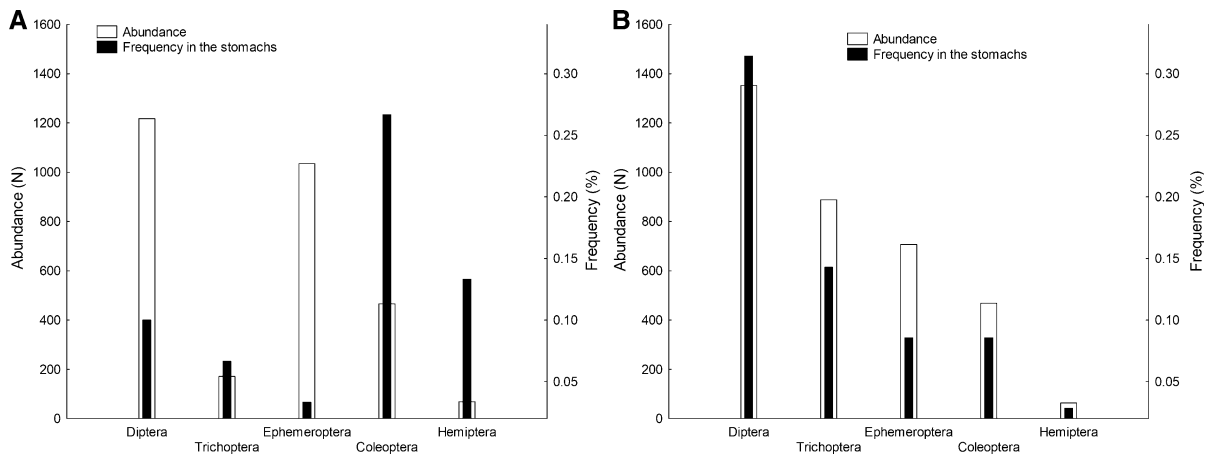


Fig. 2 Relationship between the abundance of each order of macroinvertebrates in the substrate and the frequency of each food items in the stomach of *K. moenkhausii* in natural cover streams (a) and under influence of pastures (b)

(9.20 to 13.09 ‰) than in natural cover streams (7.73–10.42‰) (Fig. 3).

Partition analyses revealed that *K. moenkhausii* resource assimilation differed between natural cover and pasture-influenced streams (Fig. 4). In natural cover streams, *K. moenkhausii* assimilated more gathering-collectors (32% of their diet), followed by filtering-collectors (20%), predators (17%), shredders (16%) and scrapers (12%). Vegetal remains from riparian vegetation contributed only 3%. Considering indirect assimilation via macroinvertebrates, the basal resources that most contributed to *K. moenkhausii* stable isotope values in natural cover streams were FPOM (39%) and CPOM (37%), followed by periphyton (13%). Contributions from algae (8%) and riparian vegetation (3%) were relatively minor (Fig. 4a). In pasture streams, *K. moenkhausii* assimilation consisted primarily of predators (42%), filtering-collectors (21%) and shredders (13%), followed by gathering-collectors and scrapers (9% each). Vegetal remains (including grasses) constituted only 6%. Considering indirect assimilation via macroinvertebrates, the contribution of CPOM and FPOM was also relevant in pastures streams (31% and 26%, respectively). However, the contribution of the autochthonous resources, periphyton (24%) and algae (12%) was double of those in the natural cover streams (Fig. 4b).

The differences in *K. moenkhausii* resource utilization between stream types were further reflected by their distributions in carbon–nitrogen bi-plot space (Fig. 3), in the amplitude of the isotopic niche

(Fig. 5a) and in its trophic position (Fig. 5b). The isotopic niche was wider in pasture streams (TA = 21.17; SEA = 7.90; SEAc = 8.42), than in natural cover streams (TA = 9.93; SEA = 3.77; SEAc = 4.00) (Fig. 5a). *Knodus moenkhausii*'s trophic position was also higher in pasture streams than in natural cover streams ($p = 0.02$) (Fig. 5b).

Results from carbon assimilation and stomach content analyses were combined to generate the *K. moenkhausii* food web (Fig. 6). In natural cover streams, the main resources in *K. moenkhausii* food webs are FPOM and CPOM (indirectly) and macroinvertebrate gathering-collectors (directly). In pasture streams, CPOM and FPOM contributed less to the food webs than in natural cover streams, and autochthonous basal resources (periphyton and filamentous algae) had larger indirect contributions to the food web. In these streams, macroinvertebrate predators were more often consumed by *K. moenkhausii*. The consumption of plant remains (in natural cover and pasture streams) and terrestrial insects (especially in natural cover streams) was observed through stomach content analysis. However, the isotopic composition of plant remains was not representative in the isotopic composition of *K. moenkhausii*.

Discussion

In the present study, we observed animal and plant material in the stomachs of *K. moenkhausii* and thus confirmed its omnivorous feeding habit. However,

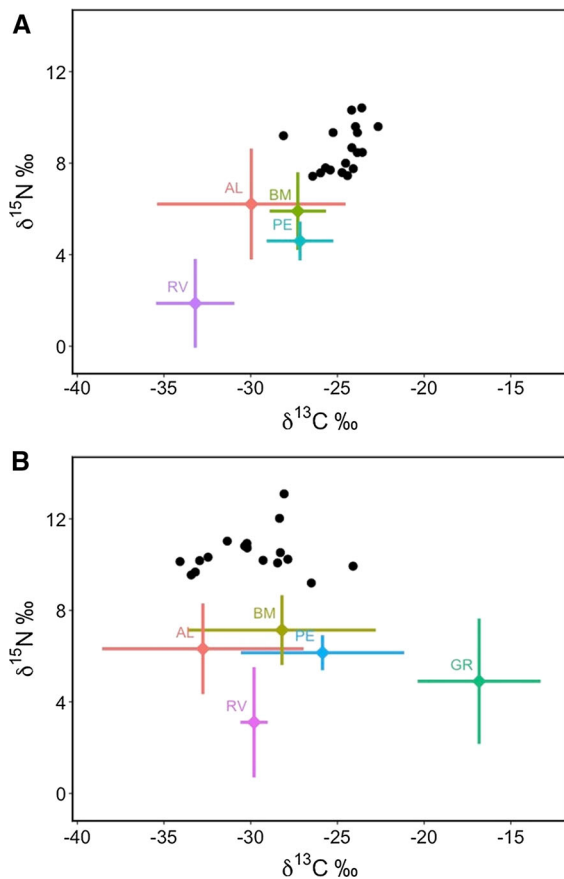


Fig. 3 Representation of trophic web (*bi-plot* space) of the species *K. moenkhausii* (solid points) sampled in natural cover streams (a) and streams influenced by pasture (b). No enrichment factor was used to construct the *bi-plot* space graph. Basal resources: AL filamentous algae, RV riparian vegetation, PE periphyton, BM benthic macroinvertebrates, and GR grasses of pasture

stable isotope analysis revealed that a large proportion of *K. moenkhausii*'s carbon and nitrogen came from aquatic macroinvertebrates, indicating a strong tendency for insectivory/invertivory. We also observed broad niche and flexible diet in response to different land uses, as well as differences in selectivity of aquatic macroinvertebrates.

Stomach content analysis produced detailed information on items consumed. In pasture streams, the abundance of aquatic macroinvertebrate groups correlated with their occurrence frequency in stomachs of *K. moenkhausii*. In streams with natural cover, *K. moenkhausii* consumed more Coleoptera despite it being only the third most abundant order in these streams. However, we were not able to distinguish

whether the coleopterans found in gut contents were terrestrial or aquatic. Relative availability of terrestrial insects was not quantified, and terrestrial insects are presumably more abundant in natural streams with intact riparian systems. Therefore, although *K. moenkhausii* exhibited some selectivity for other taxa, it is not possible to state whether or not *K. moenkhausii* consumed coleopterans in proportion to their availability or present more selectivity. Such opportunistic feeding may enable *K. moenkhausii* to allocate energy to reproduction throughout the year even in environments that are physically impacted by human disturbances (Ceneviva-Bastos and Casatti 2007).

Stable isotope analyses provided information about the food resources assimilated over time. Higher assimilation of gathering-collector macroinvertebrates in preserved streams and predators in pasture-influenced streams may be due to the relative abundance and availability of different feeding guilds under different land uses. This is not surprising, given that land-use changes can lead to shifts in resource availability and abiotic conditions and may alter the presence of different functional feeding groups of macroinvertebrates (García et al. 2017). Greater abundance of shredders and gathering-collectors is expected under natural conditions due to the greater supply of CPOM in forested covered streams than pasture streams (Graça et al. 2015; Linares et al. 2017). An increase in the number of scrapers and filtering-collectors is expected in pasture-influenced streams because reduced canopy cover frequently leads to higher periphyton production (Winkelmann et al. 2014; Neres-Lima et al. 2016, 2017).

We also expected different basal resources to contribute to the food web of *K. moenkhausii*, since land-use changes alter nutrient cycling, which can lead to differences in the quantity and quality of available food resources (Richardson et al. 2010). Aquatic macroinvertebrates may also present more generalist feeding habits in human-impacted sites, whereas more specialization may occur in macroinvertebrate assemblages under less disturbed conditions (Castro et al. 2016). Greater assimilation of CPOM and FPOM is expected under more natural environments, since the abundance of these resources is closely related to the presence of riparian forest. Pastures may also provide sources of CPOM and FPOM, especially coming from grass and manure associated with cattle grazing. The C_4 grasses from pastures usually present enriched $\delta^{13}C$

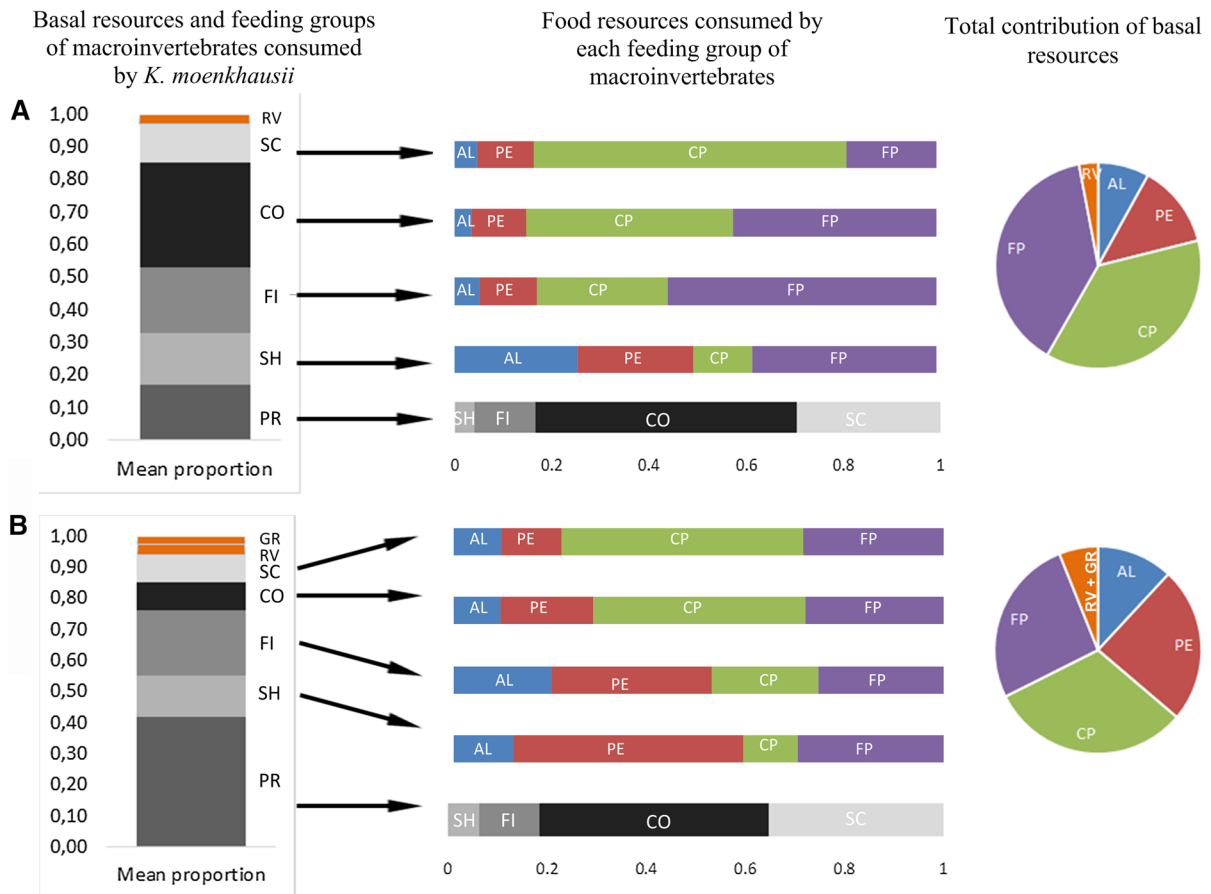


Fig. 4 Proportion of the resources assimilated by *K. moenkhausii* in natural cover streams (a) and in streams influenced by pastures (b). Feeding groups of macroinvertebrates: PR predator, SH shredder, FI filtering-collector, CO gathering-

collector and SC scraper. Basal resources: AL filamentous algae, FPOM fine particulate matter, CPOM coarse particulate matter, RV riparian vegetation, GR grasses of pasture and PE periphyton

values relative to C₃ plants from riparian vegetation (see Fig. 3), which occurs in accordance with the decarboxylation processes employed by each plant (Manetta and Benedito-Cecílio 2003). Therefore, the depleted δ¹³C values from aquatic macroinvertebrates and *K. moenkhausii* in pasture streams indicate the main source of FPOM and CPOM in these streams is from the riparian vegetation, which occurs upstream of the sampled reaches (see land use in Table 1). Grass leaves are also less nutritious and difficult to digest, which can explain the low assimilation by *K. moenkhausii* and other fish species (Carvalho et al. 2015). Increased dependence on autochthony in pasture streams may also have contributed to the depleted values of consumers at these streams (see Fig. 3). All these changes to food web dynamics demonstrate the consequences of replacing native vegetation with

pastures, which is one of the main drivers of deforestation in tropical and subtropical regions (FAO 2016).

Flexible feeding habit has been documented in other invasive fish species (Pettitt-Wade et al. 2015; Tran et al. 2015; Busst and Britton 2017) and is a key trait associated with successful colonization, establishment, and spread (Peterson and Vieglais 2001; Pettitt-Wade et al. 2015). The greater niche amplitude of *K. moenkhausii* recorded in pasture streams indicates a more generalist feeding habit, which is characteristic of species adapted to unstable environments (Levins 1968). *Knodus moenkhausii* displays this ability, as individuals fed at different trophic levels and presented broad and plastic isotopic niche in environments with different degrees of conservation. The higher assimilation of macroinvertebrate

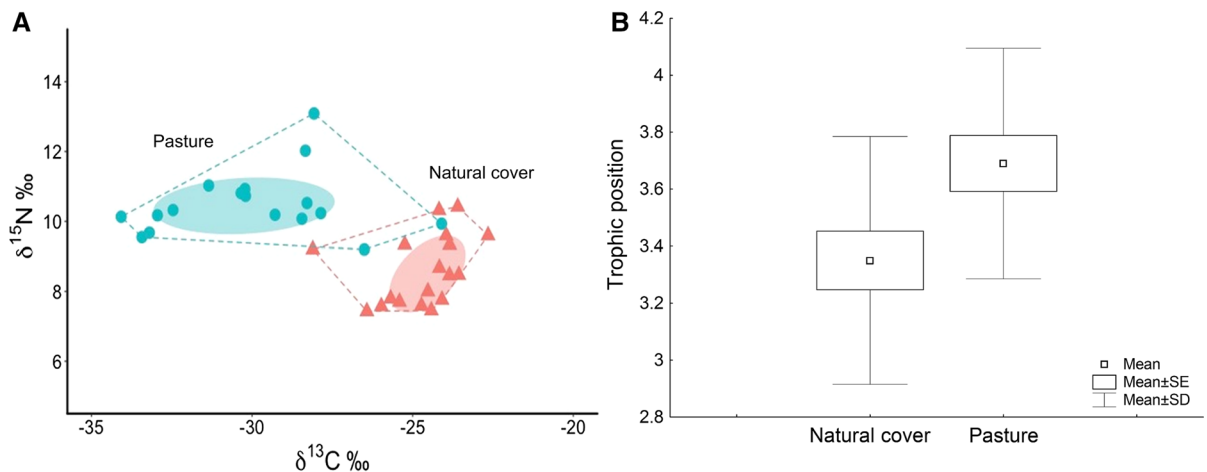


Fig. 5 Representation of amplitude of the isotopic niche (a) and trophic position (b) of *K. moenkhausii*. The points and triangles in the figure a represent the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures of each individual of *K. moenkhausii* sampled in

predators explained the higher trophic level occupied by *K. moenkhausii* in pasture streams. However, it remains unclear why *K. moenkhausii* relied heavily on macroinvertebrate predators in pasture streams, since predators (as Odonata, Naucoridae and Perlidae) were also abundant in natural cover streams (see Appendix S3). One hypothesis is a likely easiest capture of macroinvertebrates predators in pasture streams, especially when grasses from adjacent pasture enter the stream channel. In this case, macroinvertebrates predators with epiphytic habits (as Odonata) are easily consumed for fishes that forage in macrophyte banks.

Several classical studies (e.g., Hutchinson 1957; Van Valen 1965) have indicated that an absence of interspecific competition can lead to larger trophic niches. If this hypothesis is correct, we can assume that resources are not being fully exploited in pasture streams, and *K. moenkhausii* occupies previously vacant dietary niches, which has facilitated their colonization (Shea and Chesson 2002). However, if *K. moenkhausii* is actually feeding opportunistically in all streams, the differences in diet and isotopic signatures would depict differences in the underlying basal food webs (proportions of autochthonous sources) and availability of terrestrial insects.

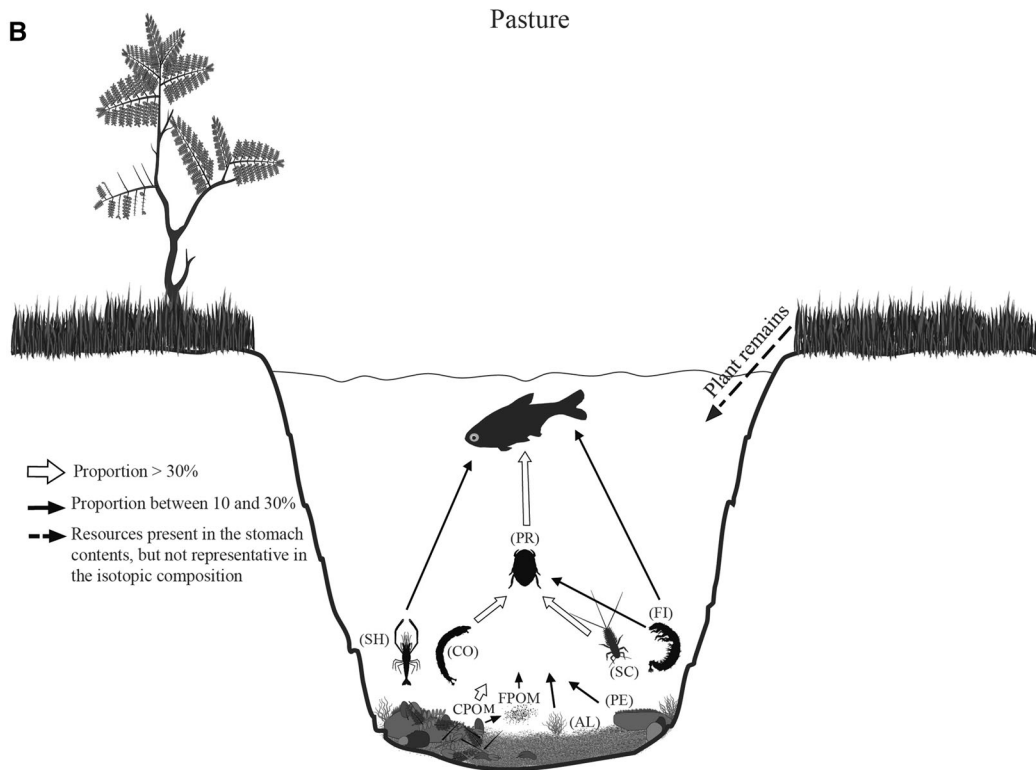
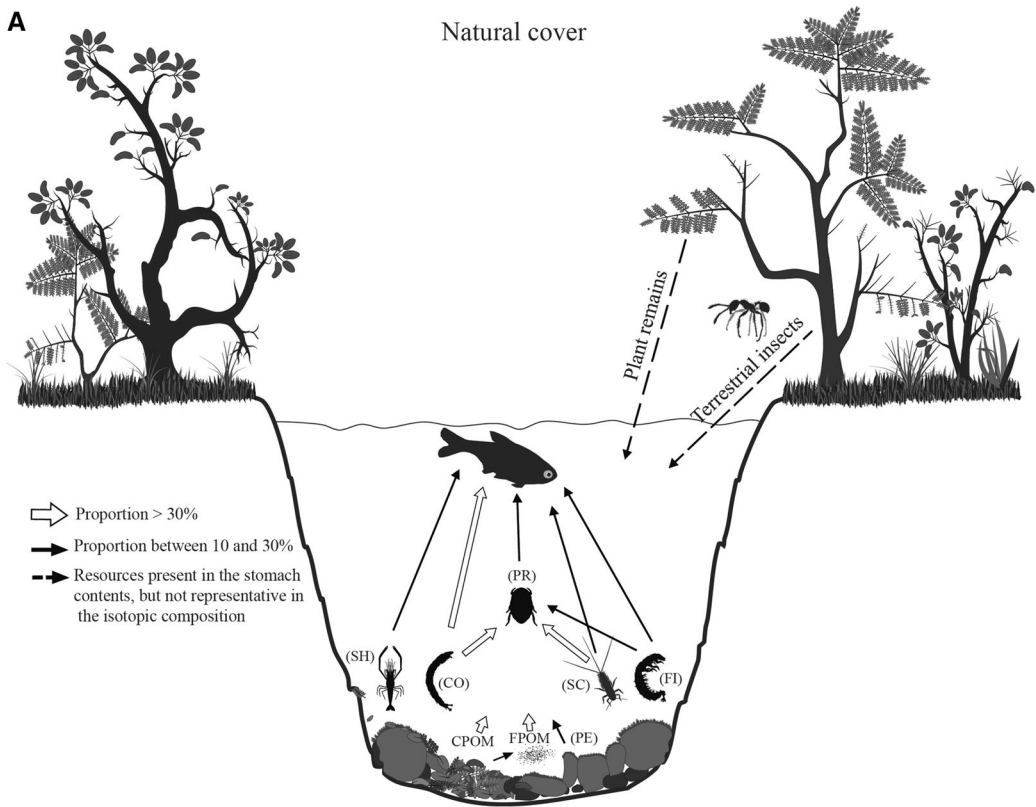
It is necessary to emphasize that dietary interactions with resident species can strongly influence and impact native communities through a variety of ways, including altering predator–prey relationships

pasture and natural cover streams, respectively. Standard ellipse areas (SEA, solid sphere) represent the core isotopic niche space and the dashed lines delimit the total area (TA)

(Alexander et al. 2014; Guo et al. 2017) and resource competition (Cucherousset et al. 2012; Busst and Britton 2017). Because predicting the ecological consequences of invasions by non-native species is a fundamental aspect of their risk-based management, it is crucial to understand the traits associated with invasive potential (Britton et al. 2007; 2011; Busst and Britton 2017). We also highlight that each invasive species presents its own particularities that allow them to be widespread or rare in the invaded environment, and in our study, we evaluated only the trophic plasticity of a single fish species.

Our study identified trophic characteristics that could be related to the success of *Knodus moenkhausii* as an invasive species. Through our results, it was also possible to evaluate how habitat degradation can change the trophic responses of such species, which reflected the aspects of ecosystem functioning. This information is important especially in developing countries, where rapid agricultural expansion leads to rapid changes in land use.

Fig. 6 Representation of food web of the species *K. moenkhausii* sampled in natural cover streams (a) and pasture streams (b) according to the analyses of stomach contents (dashed lines) and stable isotopes (solid lines). PR predator, FI filtering-collector, CO gathering-collector, SH shredder and SC scraper. Basal resources: AL algae, FPOM fine particulate matter, CPOM coarse particulate matter, PE periphyton and Plant remains = riparian vegetation and grasses (in pastures)



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