Trophic ecomorphology of Siluriformes (Pisces, Osteichthyes) from a tropical stream

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(With 4 figures)

Abstract

The present study analysed the relationship between morphology and trophic structure of Siluriformes (Pisces, Osteichthyes) from the Caracu Stream (22º 45’ S and 53º 15’ W), a tributary of the Paraná River (Brazil). Sampling was carried out at three sites using electrofishing, and two species of Loricariidae and four of Heptapteridae were obtained. A cluster analysis revealed the presence of three trophic guilds (detritivores, insectivores and omnivores). Principal components analysis demonstrated the segregation of two ecomorphotypes: at one extreme there were the detritivores (Loricariidae) with morphological structures that are fundamental in allowing them to fix themselves to substrates characterised by rushing torrents, thus permitting them to graze on the detritus and organic materials encrusted on the substrate; at the other extreme of the gradient there were the insectivores and omnivores (Heptapteridae), with morphological characteristics that promote superior performance in the exploitation of structurally complex habitats with low current velocity, colonised by insects and plants. Canonical discriminant analysis revealed an ecomorphological divergence between insectivores, which have morphological structures that permit them to capture prey in small spaces among rocks, and omnivores, which have a more compressed body and tend to explore food items deposited in marginal backwater zones. Mantel tests showed that trophic structure was significantly related to the body shape of a species, independently of the phylogenetic history, indicating that, in this case, there was an ecomorphotype for each trophic guild. Therefore, the present study demonstrated that the Siluriformes of the Caracu Stream were ecomorphologically structured and that morphology can be applied as an additional tool in predicting the trophic structure of this group.

Keywords: Loricariidae, Heptapteridae, trophic guilds, Paraná River.

Ecomorfologia trófica de Siluriformes (Pisces, Osteichthyes) de um riacho tropical

Resumo

O presente estudo investigou as relações entre morfologia e a estrutura trófica das espécies de Siluriformes (Pisces, Osteichthyes) do riacho Caracu (22º 45’ S e 53º 15’ W), afluente do rio Paraná. Foram amostrados três pontos com pesca elétrica, sendo registradas duas espécies de Loricariidae e quatro de Heptapteridae. A análise de agrupamento revelou a presença de três guildas tróficas: detritívoros, insetívoros e omnívoros. A Análise de Componentes Principais evidenciou a tendência de segregação entre dois ecomorfotipos: em um extremo do gradiente ecomorfológico estiveram dispostos detritívoros (Loricariidae), com estruturas morfológicas importantes para sustentação em substratos de corredeiras, as quais permitem a pastagem sobre detritos e materiais orgânicos incrustados no substrato. No outro extremo estiveram insetívoros e omnívoros (Heptapteridae), com estruturas morfológicas que tendem a melhorar o desempenho na exploração de recursos em hábitats estruturalmente complexos e com baixa velocidade de corrente, comumente colonizados por insetos e plantas. A Análise Discriminante Canônica revelou um caso de divergência ecomorfológica entre insetívoros e omnívoros, sendo os primeiros, detentores de estruturas morfológicas que favorecem a captura de presas que ocupam pequenos espaços entre rochas e, o segundo grupo, caracterizado por possuir corpos mais comprimidos, tendendo a explorar itens alimentares em zonas marginais de remanso. Os resultados dos testes de Mantel revelaram que a estrutura trófica apresentou relações significativas com a forma do corpo, independentemente das relações filogenéticas. Portanto, o presente estudo demonstrou que, entre os Siluriformes do riacho Caracu, existe uma estrutura ecomorfológica, o que evidenciou que a morfologia pode ser utilizada como mais uma importante ferramenta na tentativa de predizer a estrutura trófica desse grupo.

Palavras-chave: Loricariidae, Heptapteridae, guildas tróficas, rio Paraná.

1. Introduction

The study of ecomorphology involves an analysis of the relationship between body shape and environmental factors to reveal the ecological and evolutionary implications in individuals, populations, guilds and assemblages (Motta et al., 1995; Peres-Neto, 1999). At present, ecomorphological studies are based on the concept that adaptative variations in phenotype are able to produce differences in the performance of species, which consequently generate variations in resource use (Wainwright, 1994). As a result, some authors believe that morphology can predict resource use by species (Casatti and Castro, 2006; Pagotto et al., 2009; Oliveira et al., 2010).

In tributaries of the Paraná River (Brazil), Siluriformes (Osteichthyes) are one of the most abundant groups of fishes (Garutti, 1988; Agostinho et al., 1997). Considering that some species tend to exhibit trophic specialisation (Hahn et al., 2004), the ecological structure of this group can be characterised by a set of trophic guilds, with specific morphological patterns. In the present study, we evaluated the relationship of morphology with the trophic structure of Siluriformes in the Caracu Stream, a tributary of the Paraná River. Thus, we analysed the following: 1) interspecific ecomorphological patterns; and 2) relationships between morphological variables and the trophic guilds apart from the influence of phylogeny, i.e., whether trophic guilds can be predicted by body shape.

Our hypothesis was that body shape is intimately related to the exploited resource type, and consequently, morphologically analogous species tend to belong to the same trophic guild. Thus, if strong relationships of morphology with resource utilisation are found, it can be assumed that the Siluriformes of the Caracu Stream are ecomorphologically structured, which will allow ecological predictions to be made based on body shape of these species. However, if these relationships are weak, the assemblage may present an ecomorphological structure defined simply by the phylogenetic relationships among species or represent a random structure.

2. Material and Methods

2.1. Study area

The Caracu Stream (22º 45' S and 53º 15' W) is a 2nd order tributary of the left bank of the upper Paraná River (Brazil) that extends for approximately 5 km (see Figure 1). This region exhibits a warm, wet temperate climate, and the annual mean temperature is 21 °C, with December, January and February being the warmest and wettest months, and June and July the coldest and driest ones (Maack, 1981). In the present study, there were three sampling stations chosen (Sites 1, 2 and 3; see Figure 1). The means of physical and chemical variables for each sampling station are described in Table 1.

Site 1 is located in the upper stretch of the Caracu Stream (see Figure 1). It is probably the site most marked by anthropogenic alterations. The banks have a low density of vegetation, with a predominance of herbaceous species and grasses. Because it is inside an area of bovine rearing, it has an artificial enlargement that is used by animals to drink

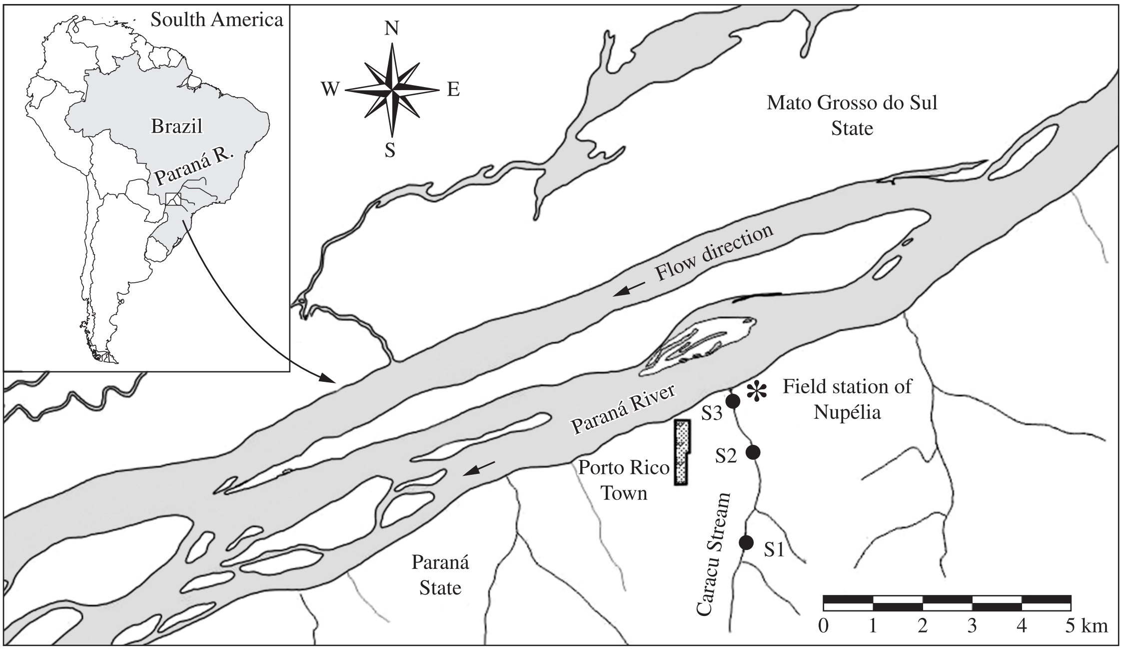

Figure 1. Map showing the studied area: Caracu Stream and its respective sample stations. Site 1 (S1), Site 2 (S2) and Site 3 (S3).

Table 1. The means (± standard deviation) of physical and chemical variables for each sampling station of the Caracu Stream.

Variables	Site 1	Site 2	Site 3
Width (m)	10.97 (± 1.97)	1.41 (± 0.51)	2.26 (± 0.42)
Depth (m)	0.33 (± 0.18)	0.25 (± 0.13)	0.25 (± 0.16)
Water velocity (m/s)	0.03 (± 0.006)	0.37 (± 0.14)	0.37 (± 0.18)
Water temperature (°C)	24.43 (± 3.23)	25.01 (± 2.18)	24.20 (± 1.1)
Dissolved O_2 (mg/L)	7.39 (± 0.66)	8.38 (± 1.73)	8.15 (± 0.17)
Conductivity (μS/cm)	51.93 (± 4.82)	50.53 (± 2.34)	47.45 (± 6.86)
pH	6.6 (± 0.21)	6.93 (± 0.1)	6.80 (± 0.32)

water. Thus, it can be considered a semi-lentic stretch (see Table 1), with the bottom typically composed of sand and mud. Site 2 is located in the middle stretch of the Caracu Stream (see Figure 1), and its banks are totally covered with grasses. In the past, the surrounding area was used as a pasture, but now it is destined for natural regeneration. Thus, the grasses are spreading homogeneously over the whole area and sometimes invading the water. Differently from Site 1, this station alternates areas of riffles with rocks on the bottom and few pools, which are sandy. Site 3 is the nearest to the mouth (see Figure 1), and it is characterised by the presence of a number of trees on its banks (*Cecropia* sp. and *Inga* sp.). Similar to Site 2, this stretch alternates areas of riffles with rocks on the bottom and few pools, which are sandy.

2.2. Sampling

Three samples were collected using electrofishing (2500 W, 500 V and 2A) in December, 2005, March, 2006 and September, 2006, at each sample station. Two electro-shock dip nets were let out longitudinally for 50 m against the stream flow, and block nets (5-mm mesh) were set at upstream and downstream positions. Three successive samples were realized for each station.

The collected fishes were taken to the field station of Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia), near the Caracu Stream (see Figure 1), where they were identified according to Graça (2004) and Graça and Pavanelli (2007), labelled and frozen. Voucher specimens were deposited in the Ichthyologic Collection of Nupélia: *Hypostomus ancistroides* NUP 332, 40 ex.; *Hypostomus cf. strigaticeps* NUP 3190, 1 ex.; *Cetopsorhamdia iheringi* NUP 3232, 1 ex.; *Imparfinis schubarti* NUP 4159, 1 ex.; *Phenacorhamdia tenebrosa* NUP 4161, 1 ex.; *Rhamdia quelen* NUP 1737, 1 ex.

2.3. Linear morphometric measures, areas and indices

Linear morphometric measures and areas, related to the trunk, fins, head, eyes and mouth of the fishes were selected according to Gatz-Jr. (1979), Breda et al. (2005) and Oliveira et al. (2010). In total, there were 23 morphological characters chosen that were related to the swimming behaviour and trophic ecology of species: standard length (SL), maximum body height (MBH), body midline height (BMH), maximum body width (MBW), caudal peduncle length (CPdL), caudal peduncle height (CPdH), caudal peduncle width (CPdW), caudal fin height (CH), anal fin length (AL), pectoral fin length (PtL), pelvic fin length (PvL), head length (HdL), head height (HdH), head width (HdW), eye height (EH), mouth height (MH), mouth width (MW), dorsal fin area (DA), caudal fin area (CA), anal fin area (AA), pectoral fin area (PtA), pelvic fin area (PvA) and eye area (EA).

To avoid variability induced by the substances used for preservation (Peterson and VanderKooy, 1996), all of the morphological measures were taken from specimens recently thawed. Considering the average length of the first maturation (Vazzoler, 1996; Suzuki et al., 2004), only adult fishes were used, because ontogenetic development can cause changes in body shape and feeding habits (Scharf et al., 2000; Novakowski et al., 2004). Linear measures were obtained by a digital pachymeter, with an approximation of 0.01 mm. The areas of eyes and fins were obtained from drawings of their outlines, which were scanned and input to AutoCAD 2004 software for the calculation of the internal area. Twenty-one ecomorphological indices were calculated from the morphological linear measures and areas (see Table 2).

2.4. Stomach contents

Fishes were eviscerated for analysis of their stomach contents, and species without identifiable stomachs had the anterior most portion of their intestines removed for analysis. The food items observed were grouped into six taxonomical and/or ecological categories: detritus/sediments (decomposed organic detritus, periphitic algae and inorganic sediment), terrestrial plants (Monocotyledons, Dicotyledons, fruits and remains of plants), aquatic insects (larvae of Trichoptera, Diptera, Chironomidae, Ephemeroptera and Coleoptera, and pupae of Diptera), terrestrial insects (adults of Chironomidae, Ephemeroptera, Hymenoptera, Homoptera and fragments), benthic invertebrates (adults of Nematomorpha) and fishes.

The procedure adopted to analyse the stomach contents was the volumetric method (Hellawell and Abel, 1971). Through this procedure, the volume of each food item was calculated as a percentage of the total volume of the stomach contents for each analysed species.

2.5. Data analysis

Similarity in species composition of trophic guilds was established by cluster analysis using the Bray Curtis index to obtain the distance matrix, and simple linkage

Table 2. Description of the ecomorphological indices and their ecological explanations.

1	Compression index - MBH/MBW: High values indicate a laterally compressed body, and would be expected in fishes occupying lentic habitats (Gatz-Jr., 1979; Watson and Balon, 1984).
2	Depression index - BMH/MBH: Low values indicate species with depressed bodies, and would be expected in fishes occupying lotic habitats (Gatz-Jr., 1979; Watson and Balon, 1984).
3	Relative length of caudal peduncle - CPdL/SL: Long caudal peduncles are related to species adapted to lotic habitats. Fishes with this structure are capable of developing short-distance displacement (Gatz-Jr., 1979; Watson and Balon, 1984).
4	Relative height of caudal peduncle - CPdH/MBH: Low values indicate great maneuverability (Gatz-Jr., 1979; Oliveira et al., 2010).
5	Relative width of caudal peduncle - CPdW/MBW: High values indicate continuous swimmers (Gatz-Jr., 1979; Oliveira et al., 2010)
6	Relative area of dorsal fin - DA/$(SL)^2$: High values indicate stabilisation in rapid starts (Breda et al., 2005).
7	Relative area of caudal fin - CA/$(SL)^2$: Large tails indicate rapid starts (Gatz-Jr., 1979; Breda et al., 2005; Oliveira et al., 2010).
8	Aspect ratio of caudal fin - $(CH)^2$/CA: High values indicate forked fins, and represent active swimmers. On the other hand, low values indicate greater fins, which represent fishes with good performance in rapid starts (Gatz-Jr., 1979; Breda et al., 2005).
9	Relative area of anal fin - AA/$(SL)^2$: High values indicate great maneuverability (Breda, 2005).
10	Aspect ratio of anal fin - $(AL)^2$/AA: High values indicate faster progressive or backward movements (Breda, 2005).
11	Relative area of pectoral fin - PtA/$(SL)^2$: High values would be expected in fishes occupying rapid flowing waters which use them to maintaining close contact with the substrate (Gatz-Jr., 1979; Watson and Balon, 1984; Kerfoot-Jr. and Schaefer, 2006).
12	Aspect ratio of pectoral fin - $(PtL)^2$/PtA: High values indicate long narrow fins which are present in faster swimmers (Breda et al., 2005). For benthic fishes which inhabit stretches of rapids, longer pectoral fins can promote the maintenance and balance in rapid flowing (Gatz-Jr., 1979; Casatti and Castro, 1998).
13	Relative area of pelvic fin - PvA/$(SL)^2$: For benthic fishes which inhabit rapid stretches. Greater pelvic fins can increase the area of contact with the substrate, and permit the fishes to maintain close contact (Gatz-Jr., 1979; Casatti and Castro, 1998; Kerfoot-Jr. and Schaefer, 2006).
14	Aspect ratio of pelvic fin - $(PvL)^2$/PvA: High values indicate long fins. For benthic fishes which inhabit stretches of rapids, longer pelvic fins can promote the maintenance into the rapid flowing (Gatz-Jr., 1979; Casatti and Castro, 1998).
15	Relative length of head - HdL/SL: High values indicate fishes feeding larger preys (Gatz-Jr., 1979; Watson and Balon, 1984).
16	Relative height of the head - HdH/MBH: High values indicate fishes feeding larger preys (Oliveira et al., 2010).
17	Relative width of the head - HdW/MBW: High values indicate fishes feeding larger preys (Oliveira et al., 2010).
18	Relative height of the mouth - MH/MBH: High values indicate fishes feeding larger preys (Gatz-Jr., 1979; Watson and Balon, 1984). Low values indicate greater suction pressure of mouth (Norton and Brainerd, 1993).
19	Relative width of the mouth - MW/MBW: High values indicate fishes feeding larger preys (Gatz-Jr., 1979). Low values indicate greater suction pressure (Norton and Brainerd, 1993).
20	Eye position - EH/HdH: Index associated with the vertical habitat preference. High values indicate species with dorsal eyes (Watson and Balon, 1984).
21	Relative area of eye - EA/$(SL)^2$: Index associated with visual acuity. High values indicate species with greater visual acuity (Pankhurst, 1989).

as the method of connection. This procedure was carried out in PC-ORD 4.1 software (McCune and Mefford, 1999).

To evaluate trends in multivariate ecomorphological space and, then, to find patterns of interspecific diversification, there was a principal components analysis (PCA) applied to the correlation matrix (Pearson) formed by 21 ecomorphological indices. The axes were selected using a broken-stick model (Jackson, 1993), and the analysis was performed in PC-ORD 4.1 (McCune and Mefford, 1999).

Canonical discriminant analysis (CDA) was applied to verify the ecomorphological indices that maximised the differences between the trophic guilds using a stepwiseforward method ($p < 0.05$) (Johnson, 1998). Additionally, the CDA reclassified the groups based on the minimal distance between the observations inside the groups. The percentage of correct reclassification can be an indicative of success in the prediction (Gotelli and Ellison, 2004). This test was performed in Statistica 7.0 software.

A Mantel test was carried out to check whether the species that used the same ecological resource were the most similar morphologically. This method compared the matrix of morphological distance between the species with the models matrices for trophic structure and phylogeny. The null hypothesis was that the morphological patterns of Siluriformes from the Caracu Stream are independents of resource used and of species phylogeny.

The morphological distances were calculated based on the mean Euclidian distance among the ecomorphological indices for each pair of species, according to the expression (Equation 1):

$$D_{jk} = \left[\sum_{i=1}^{n} \left(x_{ij} - x_{ik} \right)^2 \right]^{1/2} \qquad (1)$$

in which: D_{jk} = Euclidian distance, n = number of the ecomorphological indices, and x_{ij} e x_{ik} = values of ecomorphological index i to j and k species, respectively (Gotelli and Ellison, 2004).

The model matrices were obtained by attributing the value of 1 to the pair of species from the same trophic guild and 0 to the pair of species that did not satisfy these conditions. In building the model matrix of taxonomic distance, the method proposed by Pouilly et al. (2003) was used, which consists of a standardized counting of the number of nodes that separate each species along the taxonomical tree. Value 1 was attributed to species from the same genera, value 2 to different genera, but in the same family, and value 3 to those that were not in the same family.

The relationship between morphology and trophic structures could be an artifact derived from the phylogenetic distance among the species (Douglas and Matthews, 1992). A partial Mantel test was performed to evaluate the effect of phylogeny, which tested the partial correlation between two matrices, controlling the effect of a third. Initially, regressions of morphological distance by taxonomical distances and regressions of model matrices of trophic structure by taxonomical distances were carried out. Then a partial Mantel test correlating the residual matrix from the first regression (morphology x phylogeny) with the residual matrix from the trophic structure x phylogeny regression was performed. Thus, the correlation tests between the morphological distance matrix and trophic structure were performed independent of the effect of phylogeny. Both the Mantel and partial Mantel test were carried out in NTSYS-pc software (Rohlf, 1988) and the statistical significance was estimated using 20,000 permutations.

3. Results

A total of six Siluriformes species, representing two families and five genera, were sampled and analysed (see Table 3).

The diets of *H. ancistroides* and *H. strigaticeps* were dominated by organic detritus (periphytic algae and decomposing organic material) and inorganic sediments. Thus, they were classified as detritivores. *Cetopsorhamdia iheringi*, *I. schubarti* and *P. tenebrosa* formed the group of insectivores. All of these species were characterised by insects (terrestrial or aquatic) as their main food item. *Rhamdia quelen*, which fed on a large diversity of food resources, with a tendency toward the consumption of plants, was classified as an omnivore (see Table 4 and Figure 2).

The PCA showed that only the first axis was significant in explaining the ordination of the data, accounting for 49.6% of the total variability (see Table 5). According to the ordination (see Figure 3), the variation tendency of the data demonstrated clear segregation between the Loricariidae and Heptapteridae. Thus, the Loricariidae, with negative scores, presented individuals with more depressed bodies (low values for the depression index), long caudal peduncles and developed fins (except for the

Table 3. The systematic position of Siluriformes from the Caracu Stream; N represents the number of individuals analysed for each species, SL represents the mean of standard length (in mm) and SD the respective standard deviation. The systematic position of the species followed Reis et al. (2003).

Species	N	SL ± SD
SILURIFORMES		
LORICARIIDAE		
HYPOSTOMINAE		
Hypostomus ancistroides (Ihering, 1911)	51	73.25 ± 9.85
Hypostomus cf. strigaticeps (Regan, 1908)	4	79.16 ± 15.01
HEPTAPTERIDAE		
Cetopsorhamdia iheringi Schubart and Gomes, 1959	4	44.38 ± 4.69
Imparfinis schubarti (Gomes, 1956)	21	51.65 ± 5.21
Phenacorhamdia tenebrosa (Schubart, 1964)	8	41.47 ± 6.30
Rhamdia quelen (Quoy and Gaimard, 1824)	14	118.10 ± 23.76

Table 4. The volumetric frequency of each food item exploited by Siluriformes from the Caracu Stream: Ha = *H. ancistroides*; Hs = *H. strigaticeps*; Ci = *C. iheringi*; Is = *I. schubarti*; Pt = *P. tenebrosa*; and Rq = *R. quelen.*

Trophic category	Ha	Hs	Ci	Is	Pt	Rq
Detritus/Sediments	100	100	1.16	1.04	5.88	0.02
Plants						
Monocotyledons	-	-	-	-	-	46.00
Dicotyledons	-	-	11.63	0.83	-	23.21
Fruits	-	-	-	-	-	3.47
Remains of plants	-	-	-	9.80	2.94	-
Aquatic insects						
Trichoptera larvae	-	-	30.23	3.54	2.94	-
Diptera larvae	-	-	2.33	7.5	14.71	-
Diptera pupae	-	-	-	4.37		-
Ephemeroptera larvae	-	-	-	0.21	2.94	-
Coleoptera larvae	-	-	9.3	2.08	35.30	-
Terrestrial insects						
Diptera adults	-	-	-	-	-	0.05
Ephemeroptera adults	-	-	-	2.92	-	-
Hymenoptera adults	-	-	16.28	5.00	2.94	1.78
Homoptera adults	-	-	-	-	-	10.4
Fragments	-	-	29.07	62.29	32.35	4.35
Benthic invertebrates						
Nematomorpha adults	-	-	-	-	-	3.44
Fishes						
Remains of fishes	-	-	-	0.42	-	7.28

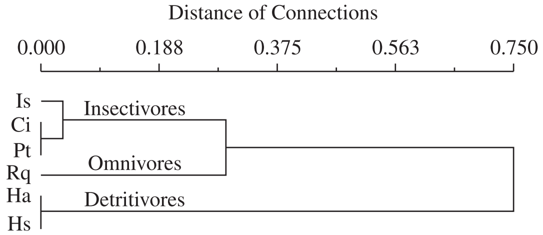

Figure 2. Dendrogram of trophic similarity for Siluriformes from the Caracu Stream: Is = *I. schubarti*; Ci = *C. iheringi*; Pt = *P. tenebrosa*; Rq = *R. quelen*; Ha = *H. ancistroides*; and Hs = *H. strigaticeps*. Species with similar diets presented the shorter distance of connections.

anal). The second family, Heptapteridae, with positive scores, presented individuals with higher and proportionally more compressed bodies, anal fins with large areas and relatively larger mouths (see Figure 3).

The models predicted by the CDA selected the 16 ecomorphological indices that most contributed to the discrimination among members of the trophic guilds (see Table 6). Therefore, the first axis, responsible for explaining 94.7% of the total variance, demonstrated clear segregation of the group of detritivores (Loricariidae) compared to the others (see Figure 4). Canonical axis 2 (5.3% of explained variability) showed the segregation between insectivores and omnivores. The insectivores, with positive scores, presented wider heads, caudal fins with a tendency toward bifurcation and larger anal fins, while the omnivores were more compressed (see Table 6 and Figure 4). The classification matrix predicted by the CDA model indicated that all of the Siluriformes species of the Caracu Stream were correctly classified into their respective trophic guilds.

The Mantel test revealed a significant correlation between morphology and diet (p = 0.02; see Table 7). However, when the matrices of morphological and phylogenetic distances were correlated, the possibility of phylogeny affecting these ecomorphological correlations could not be discarded (p = 0.07; see Table 7). Thus, a partial Mantel test was performed to control the effect of historical factors in the ecomorphological relationships. It revealed that, independent of phylogenetic relationships, the body shapes of the fishes were related to the local trophic structure (p = 0.03; see Table 7).

4. Discussion

In the Caracu Stream, the Siluriformes were grouped in three trophic guilds: detritivores, insectivores and omnivores. Despite the small number of individuals for some species, the trophic structure described in the Caracu Stream cannot be considered a random result, as shown by the Mantel tests. Moreover, our results confirm the feeding habits observed by other authors in studies with these species in streams of the same hydrographic basin (Castro and Casatti, 1997; Casatti and Castro, 1998; Casatti, 2003).

We found that the ecomorphological gradient formed two groups in multivariate space: detritivores (Loricariidae) and insectivores/omnivores (Heptapteridae). Detritivores presented long caudal peduncles and large middle fins (except for the anal), which are morphological structures that are fundamental to their success in exploiting lotic environments. Because of these structures, they are capable of performing short displacements and stabilise their bodies while they move through the flowing water (Breda et al., 2005). Additionally, the greatest problem encountered by fishes that exploit the currents of rivers and streams is remaining on the substrate. In these environments, they

Table 5. The eigenvectors of morphological indices at the first axis (PC1) of Principal Component Analysis. At the lower level there are the eigenvalue of PC1, the eigenvalue predicted by the broken-stick model and the explained variability by this axis (in percentage). Eigenvectors (bold numbers) were chosen to explain the ordination of the data in the multivariate ecomorphological space.

Ecomorphological indices	PC1
Compression index	**0.235**
Depression index	**0.271**
Relative length of caudal peduncle	**-0.293**
Relative height of caudal peduncle	0.155
Relative width of caudal peduncle	0.113
Relative length of the head	-0.101
Relative height of the head	-0.174
Relative width of the head	0.146
Relative height of the mouth	**0.266**
Relative width of the mouth	**0.288**
Eye position	0.065
Relative area of eye	-0.217
Relative area of dorsal fin	**-0.278**
Relative area of caudal fin	**-0.257**
Aspect ratio of caudal fin	0.176
Relative area of anal fin	**0.245**
Aspect ratio of anal fin	-0.084
Relative area of pectoral fin	**-0.259**
Aspect ratio of pectoral fin	**-0.252**
Relative area of pelvic fin	**-0.253**
Aspect ratio of pelvic fin	-0.210
Eigenvalue	10.42
Predicted eigenvalue: *broken-stick*	3.64
Explained variability (%)	49.64

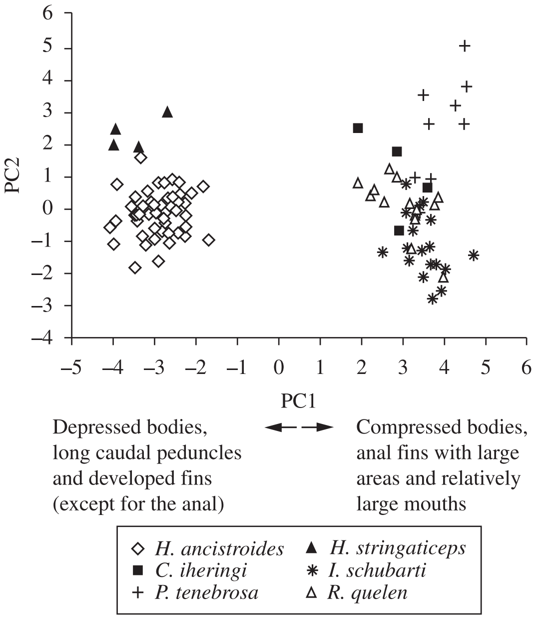

Figure 3. The multivariate ecomorphological space occupied by Siluriformes from the Caracu Stream. The scores are differentiated according to each species. The arrows indicate more representative indices, correlated negatively and positively with PC1.

Table 6. The values of ecomorphological indices correlated with the axes produced by canonical discriminant analysis. At the lower level are described the eigenvalues to both axis 1 and 2, and the explained variability by theses axes (in percentage). Representative indices of each axis (bold numbers) were chosen to explain the ordination of the data in the multivariate ecomorphological space.

Ecomorphological indices	Axis 1	Axis 2
Compression index	**0.624**	**-1.578**
Depression index	0.388	-0.212
Relative length of caudal peduncle	**-0.547**	-0.128
Relative height of caudal peduncle	0.414	-0.602
Relative length of the head	0.001	-0.281
Relative height of the head	0.053	-0.379
Relative width of the head	-0.224	**0.757**
Relative height of the mouth	**0.515**	0.171
Relative width of the mouth	0.229	-0.204
Relative area of eye	-0.078	-0.281
Relative area of dorsal fin	-0.247	-0.126
Relative area of caudal fin	**-0.366**	-0.031
Aspect ratio of caudal fin	0.314	**0.610**
Relative area of anal fin	**0.678**	**0.869**
Relative area of pectoral fin	**-0.275**	0.302
Aspect ratio of pectoral fin	-0.238	0.203
Eigenvalue	64.32	3.59
Explained variability (%)	94.7	5.3
Accumulated variability (%)	94.7	100.0

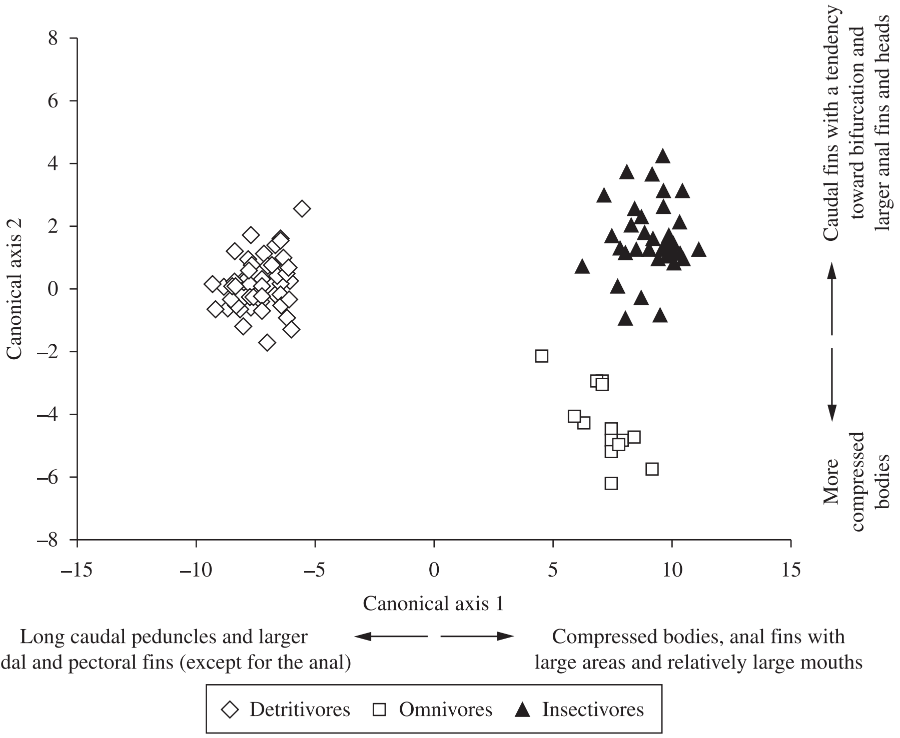

Figure 4. Diagram of canonical discriminant analysis showing the segregation among the trophic guilds in ecomorphological space. The arrows indicate more representative indices, correlated negatively and positively at each canonical axis.

Table 7. A Mantel test comparing the matrix of morphological distance with the model matrices of trophic guilds and phylogenetic distance, respectively. At the lower level is described the result of partial Mantel test comparing the matrix of residuals of morphological distance (dependent variable) by the phylogenetic distance (independent variable) with the matrix of residuals of trophic guilds (dependent variable) by the phylogenetic distance (independent variable).

Mantel test	**$Z_{observed}$**	**$p(Z_{random} < Z_{observed})$**	**$p(Z_{random} > Z_{observed})$**
morphology x trophic guilds	- 0.80	**0.02**	0.98
morphology x phylogeny	0.73	0.93	**0.07**
Partial Mantel test			
residuals (morphology x phylogeny) x residuals (trophic guilds x phylogeny)	- 0.60	**0.03**	0.97

suffer the effect of forces of resistance that tend to elevate their body, in particular the net pressure force, which is composed of two components: a lift force, acting normal to the axis of motion, and a drag force, acting along that axis and retarding the motion (Webb, 1974). It results from the more rapid movement of water molecules across the upper surface than the lower surface of the body (Bernoulli effect). However, this effect is eliminated when the fish remains in contact with the substrate, because there is no water pressure underneath its body. Therefore, the dorsoventral flattening and the development of paired fins (which increase the area of contact with the substrate; Kerfoot-Jr. and Schaefer, 2006) are morphological adaptations that allow the Loricariidae to fix themselves to the substrate associated with rushing torrents, minimising adverse effects on these fish.

On the other side of the ecomorphological gradient were the insectivores/omnivores, which exhibit compressed bodies and large anal fins and possess a greater capacity for maneuverability (Breda, 2005). Maneuverability is defined as the ability of organisms to perform quick small-angled maneuvers (Webb et al., 1996). Thus, species with these characteristics exhibit a superior performance in the exploitation of structurally complex habitats with low current velocity (Breda, 2005).

As in the principal components analysis, the CDA results confirm that the greatest segregation tendency was between detritivores and the other guilds. Moreover, this analysis showed that, in terms of morphology, the most similar individuals were correctly classified into the same guilds, with 100% precision and a high prediction success.

According to Casatti (2003), Loricarid detritivores use pasturing as a feeding tactic. In this type of behaviour, the organisms are supported on submerged rocks or branches, generally in stretches of river rapids, where they graze on the encrusted organic material on the surface of these substrates. Consequently, they are benefitted by the long caudal peduncle and the large proportions of the caudal and pectoral fins, which aid movement through the flowing water by using quick short-distance displacements, in addition to allowing maintenance of position and balance while the fish feed in the turbulent conditions of the river rapids. In contrast, the insectivores and omnivores that we collected presented characteristics that give them a great capacity for maneuverability and efficiency in the capture of relatively large preys and plants in refuges among rocks and backwater zones (greater compression of the body, development of the anal fin and large mouths). In these habitat types there is a large deposition of allochthonous (e.g., insects and plants from the terrestrial environment) and autochthonous material (e.g., insect larvae) (Casatti and Castro, 1998).

The large variability explained by axis 1 of the CDA did not represent anything unexpected, because the segregated groups are especially distant phylogenetic lineages, thus presenting the tendency to be ecomorphologically distinct. In fact, what most attracted our attention was the separation of the insectivores and omnivores on axis 2. These two guilds belong to close phylogenetic lineages, and, consequently, exhibit great morphological similarity (thus representing a lower proportion of variability in the multivariate space); however, we found that they demonstrate a case of ecomorphological divergence.

Rhamdia quelen, as observed by Casatti and Castro (2006), possesses a more compressed body than the other Heptapterids and, thus, presents a greater capacity for maneuverability, tending to occupy marginal backwater zones, where the flooded vegetation presents a great deal of structuring and spatial complexity. In these environments, this fish assumes a generalist profile (Gomes et al., 2001) and can be considered a bottom sweeper (Casatti and Castro, 1998). On the other hand, the insectivores prefer to inhabit areas near stretches of rapids (e.g., small spaces among the rocks, where the deposition of both terrestrial and aquatic insects is intense). In these environments, these organisms actively swim among rocks, where they capture their prey individually by excavating (while moving) and turning over the substrate (Casatti and Castro, 1998). In this way, they are benefitted by high aspect ratio values of the caudal fin and by large anal fin areas that confer a greater ability for continuous swimming while looking for food and aid in maneuvers during the capture of prey deposited near the bottom, respectively.

The results of the Mantel test revealed that body shape was intimately correlated with diet, i.e., morphologically similar species tend to be grouped into the same trophic guild. However, the relationships between morphology and ecology may be simply an artifact produced by phylogenetic relationships (Douglas and Matthews, 1992). Consequently, ecomorphological studies are more convincing when developed together with methods that prove whether the relationships between morphology and ecology originated from adaptive responses to selective environmental pressures. Thus, with the aid of a partial Mantel test, which permits the control of the effect of historical factors in ecomorphological relationships, the present study revealed that independent of the phylogenetic relationships, the body shape of the fishes of the Caracu Stream was related to local trophic structure. This suggests that the effects of phylogeny, even if apparently significant, did not limit the identification of adaptive relationships between morphology and ecology. Therefore, the Siluriformes of the Caracu Stream were ecomorphologically structured and morphology can be applied as an additional tool in predicting the trophic structure of this group.

In summary, this study revealed that among the Siluriformes of the Caracu Stream, trophic structure is related to the morphology of the species, independent of their phylogenetic relationships. This structure can be explained by the interspecific ecomorphological diversification pattern, which revealed differences in the occupation of the ecomorphological space by the trophic guilds. However, it is not possible to ignore the influence of behavioural, physiological and stochastic factors on the lifestyle of the species. Therefore, despite the fact that ecomorphology can be considered an important tool in the prediction of the exploited niche, it is of interest to combine behavioural and physiological experiments with ecomorphological studies. The predictive character of these approaches would provide greater precision in the analyses and significantly contribute to our understanding about mechanisms that allow the coexistence of species.

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