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Dry Season Feeding Profiles of a Characiformes Assemblage in a Brazilian Tropical Stream

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Trophic interactions between fish and their resources depends on resource availability and interspecific competition. To understand dry season trophic profiles of a speciose Characiformes assemblage we performed stomach content analysis to describe diet and determine levels of niche partitioning and morphological adaptations among eight Characiformes species in the dry season in Mata de Itamacaoca, Chapadinha Municipality, State of Maranhão, northeastern Brazil. Insectivory dominated most diets, with *Astyanax* cf. *bimaculatus* and *Characidium* cf. *bimaculatum* exhibiting the broadest niches. Specialization occurred in *Curimatopsis* cf. *cryptica* (85.07% plant material) and there was significant dietary segregation with indicator species analysis linking *Astyanax* cf. *bimaculatus* to piscivory and *Knodus guajajara* to vermivory. Pianka index showed extreme niche overlap variations, with the highest overlap between *Bario oligolepis* and *Characidium* cf. *bimaculatum* (1.68), and between *Astyanax* cf. *bimaculatus* and *Nannostomus beckfordi* (1.64). Morphological PCA associated traits with feeding strategies: caudal fin length (*Astyanax* cf. *bimaculatus*), body depth (*Curimatopsis* cf. *cryptica*), and oral gape width (*Bario oligolepis*). Mixed models confirmed insects and plant material with a marginally significant effect as key drivers of dietary variation. Therefore, the assemblage shows high niche overlap combined with diverse trophic profiles. Results presented here demonstrate how dry season resource scarcity promotes trophic divergence via morphological specialization, with generalists (*Astyanax* cf.

bimaculatus) coexisting with specialists through niche partitioning, which is critical for conservation in this threatened urban-protected area.

Keywords: Morphological adaptations, Neotropical fishes, Resource partitioning, Seasonality, Trophic ecology

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BACKGROUND

Neotropical aquatic ecosystems harbor one of the most diverse ichthyofaunas on the planet (Albert et al. 2020; Tonella et al. 2022), where Characiformes play a fundamental role in structuring trophic networks (Barreto and Aranha 2006; Silva-Camacho et al. 2014; Meira et al. 2022; Oliveira et al. 2024). In seasonal environments, hydrological variation acts as an environmental filter, shaping patterns of trophic and morphological adaptations (Junk et al. 1989; Correa and Winemiller 2014; Duarte et al. 2022). Previous studies have shown that the dry season imposes critical constraints on resource availability, leading to increased interspecific competition (Prejs and Prejs 1987), the emergence of distinct morphological strategies (Gomiero et al. 2010), and dietary specialization (Novakowski et al. 2008). Although trophic segregation has been highlighted as the primary mechanism structuring fish assemblages (Ross 1986), this dynamic may vary according to local conditions, including dry season factors (Bouton et al. 1997). However, gaps remain in understanding the mechanisms that allow the coexistence of multiple sympatric species under such extreme conditions (Ross 1986; Neves et al. 2018).

Aquatic environments are generally strongly influenced by seasonal periods and flood pulse dynamics (Junk et al. 1989; Pazin et al. 2006; Espírito-Santo and Zuanon 2017). As flood peaks reach their maximum and the system transitions into the dry season, periods that are becoming increasingly pronounced, there is a progressive decline in turbidity, resource availability, flow velocity, and water level (Alho and Silva 2012). These abiotic changes result in significant transformations in fish assemblages (Saint-Paul et al. 2000). While some species exhibit expansion and contraction dynamics aligned with dry season reproduction, others persist throughout the entire hydrological cycle (Fialho et al. 2008; Arthington and Balcombe 2011; Fitzgerald et al. 2018). Dry season variation, particularly in tropical regions, plays a crucial role in shaping food resource availability and structuring trophic networks (Medeiros et al. 2014; Pelage et al. 2022; Londe et al.

2024). During the dry season, reduced water volume can lead to increased population density and the concentration of organisms in remnant habitats, intensifying ecological interactions such as competition and predation (Duarte et al. 2022). This scenario can directly impact niche partitioning, leading to shifts in dietary composition and potential trophic displacements among sympatric species (Silva-Camacho et al. 2014; Bloomfield et al. 2022; De Andrade et al. 2024).

In the context of dry season persistence, intraspecific morphological variation becomes a crucial factor for fish survival in stochastic ecosystems, as species evolve in response to persistent hydrological regimes (Poff and Ward 1989; Lytle and Poff 2004). Morphological adaptations and diversity can confer specializations to specific environmental parameters, thereby increasing survival among cohorts (Langerhans and Reznick 2010). morphological theory predicts that coexistence in restrictive environments is mediated by three main mechanisms: (a) divergence in functional traits (Winemiller 1991), (b) behavioral plasticity (Correa and Winemiller 2014), and (c) temporal resource partitioning (Ross 1986). However, the application of these principles to small Characiformes assemblages in seasonal microhabitats remains insufficiently tested. Studies in analogous systems suggest that body and oral apparatus morphology explain up to 80% of the variation in resource use (Neves et al. 2018; Duarte et al. 2022), but these patterns may differ significantly in fragmented environments such as the Mata de Itamacaoca.

The order Characiformes is one of the most diverse among Neotropical fishes, comprising approximately 1,700 described species (Reis et al. 2016) and encompassing a wide range of feeding habits, from herbivores and detritivores to carnivores and piscivores (Barbosa et al. 2017; Burns and Sidlauskas 2019). This functional diversity grants these fishes a crucial role in mediating energy and matter flow in aquatic ecosystems, directly influencing the availability and renewal of trophic resources (Burns and Sidlauskas 2019; Burns 2021; Burns et al. 2024). Moreover, their abundance and distribution across different habitats make them ideal models for investigating trophic interactions and adaptive strategies in dry season environments (Burns and Sidlauskas 2019; Burns et al. 2024). Trophic ecology among Characiformes species is often associated with morphological differences, particularly in mouth shape, dentition, and digestive tract structure (Silva-Camacho et al. 2014; Benone et al. 2020; Burns 2021; Meira et al. 2022). Specialized morphological traits enable differential exploitation of available resources (Sibbing and Nagelkerke 2000; Bower and Winemiller 2019), reducing dietary overlap (Mise et al. 2013) and promoting the coexistence of multiple species within the same environment (Oliveira et al. 2024; Oliveira et al., 2025). In environments influenced by seasonal hydrological regimes, these adaptations can be essential for species survival, allowing diversification of feeding strategies as resource availability fluctuates throughout the hydrological cycle (Porter et al. 2022; Bloomfield et al. 2022; De Andrade et al. 2024).

The Munim River Basin (16,000 km²), an important hydrographic system of Maranhão (Koerber et al. 2022), which is located in a transitional zone between the Amazon and Cerrado biomes (NuGeo 2016), harboring a still understudied ichthyofauna (Abreu et al. 2019; Vieira et al. 2023). Within this context, the Mata de Itamacaoca stands out as a unique ecological enclave embedded within an urban matrix (Oliveira et al. 2020), sustaining a diverse assemblage of small Characiformes (Oliveira et al. 2020), characterized by significant morphological and trophic overlap (Oliveira et al. 2024). The coexistence of functionally similar species in a seasonally dynamic environment suggests (i) the presence of sophisticated resource partitioning mechanisms (Burns and Sidlauskas 2019) and (ii) an increased vulnerability to anthropogenic disturbances (Daufresne and Boet 2007). Although preliminary studies have identified trophic segregation patterns (Oliveira et al. 2024), possible mechanisms are unexplored as these studies combined both wet and dry season than accounting for increased resource abundance in the wet season. Thus, dry-season ecological processes in the Munim River Basin remain poorly understood, particularly regarding how seasonal reductions in water volume and resource availability shape trophic interactions among fish species (Junk et al. 1989; Lytle and Poff 2004; Correa and Winemiller 2014).

Given the above, this study aims to investigate the dietary composition and trophic structure of Characiformes species in the Mata de Itamacaoca during the dry season through stomach content analysis, correlating it with food resource availability and species' morphological adaptations. Specifically, we seek to: (1) describe dietary composition and identify the main food items consumed based on stomach content analysis, (2) assess patterns of overlap and segregation in resource use among species, (3) examine the relationship between morphological attributes and dietary preferences, and (4) discuss the ecological implications of resource partitioning and interspecific competition.

MATERIALS AND METHODS

Study area and sampling methodology

This study was conducted in the Mata de Itamacaoca (middle Munim River Basin), a protected urban fragment (460 ha) within the Cerrado biome 03°44'45.2"S 43°19'15.1"W; ~90 m elevation), located in the Chapadinha municipality, State of Maranhão, northeastern Brazil (Fig. 1, Table 1). Mata de Itamacaoca encompasses a diverse array of microhabitats, including riparian forests, gallery forests, and perennial streams that collectively support a rich biodiversity representative of the Cerrado biome (Silva et al. 2008; Oliveira et al. 2020). The vegetation consists primarily of closed-canopy formations with trees exceeding 10 meters in height, particularly around springs and water bodies, which are essential for maintaining local water supplies (Silva et al. 2008). The area was officially designated as an Area of Relevant Ecological Interest (Decreto Nº 05/2018) due to its critical role in watershed protection, microclimate regulation, and the conservation of regional biodiversity (Silva et al. 2008). Despite its protected status, the reserve faces increasing anthropogenic pressures, including illegal resource extraction (*e.g.*, timber, fish, and game), agricultural burning practices, urban encroachment, and inadequate enforcement of conservation measures (Oliveira et al. 2020). These threats have significantly affected both the hydrological dynamics of the reservoir system and the conservation status of aquatic biodiversity in recent years. The area's high accessibility and complete urban encroachment make it particularly vulnerable to such disturbances, despite its recognized ecological importance for regional water supply and climate regulation (Oliveira et al. 2020).

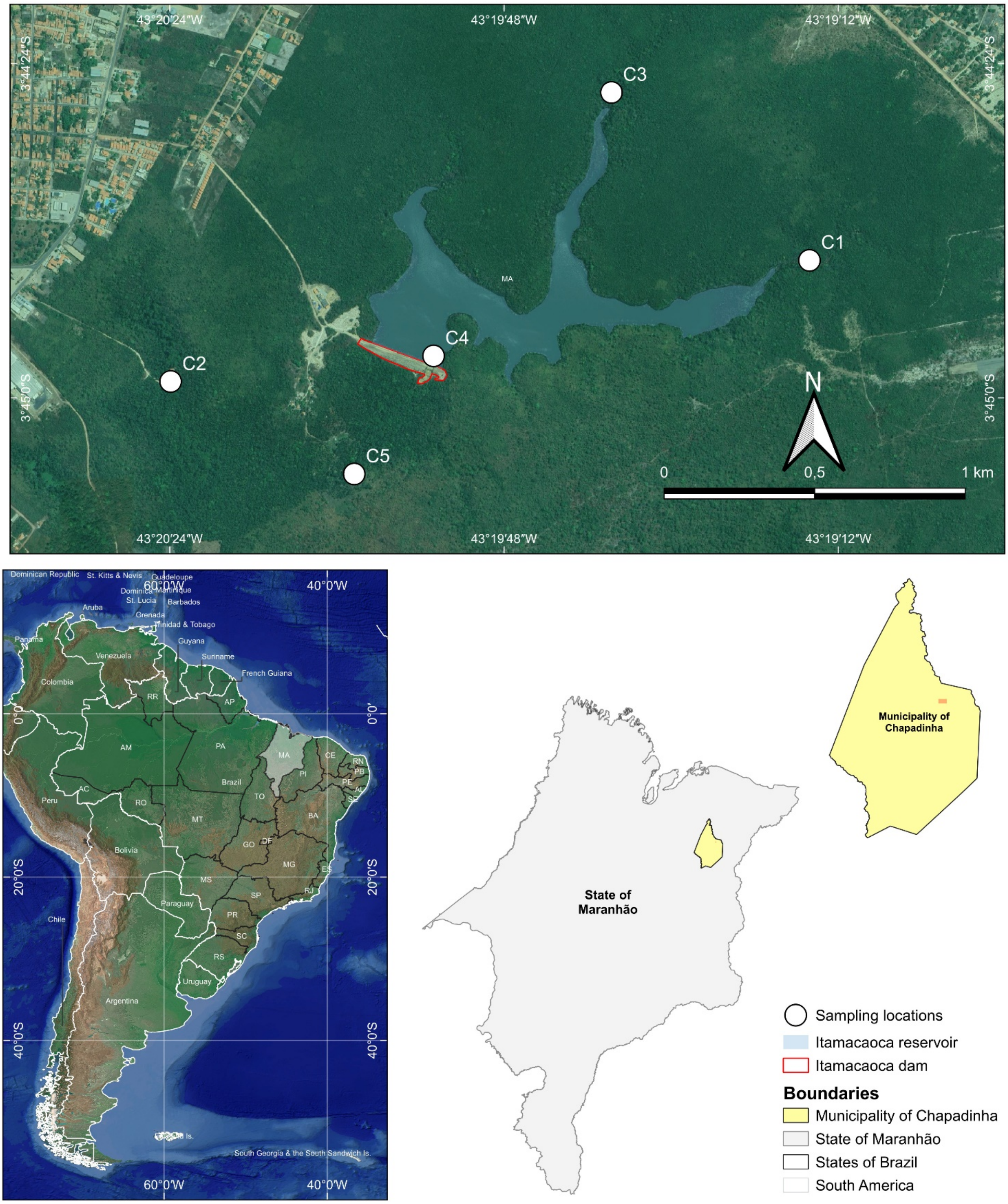

Fig. 1. Location of the colleting sites (C1-C5) distributed across the Mata de Itamacaoca, Chapadinha municipality, State of Maranhão, northeastern Brazil.

Table 1. Description of the collecting sites, including coordinates and habitat characteristics, in Mata de Itamacaoca, Chapadinha, Maranhão, Brazil

Collecting Site	Coordinates	Habitat Characteristics
C1	3°44'45.20"S 43°19'15.10"W	Stream near a spring, surrounded by gallery and riparian forest, in Mata de Itamacaoca, Chapadinha, Maranhão. Sampling covered ~200 meters of the watercourse.
C2	3°44'58.24"S 43°20'23.91"W	Stream in the Repouso do Guerreiro area, within Mata de Itamacaoca, Chapadinha, Maranhão.
C3	3°44'27.1"S 43°19'36.4"W	Stream near a natural water source, with gallery and riparian forest, in Mata de Itamacaoca, Chapadinha, Maranhão.
C4	3°44'55.16"S 43°19'57.10"W	Itamacaoca Dam, located in Chapadinha, Maranhão.
C5	3°45'8.20"S 43°20'4.13"W	Stream downstream of the dam, within Mata de Itamacaoca, Chapadinha, Maranhão.

The regional climate exhibits strong seasonality, with a well-defined dry season lasting five to six months (July to November/December), characterized by significant water deficits (150–300 mm), followed by an equally distinct rainy season from January to May/June, with peak precipitation occurring between February and March (Passos et al. 2016; IMESC 2021). This marked seasonal variation may create dynamic environmental conditions that profoundly influence the aquatic ecosystems within the protected area.

Sampling was conducted during the dry season (from July to December 2019) at five previously established collecting sites (C1-C5) distributed across the Mata de Itamacaoca within the middle Munim River Basin (Fig. 1, Table 1). All sampling procedures were authorized under SISBIO permit N° 64415. Because the study involved only the collection of wild fish specimens for taxonomic and ecological analyses, it did not require approval from an Institutional Animal Care and Use Committee (CEUA). These sites included both natural stream sections and one dam-impacted area (C4), as described in Oliveira et al. (2020) (Fig. 1, Table 1). Fish collections were performed using standardized techniques with dip nets (80 cm × 54 cm, 2 mm mesh) and trail nets (240 cm × 100 cm, 2 mm mesh) following the methodology of Souza and Auricchio (2002). All collection procedures adhered to animal welfare guidelines (Underwood and Anthony 2020), with specimens euthanized in a solution of ethyl-3-amino-benzoate-methanesulfonate (MS-222; 250 mg/L) until cessation of opercular movement. Following euthanasia, specimens were initially preserved in 10% formalin and subsequently transferred to 70% ethanol after 10-15 days for long-term storage. Voucher specimens are housed at the Coleção Ictiológica do Centro de Ciências Agrárias e Ambientais (CICCAA) of the Universidade Federal do Maranhão (UFMA); the complete information spreadsheets are provided in table S1. This sampling design-maintained consistency with previous studies in the area while specifically targeting the dry season to investigate trophic and morphological adaptations under seasonal stress conditions.

Fish Identification

Fish were identified to the lowest possible taxonomic level, based on specific literature for each taxonomic group. Species names, authorship and year of description, geographical distribution, taxonomic classification, as well as other additional information were checked in Fricke et al. (2025a, b).

Stomach content analyses

Only adult individuals were included in all analyses to avoid ontogenetic effects on trophic composition and morphological traits (Winemiller 1991; Gerking 1994). This was confirmed by examining standard length (SL) ranges for each species (Table 2), which consistently corresponded to adult size classes reported in the literature. We analyzed the dietary composition of 173 specimens belonging to eight Characiformes species: *Astyanax* cf. *bimaculatus* (*n* = 26; Acestrorhamphidae), *Characidium* cf. *bimaculatum* (*n* = 27; Crenuchidae), *Curimatopsis* cf. *cryptica* (*n* = 23; Curimatidae), *Holopristis* cf. *ocellifera* [*Hemigrammus* sp. 1 *sensu* Oliveira et al. (2020)] (*n* = 30; Acestrorhamphidae), *Hyphessobrycon piorskii* Guimarães, Brito, Feitosa, Carvalho-Costa & Ottoni 2018 (n = 16; Acestrorhamphidae), *Knodus guajajara* Aguiar, Brito, Ottoni & Guimarães 2022 [*Knodus victoriae* (Steindachner, 1907) sensu Oliveira et al. (2020)] (*n* = 10; Stevardiidae), *Bario oligolepis* (Günther 1864) (*n* = 11; Acestrorhamphidae), and *Nannostomus beckfordi* Günther, 1872 (*n* = 30; Lebiasinidae) (Table S1, Table 2). An ideal sample size of 30 individuals per species was initially established to standardize comparisons. However, some species did not reach this number due to their low abundance in the sampled environment during the dry season. Despite this limitation, the available sample sizes were considered adequate for descriptive dietary and morphological analyses.

Table 2. Standard length (SL) variation of Characiformes fishes sampled in Mata de Itamacaoca during the dry season of 2019. Values represent: N = sample size per species, size range (min-max), mean ± standard deviation (SD), and median SL in millimeters

Family	Species	N	SL Range (mm)	SL Mean ± SD (mm)	SL Median (mm)
Acestrorhamphidae	*Astyanax* cf. *bimaculatus*	26	27.5-76.96	53.35 ± 9.1	53.86
	Bario oligolepis	11	45.86-68.44	52.65 ± 6.02	51.73
	Holopristis cf. *ocellifera*	30	25.09-34.15	30.76 ± 2.08	31.17
	Hyphessobrycon piorskii	16	21.02-28.5	25.2 ± 2.01	25.26
Crenuchidae	*Characidium* cf. *Bimaculatum*	27	22.91-27.55	24.99 ± 1.07	24.77
Curimatidae	*Curimatopsis* cf. *cryptica*	23	30.48-40.42	33.57 ± 2.94	32.63
Lebiasinidae	*Nannostomus beckfordi*	30	25.83-29.8	27.75 ± 1.04	27.89
Stevardiidae	*Knodus guajajara*	10	23.88-36.48	30.00 ± 4.57	30.56

To achieve this, we removed the stomach and intestine of each individual and placed the digestive contents in a Sedgwick-Rafter cell, which contains 1 × 1 mm grid divisions, allowing for visualization and quantification under a stereomicroscope, following the protocol described by Martin and Wainwright (2013). The frequency of occurrence (FO) of each dietary item was determined as the proportion of stomachs in which the item was identified relative to the total number of stomachs analyzed (Hyslop 1980). The volume (V) of each item was estimated using the volumetric method described by Hellawell and Abel (1971) and Hyslop (1980). Based on these values, we calculated a modified alimentary index (IAi) for each species, excluding empty stomachs, as proposed by Kawakami and Vazzoler (1980). The obtained proportions were rounded to 0.1% and expressed as percentages. Additionally, we calculated the mean and standard deviation of the proportions of prey items consumed by each species. Dietary items were identified based on partially digested remains, including exoskeletal fragments, plant material, and organic matter. To facilitate analysis, all prey items were classified into taxonomic and functional categories based on size, shape, and movement patterns, including insect larvae, plant material, insects, crustaceans, zooplankton, worms, fish, and detritus (Table 3).

Table 3. (a) Stomach content analysis of Characiformes fishes from Mata de Itamacaoca (dry season 2019; N = 8 specimens), showing dietary composition by: frequency of occurrence (F%), volumetric proportion (V%), and Index of Alimentary Importance (IAI). Food items are categorized by taxonomic group, with dominant resources (IAI) indicating key dietary components. (b) Relative contribution of autochthonous and allochthonous food resources to the diet of Characiformes assemblage in Mata de Itamacaoca during the 2019 dry season, based on the Index of Alimentary Importance (IAI)

(a)

Food items/Groups	Frequency of Occurrence (%)	Volume (%)	IAI
Insects			
Coleoptera	19.653	10.268	4.036
Diptera	9.2455	4.4009	0.8140
Ephemeroptera	4.0462	1.9588	0.1585
Hemiptera	8.6705	5.1450	0.8922
Isoptera	4.0462	1.4471	0.1171
Tricophtera	3.4682	2.0771	0.1440
Insect remains	35.260	13.388	9.4413
Insect larvae			
Coleoptera larvae	7.5144	3.1509	0.4735
Diptera larvae	11.560	6.7482	1.5602
Hemiptera larvae	3.4682	1.6484	0.1143
Tricophtera larvae	0.5780	0.2600	0.0030
Plant material			
Flowers	2.8901	1.4261	0.0824
Seeds	18.497	12.898	4.771
Filamentous algae	7.5144	4.6643	0.7010
Plant remains	26.011	12.079	6.2841
Zooplankton			
Hydracarina	3.4682	0.5327	0.0369
Cladocera	0.5780	0.0209	0.0002
Detritus			
Debris	16.184	7.4193	2.4016

Sediment	10.404	3.9495	0.8218
Fish			
Fish scale	9.2485	2.7751	0.5133
Fish remains	0.5780	0.2516	0.0029
Worms			
Nematodeo	1.7341	1.1694	0.0405
Crustaceans			
Decapoda	4.6242	2.3195	0.2145

(b)

Origin of food items	Main items included	IAI (%)
Allochthonous	Adult insects (Coleoptera, Diptera, Ephemeroptera, Hemiptera, Isoptera, Trichoptera, insect remains), flowers, seeds, plant remains	79.5
Autochthonous	Insect larvae (Coleoptera, Diptera, Hemiptera, Trichoptera), filamentous algae, zooplankton (Hydracarina, Cladocera), detritus (debris, sediment), fish tissues (scales, remains), worms (Nematodea), crustaceans (Decapoda)	20.5

To assess the trophic organization patterns of Characiformes species, we employed a multivariate approach based on the proportions of dietary items identified in stomach contents. As input data, we used the mean proportions (expressed as percentages) of the following dietary items per species: adult insects, insect larvae, plant material, fish, detritus, crustaceans, worms, and zooplankton.

We performed a non-metric multidimensional scaling (nMDS) ordination using a Bray-Curtis dissimilarity matrix calculated from the proportions of dietary items. The analysis was configured with two dimensions and 3,000 iterations, yielding a final stress value of 0.13, indicating a good representation of the data (Clarke 1993). ANOSIM was used to test the hypothesis that differences in dietary item proportions among species were greater than intraspecific variations. Additionally, we conducted an indicator species analysis using the *indicspecies::multipatt* function in R to determine which dietary components significantly contributed to the stomach contents of each species (α = 0.05) (Dufrêne and Legendre 1997; De Cáceres et al. 2010). Indicator values were calculated based on the point-biserial correlation coefficient (r.g) between the proportions of each dietary item and species occurrence.

To investigate dietary similarity patterns among species, we performed a hierarchical clustering analysis using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) method, based on trophic niche overlap (Pianka 1973). Proportional dietary data were standardized using Z-score transformation (scale function). Trophic similarity between species pairs was quantified using the modified Pianka index (Pianka 1973), calculated as:

$$O_{ij} = \frac{\sum_{k=1}^{n}(p_{ik} * p_{jk})}{\sqrt{\sum_{k=1}^{n} p_{ik}^{2} * \sum_{k=1}^{n} p_{jk}^{2}}}$$

Where p_{ik} e p_{jk} represent the proportions of dietary item k for species i and j, respectively. This index ranges from 0 (no overlap) to 1 (complete overlap). To convert this similarity measure into a dissimilarity, measure suitable for clustering analysis, we calculated D = 1 - O.

In addition to its use in clustering analysis, the Pianka index was also applied independently to quantify niche overlap between species pairs. The calculated values were compiled in a matrix to identify species with the highest and lowest trophic overlap (Pianka 1973).

To complement niche overlap analysis, we estimated niche breadth using the Levins' index (Levins 1968), defined as:

$$B = \frac{1}{\sum \mathrm{i}_{i=1}^{n} p_i^2}$$

Where: B: Niche breadth index; p_i: Proportion of resource i use relative to the total resources used; n: Total number of resource categories.

The index was standardized (Ba) to a 0–1 scale for cross-species comparisons:

$$Ba = \frac{\mathrm{B} - 1}{\mathrm{n} - 1}$$

Where $Ba = 0$: Specialist (uses only one resource); $Ba = 1$: Perfect generalist (equally uses all n resources).

To summarize dietary patterns at the assemblage level, we fitted linear models (LMs) in R version 4.0.3 (R Core Team 2021) using pooled proportional dietary data from the eight Characiformes species. Proportional data were transformed using the arcsine square root to improve variance homogeneity and normality (Zar 2010; Warton and Hui 2011). The models were used descriptively to evaluate whether the mean proportional contribution of major food categories differed from zero, rather than to test interspecific differences. Model coefficients were therefore interpreted as summaries of assemblage-level dietary composition.

To identify significant differences in dietary proportions among Characiformes species, we performed multiple comparisons using the non-parametric Dunn test (Dunn 1964), with Benjamini-Hochberg correction to control the false discovery rate (Benjamini and Hochberg 1995). The analysis was applied to the transformed data (arcsine square root of proportions; Zar 2010) and considered all paired combinations between species, with a significance level of $\alpha = 0.05$.

Functional morphology analyses

To assess the morphological diversity related to trophic resource use, we performed standardized linearly measurements on 20 morphological characters associated with feeding, locomotion, and habitat use, following the morphological scheme illustrated in Oliveira et al. (2024, Table S1) (see Table S2, Table 2). All morphological analyses were performed exclusively on adult individuals, using the same 173 specimens analyzed in the dietary assessments (Table 2). Standard length (SL) ranges confirmed that all individuals fell within adult size classes (Table 2). For this, we adapted protocols from Balon et al. (1986), Sibbing and Nagelkerke (2000), and Breda et al. (2005). Measurements were obtained using a digital caliper (precision of 0.01 mm) and a stereomicroscope, ensuring data accuracy.

To isolate shape variation independently of body size, we applied the Mosimann standardization method, calculating the geometric mean of all measurements per individual and using this value as a divisor for each character. This approach, preferred in recent comparative analyses, allows for a more robust evaluation of morphological adaptations while maintaining the original proportions between characters (Jungers et al. 1995). The geometric mean (GM) was included as an independent variable in subsequent analyses to represent total body size instead of standard length (SL) (Nawa et al. 2024).

To investigate morphological divergence patterns between species, we conducted a Principal Component Analysis (PCA) on the correlation matrix of the standardized measurements. This multivariate analysis allowed us to identify the axes of greatest morphological variation and assess the overlap in the morphospace between species, revealing patterns of morphological segregation. All analytical procedures were performed in the R environment (version 4.1.0).

RESULTS

Dietary composition

During the dry season, adult insects (61.8%), plant material (54%), and insect larvae (44.1%) dominated the diet of most individuals (Table 3a, b). When dietary items were grouped into autochthonous and allochthonous categories based on their Index of Alimentary Importance (IAI) (Table 3a, b), allochthonous resources (adult insects and terrestrial plant material) accounted for approximately 79.5% of the total dietary importance (Table 3a, b), whereas autochthonous items (insect larvae, algae, zooplankton, detritus, and aquatic invertebrates) contributed the remaining 20.5% (Table 3a, b). Among the species, the highest proportions of adult insect consumption were observed in *Astyanax* cf. *bimaculatus* (42.6%), *Characidium* cf. *bimaculatum* (59.9%), *Holopristis* cf. *ocellifera* (52.2%), *Nannostomus beckfordi* (43.5%), *Knodus guajajara* (34.1%), and *Hyphessobrycon piorskii* (49.9%) (Fig. 2, Table 3a, b). In contrast, *Curimatopsis* cf. *cryptica* (85.1%) and *Bario oligolepis* (39.2%) primarily consumed plant material (Fig. 2, Table 3a, b). Some species, such as *Astyanax* cf. *bimaculatus* and *Characidium* cf. *bimaculatum*, exhibited higher dietary diversity, incorporating detritus and other resources in smaller proportions (Fig. 2, Table 3a, b).

Although some dietary components were rare, such as fish consumption, which was recorded only in *Astyanax* cf. *bimaculatus* (6.86%), other items like crustaceans were observed in *Astyanax* cf. *bimaculatus* (2.81%) and *Characidium* cf. *bimaculatum* (9.02%) (Fig. 2, Table 3a, b). Zooplankton consumption was recorded in *Characidium* cf. *bimaculatum* (2.97%), *Hyphessobrycon piorskii* (2.15%), *Knodus guajajara* (1.05%), and *Nannostomus beckfordi* (1.95%) (Fig. 2, Table 3a, b). Additionally, worms were recorded exclusively in *Hyphessobrycon piorskii* (3.35%) and *Knodus guajajara* (8.21%) (Fig. 2, Table 3a, b).

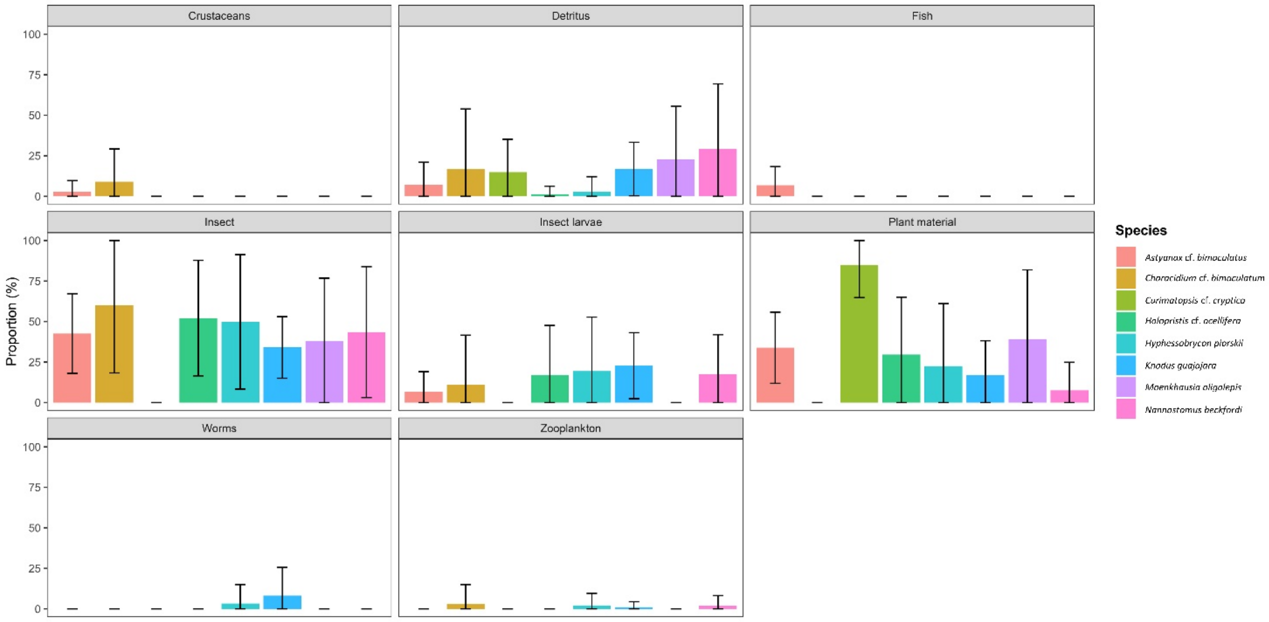

Fig. 2. Proportion of food items in the diet of the analyzed species. The graphs show the percentage composition (%) of each food category identified in stomach/intestinal contents.

Clustering, Similarity, and Indicator Species

The NMDS ordination analysis (stress = 0.13, k = 2) revealed a weak clustering of species based on their dietary components, with considerable overlap among them (Fig. 3). However, a statistically significant difference in diet among species was identified (ANOSIM: R = 0.26, p = 0.001).

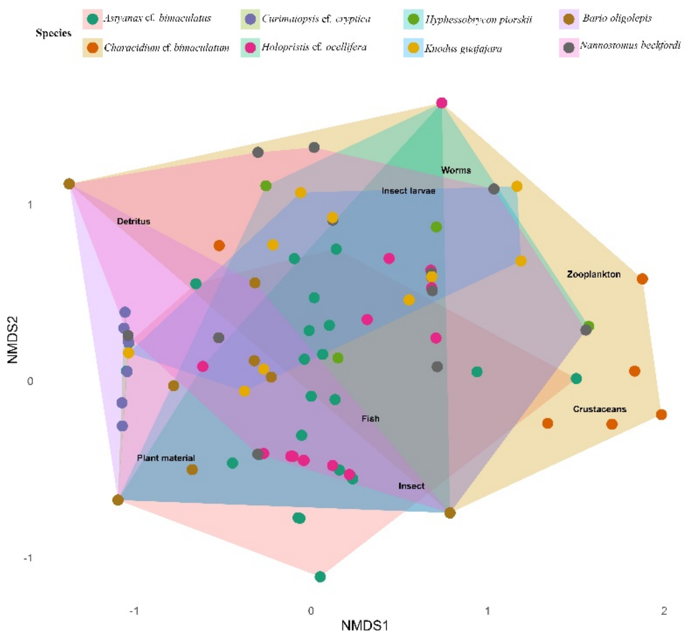

Fig. 3. Non-metric Multidimensional Scaling (NMDS) ordination of dietary overlap among of the eight Characiformes species based on stomach content composition (Bray-Curtis dissimilarity). Convex hulls enclose each species' dietary niche space, with closer positions indicating greater similarity in prey composition. Stress value = 0.13, indicating acceptable representation of multidimensional dietary patterns in 2D space.

The results of the indicator species analysis showed significant associations between species and their dietary categories (Table 4). *Astyanax* cf. *bimaculatus* was associated with fish consumption (p < 0.001), while *Knodus guajajara* was associated with worms (*p* = 0.0104) (Table 4). Species combinations showed specific preferences - crustaceans (*Astyanax* cf. *bimaculatus* + *Characidium* cf. *bimaculatum*, *p* = 0.011), insects (*Astyanax* cf. *bimaculatus* + *Bario oligolepis*, p = 0.0009), and plant material (*Astyanax* cf. *bimaculatus* + *Curimatopsis* cf. *cryptica* + *Bario oligolepis*, *p* = 0.0001) (Table 4). Larger groups favored insect larvae (p = 0.007) and detritus (p = 0.0094) (Table 4).

Table 4. Results of the indicator species analysis (indicspecies) testing for significant dietary preferences among fish species based on stomach content composition. Bold values indicate the most strongly associated prey items for each predator species

Associated Species Group	Prey Category	Indicator Value (stat)	*p*
Astyanax cf. *bimaculatus*	Fish	0.556	**0.0001*****
Knodus guajajara	Worms	0.385	**0.0001*****
Astyanax cf. *bimaculatus* + *Characidium* cf. *bimaculatum*	Crustaceans	0.364	**0.0104***
Astyanax cf. *bimaculatus* + *Curimatopsis* cf. *cryptica* + *Bario oligolepis*	Plant material	0.532	**0.0001*****
Astyanax cf. *bimaculatus* + *Bario oligolepis*	Insects	0.426	**0.0009****
Astyanax cf. *bimaculatus* + *Hyphessobrycon piorskii* + *Knodus guajajara* + *Nannostomus beckfordi*	Insects larvae	0.361	**0.007****
Astyanax cf. *bimaculatus* + *Curimatopsis* cf. *cryptica* + *Knodus guajajara* + *Bario oligolepis* + *Nannostomus beckfordi*	Detritus	0.354	**0.0094****

Trophic structure and variation in trophic resource use

The Levins' index ranged from *Ba* = 0.132 for *Curimatopsis* cf. *cryptica* to *Ba* = 0.593 for *Knodus guajajara*, with *Hyphessobrycon piorskii* (*Ba* = 0.577) and *Astyanax* cf. *bimaculatus* (*Ba* = 0.562) exhibiting the highest values (Table 5). The species utilized between two (*Curimatopsis* cf. *cryptica*) and six food resources, with *Characidium* cf. *bimaculatum* and *Nannostomus beckfordi* displaying intermediate values (*Ba* ≈ 0.478) (Table 5). *Bario oligolepis* (*Ba* = 0.268) and *Holopristis* cf. *ocellifera* (*Ba* = 0.372) completed the observed range of variation (Table 5).

Table 5. Levin's niche breadth measures: prey proportions (rows 1-8), resource count (N), raw (*B*) and standardized (*Ba*) indices

Dietary component	*Astyanax* cf. *bimaculatus*	*Characidium* cf. *bimaculatum*	*Curimatopsis* cf. *cryptica*	*Holopristis* cf. *ocellifera*	*Hyphessobrycon piorskii*	*Knodus guajajara*	*Bario oligolepis*	*Nannostomus beckfordi*
Insects larvae	0.156	0.2061	0	0.1877	0.272	0.1841	0	0.232
Plant material	0.197	0	0.5971	0.2815	0.1786	0.1439	0.3242	0.1787
Insects	0.3149	0.2482	0	0.371	0.2206	0.2274	0.4226	0.2862
Fish	0.0727	0	0	0	0	0	0	0
Detritus	0.1025	0.1248	0.4029	0.1598	0.1294	0.1319	0.2532	0.242
Crustaceans	0.1568	0.315	0	0	0	0	0	0
Worms	0	0	0	0	0.1605	0.26	0	0
Zooplankton	0	0.1058	0	0	0.0388	0.0528	0	0.0611
N	6	5	2	4	6	6	3	5
B	4.933	4.346	1.927	3.601	5.036	5.153	2.875	4.349
Ba	0.562	0.478	0.132	0.372	0.577	0.593	0.268	0.478

Dietary niche overlap varied substantially among species (Pianka index: 0.20–1.68) (Table 6). The lowest overlap occurred between *Hyphessobrycon piorskii* and *Knodus guajajara* (0.20), followed by *Curimatopsis* cf. *cryptica* and *Holopristis* cf. *ocellifera* (0.72) (Table 6). Conversely, several species pairs showed high overlap (>1.4), particularly *Bario oligolepis* with *Characidium* cf. *bimaculatum* (1.68) and *Astyanax* cf. *bimaculatus* with *Nannostomus beckfordi* (1.67) (Table 6). *Curimatopsis* cf. *cryptica* exhibited low to moderate overlap with most species (0.71–1.42) (Table 6).

Table 6. Pianka's measure of niche overlap (Pianka 1973) among Characiformes species from Mata de Itamacaoca. Values range from 0-1, with 0 being no niche overlap and 1 being complete niche overlap

Species	*Astyanax* cf. *bimaculatus*	*Characidium* cf. *bimaculatum*	*Curimatopsis* cf. *cryptica*	*Holopristis* cf. *ocellifera*	*Hyphessobrycon piorskii*	*Knodus guajajara*	*Bario oligolepis*	*Nannostomus beckfordi*
Characidium cf. *bimaculatum*	1.1311	1.0000						
Curimatopsis cf. *cryptica*	1.4241	1.3096	1.0000					
Holopristis cf. *ocellifera*	1.0375	1.4281	0.7242	1.0000				
Hyphessobrycon piorskii	1.2865	0.9031	1.4173	1.0622	1.0000			
Knodus guajajara	1.4006	0.8876	1.3554	1.4127	0.1959	1.0000		
Bario oligolepis	0.9190	1.6867	0.7074	0.8392	1.6209	1.411	1.0000	
Nannostomus beckfordi	1.6715	0.5843	0.7844	0.9553	0.8329	0.9763	1.3218	1.0000

Pairwise comparisons of species' diets revealed significant differences ($p < 0.05$, Benjamini-Hochberg adjusted) in feeding composition among most analyzed pairs. *Astyanax* cf. *bimaculatus* showed significantly distinct dietary patterns compared to all other species except *Knodus guajajara* (p = 0.483) (Table 7). Conversely, *K. guajajara* exhibited pronounced dietary differentiation from most sympatric species, including *Characidium* cf. *bimaculatum* ($p < 0.001$), *Curimatopsis* cf. *cryptica* ($p < 0.001$), *Holopristis* cf. *ocellifera* ($p = 0.0003$), *Hyphessobrycon piorskii* ($p = 0.001$), *Bario oligolepis* ($p = 0.020$), and *Nannostomus beckfordi* ($p = 0.003$) (Table 7). The cluster analysis based on the eight prey categories formed three distinct groups: (1) *Hyphessobrycon piorskii*, *Knodus guajajara*, *Characidium* cf. *bimaculatum*, and *Nannostomus beckfordi*; (2) *Astyanax* cf. *bimaculatus*; and (3) *Holopristis* cf. *ocellifera*, *Curimatopsis* cf. *cryptica* and *Bario oligolepis* (Fig. 4).

Table 7. Mean comparisons between groups adjusted using the Benjamini-Hochberg method. The table displays pairwise mean differences and adjusted *p*-values among species groups. ns (not significant). Significant results ($p \leq 0.05$) indicate substantial differences between species pairs

Group 1	Group 2	Mean Difference	Adjusted *p*-value	Significance
Astyanax cf. *bimaculatus*	*Characidium* cf. *bimaculatum*	-6.097	0.001	**
	Curimatopsis cf. *cryptica*	-5.337	0.001	**
	Holopristis cf. *ocellifera*	-4.829	0.001	**
	Hyphessobrycon piorskii	-4.007	0.0001	***
	Knodus guajajara	-0.043	0.483	ns
	Bario oligolepis	-2.776	0.007	**
	Nannostomus beckfordi	-3.866	0.0002	***
Characidium cf. *bimaculatum*	*Curimatopsis* cf. *cryptica*	0.238	0.437	ns
	Holopristis cf. *ocellifera*	1.689	0.080	ns
	Hyphessobrycon piorskii	0.979	0.241	ns
	Knodus guajajara	5.097	0.001	**
	Bario oligolepis	1.969	0.049	*
	Nannostomus beckfordi	2.154	0.034	*
Curimatopsis cf. *cryptica*	*Holopristis* cf. *ocellifera*	1.319	0.146	ns
	Hyphessobrycon piorskii	0.723	0.299	ns
	Knodus guajajara	4.562	0.001	**
	Bario oligolepis	1.674	0.078	ns
	Nannostomus beckfordi	1.774	0.071	ns
Holopristis cf. *ocellifera*	*Hyphessobrycon piorskii*	-0.411	0.381	ns
	Knodus guajajara	3.862	0.0002	***
	Bario oligolepis	0.669	0.307	ns
	Nannostomus beckfordi	0.590	0.324	ns
Hyphessobrycon piorskii	*Knodus guajajara*	3.495	0.0007	***
	Bario oligolepis	0.912	0.253	ns
	Nannostomus beckfordi	0.866	0.258	ns
Knodus guajajara	*Bario oligolepis*	-2.424	0.018	*
	Nannostomus beckfordi	-3.154	0.002	**
Bario oligolepis	*Nannostomus beckfordi*	-0.189	0.441	ns

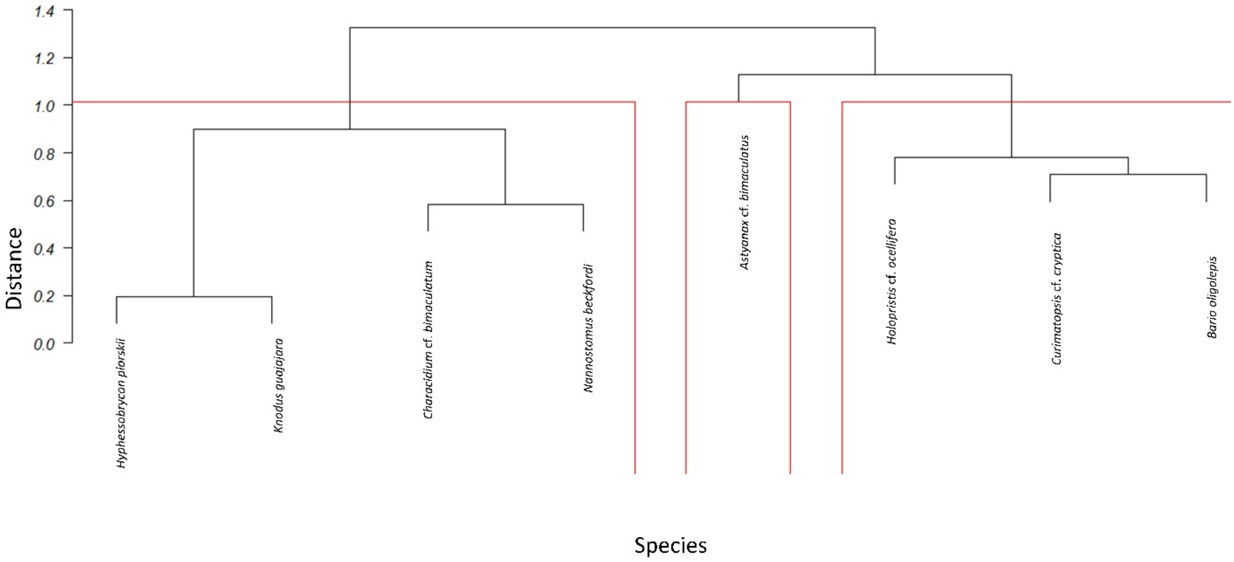

Fig. 4. Dendrogram from cluster analysis on Index of Trophic similarity between species pairs quantified using the modified Pianka index (Pianka 1973) for the eight examined Characiformes fish species in Mata de Itamacaoca, dry season.

The linear model indicated that the overall mean dietary proportion differed from zero (β = 0.605; p = 0.001; Table 8). Among food categories, insects showed a significant positive coefficient (β = 0.368; p = 0.011; Table 8). Whereas plant material exhibited a marginally significant contribution (β = 0.285; p = 0.051; Table 8). Other food categories, including detritus, fish, insect larvae, worms, and zooplankton, did not differ significantly from zero (p > 0.05; Table 8).

Table 8. Table 8. Results of linear models (LMs) summarizing assemblage-level dietary composition of Characiformes during the dry season. The table presents estimated coefficients, standard errors, t-values, and significance levels for major food categories. Model coefficients indicate whether the mean proportional contribution of each food category differs from zero. Proportional data were variance-stabilized using an arcsine square root transformation. ms = marginally significant. Statistically significant predictors (p < 0.05) are shown in bold

Coefficients	Estimate	Std. Error	T value	*p*
Intercept	0.605	0.138	4.358	**0.001*****
Detritus	0.155	0.151	1.028	0.305
Fish	-0.194	0.186	-1.043	0.298
Insect	0.368	0.144	2.545	**0.011***
Insect larvae	0.147	0.152	0.963	0.335
Plant material	0.285	0.146	1.955	**0.051 ms**
Worms	0.087	0.266	0.328	0.743
Zooplankton	-0.116	0.212	-0.550	0.582

Morphological Variation

The Principal Component Analysis (PCA) explained 41.6% of the total variance, with the first two principal components (PC1 = 25.4%; PC2 = 16.2%) accounting for most of this variance (Fig. 5). Species distribution in the morphological space revealed distinct groupings. *Astyanax* cf. *bimaculatus* was primarily influenced by Caudal fin length (CFiL), while *Characidium* cf. *bimaculatum* was determined by Caudal peduncle depth (CPD) (Fig. 5). For *Curimatopsis* cf. *cryptica*, the most important variable was Body depth (BD), whereas *Holopristis s* cf. *ocellifera* was more influenced by Body width (BW) (Fig. 5). *Hyphessobrycon piorskii* had Head depth (HD) as the predominant variable, while *Knodus guajajara* was influenced by Eye diameter (ED) (Fig. 5). In *Bario oligolepis*, Dorsal fin length (DFiL) had the greatest impact, while *Nannostomus beckfordi* was influenced by Pectoral fin length (PFiL). *Bario oligolepis* was influenced by Oral gape width (GW) (Fig. 5).

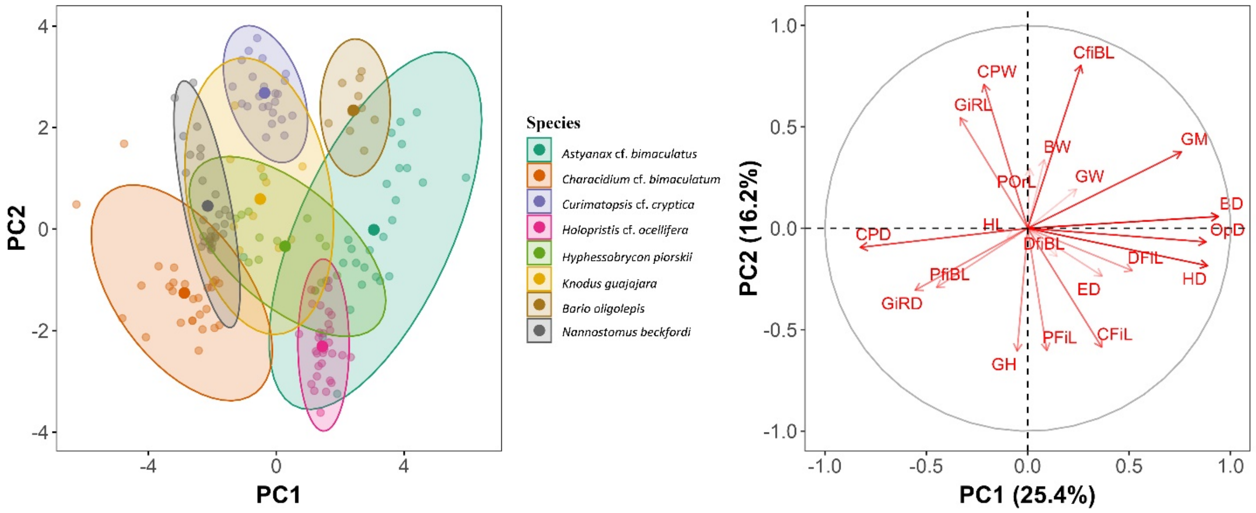

Fig. 5. Biplot of Principal Component Analysis (PCA) of morphological trait space between Characiformes species; and variable loadings on the PC axes.

DISCUSSION

Here, we present the results of the trophic ecology and morphological analyses of Characiformes species inhabiting the Mata de Itamacaoca, a protected area within the middle Munim River Basin, Maranhão, Brazil. The study was conducted during the dry season and focused on the stomach contents and morphological traits of eight fish species from four different families:

Acestrorhamphidae (*Astyanax* cf. *bimaculatus*, *Bario oligolepis*, *Holopristis* cf. *ocellifera*, and *Hyphessobrycon piorskii*), Stevardiidae (*Knodus guajajara*), Lebiasinidae (*Nannostomus beckfordi*), Crenuchidae (*Characidium* cf. *bimaculatum*), and Curimatidae (*Curimatopsis* cf. *cryptica*). Despite the protected status of the area, the presence of urban influences, such as such as illegal resource extraction, agricultural burning practices, urban encroachment, and inadequate enforcement of conservation measures, highlights the importance of understanding the ecological dynamics of these fish communities (Oliveira et al. 2020 2024). The analyses revealed significant dietary and morphological adaptations, revealing into the mechanisms that allow these species to coexist in a spatially limited and environmentally sensitive habitat during the dry season. Although seasonal hydrological fluctuations broadly influence neotropical aquatic ecosystems, our findings highlight the specific ecological dynamics occurring during the dry season, a critical period of resource scarcity and intensified biotic interactions (Pelage et al. 2022; Londe et al. 2024). While some species presented relatively low sample sizes (*e.g.*, *Knodus guajajara*, *Bario oligolepis*), these numbers are consistent with their observed rarity in the field during the dry season. We interpret these values as biologically meaningful, as they reflect true patterns of local abundance rather than sampling bias.

At the assemblage level, dietary patterns during the dry season were characterized by the predominance of insects and, marginally, plant material, as indicated by the linear model analysis (Table 8). This descriptive overview provides a community-scale context for the morphological patterns discussed below. Although the first two PCA axes accounted for a moderate proportion of total variance (41.6%), such values are common in multivariate ecomorphological datasets that include numerous correlated morphometric traits (Gatz 1979; Winemiller 1991; Jolliffe 2011; Zelditch et al. 2012; Oliveira et al. 2024). Despite this, the PCA revealed clear species-level segregation in morphospace, indicating consistent morphological divergence related to trophic structure. Morphological adaptations among species reflects their feeding preferences: *Astyanax* cf. *bimaculatus*, with a long caudal fin, captures mobile prey (Balon et al. 1986; Breda et al. 2005); *Characidium* cf. *bimaculatum*, with a deep caudal peduncle, enhances burst impulse for insectivory (Sibbing and Nagelkerke 2000); *Curimatopsis* cf. *cryptica*, with a deep body, improves maneuverability (Balon et al. 1986); *Holopristis* cf. *ocellifera*, with a wide body, adapts to vertical movements (Balon et al. 1986); *Hyphessobrycon piorskii*, with a high head, has a varied diet; *Knodus guajajara*, with large eyes, aids in benthic prey detection (Balon et al. 1986); *Bario oligolepis*, with a long dorsal fin, processes vegetation efficiently (Balon et al. 1986; Breda et al. 2005); and *Nannostomus beckfordi*, with extended pectoral fins, controls propulsion (Balon et al. 1986; Breda et al. 2005). Insectivory in *Astyanax* cf. *bimaculatus*, *Characidium* cf. *bimaculatum*, and *Hyphessobrycon piorskii* aligns with Neotropical floodplain patterns (Petry et al. 2011; Esteves et al. 2021), while phytophagy in *Curimatopsis* cf. *cryptica* (85.07%) and *Bario oligolepis* (39.24%) reflects trophic plasticity (Goulding 1980; Vanni et al. 2006; Medeiros et al. 2014; Allan et al. 2021). Trophic segregation between euryphagous (e.g., *Astyanax* cf. *bimaculatus*) and stenophagous species (*e.g.*, *Knodus guajajara*) supports the "limiting similarity" paradigm (Abrams 1983; Duarte et al. 2022), promoting niche partitioning and reducing competition in seasonal ecosystems (Abrams 1983; Pelage et al. 2022; Londe et al. 2024; Pastore et al. 2021; Zhang et al. 2024).

The consistency between our results and those of Oliveira et al. (2024), conducted in the same area but without accounting for dry season, underscores the significance of insects and plant material as key resources for Characiformes species in the Mata de Itamacaoca during the dry season. *Astyanax* cf. *bimaculatus* diet was characterized by fish and crustaceans in our study, whereas data from Oliveira et al. (2024) emphasized seed intake thus reflecting dry season abundance of resources. Similarly, *Hyphessobrycon piorskii* displayed the presence of worms in our analysis, a dietary component not previously recorded. These discrepancies may reflect dry season fluctuations in resource availability or dietary plasticity, a phenomenon frequently observed in fish inhabiting seasonally dynamic environments, particularly during the dry season (Keller et al. 2019). Nevertheless, the consistent consumption of insects by *Characidium* cf. *bimaculatum* and plant material by *Holopristis* cf. *ocellifera* suggests that these resources play a fundamental role in the trophic ecology of Characiformes species in the Mata de Itamacaoca regardless of environmental variability.

Although species-specific trophic ecology studies were not available for most of the taxa analyzed, we compared our findings with the general trophic patterns reported for their respective genera. Our results generally align with these broader patterns, although notable species-specific differences emerged. For instance, while literature suggests that species of the genera *Knodus* Eigenmann 1911 and *Hyphessobrycon* Durbin 1908 are typically generalist insectivores (Ceneviva-Bastos and Casatti 2007; Prado et al. 2016; Benone et al. 2020), we recorded high insectivory in *Knodus guajajara* (34.1% adult insects) and *Hyphessobrycon piorskii* (49.9%), but also observed niche diversification, such as *Hyphessobrycon piorskii* consumption of worms (3.4%), a resource rarely mentioned in prior studies. Similarly, *Holopristis* cf. *ocellifera* (52.2% insects) and *Bario oligolepis* (39.2% plant material) matched the insectivorous tendency described for their genera (Castro 1999; Graciolli et al. 2003), although *Bario oligolepis* reliance on plant matter was unexpectedly high. *Astyanax* cf. *bimaculatus* and *Characidium* cf. *bimaculatum* exhibited the generalist omnivory documented in earlier work (Casatti et al., 2001; Silva-Camacho et al., 2014), including detritus and crustaceans, but in our data, *A.* cf. *bimaculatus* also consumed fish remains (6.9%), a trophic behavior less frequently reported for the genus. Both species showed elevated insectivory (42.6% and 59.9%, respectively), surpassing values commonly described in the literature. *Nannostomus beckfordi*, consistent with the varied diet described for its genus (Silva 1993), also showed high insectivory (43.5%), while incorporating zooplankton and detritus. The most striking divergence was observed in *Curimatopsis* cf. *cryptica*, which predominantly consumed plant material (85.1%) rather than the fine organic matter commonly reported for the genus (Brejão et al. 2013).

These findings corroborate the well-established paradigm that morphological traits are critical determinants of trophic niche specialization, facilitating the efficient exploitation of specific resources through adaptive divergence (Gatz 1979; Sibbing and Nagelkerke 2000; Novakowski et al. 2016). Such morphological relationships are particularly pronounced in freshwater ecosystems, where selective pressures drive functional trait diversification, thereby promoting dietary specialization and mitigating niche overlap via resource partitioning (Ferry-Graham et al. 2002; Montaña and Winemiller 2013; Montaña et al. 2020; Paz Cardozo et al. 2021). The observed congruence between morphology and diet aligns with niche theory (Hutchinson 1957; Chase and Leibold 2009), which posits that phenotypic divergence reduces interspecific competition by enabling differential resource acquisition (Breda et al. 2005; Oliveira et al. 2024). However, the presence of dietary overlap among morphologically distinct species suggests that niche differentiation may also be mediated by non-morphological mechanisms (Chesson 2000; Leibold and McPeek 2006). These could include behavioral plasticity (Gomiero et al. 2010; Garcia et al. 2020), temporal or microhabitat segregation (Schoener 1974; Brandão-Gonçalves and Sebastien 2013), or differential prey selectivity driven by foraging strategies (Lubich et al. 2024). Such compensatory mechanisms may stabilize coexistence in high-diversity assemblages, underscoring the multidimensional nature of niche partitioning (Chesson 2000; Leibold and McPeek 2006). Future studies should integrate functional morphology with spatiotemporal foraging data to disentangle the relative contributions of these factors in structuring trophic interactions.

CONCLUSIONS

Finally, the ecological implications of resource partitioning and interspecific competition are evident in the coexistence strategies adopted by these species. The observed dietary plasticity, combined with morphological adaptations, suggests that dry season changes in resource availability drive adaptive feeding behaviors that minimize direct competition. This finding supports the hypothesis that environmental dry season acts as a selective pressure, shaping trophic interactions and promoting species coexistence (Bloomfield et al. 2022). However, the proximity of the Mata de Itamacaoca to urban areas raises concerns about anthropogenic disturbances, such as habitat degradation and water quality deterioration, which could disrupt the delicate balance of resource availability and trophic dynamics (Daufresne and Boet 2007; Matono et al. 2014; Iacarella et al. 2018; Candolin and Rahman 2023). In this context, our study has important conservation implications by identifying functionally vulnerable guilds (*e.g.*, species with restricted diets), establishing baseline data for long-term monitoring, and highlighting critical microhabitats for conservation. Effective protection of this ecosystem thus requires strategies that consider both natural dry season ecological processes and cumulative anthropogenic impacts, integrating aquatic connectivity and the maintenance of habitat heterogeneity.

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Consent for publication: Not applicable.

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Supplementary materials

Table S1. Sample Codes, Species Names, Voucher Numbers, and Number of Individuals Analyzed in this work. (download)

Table S2. Traits measured, morphological descriptions and ecological interpretation of Characiformes of the dry season in Mata de Itamacaoca, middle Munim River basin, Chapadinha municipality, State of Maranhão, northeastern Brazil. (download)