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Integrative Analysis to Manage Aquatic Resources Based on Fish Feeding Patterns in Neotropical Rivers

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Abstract: Feeding ecology is an integrative procedure to highlight different diets, associating feeding trends with governing and regulation factors characterizing foraging species and their environments, respectively. The diet variability of seven fish species forming a community in a Neotropical riverine system was analyzed to characterize the resource and consumer linkages, providing a detailed assessment of adaptive feeding behaviors of fishes living in different ecological states transiting from natural/resilient spaces to anthropic pressions-linked disturbed ones. Fishes were sampled along four sites during a year, and their stomach contents were analyzed. Feeding data were analyzed by applying quali- and quantitative methods with multi-levels and multifactor aspects to determine target food categories (percentage of occurrence) and identify feeding patterns (correspondence and cluster analyses, CA-HCA). Factors and scales governing target food categories were also tested. A total of 483 stomachs were dissected, and 30 food categories were identified. CA-HCA highlighted 10 feeding trends (FTs) combining several foods co-occurring at distinct levels. These FTs indicated characteristic diets and high diversity of feeding behaviors concerning multiple and narrow diets, different alimentary needs related to ecomorphological features, different plasticity ranges (adaptability, tolerance) and a spatial governing effect (headwater to river mouth environmental quality loss). These multiple factors provided essential information on overcoming ways of environmental constraints and optimization ways of food balances helping to better manage the richness and working of neotropical river systems.

Keywords: stomach content analysis; percentages of occurrence; multivariate analysis; feeding trends; fish community interactions

Key Contribution: Fish feeding patterns in the Neotropical region are complex; based on widely diversified foraging factors at intra-specific, inter-specific and ecosystem scales. A deep integrative approach was applied focused on the understanding of this complexity in a riverine system chosen as a model.



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1. Introduction

Ecological systems are characterized by high complexity due to multiple interactions between biological species and environmental factors [1,2]. Their management requires assessment methods of their compositional and functional states. Such states are strongly memorized through feeding systems linking consumer and consumed species with variations resulting from several biotic and abiotic factors [2,3]. Foraging efficiency is enhanced when feeding items and related activities generate more benefits than costs, the basis of optimal foraging theory, widely applied for animals [2]. The optimal foraging theory looks

to explain the mechanisms for weighing the benefits and costs of the choices for some food items instead of other ones [2–4]. Several foraging factors interact and drive these complexes feeding systems, varying a lot among animal species and their habitats [5–9].

In aquatic ecosystems, this complexity increases, as well as the ability for harvesting resources, due to the environmental three-dimensionality and water characteristics (e.g., density, visibility, depth and velocity, among others) [4,10–12]. Fishes present varied phenotypic and behavior adaptations to optimize their ability for harvesting resources once they occupy almost every trophic level, from 2 (detritivores) up to 4.7 (piscivorous predators) [3,12,13]. Helfman and collaborators [11] summarize fish's feeding steps as follows: searching/detecting, pursuing and attacking (in predators), capturing and handling prey. The foraging efficiency previously mentioned can be also applied for fishes [2,11,14,15]. Additionally, functionality of resource and consumer linkages depend on a set of elements that varies along a watercourse [12].

Studies on feeding ecology of fishes are of integrative nature, requiring robust and detailed trophic assessments of consumed food categories by considering intrinsic and extrinsic factors to the consumers [10,12,16,17]. Exploited food sources by fish consumers can be quantified by several ways (e.g., occurrence, amount and bulk) whose analysis highlights trophic interactions at intra- and interspecific levels with various associated effects on biodiversity including: (i) ecomorphological constraints, (ii) learning factors (iii) diet shifts, (iv) resource partitioning, (v) competition, (vi) predator–prey relationships, and (vii) predator responses to nutritional needs [3,4,10,12,13,16–26]. All of these elements have long been a backbone of ecological studies, including fish communities, in which the routine questions “what”, “where” and “how much” remain [10,16].

In the Neotropical region, trophic relationships are more complex due to the high diversity of aquatic habitats and freshwater fish species (more than 6200 species), making it the richest of the world [12,27,28]. The ichthyofauna from this ecoregion present high phenotypic plasticity concerning trophic structures and behaviors [11,12,27]. Considering this, a Neotropical riverine system was chosen as a model to investigate fish feeding patterns due to different physical–chemical and biological states along its watercourse. We aimed to characterize the resource and consumer linkages in this Neotropical riverine system, providing a detailed assessment of adaptive feeding behaviors of fishes living in different ecological states transiting from natural/resilient spaces to anthropic pressions-linked disturbed ones. This wide variation provides propitious space for highlighting different adaptive (reactive, defensive, competing) trends in different biological populations according to local environment conditions within and between sites [29]. These goals are based on the premise from the optimal foraging theory that fishes forage looking for the most efficiency [3,4,11–14].

In order to attain the proposed objectives, we employed accurate and integrative methods to extract and deeply analyze fish feeding patterns, both ecologically and quantitatively [16,29–31]. Advanced exploratory statistical analyses were applied to highlight the multiple biological patterns associated with several responses of fishes. Stomach contents analysis of fishes were conducted by means of two complementary ways: by considering (i) separated and (ii) co-occurring food categories [16,32]. Co-occurrence ways and levels of different food categories in fishes' stomachs were analyzed by multivariate methods, including topological analysis (correspondence analysis, CA) and a typological one (hierarchical cluster analysis, HCA) [1,16,17,33,34]. The results allowed us to evaluate the intra- and interspecific variation of feeding patterns in different fish species under multiple factors operating on the aquatic and terrestrial landscapes, a basis for the use and conservation of Neotropical riverine systems.

2. Materials and Methods

2.1. Sampling Area

The study case of a Neotropical river in this work concerned the Verde River (VR) (Brazil) (Figure 1). It is an important tributary of the Upper Paraná River Ecoregion (UPRE),

partially inside two Brazilian protected areas (PAs), the Campos Gerais National Park (CGNP) and the Devonian Escarpment Environmental Protection Area (DEEPA). Both PAs are characterized by original and unique geomorphology and species richness [35–38], presenting more than 300 fish species, many of them endemic, concentrating 1 among the richest and diversified Neotropical ichthyofauna [28,39]. In some areas, VR soils are extremely susceptible to erosion due to native vegetation suppression and inadequate practices of soils handling, which are common to the region [37,38,40,41]. In this way, it represents a good model of an interactive space between natural conditions and several anthropic factors (economic, political, social).

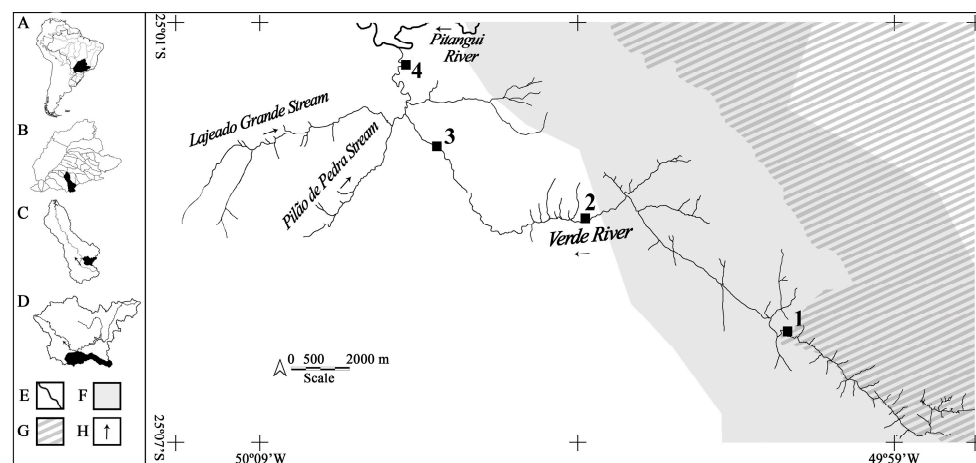


Figure 1. Verde River basin and sampling sites. (A) South America and the Upper Paraná River Ecoregion (UPRE, in black); (B) UPRE and the Tibagi River basin (TRB, in black); (C) TRB and the Pitangui River basin (PRB, in black); (D) PRB and the Verde River basin (in black); (E) Hydrography; (F) Devonian Escarpment Environmental Protection Area; (G) Campos Gerais National Park; (H) Water flow direction. Adapted and modified from [38].

In the current study, variability of fishes' occurrence and behaviors was followed in VR through four sampling sites: headwater (site 1, 25°06'19.67" S 50°01'23.21" W), upper middle stretch (site 2, 25°04'46.29" S 50°04'56.53" W), lower middle stretch (site 3, 25°03'26.11" S 50°07'25.06" W), and river mouth (site 4, 25°02'28.85" S 50°07'35.59" W). A rapid bioassessment protocol was applied [38,41–43], characterizing the sampling sites (for details see Supplementary Material S1: sampling area). Their major features are summarized as follows.

Headwater has a shallow soil that supports steppe-type vegetation and stable riverbanks associated with rock outcrops and wetland depressions; intensive agricultural and livestock activities are developed at headwater surrounding landscapes. Downstream of this area, there is a small reservoir (about 2 m height) followed by a large cascade (about 10 m height). Following the water course, in the middle and river mouth stretches, soils support more complex vegetation. The upper middle stretch presents sequential riffle-pools, fragmented riparian vegetation, stable riverbanks and complex riverbed surrounded by intensive agricultural and livestock activities. Below this site, an urban zone and semi-intensive agriculture, which dump untreated sewage, garbage and agrochemical wastes into VR. Due to it, in the lower middle stretch, riffle stretches are short and pool stretches are sandy covered, due to siltation. Riparian vegetation also is highly degraded. Between sites 3 and 4, VR receives inputs from the Pilão de Pedra and Lajeado Grande streams, rivers that also receive untreated sewage and garbage into them. At this place, VR also receives inputs of treated effluents from the municipal sewage treatment plant (Companhia de Saneamento do Paraná—SANEPAR). As a consequence, the riverbed at the river mouth is in an advanced siltation process and presents vast amounts of sludge. Sampling sites features evidenced a gradient from natural/resilient to anthropic pressures-linked

disturbed ones [38], in an empirical rating scale from “best” (headwater), “good” (upper middle stretch), “bad” (lower middle stretch), and “worst” (river mouth).

2.2. Data Sampling

Monthly samplings were performed from May 2016 to April 2017 in the four sites following standardized procedures [38]: 24 h of fishing effort using gillnets (1.2-, 1.5-, 2-, 3-, 4-, 5-, 6-, 7- and 8-cm mesh) and hook and line, with fish removals at each 12 h, and 1 h of fishing effort using cast nets and scoop nets. Specimens caught were sacrificed (250 mg/L benzocaine) and eviscerated, and their stomachs were removed and conserved at formalin 4%. Afterward, stomach contents were analyzed under stereoscope and microscope. Consumed prey items were identified until the lowest possible taxa level [11].

2.3. Data Analysis

Specimens of each species associated with the same site and month were merged in sample units. For each food category in each sample unit, the percentage of occurrence (% O_{fi}) was calculated by relativizing the number of its containing stomachs by the total number of analyzed stomachs [16]. A preliminary permutational multivariate analysis of variance indicated that only species and sites were significant, but not the temporal variation (months) (Supplementary Material S2: PERMANOVA).

Diet patterns were highlighted by analyzing relative levels of co-occurrence of different food categories in different individuals (sample units) of different fish species. This was conducted by means of a multivariate analysis, Correspondence Analysis (CA) [1,17,33,44]. CA standardizes the occurrence level of each food category relatively to (i) the sum of all the other food categories in the same fish sample (i.e., row sum) and to (ii) the sum of its occurrence levels in all the fish samples (i.e., column sum). This double standardization makes feeding trends to be analyzed at both intra- and inter-sample unit levels [33].

The set of principal components covering 70% of total inertia in CA was used as basis to carry out a classification analysis of sample units by means of Hierarchical Cluster Analysis (HCA) using Euclidian distance and Ward aggregation rule [1,17,44]. HCA classified the fish sample units into homogeneous clusters associated with well-distinct feeding trends (FTs). Both CA and HCA were performed using ADE4 statistical software [45]. Association levels between FTs and food categories, fish species and river sites were graphically analyzed using box plots and stacked columns [46].

3. Results

In all, a total of 483 stomach contents were analyzed to provide integrative information on several food categories consumed by the 7 fish species in different sampling sites of VR (Supplementary Material S3: fish species size structure). Specimens of each species associated with the same site and month resulted in 97 analyzed sample units.

3.1. Spatial Distribution Analysis of Fish Species

Verde River showed several abundance levels of fish species varying with sampling sites (Figure 2). The highest diversity and abundance of fish species were recorded at the upper (48.4%) and lower (24.6%) middle stretches. *Psalidodon paranae* (Eigenmann, 1914) was related to upstream sites, mainly occurring at headwater (48%), upper (44%) in addition to lower (7.4%) middle stretches. *Psalidodon* aff. *fasciatus* (Cuvier, 1819), generally showed downstream distribution by occurring at upper (20%) vs. lower (40%) and river mouth stretches (40%). Several species exclusively occurred at upper and lower middle stretches, including *Apareiodon* sp. (68.8% and 31.2% of abundance, respectively), *Corydoras ehrhardti* Steindachner, 1910 (53.6% and 43.7%), *Hypostomus strigaticeps* (Regan, 1908) (80% and 20%) and *Rhamdia quelen* (Quoy & Gaimard, 1824) (50% and 50%). Only *Geophagus brasiliensis* (Quoy & Gaimard, 1824) occurred in all the sampling sites.

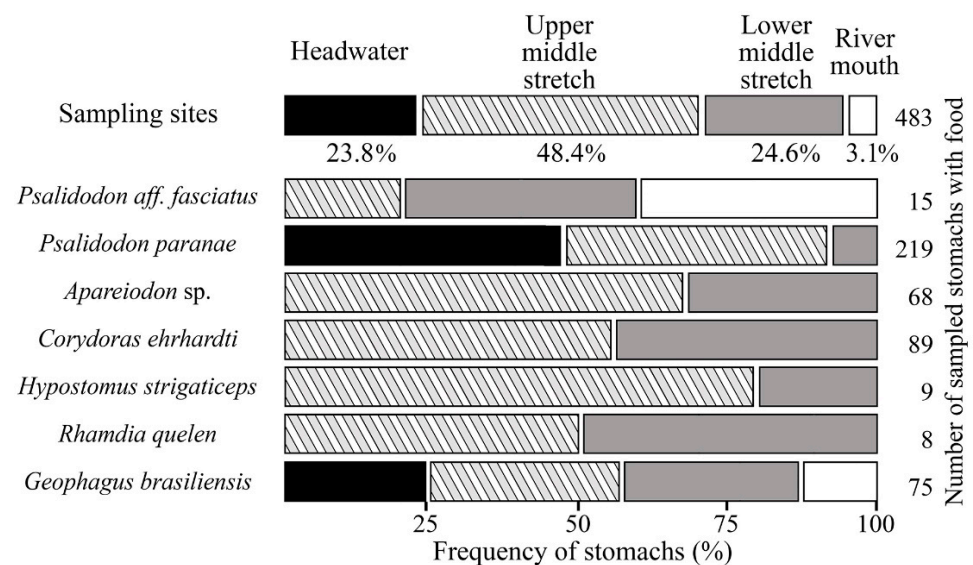


Figure 2. Spatial distribution of fish species sampled with stomachs contents of the fish community from Verde River.

3.2. Highlighting of Feeding Trends

The stomach contents provided 30 food categories in the fish community of Verde River (Supplementary Material S4: percentages of occurrence of consumed foods). The first 10 principal components of CA covered 70% of total inertia, and they were used to carry out HCA. Dendrogram given by HCA highlighted 10 distinct clusters corresponding to 10 feeding trends (FTs) which were associated with different fish species (Figure 3). The 10 FTs were characterized by relatively high levels of different food categories consumed by the different fish species. The 4 majors FTs (FTs 2, 3, 6, 8) concerned the most abundant fish species (*P. paranae*, *Apareiodon* sp., *C. ehrhardti* and *G. brasiliensis*), whilst the 2 minor (FTs 1, 7) and 4 outlier groups (FTs 4, 5, 9, 10) concerned the less abundant species (*P. aff. fasciatus*, *H. strigaticeps* and *R. quelen*). FTs 4–10 showed higher distinctness and compactness than FTs 1–3. These classification aspects indicated higher differentiation and homogeneity of clusters 4–10 vs. more heterogeneity and diversity for clusters 1–3. Homogeneous FTs could be associated with different targeted feeding patterns (behaviors) in different fish species.

The 10 principal components of CA (P1–P10) were defined by high contributions of different food variables, which were associated with different FTs (Figure 4 and Supplementary Material S5: feeding profile of ten identified feeding trends):

- Along P1, Diptera and sediments separated FTs 3, 6–8 from the rest of data with relatively high associations between FT6, FT8 and Diptera, Sediments, respectively (Figure 4a,b). However, FT2 showed opposite projection along P1 indicating relatively low consumption of Diptera and Sediments (Figure 4b). Moreover, on the negative side of P1, FTs 1 and 2 were distinguished by relatively high consumptions of Lepidoptera (absent elsewhere). This was indicative of different feeding behaviors combining targeting/preferences for some food categories and avoidances for other ones.
- Along P2, Orthoptera, Acarina and Cyanophyta were the most contributing food variables (Figure 4a) with relatively high consumption levels in FTs 10, 5 and 9, respectively (same factorial subspaces) (Figure 4b).
- Along P3, FTs 10, 5, 9 were further distinguished by relatively high consumptions of specific food categories (Orthoptera, Acarina, Cyanophyta, respectively) (quasi-absent elsewhere) (Figure 4d).
- Along P4, Orthoptera and Teleostean (were the most contributing food variables. Their opposition separated FT10 from FT1 with relatively high consumption of Orthoptera in FT10 (null in FT1) and Teleostean in FT1 (null in FT10) (Figure 4c,d).

- Along P5, *FT1* and *FT2* opposed because of higher relative consumption levels (preference) of *Lepidoptera* in *FT1* (lower in *FT2*) vs. opposite pattern for *Aquatic Angiosperm*, *Gastropoda* and *Isoptera* showing high consumption in *FT2* (and low in *FT1*) (Figure 4c,d).
- Along P6, *Ephemeroptera* was the most contributing variable with relatively high consumptions in *FT9* and some individuals of *FTs* 2 and 6 (Figure 4e,f). On the opposite side of P6, *FT10* was marked by the absence of *Ephemeroptera* feeding.
- Along P7, *FTs* 3, 4, 5 were opposed to *FTs* 1, 2, 10 along P7 due to their relatively higher consumptions of *Undetermined Insects* (the most contributive variable to P7) (Figure 4g–h). Moreover, *FTs* 3, 5 were characterized by relatively high consumption of *Isopoda* and *Acarina*, respectively. Further, *FT9* was revealed to be distinguished by *Cyanophyta* in addition to *Undetermined insects*. On the opposite side, *Invertebrate Eggs* characterized *FT2*.
- Along P8, *Bacillariophyta* and *Bryophyta* were the most contributing variables and characterized *FT7* (Figure 4g–h). *Bryophyta* consumption was quasi-absent in the other *FTs*. By this way, *FT7* was revealed to be specific feeding patterns of *Bryophyta*.
- Along P9, *Plant Fragments*, *Coleoptera* and *Trichoptera* were the most contributing variables (Figure 4i). *Trichoptera* consumption was shared by *FTs* 2, 3 and 8 (on the positive side of P9) (Figure 4j). *Plant Fragments* characterized more particularly *FT4*. On the opposite side, *FT1* was characterized by *Coleoptera* in addition to *Lepidoptera* and *Teleostean* with absence of *Trichoptera*).
- Along P10, *Bacillariophyta* was the most contributing variable by characterizing *FT7* (Figure 4i,j) by representing 20–50% a whole feeding profile.

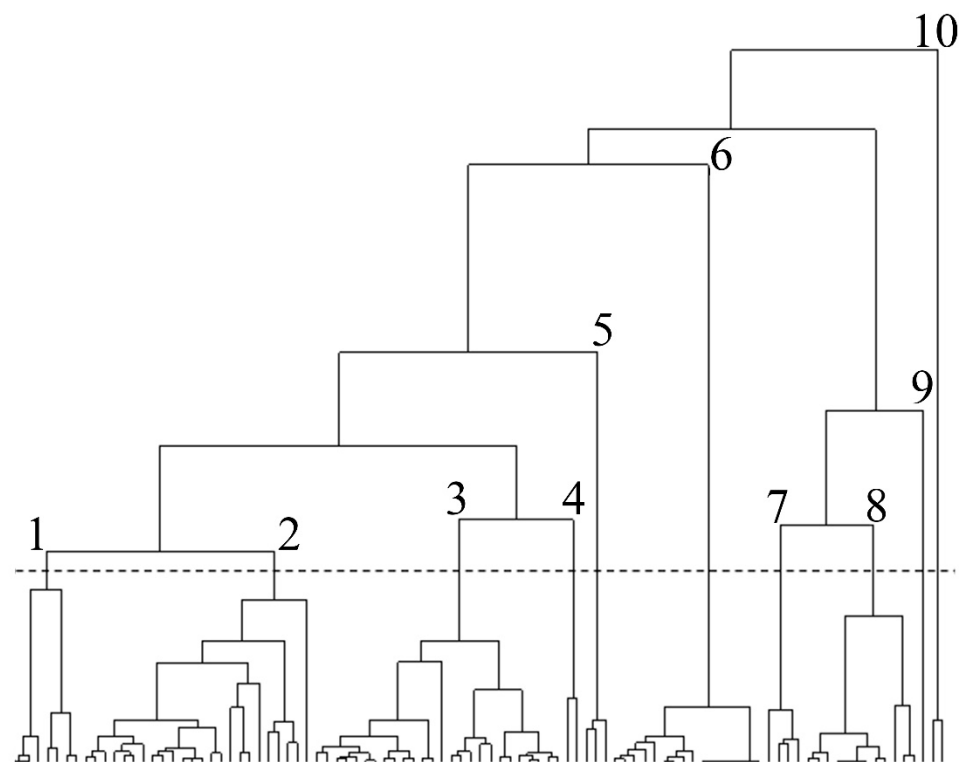


Figure 3. Dendrogram highlighting ten feeding trends characterized by high relative consumptions of different food types of the fish community from Verde River.

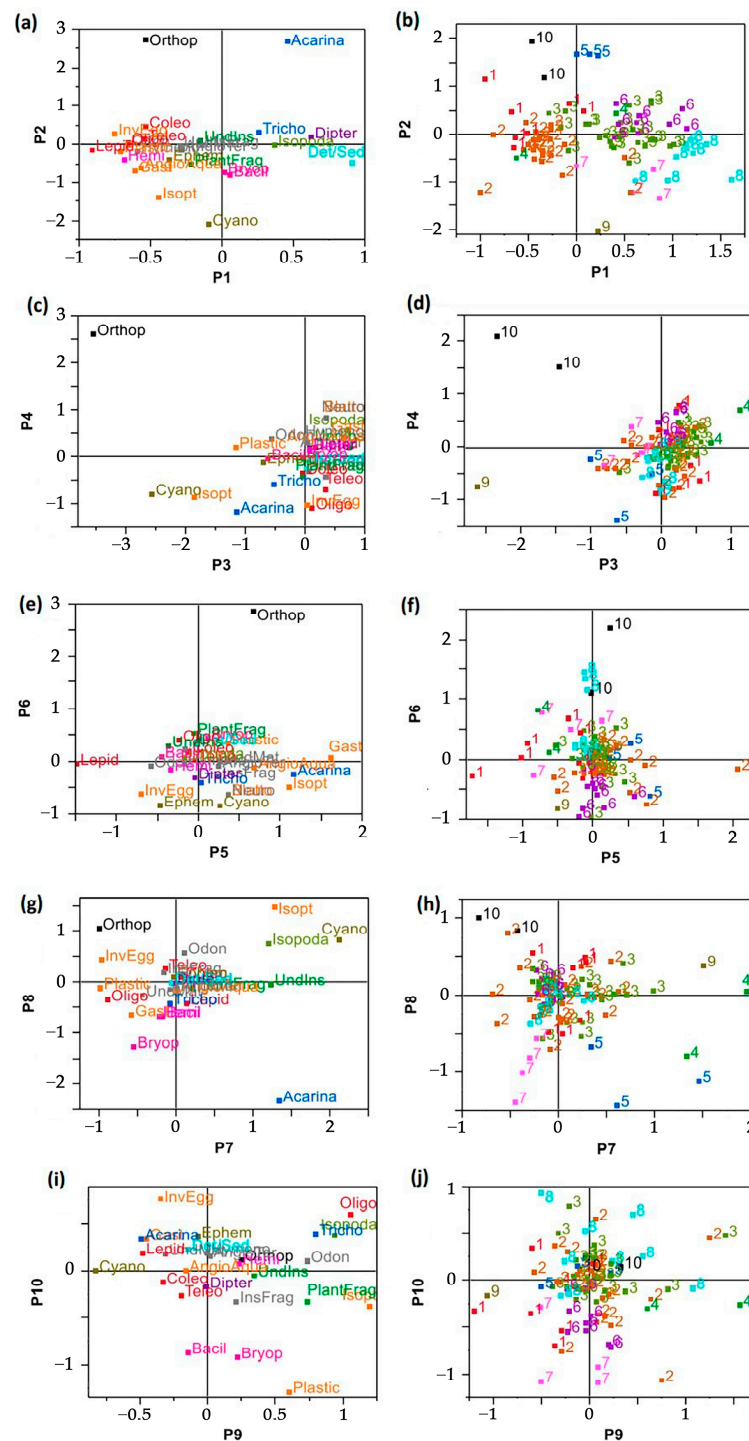


Figure 4. Factorial plots given by the 10 principal components of correspondence analysis applied on food data of the fish community from Verde River. (a,c,e,g,i) Food variables' plots. (b,d,f,h,j) Feeding trends of individual fishes. Different colors were used to distinguish between different food categories (left plots) and between feeding trends (right plots). (Acarina: Acarina; Bacil: Bacillariophyta; Blatto: Blattodea; Bryo: Bryophyta; Coleo: Coleoptera; Cyano: Cyanophyta; Det/Sed: Detritus/Sediments; Dipter: Diptera; Ephem: Ephemeroptera; Gast: Gastropoda; Hemi: Hemiptera; InsFrag: Insect fragments; InvEgg: Invertebrates eggs; Isopoda: Isopoda; Lepid: Lepidoptera; Neuro: Neuroptera; Odon: Odonata; Oligo: Oligochaeta; Orthop: Orthoptera; PlantFrag: Plant Fragments; Plastic: Plastic; Teleo: Teleostei; Tricho: Trichoptera; UndIns: Undetermined Insects).

Based on the above results, several FTs of the fish community at VR were highlighted as multivariate patterns showing specific food and differential feeding ratios (Table 1). These served as basis for analyses of feeding behaviors of fish species under interspecific and spatial aspects.

Table 1. Description of the feeding trends identified in the diets of the fish community from Verde River.

| Feeding Trend | Sample Units | Feeding Trend Description |
|---------------|--------------|---|
| FT1 | 7 | Characterized by high consumption of Teleostei (up to 50% of total diet, TD) (Figure 2aSM) and Lepidoptera (up to 35% TD; Figure 2bSM). Some sample units showed high consumption of Coleoptera (50–100% TD; Figure 2cSM) and Hymenoptera (20–35% TD; Figure 2dSM), demonstrating ability to exploit terrestrial resources. |
| FT2 | 24 | Characterized by high consumption of Aquatic angiosperms (up to 25% TD; Figure 2eSM) and Ephemeroptera (up to 18% TD; Figure 2fSM). FT2 showed the most diversified diet profile, presenting consumed food categories that were absent in other FTs, such as Blattodea, Gastropoda, Isoptera, Invertebrate Eggs, Neuroptera and Plastic debris (Figure 2g-ISM). |
| FT3 | 26 | Also presented heterogeneous diet pattern, consuming Terrestrial angiosperms, Sediments and Diptera (up to 50% TD for each one; Figure 2m-oSM), in addition to Undetermined invertebrates, Undetermined matter, Invertebrate fragments, Trichoptera and Isopoda (Figure 1p-tSM). |
| FT4 | 2 | Characterized by relatively high consumption of Undetermined invertebrates (35–50% TD; Figure 2pSM), in addition to Diptera (Figure 2oSM), Hemiptera and Plant fragments (Figure 1u-vSM). |
| FT5 | 3 | Characterized by relative high consumption of Acarina (10–20% TD; Figure 2wSM), Trichoptera (up to 20% TD; Figure 2sSM) and Coleoptera (up to 35% TD, Figure 2cSM). |
| FT6 | 16 | Characterized by relative high consumption of Diptera (up to 50% TD; Figure 2oSM), in addition to Invertebrate fragments (Figure 2rSM). |
| FT7 | 4 | Characterized by relative high consumption of Bacillariophyta (20–50% TD; Figure 2xSM) and Sediments (up to 50% TD; Figure 2nSM), in addition to Bryophyta (Figure 2ySM). |
| FT8 | 12 | Characterized by relative high consumption of Sediments (40–100% TD; Figure 2nSM) associated with Plant fragments (Figure 2vSM) and Trichoptera (Figure 2sSM). |
| FT9 | 1 | Characterized by consumption peaks of Cyanophyta, Bacillariophyta and Ephemeroptera (each one up to 25% TD; Figure 1zSM, 1xSM and 1fSM) in addition to relative high levels of Sediments (25% TD; Figure 2nSM). |
| FT10 | 2 | Characterized by relative high consumption of Hymenoptera, Orthoptera and Coleoptera (15–25% TD for each one; Figure 1dSM, 1aSM and 1SMc). |

3.3. Association between Feeding Trends and Fish Species

Different fish species were characterized by different FTs patterns (Figure 5A). Some species were restricted to few FTs, including *P. aff. fasciatus* that was concerned only with FT3 (80%) and FT2 (20%), *H. strigaticeps* concerned with FT8 (60%), FT7 and FT9 (20% each one), and *R. quelen*, concerned with FT1 (50%), FT10 (33.3%) and FT6 (16.7%). The other fish species showed larger FTs patterns: *P. paranae* characterized by: FT2 (80%), FT1 (12%), FT3 and FT4 (4% each one); *Apareiodon* sp.: FT8 (43.7%), FT3 (31.3%), FT2 and FT7 (12.5% each one); *C. ehrhardti*: FT6 (56.3%), FT3 (31.3%), FT5 and FT8 (6.2% each one); *G. brasiliensis* showing the broadest FT pattern with FTs 3 (45.7%), 6 (25%), 5 (8.3%), and 1, 2, 4, 7 and 8 (4.2% each one). These patterns highlighted a highly structured complex feeding system of fish species which were distinguished by multiple (compensatory) diets or by narrow (specific) ones. These feeding strategies could be linked to fish species morphologies, living micro-environments and/or needs to overcome interspecific competitions.

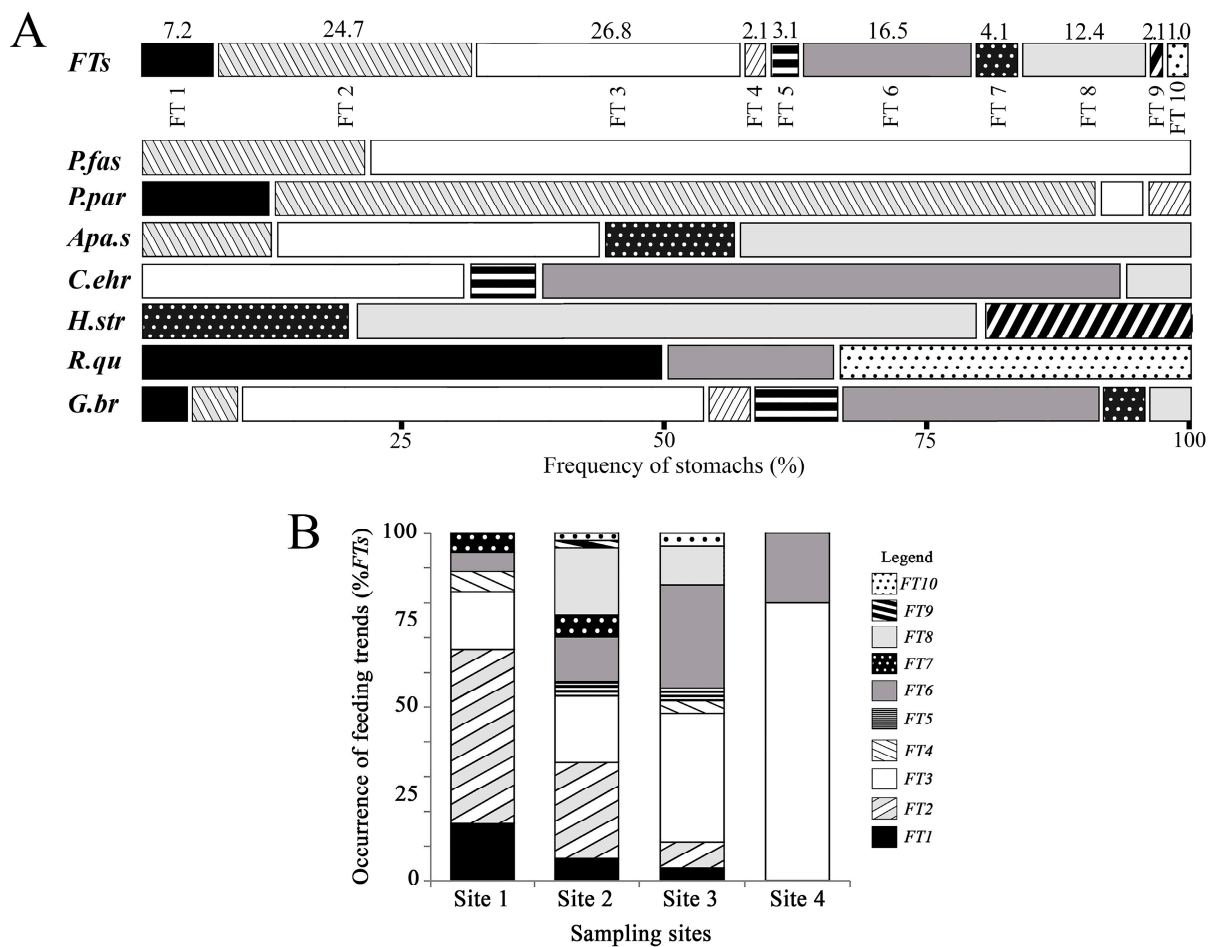


Figure 5. Feeding trends identified in the diet of the fish community from Verde River (A) by species and (B) by site. FTs = Feeding trends; *P.fas* = *Psalidodon aff. fasciatus*; *P.par* = *Psalidodon paranae*; *Apa.sp* = *Apareiodon sp.*; *C.ehr* = *Corydoras ehrhardti*; *H.str* = *Hypostomus strigaticeps*; *R.que* = *Rhamdia quelen*; *G.bra* = *Geophagus brasiliensis*.

3.4. Distribution Analysis of Feeding Trends in Sampling Sites

Different FTs showed opposite distributions through different sampling sites, highlighting a governing spatial effect on feedings of different fish species (Figure 5B). In total, 6 FTs characterized the headwater with the predominance of FT2 (50%). The upper and lower middle stretches showed higher feeding variability (nine and eight FTs, respectively) than other river sites. The upper middle was the most heterogeneous, with predominance of FT2 (27.7%), FT3 (19.1%) and FT8 (19.1%). At the lower middle stretch, FT3 (37%) and FT6 (29.6%) predominated. However, the river mouth was the most homogeneous site, characterized only by FT3 (80%) and FT6 (20%). There were two opposite variations showing relatively higher omnivory (i.e., plant-animal-based diets) in headwater and upper middle stretch versus more insect consumption in lower middle and river mouth stretches. Fish species and sites were mutually considered for further analysis.

3.5. Link Analysis between Feeding Trends and Species–Sites Interaction

By considering the different fish species in the 4 sampling sites separately, their diets were revealed to be mainly associated with the major FTs 1, 2, 3 and 6 with complementary/alternative/compensatory other FTs (Figure 6):

- For *P. paranae*, FT2 was the main feeding way and was completed by FTs 1, 3 and 4 at headwater, upper and lower middle stretches, respectively. Percentages of FT2 in *P. paranae* were higher at headwater and upper middle stretch than lower middle stretch,

being positively associated with the occurrence levels of the species in these sites. This leads to a positive trend (attractive feeding process) between *P. paranae* and FT2. Plant and insect consumptions varied by opposite ways between headwater, upper (showing plant dominance; FTs 1, 2) and lower middle stretches (showing relatively more captured insects, FT4).

- In *G. brasiliensis*, diets showed differential variations alternating between FTs 3 and 6 according to the different sites. FT3 occurred in all the sites and was particularly dominant at headwater and river mouth, where the species consumed plants and aquatic and terrestrial insects. However, FT6 represented a main food source at headwater and lower middle stretch, highlighting insectivorous diets focused on dipterids.

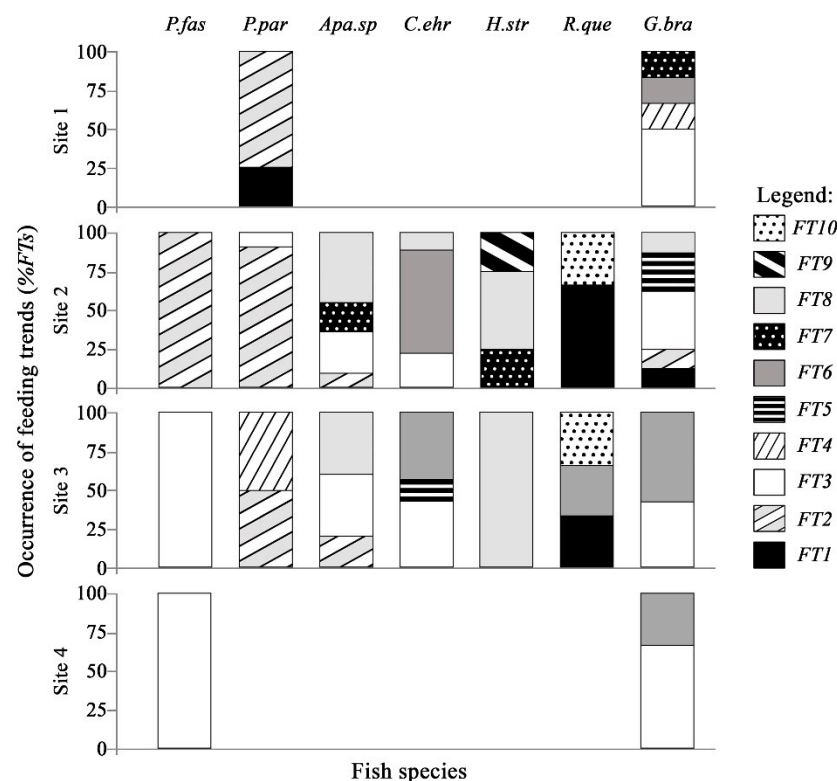


Figure 6. Spatial distribution of the feeding trends (FT) identified in the diet of the fish community from Verde River. *P.fas* = *Psalidodon* aff. *fasciatus*; *P.par* = *P. paranae*; *Apa.sp* = *Apareiodon* sp.; *C.ehr* = *Corydoras ehrhardti*; *H.str* = *Hypostomus strigaticeps*; *R.que* = *Rhamdia quelen*; *G.bra* = *Geophagus brasiliensis*.

Four fish species occurred only in middle stretches by showing different characteristic feeding patterns:

- *Apareiodon* sp. showed heterogeneous diet based on FTs 2, 3 and 8 in both upper and lower middle stretches. Moreover, the fish species showed some occurrence of FT7 in the upper middle stretch.
- *Corydoras ehrhardti* (occurring in upper and lower middle stretch) showed diet mainly based on FTs 3 and 6. It was the fish species to be associated with FT6 at upper middle stretch, indicating a strong preference of Diptera.
- *Hypostomus strigaticeps* showed a diversified diet at upper middle stretch, combining FTs 8, 7 and 9 (including Bacillariophyta, Cyanophyta, Bryophyta, plant fragments). However, FT8-based exclusively diet (highlighting Sediments) occurred at lower middle stretch. This indicated a constrained feeding response to a loss of environmental quality. FT9 was particularly concerned with *H. strigaticeps* and manifested only at upper middle stretch.

- *Rhamdia quelen* showed a diet based on FTs 1 and 10 occurring at upper and lower middle stretches. FT10 was specific to *R. quelen* indicating feeding motivation for big insects. Further, the occurrence of FT1 highlighted the feeding motivation of *R. quelen* for big prey (Orthoptera, Coleoptera, Teleostei). However, this fish species manifested FT6 at lower middle stretch, highlighting a higher trend for insect consumption. Moreover, the occurrence of FT6 in site 3 (versus absence in site 2) could be indicative of feeding response to a loss of environmental quality.

Finally, *P. aff. fasciatus* showed more restricted (selective/constrained) diets based exclusively on FT2 at upper middle stretch and FT3 at lower middle and river mouth stretches. This provided further information on the ability of genera *Psilidodon* to combine or alternate plant and insect-based diets according to the local conditions.

4. Discussion

Ecological states of VR were approached based on feeding behaviors of several fish species by using integrative information from stomach contents and consisting of different consumed food categories varying quantitatively and qualitatively at intra- and interspecific levels, and spatially within and between sampling sites. The 10 FTs highlighted from stomach content analyses were differently distributed or specifically associated with the different studied fish species (Figure 7). Feeding behaviors and patterns were related to intrinsic factors (e.g., morphology, sensorial way, habit, and habitat type), and extrinsic ones (e.g., interactive effect of sampling sites on such feeding patterns), discussed as follows.

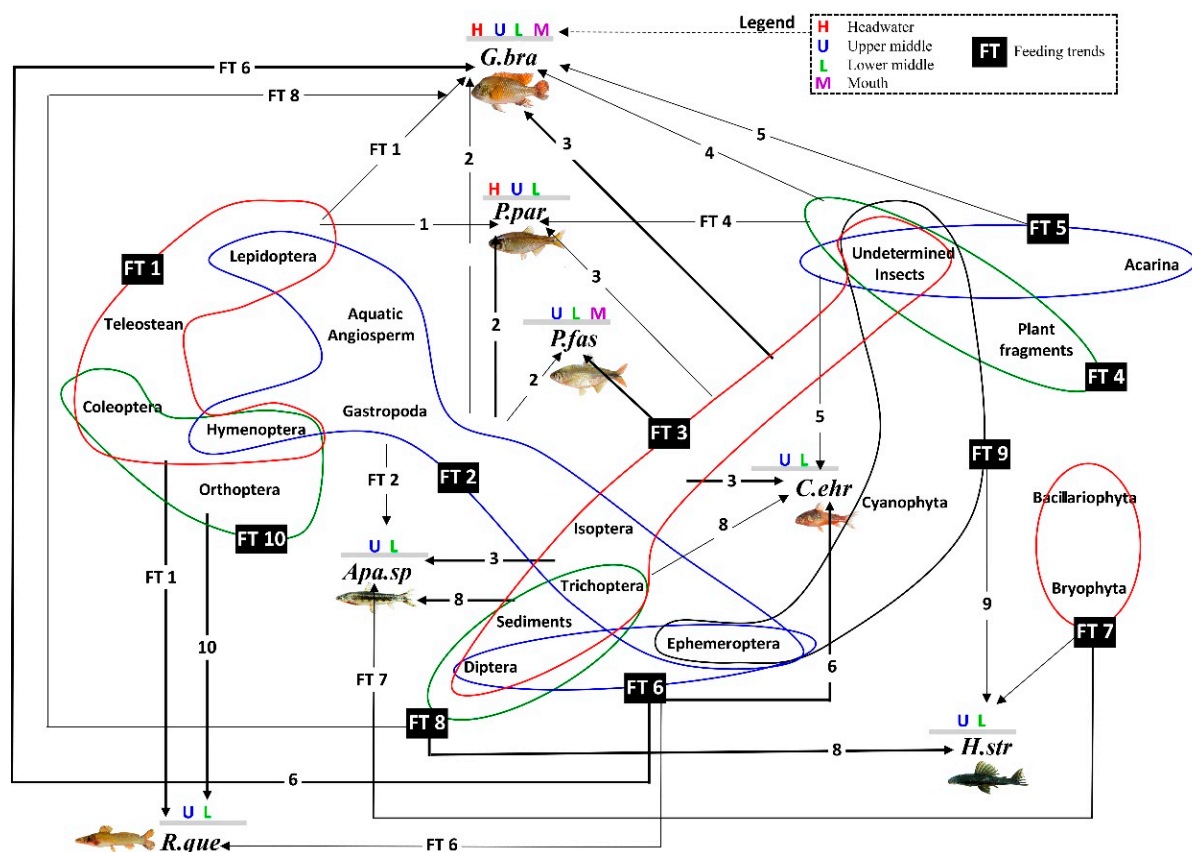


Figure 7. Schematic network showing the different feeding characteristics and interactions of the fish community from Verde River. H: headwater (red lines); U: upper middle stretch (blue lines); L: lower middle stretch (green lines); M: river mouth (purple lines); FTs = Feeding trends; *Pfas* = *Psilidodon aff. fasciatus*; *P.par* = *Psilidodon paranae*; *Apa.sp* = *Apareiodon sp.*; *C.ehr* = *Corydoras ehrhardti*; *H.str* = *Hypostomus strigaticeps*; *R.que* = *Rhamdia quelen*; *G.bra* = *Geophagus brasiliensis*.

4.1. Phenotypic and Behavioral Dietary Adaptations

At VR, *Psalidodon* aff. *fasciatus* and *P. paranae* presented a generalist and opportunistic feeding behavior, consuming a high diversity of prey from autochthonous (highlighting Diptera larvae and aquatic angiosperm) and allochthonous origins (highlighting Hymenoptera, Coleoptera and terrestrial angiosperm). *Psalidodon* species are diurnal and present high visual sensitivity and acuity to prey seek, with ability to fast movements up- and downward in the water column, exploiting food resources present since the water surface to the river bottom [23–25]. These abilities are related to morphoecological features that include high compressed and tall body, short pectoral and dorsal fins, compressed caudal peduncle, high caudal fin aspect ratio, large eyes, and terminal mouth [24,47–50]. Due to this set of characteristics, *P. aff. fasciatus* and *P. paranae* can show high trophic plasticity, adopting different degrees of herbivory, insectivory and detritivory [23,41,47,51–55]. These features make the genus efficient colonizers, able to modulate feeding behaviors as response to temporal fluctuations and to environmental changes [47,55,56]. As a resource, *P. aff. fasciatus* and *P. paranae* are prey for the top predators *H. aff. malabaricus* and *R. quelen* that cooccur in the VR [38,57,58]. Considering that the presence of predators changes the feeding behaviors of its prey organisms [19], phenotypic plasticity represents an eco-evolutionary response to a high diversity of habitats and food supplies [59]. This is the case of these species in VR as well as in the Neotropical region as a whole, which modulate their strategies for habitat colonization, resources partitioning, predator avoidance and fitness [12,59].

The pearl cichlid, *G. brasiliensis*, also presents high phenotypic plasticity, modulating its morphoecological features [60] and feeding strategies [61–63] to inhabit a wide range of habitats with different environmental features and food availability [43,64,65]. It presents a relatively compressed body, large head, large and terminal mouth, highly protrusible jaws, large eyes, large caudal peduncle, rounded caudal fin and low body ratio [66,67]. These morphoecological features are common for not good swimmers, which inhabit spatially heterogeneous areas and use their flexible fins to fine position adjustments [66]. *Geophagus brasiliensis* is nocturnal and occupies marginal areas of the river [67,68]. At VR, a key issue to understand the species is its feeding behavior, detailed described by Sazima [69] and summarized as follows: during feeding, it tilts its body in an oblique position in relation to the bottom and moves its pectoral and caudal fins, propelling the body forward; at the same time, the fish protrudes its upper jaw, burying the mouth in the sediment. Afterward, the fish adopts a horizontal or slightly inclined position while sorting the food captured in the mouth, expelling sand and clay particles through the mouth and opercular opening. During the food sorting, the pectoral fins perform movements of large amplitude to keep its body position in the water column.

These adaptations allow *G. brasiliensis* to shift its feeding behavior between visually oriented to pump-filter according to prey availability. This enables the species to adopt omnivorous feeding behavior and consuming benthic aquatic invertebrates (highlighting Chironomidae), algae and plants, usually associated with the ingestion of large amounts of sediments [61,62,67,69–71]. This pattern was observed for *G. brasiliensis* species at VR.

The armored fish *H. strigaticeps* present morphometric body features related to fishes constrained to benthic habitats, including depressed and low body shape, wider pectoral-, pelvic and caudal fins, developed caudal peduncle, dorsally positioned eyes, ventrally oriented mouth, and teeth resembling a spatula to scrape foods from different substrates [20,43,48,72]. The species has a large intestine that allows them to feed on periphyton and ingest algae, small invertebrates and particulate organic matter associated with amounts of detritus and sediments [20,73,74]. The *Hypostomus* spp. are nocturnal and associated with fast-flowing water that seek food by chemical signals [20,48,75]. In the VR, *H. strigaticeps* mainly consumed Diptera, highlighting Chironomidae, and Bacillariophyta associated with large amounts of sediments, characterizing it as an aufwuchs-eater [76].

A similar aufwuchs feeding behavior was also observed for *Apareiodon* sp., a small size endemic species of VR not yet described [77]. This genus also presents body features

related to benthic habitats, such as depressed body shape, wider pectoral and pelvic fins, developed caudal peduncle, scrape-specialized jaw, spatulate teeth, subterminal mouth and large eyes [43,48]. These morphological features enable the species to swim near the river bottom, mainly on rocky riverbeds [43,78]. The *Apareiodon* sp. is diurnal, found in fast-flowing environments [78]. During feeding, it uses visual orientation to exploit small benthic arthropods and aquatic plants, such as algae and macrophytes, usually ingesting them associated with sediments [72,78,79]. Due to their ecomorphological constraints, the consumption of terrestrial resources by *Apareiodon* sp (and *H. strigaticeps* too) in VR seems to be an opportunistic behavior related to allochthonous prey that sank until the river bottom.

Concerning the diet of *C. ehrhardti* in VR, it was focused on the consumption of Diptera, highlighting Chironomidae, associated with the ingestion of large amounts of sediments. The species has a well-known selective feeding behavior on dipteran larvae, highlighting chironomids [47,80]. *Corydoras ehrhardti* is more active during crepuscule and night periods [80]. The species present subterminal mouth, elongated snout, sensory barbels and short caudal peduncle, being well adapted to sandy and lentic habitats [50,80–82]. During the seek on aquatic benthic invertebrates, *C. ehrhardti* probes the river substrates by using its paired barbels, which are rich in taste bud cells [83,84], and it loosens sandy and muddy substrates by using its snout [18,81,85]. Ingested sediments may be expelled by *Corydoras* in bursts through its opercular openings, a well-known substrate-sifting behavior [82]. Stomach content analyses in *Corydoras* have shown that food resources are usually ingested with sediments [50,80].

Another important body feature of *Corydoras* is the presence of pectoral- and dorsal-fin spines [81]. When armed, these spines increase the effective size of the fish, exceeding the mouth opening dimensions of several predators, hampering its manipulation and, afterward, its capture as response to predator learning processes [85,86]. Moreover, *Corydoras* show monochromic and abstract pigmentation patterns that are related to crypsis in different river substrates [81,87]. Furthermore, when exposed to simulated threats and predators (e.g., *H. aff. malabaricus*), *Corydoras* presents several anti-predator responses, including freezing behavior, shoal compaction with coordinated and alerting movements, and the use of submersed plants, roots and branches as cover for refuge [87,88]. Studies showed that *Corydoras* is prey of *H. aff. malabaricus*, although this predation seems to be very low [81,89]. Probably, the set of morphological and behavioral features exhibited by *C. ehrhardti* contribute to avoid predation [71,85,87,89], reducing the time spent by the species in anti-predator behaviors and allowing feeding strategies focused on high nutritive prey [90], as was observed in the VR.

The diet of *R. quelen* at VR was focused on nutritive prey, mainly consuming Diptera, Coleoptera, Hymenoptera and Orthoptera. It presents depressed and longer body shape, wider pectoral and caudal fins, and specific top-predator features such as higher and wider mouth terminally positioned, higher and longer head, and sensory barbels [43,47,50,68,91,92]. *Rhamdia quelen* is nocturnal and inhabits marginal areas close to the river bottom [43,50,68,91]. Although not detected at VR due to the scarcity of *H. aff. malabaricus* [38], *R. quelen* and it could be antagonistic predators, with adults of one species predating on juveniles of the other species [57,58,93]. The current scenario at VR indicates a low or an absent prey–predator interaction between *R. quelen* and *H. aff. fasciatus* in the area [19,22,90].

4.2. Spatial-Interspecific Diet Trends

Fish diets in VR were modulated by spatial availability and distribution of food resources, which depended on environment structure, shifts in environmental quality, and variable anthropic effects in the surrounding landscapes, as observed in other Neotropical riverine systems [36,38,55,94–96]. In VR, this set of factors affected the longitudinal occurrence of fish species and, consequently, their adaptive feeding behaviors, revealed by FT responses.

At headwater the presence of riparian vegetation and the relative well environmental quality influenced the diet of *P. paranae* and *G. brasiliensis*. Riparian vegetation brings

several benefits for aquatic environments by controlling environmental conditions (e.g., temperature, pH, conductivity, turbidity, suspended solids inputs), increasing habitat complexity (e.g., by providing wood debris, roots, branches and trunks), and providing terrestrial energetic resources (e.g., seeds, flowers, leaves, and a high diversity of invertebrates) [38,94,97]. The adopted FTs at headwater were characterized by the consumption of these diverse terrestrial resources:

- *Psalidodon paranae* mainly exploited terrestrial invertebrates (highlighting Coleoptera and Hymenoptera) and angiosperms (seeds and leaves), confirming its generalist and opportunistic behaviors, exploiting prey items from riparian origin [41,47,49,55,94–96,98].
- The diet of *G. brasiliensis* was focused on benthic prey items and complemented by terrestrial items, such as Hymenoptera and seeds. This trend is common in freshwater fishes inhabiting areas with good status of riverbank conservation that tend to be energetically dependent on allochthonous resources [61,62,99].

The high variability of fish species and FTs observed in the upper middle stretch reflects the structural complexity of this area related to the riverbed conditions. Its features favor the establishment of rich and complex communities of periphyton [100,101] and macroinvertebrates [102], contributing to the occurrence of several fish species [43,103]:

- Both *Psalidodon* species recurrently consumed aquatic plants, highlighting Podostemaceae, followed by terrestrial resources (angiosperms, Coleoptera and Hymenoptera). These results reinforce them as generalist and opportunistic feeding species [41,47,55,98].
- In contrast, *C. ehrhardti*, *G. brasiliensis* and *R. quelen* adopted highly selective diets. The former and the second species mainly consumed Diptera larvae. The latter mainly exploited big terrestrial insects (Coleoptera and Orthoptera), highlighting the relevance of the riparian vegetation in providing energetic resources for the aquatic systems [41,97]. These focused diets reflect the intrinsic features of each species, considering the effectiveness of their sensory and mechanical apparatus for seeking and selecting nutritious foods [69,80,82,84,92,104].
- Finally, *Apareiodon* sp. and *H. strigaticeps* consumed aquatic resources, focusing on Diptera larvae and Bacillariophyta with recurrent ingestion of sediments. Both species are morphologically well adapted to inhabit stable riverbeds [43,48,78], commonly ingesting large amounts of sediments and detritus associated with benthic invertebrates [75,78].

The ichthyofauna of the lower middle stretch was also rich and adopted a high diversity of FTs, although with different feeding patterns. The consumption of terrestrial plants and invertebrates decreased in opposition to an increase in the feeding of aquatic insects and sediments. This scenario reflects the riparian vegetation suppression, adjacent soil erosion, riverbanks instability and riverbed siltation, influencing the FTs:

- *Psalidodon* aff. *fasciatus* mainly consumed Diptera larvae, in addition to terrestrial plants and invertebrates, whilst *P. paranae* showed a generalist diet, consuming aquatic plants and invertebrates. The environmental conditions of this area reduced the influx of terrestrial energetic resources into the river, leading fishes to exploit foods from aquatic origin [41,55,95].
- *Apareiodon* sp., *C. ehrhardti*, *G. brasiliensis* and *H. strigaticeps* mainly consumed Diptera larvae and sediments, while *R. quelen* recurrently consumed Diptera larvae and big terrestrial insects (Coleoptera and Orthoptera). An increase in the ingestion of sediments is a consequence of the environmental changes noticed in the lower middle stretch, changing the availability of potential foods for the ichthyofauna [64,95–97].

The ichthyofauna of the river mouth was low diverse and high dependent on aquatic energetic resources when compared with the other sampled sites. The consumption of large amounts of sediments followed a trend observed at the lower middle stretch. The species recorded in this site are adaptable to high degraded habitats [38,64,65,105–107], the case of river mouth:

- *Psalidodon* aff. *fasciatus* and *G. brasiliensis* were highly dependent on Diptera chironomids larvae and sediments. Although chironomids represent a highly diversified, abundant, and nutritive insect group distributed in worldwide freshwater environments [72,91,108], their strongest predominance in the diet of *P. aff. fasciatus* and *G. brasiliensis* indicate a decrease in the diversity and abundance of other aquatic macroinvertebrates [104,108–110].

4.3. Methodological Considerations

Stomach contents represent rich information compartments correlated with forager behaviors, foods' availability/accessibility, and environment states [16,29,32]. It has the advantage to be both a soft and highly collective way of information concerning biological diversity, fish feeding patterns and ecosystem states with minimal costs and disturbances vs. highly acquired information on structural and functional aspects of the studied system (fish community, river). Herein, analysis of stomach contents provided both structural and functional biological/ecological information consisting of occurrence of prey on one hand vs. behaviors of predators on other hand, the basis of resource and consumer linkages [10,12,16,29].

Single counting values (occurrence) are not informative of diet because they only inform on the availability and consumption level of prey without consideration of the consumption states of other prey types. To solve this limitation, the use of multivariate techniques (CA-HCA-based method) provided an integrative approach helping to highlight differential organization of a big set of food profiles into original feeding trends (FTs) defined by high affinities of consumers toward some food types.

Correspondence analysis is a strong relativization method and is appropriate for analysis of the regulation ratios controlling observed profiles (balance states) in any studied system (population, community, etc.) [33,34]. Moreover, CA is an efficient preparative step for HCA, helping to obtain well-interpretable clusters in terms of foraging trends at population/community scale. This integrative approach was chosen because direct clustering (without CA) would provide fewer specific trends to analyze foraging patterns.

Together with the biological results, this is another novelty of the current study: the deep ecological–quantitative characterization, not restricted to a simple description of the most evident trends. Feeding patterns were highlighted from relatively high consumption levels of a given food type by a consumer compared with other food types in the same consumer on one hand, and with other consumers toward the same food type on other hand. The results provided by the CA-HCA-based method advantageously classified the large population/community dataset into homogeneous clusters representing different feeding trends in the VR. This provided the most original cases in terms of feeding behaviors and diet characterization within the studied community, a method recommended for complex Neotropical riverine systems evaluation.

5. Conclusions

The resource and consumer linkages at Verde River were detailed, and fishes have shown their ability to access the relative profitability of different food patches and to switch among patches as resources are depleted. The adaptive processes included generalist and specialist feeding behaviors implying extension of food categories' ranges (e.g., *P. aff. fasciatus*, *P. paranae*, *G. brasiliensis*); selection of well-located, high-size or energetic prey (e.g., *H. strigaticeps*, *Apareiodon* sp., *C. ehrhardti*, *R. quelen*); and sediment ingestions under critic conditions (e.g., *P. aff. fasciatus*, *G. brasiliensis*). These adaptive feeding trends, constrained by environmental conditions, were associated with several intrinsic characteristics of fish species, including ecomorphology (*i.e.*, mechanistic and orobranchial movements, sensitivity/acuity capacities and sensorial apparatus, inter alia) and specific behaviors (e.g., aufwuchs-eater and others herein described).

The interactive fish–river processes provided a wide and complex panel of essential information, allowing us to understand overcoming ways of environmental constraints and

optimizing ways of food balances. At VR, the fish community was modulated by paleogeomorphology, environmental conditions and ecological interactions operating on the aquatic environments and their surrounding terrestrial landscapes [28,111,112]. The assessment of resource and consumer linkages provided useful information about the availability of prey, valuable information to evaluate changes on fish feeding patterns as responses to shifts in Neotropical riverine systems [24,41,47,95]. This set of information is also essential to identify potential disturbing factors for fish communities and to establish policies that ensure suitable management of the aquatic and terrestrial environments [24,113].

Management recommendations include long-term environmental monitoring and the adoption of restoration practices [114]. Conservation plans must be based on cost-effective scenarios (including ecological and socio-economic values), and a systematic conservation planning (SCP) is recommended to be applied on Verde River [115]. This would lead to previous and post-management scenarios, evidencing the conservation effectiveness in an updated and modern approach.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fishes8030157/s1>, Supplementary Material S1: Sampling area; Supplementary Material S2: PERMANOVA; Supplementary Material S3: fish species size structure; Supplementary Material S4: frequency of occurrence of consumed foods; Supplementary Material S5: feeding profile of ten identified feeding trends.

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