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Predictive factors of species composition of follower fishes in nuclear-follower feeding associations: a snapshot study

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We tested whether habitat, identity, size of nuclear fishes, and intensity of bottom disturbance caused by their foraging can predict the composition of fish followers in nuclear-follower feeding associations. The study was carried out in a stream of the Serra da Bodoquena, Mato Grosso do Sul State, Southwestern Brazil. We performed underwater observational sessions (total 12 h) of such interspecific interactions to obtain data about the identity and abundance of the followers in the association, as well as the identity and size of the nuclear fish. We also evaluated whether different intensities of bottom disturbance due to the nuclear fish foraging and type of habitat may influence interactions. We recorded 38 episodes involving nuclear and follower species. Using a multivariate analysis with distance matrices, we noted that the intensity of bottom disturbance caused by nuclear fishes was the main predictor of the composition of the follower species ($r = 0.55$, $p < 0.01$), as well as the identity of the nuclear species, although this latter relation was weak ($r = 0.09$, $p = 0.05$). Such results indicate that followers react readily to sediment suspension, which reflects the trophic plasticity and opportunistic foraging characteristic of most tropical freshwater fishes.

Neste estudo testamos se o hábitat, a identidade e o tamanho da espécie nuclear, bem como a intensidade do distúrbio causado pela atividade do nuclear podem predizer a composição de seguidores na associação alimentar do tipo nuclear-seguidor. O estudo foi conduzido em um riacho da Serra da Bodoquena, estado do Mato Grosso do Sul, bacia do alto Rio Paraguai. Foram realizadas sessões de observação subaquática (totalizando 12 h), visando a obter informações sobre identidade e abundância dos seguidores, assim como identidade e tamanho da espécie nuclear, hábitat e intensidade do distúrbio causado pela atividade de forrageamento da espécie nuclear. Foram registradas 38 associações envolvendo cinco espécies nucleares e nove espécies seguidoras. A análise multivariada com matrizes de distância demonstrou que a intensidade do distúrbio causado pelos nucleares foi o principal preditor da composição de seguidores ($r = 0,55$, $p < 0,01$), assim como a identidade da espécie nuclear, embora essa relação tenha sido fraca ($r = 0,09$, $p = 0,05$). Esses resultados indicam que os seguidores respondem prontamente à suspensão de sedimento, refletindo a plasticidade trófica e o oportunismo de forrageio característico da maioria dos peixes tropicais de água doce.

Key words: Communities, Interspecific interactions, Ichthyofauna, Foraging behavior.

Introduction

The nuclear-follower feeding associations between fishes are composed of species that dig in, or otherwise disturb, the bottom (nuclear species), usually during foraging, and follower species that associate with the former, taking the food made available by this disturbance (Strand, 1988). Although such interactions are commonly recorded in marine environments (Strand, 1988; Lukoschek & McCormick, 2000; Sazima *et al*., 2006; Sazima *et al*., 2007), there are studies on such interactions in tropical freshwater environments as well, mostly in tropical waters (*e.g.*, Baker & Foster, 1994; Leitão *et al*., 2007; Ott, 2007; Teresa & Carvalho, 2008; Garrone-Neto & Sazima, 2009; Teresa *et al*., 2011). Despite efforts to describe this type of association, knowledge of its modulating factors is still incipient (see Sazima *et al*., 2005; Krajewski, 2009).

Some studies indicate that bottom disturbance is the main factor responsible for variation in the composition and abundance of followers in nuclear-follower interactions (Strand, 1988; Sazima *et al*., 2006). Indeed, the importance of bottom disturbance was emphasized by Krajewski (2009), who experimentally demonstrated that bottom disturbance is a factor more important than the identity of the nuclear species in attracting followers. Thus, the features directly or indirectly associated with sediment suspension would be

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important for the occurrence and variation in the composition of followers. Recently, Teresa *et al*. (2011) showed that different substrata types may interfere in the profile of this association type, influencing the composition of nuclear and follower species. For example, stream stretches with unconsolidated substrate (sand, mud) and with apparently greater availability of organic matter would show a high sediment suspension capacity during the feeding activity of benthivorous fishes, thereby attracting larger groups of followers (Teresa *et al*., 2011).

Attributes of the nuclear species may also be important in determining which follower species are attracted, as well as their abundance. Although it is well known that nuclear species share the behavior of inspecting or disturbing the bottom during feeding (Strand, 1988; Sazima *et al*., 2006), behavior variations and changes in other biological attributes such as size can also have predictive power about the composition and abundance of followers. For example, the nuclear species can adopt distinct feeding tactics according to the characteristics of the substrate and, consequently, vary in the degree of bottom disturbance they cause, thus influencing the attraction of followers. A study of the interactions between the nuclear species *Goniistius zonatus* (Cheilodactylidae) and the follower species of the genus *Pseudolabrus* (Labridae) in Southeastern Japan, demonstrated that different substrata types result in differences in behavior and frequency with which the nuclear species contacts the bottom to obtain food (Matsumoto & Kohda, 2001). In sites with seaweed banks, these nuclear fishes forage by repeatedly biting the substrate and attract a greater number of follower fishes (Matsumoto & Kohda, 2001). Size variations of nuclear fishes may also influence the composition of followers (Strand, 1988; Lukoschek & McCormick, 2000). Such effect is probably related to the ontogenetic changes in the way fishes explore the substrate (Lukoschek & McCormick, 2000), but may also reflect interspecific differences related to the ability of nuclear species to cause disturbances in the substrate according to their size.

Most records of feeding associations in freshwater were made in Neotropical headwater streams (Leitão *et al*., 2007; Teresa & Carvalho, 2008; Teresa *et al*., 2011, but see Ott, 2007). These environments feature a mosaic of environmental conditions (Frissel *et al*., 1986) and many of them have high variability in microhabitats, heterogeneous bottom composition, high water transparency and species diversity, conditions that favor the study of the modulating factors of such associations. The streams of the Serra da Bodoquena, in particular, situated in the Central-West region of Brazil, share the above-mentioned characteristics (Casatti *et al*., 2010). Moreover, recent studies show that significant part of the species living there participate in feeding associations (*e.g.*, Teresa *et al*., 2011). In this context, we conducted a snapshot study in a stream of the Bodoquena region as a model to evaluate the factors that may influence the composition of follower species in the nuclear-follower associations. More specifically, we tested whether habitat characteristics where the associations occur, the identity of the nuclear species, the size of the nuclear fishes, and the intensity of bottom disturbance caused by the activity of the nuclear fishes can predict the composition of the followers in the association.

Material and Methods

The study was conducted in the Olho d'Água stream (21°26'15.8"S 56°26'41.5"W) in the upper Paraguay basin located in the Planalto da Bodoquena, Mato Grosso do Sul State, Southwestern Brazil. This stream has high underwater transparency (in general more than 30 m horizontally) that makes underwater observation easier for fish studies. The observations were made on the whole length of the stream (1,450 meters), which is 10 to 12 m wide and 0.3 to 3 m deep, and has a great variety of habitats.

Underwater observations were carried out in sessions of about 180 min (totaling 12 h), between 1000 and 1400 h on 3 to 6 May 2011 by two observers jointly. In order to avoid resampling of individuals, observations were carried out by moving constantly from upstream to downstream. For each episode of a nuclear-follower interaction, we determined the identity of the nuclear species, the size of the nuclear fish, the identity and abundance of the follower species in the association, as well as the intensity of the bottom disturbance caused by the nuclear species and the habitat in which the interaction occurred. The approach of followers within a radius of approximately 50 cm of another individual causing disturbance to the bottom (nuclear) was considered to be an interaction episode. The intensity of the disturbance caused by the nuclear fish was determined, considering the size of the suspended sediment cloud (small: cloud of sediment near of the nuclear fish mouth; medium: cloud of sediment around 30 cm; large: cloud of sediment larger than 30 cm) as well as the time the sediment remained in suspension in the water column (short: time of suspension of the sediment cloud inferior to five seconds; medium: time of suspension between six and 15 seconds; long: time of suspension superior to 15 seconds). These two parameters were graded from 1 to 3, indicating the lowest and highest intensity, respectively. The habitat was defined as the place where the interaction occurred and was classified qualitatively in accordance with the type of predominant substrate on the site (sand, gravel, rock, algae, and macrophytes).

The importance of predictive variables of the composition of follower species was evaluated by multiple regression on distance matrices (MRM). This analysis is similar to the Mantel test, but allows testing several distance matrices as predictive variables while at the same time it allows assessing the degree of relationship of predictive variables separately (Lichstein, 2007). Two matrices of species composition were used as dependent variables, the one lending more weight to less abundant species (Jaccard similarity coefficient) and the other giving more importance to abundant species (Bray-Curtis index). The predictive matrices were constructed from the Jaccard similarity coefficient (habitat and identity of nuclear species) and from the Euclidean distance coefficient (size of the nuclear fish and intensity of the disturbance). Correlation between the distance matrices was evaluated by means of the Spearman correlation coefficient. This analysis was performed using the "MRM" function of the "ecodist" package of the software R 2.11.1 (R Development Core Team, 2010). To enable a graphical view of the data variation, a non-metric multidimensional analysis (NMDS) was performed, emphasizing the predictive variables significantly associated with the follower species composition in the MRM analysis. In addition, the degree of autocorrelation between the predictive variables significantly associated with follower composition was evaluated by 2Stage analysis. This analysis calculates the correlation coefficient (Spearman) between pairs of matrices. The analyses were performed using Primer 6 software (2006).

Results

We recorded 38 episodes of nuclear-follower association, involving 15 species. Five acted strictly as nuclear species and nine strictly as followers, whereas one (*Leporinus striatus*) acted in both roles. After the name of each recorded species, N is the number of episodes in which this species was recorded. *Leporinus macrocephalus* (N= 15), *Prochilodus lineatus* (N= 16), *Leporinus striatus* (N= 03), *Leporellus vittatus* (N= 02), and *Parodon nasus* (N= 02) acted as nuclear species. The followers were *Odontostilbe pequira* (N= 38), *Jupiaba acanthogaster* (N= 19), *Astyanax marionae* (N= 12), *Crenicichla lepidota* (N= 09), *Crenicichla vittata* (N= 04), *Astyanax lineatus* (N= 04), *Astyanax asuncionensis* (N= 03), *Hypessobrycon eques* (N= 03), *Leporinus striatus* (N= 01), and *Characidium zebra* (N= 01). *Prochilodus lineatus* and *L. macrocephalus* were the two species that played the most important roles as nuclear fishes (Figs. 1-2).

The intensity of bottom disturbance caused by the nuclear fishes was the main predictor of the follower composition in the association, independently of the weight attributed to rare or abundant species (MRM, $r=0.55$, $p<0.01$, Table 1). The similarity in the followers' composition was also correlated with the identity of the nuclear species, although this relation was weak (MRM, $r = 0.09$, $p=0.05$, Table 1). Furthermore, the intensity of bottom disturbance was weakly related with the identity of the nuclear species (2Stage, $R = 0.10$).

The importance of the gradient of substrate disturbance caused by nuclear fishes in determining the follower species composition in the association can be viewed in the ordination produced from NMDS (Fig. 2A-B). On the other hand, when the identity of the nuclear species is highlighted, this relationship became less obvious (Fig. 2C). The identity of the nuclear species was the second most significant element associated with the composition of the follower species (Table 1). The differences attributable to identity are related to differences in behavioral characteristic. This trend may be exemplified by *P. nasus*, whose groups of 7-14 individuals bit out substrate portions (algae) in quick movements, creating large sediment clouds and attracted a distinct set of followers when compared with *L. striatus* that fed with subtle bites on the river bottom, causing minimum bottom disturbance, and thus attracted few followers. On the other hand, *L. macrocephalus* and *P. lineatus* caused varying levels of disturbance and showed high variability in the composition of followers (Fig. 1C-F). As to the follower species, the one that influenced most the ordination pattern of samples was *O. pequira*, whose abundance was positively correlated with the size and duration of the sediment cloud caused by the nuclear fish (Figs. 1C-F and 2D).

Discussion

We found that the intensity of bottom disturbance caused by nuclear fishes and their identity are the main predictors of the composition of followers in the nuclear-follower feeding associations in a freshwater stream in Southwestern Brazil. Among these factors, bottom disturbance intensity is the most important, influencing not only the abundance pattern of follower species, but also their incidence (presence/absence), since the results of the correlation between predictor variables and follower composition were similar for presence/absence and abundance data. Recently, Krajewski (2009) demonstrated experimentally that sediment suspension is an important stimulus *per se* to attract followers, probably because the suspension signals availability of food for the followers. This is consistent with studies conducted in marine (Strand, 1988; Sazima *et al*., 2006; Sazima *et al*., 2007) and freshwater environments (Matsumoto & Kohda, 2001; Teresa & Carvalho, 2008; Teresa *et al*., 2011), which emphasized the importance of the intensity of substrate disturbance to attract follower species.

The importance of bottom disturbance intensity to attract followers is exemplified by the abundance pattern of *O. pequira*, the most common species in the associations recorded in this study. The abundance of this fish in the associations increased proportionally to substrate disturbance (see Fig. 2). Such relationship can be associated with the ability of potential followers to detect the sediment cloud (Krajewski, 2009). In this sense, the greater and longer lasting the sediment cloud is, the more probable it is for the fish nearby to spot it and to move to join the association. In this case, locally abundant species have more chance to detect sediment clouds, quickly taking part in the interaction. Indeed, the ubiquitous and abundant *O. pequira* was the species that joined almost every species of nuclear species even in very short periods of substrate disturbances.

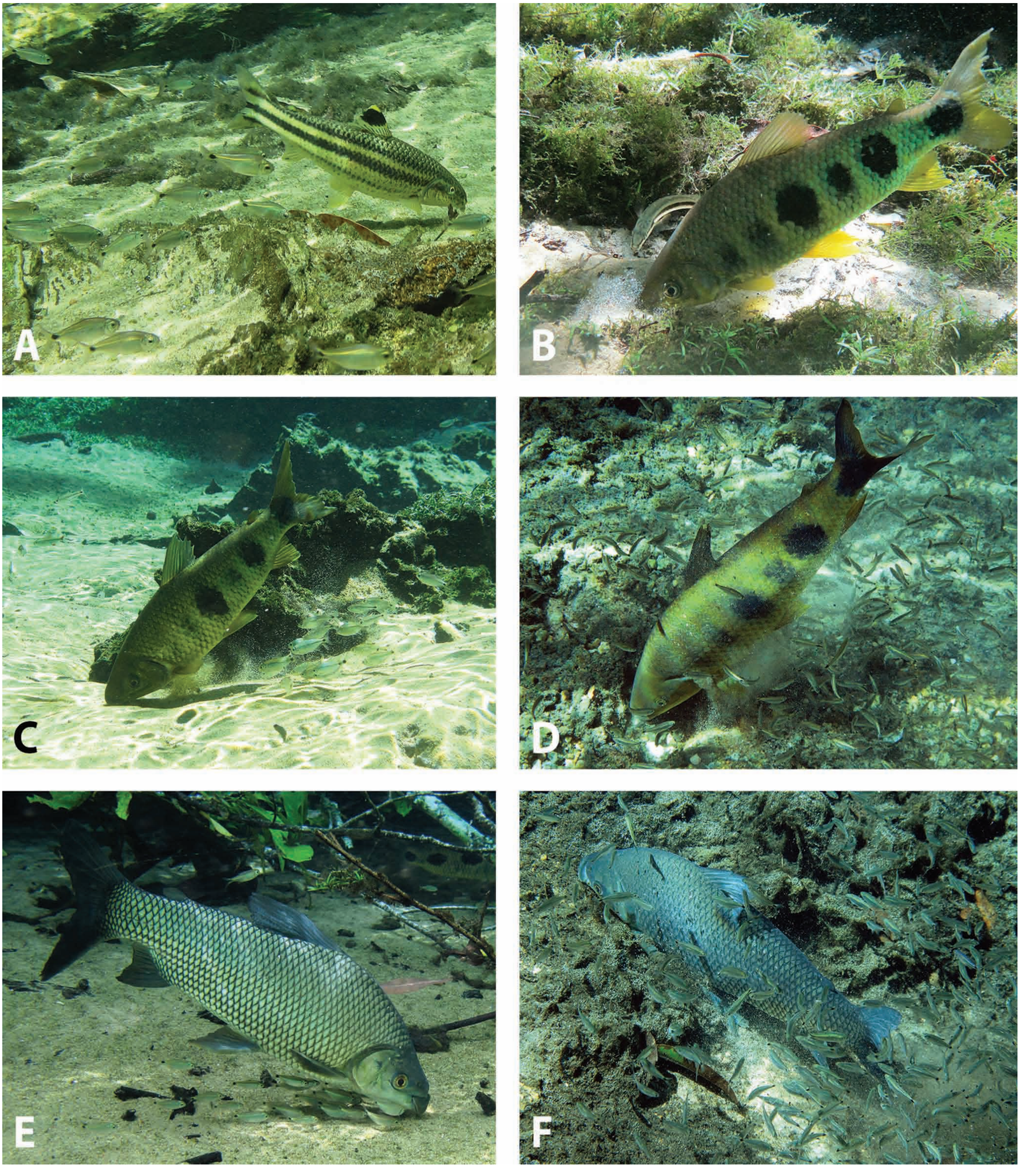

Fig. 1. Selected examples of nuclear-follower fish associations recorded in a stream in Southwestern Brazil: *Leporellus vittatus* begins to approach the bottom, while followed by a small group of *Jupiaba acanthogaster* (A); *Leporinus macrocephalus* disturbs the bottom, while *Crenicichla vittata* approaches to feed on fleeing or uncovered prey (B); *L. macrocephalus* stirs a little cloud, while a small group of *Odontostilbe pequira* and *J. acanthogaster* approaches (C); the same nuclear species stirs a large cloud, which congregates large numbers of *O. pequira* (D); *Prochilodus lineatus* begins to probe on the bottom, readily attracting a small group of *O. pequira* and *J. acanthogaster* (E); the same nuclear species stirs a large sediment cloud, which attracts large numbers of *O. pequira* (F). Photo credits: Sergio R. Floeter (A, E); José Sabino (B); Guilherme Ortigara Longo (C); Ivan Sazima (D, F).

The identity of the nuclear species was the second most significant element associated with the composition of the follower species, as seen in the case of *P. nasus* and *L. striatus*. Thus, the difference in the composition of followers in the association may be related with behavioral characteristics and the way nuclear species interact with the substrate. If, on one hand, *P. nasus* and *L. striatus* cause disturbances to the substrate in a characteristic way, the same cannot be said of *L. macrocephalus* and *P. lineatus*, whose disturbance pattern is quite variable, as can be seen in the ordination analysis (see Figs. 1C-F and 2C). This may explain the low correlation between the identity of the nuclear species and the intensity of bottom disturbance caused by the nuclear fishes, as well as the low explanatory power of the identity of nuclear fishes in relation to the composition of followers. Indeed, Teresa *et al*. (2011) found changes in the feeding behavior of *P. lineatus* and *L. macrocephalus* due to variations in substrate composition and food availability, which affected the pattern of sediment disturbance and suspension. Other factors such as feeding motivation, food availability and predation risk potentially contribute to variation in the foraging behavior of nuclear fishes (Gerking, 1994).

Contrary to what would be expected, habitat did not explain the composition of follower species, which contrasts with other studies that showed changes in the interaction profile due to the environment (Matsumoto & Kohda, 2001; Teresa *et al*., 2011). Such discrepancy may be related to differences in the spatial scale at which habitats have been assessed. The present study considered the immediate environment of the interactions (*i.e.*, microhabitat) for habitat classification, unlike other studies that used the meso/macrohabitat approach scale. Thus, differences in scales used in the environmental characterization would explain some of the differences between studies. Indeed, the predictive power of habitat characteristics at meso/macrohabitat scales for the structuring of fish communities has been extensively documented (Gorman & Karr, 1981; Angermeier & Karr, 1983; Teresa & Romero, 2010). Ongoing studies in the Olho d'Água stream have shown that the fish community composition is influenced by the habitat at scales wider than the one used in the present study.

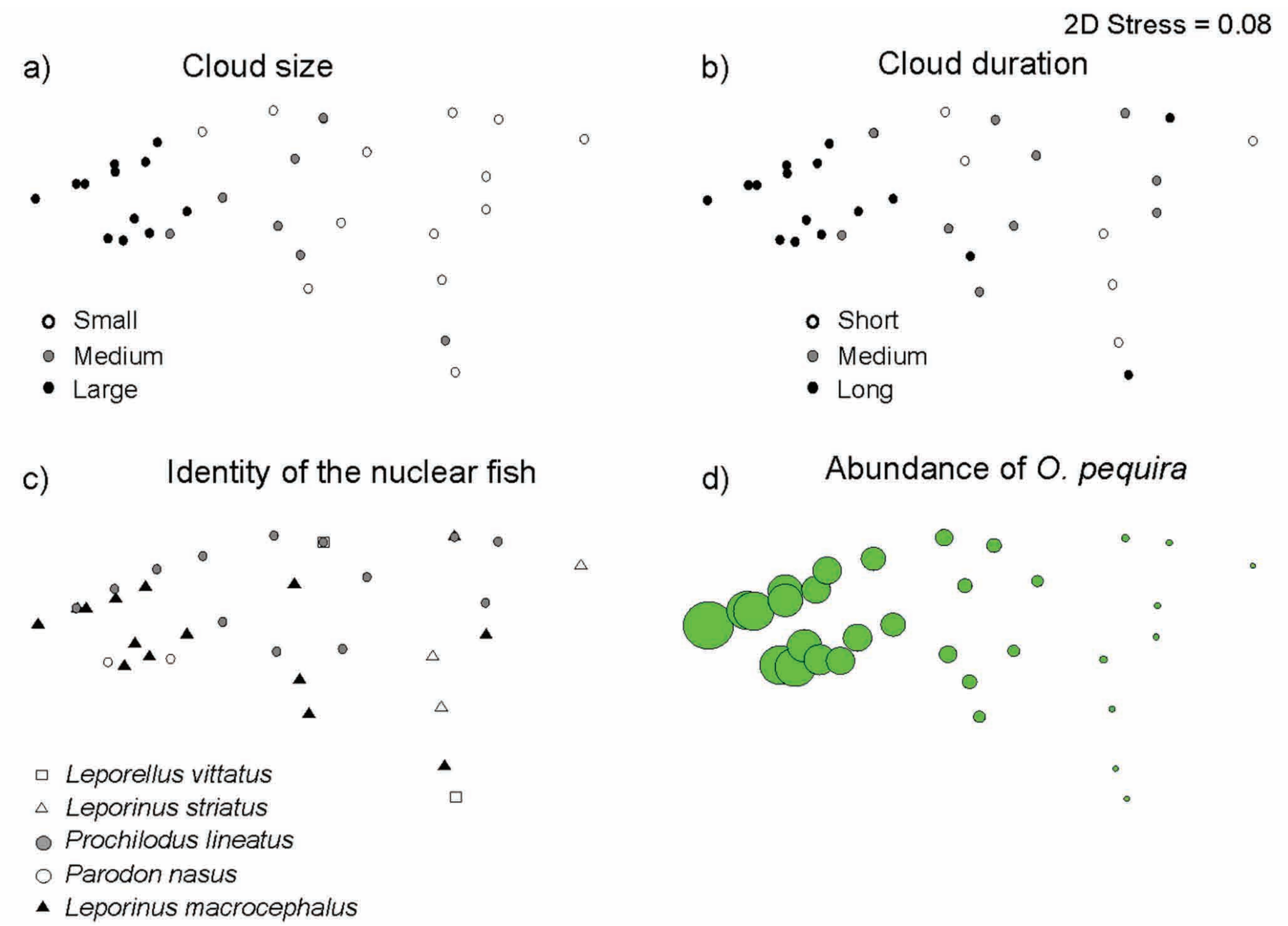

Fig. 2. Two-dimensional ordination of samples, considering the composition of follower fish species in the associations from Bray-Curtis similarity coefficient, and emphasizing the size of the sediment cloud (A), the duration of the sediment cloud (B), the identity of the nuclear species (C) and the abundance of the follower species *Odontostilbe pequira*, represented by the circumferences' sizes (D).

Table 1. Results of the analyses of multiple regression on distance matrices (MRM) indicating the relationship coefficient between the predictive and response variables and the respective values of p, in a study of nuclear-follower associations among fishes in a stream in Southwestern Brazil.[1] Similarity matrix constructed from Bray-Curtis similarity coefficient. [2] Similarity matrix constructed from Jaccard similarity coefficient. [3] Similarity matrix constructed from Euclidean distance.

Response variables	Predictive variables	Correlation coefficient	P
Quantitative structure[1]			
	Identity of the nuclear species[2]	0.09	0.05
	Size of the nuclear species[3]	0.002	0.98
	Intensity of disturbance[3]	0.55	< 0.01
	Habitat[2]	0.06	0.24
Composition (presence/absence)[2]			
	Identity of the nuclear species[2]	0.09	0.05
	Size of the nuclear species[3]	0.002	0.94
	Intensity of disturbance[3]	0.55	< 0.01
	Habitat[2]	0.06	0.20

The size of nuclear fishes was not important in determining the composition of follower species. Larger individuals could cause more bottom disturbance and thereby influence the attraction pattern of followers. However, the unconsolidated substrate of the Olho d'Água stream, being easy to suspend even with subtle touches, may favor the production of large sediment clouds, even when disturbed by small individuals. Regardless of the size of the nuclear fish, the foraging behavior seems to be the most important factor to rank the intensity of the bottom disturbance. For example, *P. lineatus* is an illiophagous species that feeds on detritus embedded in the sediment applying its lips to the bottom and biting out substrate portions (Fugi *et al*., 1996) with less vigorous movements than the smaller (and less adapted to detritivory) *L. macrocephalus*. Another example is *P. nasus*, one of the smallest among the nuclear fishes recorded in this study, which, nevertheless, is able to cause intense disturbances to the substrate while foraging in groups.

Our study was carried out in the dry season and does not encompass different seasonal periods. Even if there are no evidence for seasonal changes in fish composition in plateau streams of Paraguay basin (Valério *et al*., 2007), temporal changes on nuclear-follower association may occur. As had been show in a spatial context (Matsumoto & Kohda, 2001), temporal changes on stream conditions and resources availability can potentially influence the composition and abundance of follower species. The increased turbidity, as is typical in headwater streams immediately after rain events (Rocha *et al*., 2009), could affect the ability of most fish to visually detect the sediment cloud produced by the nuclear species. Furthermore, alterations on food availability and in the substrate composition across seasons may also influence behavior of nuclear species and the frequency and intensity of disturbance caused in the substrate (Matsumoto & Kohda, 2001). In this sense, the study of seasonal and annual dynamics of nuclear-follower association would provide interesting insights into how patterns observed in this study are consistent across temporal scales.

In summary, this snapshot study allows us to conclude that the composition of followers in the nuclear-follower associations is primarily related to variations in the intensity of bottom disturbance, with low fidelity with regard to the identity of the nuclear fishes. Contrary to what is recorded for marine environments, where some follower species associate with certain nuclear species even when these latter are not foraging (*e.g.*, Montgomery, 1975; Strand, 1988), the activity of followers in freshwater seems to be a generalized response to substrate disturbance as illustrated by sediment stirring animals other than fishes, including large mammals (Costa-Pereira, 2011). This generalized response is another example of the trophic plasticity and opportunistic foraging characteristic of tropical freshwater fishes (Goulding, 1980; Lowe-McConnell, 1995; Carvalho *et al*., 2009; overview in Abelha *et al*., 2001).

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