Facilitation underpinning the success of the non-native catfish *Hoplosternum littorale* (Callichthyidae) in lakes of the Middle Doce River Basin, southeastern Brazil

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**Abstract**

Facilitation is defined as an interaction between two or more species, which benefits at least one of them and causes harm to neither. The establishment of non-native species in new areas is a global phenomenon that raises the question of how facilitation may help in successful biological invasions. We describe a possible facilitation process between the catfish *Hoplosternum littorale* (Tamboatá) and its predators: *Pygocentrus nattereri* (piranha) and *Cichla cf kelberi* (tucunaré), all non-native fish that live in the lakes of the Middle Doce River Basin, southeastern Brazil. We found evidence of indirect facilitation, where non-native predators probably release *H. littorale* from competition, as they prefer to prey on native fish. Our main evidence in favor of this interpretation was a difference in the abundance of *H. littorale* between lakes where these species co-occur and lakes where *H. littorale* is the only non-native fish species. This difference was not associated with environmental differences between lakes or spatial segregation of age classes of *H. littorale*. Differences in peak activity among *H. littorale* and non-native predators are probably the main driver of co-occurrence.

**Keywords**: biological invasion, tropical lakes, fish, non-native species

**Introduction**

Ecology has been heavily influenced by ideas and theories related to interspecific competition, competitive exclusion, and niche and species packing, and there has been much less emphasis on mutualism and facilitation (Bruno et al. 2003). Studies on positive interactions are comparatively modest, and so is our knowledge of this phenomenon (Callaway 1995; 1997; Stachowicz 2001; Bruno et al. 2003).

Facilitation or positive interactions are encounters between organisms that benefit at least one of them and cause harm to neither (Bruno et al. 2003). It may be considered a type of mutualism that can occur between native species, native species and non-native species, or non-native species (Richardson et al. 2000). This mechanism may occur in two different forms: (i) direct facilitation, when a species alters the environmental conditions to favor another species (e.g., reduction in temperature and wind incidence, increase in pollination rate or propagule dispersal rate); or (ii) indirect facilitation, which occurs when there is a positive indirect effect of one species on
another (e.g., reduction in predation pressure, increased opportunities for competition refuge, reduced competitor populations) (Levine 1999; Richardson et al. 2000; Stachowicz 2001).

New interactions between species in natural ecosystems stemming from the colonization of non-native species constitute real threats to native ecosystems worldwide (Vitousek et al. 1997; Mack et al. 2000; Clavero & García Bertou 2005) and drive global biodiversity toward homogenization (McKinney & Lockwood 1999; Olden 2006). To date, the best studied causes of biodiversity decline due to the invasion of non-native species are competition and predation (Barel et al. 1985; Baltz & Moyle 1993; Lodge 1993; Richardson et al. 1995; Johnson & Padilla 1996; Kitchell et al. 1997), but positive interactions among non-native species are an important factor in invasion processes (Simberloff & Von Holle 1999; Bruno et al. 2003; O’Dowd et al. 2003; Grosholz 2005; Green et al. 2011).

In Brazil, the lake system of the Middle Doce River Basin is well-suited for studying the effects of non-native fish establishment and facilitation on other non-native species. The region has approximately 140 natural lakes, and non-native fish have been introduced into these lakes in the 1970s (Sunaga & Verani 1985). Among seven non-native fish already established, stand out the red piranha Pygocentrus nattereri (Kner 1858) and the peacock bass Cichla cf. kelberi (Latini et al. 2004). The predatory behavior of these two fishes, which places them at top positions in the food webs of local lakes, as well as their parental care behavior, may explain their successful colonization of these lakes (Latini & Petreere Jr. 2004). The other five non-native species are the oscar Astronotus ocellatus (Agassiz, 1831), the African catfish Clarias gariepinus (Burchell, 1822), the Nile tilapia Oreochromis niloticus (Linnaeus, 1758), the tambaqui Colossoma macropomum (Curvier, 1818), and the tambaqui Hoplosternum littorale (Hancock, 1828).

Hoplosternum littorale is a common catfish in most Cis-Andean South American river systems draining the northern region of Buenos Aires (Froese & Pauly 2004; Berra 2007). This species does not occur naturally in the basins of Eastern Brazil (Oliveira & Moraes Júnior 1997) and was introduced in the 1990s after the introductions of P. nattereri and C. kelberi (Latini et al. 2004), probably as a bait for fishing in the Lakes District of the Rio Doce Basin (Latini et al. 2004). Hoplosternum littorale is a benthic species that preys on invertebrates and has a broad diet (Hahn et al. 1997; Froese & Pauly 2004). Its reproductive behavior includes the construction and guarding of a floating nest by males: the floating nest protects eggs and larvae against opportunistic predators. The male guarding behavior discourages intruders and larger predators (Hostache & Mol 1998; Nico & Muench 2004). In these lakes, H. littorale is either the only non-native species in a given lake, or it co-occurs with other non-native fish, such as P. nattereri and C. kelberi (Latini et al. 2004). In all cases, H. littorale only became established after the establishment of P. nattereri and C. kelberi. Although there are no studies on the negative impacts of H. littorale on native fish, field experiments in Florida (USA) have suggested that introduced H. littorale alter the structure of macroinvertebrate assemblages (Duxbury et al. 2010).

The previous colonization by non-native fish has reduced the abundance of native species and modified the assemblage structure (α and β diversity) of those lakes (Latini & Petreere Jr. 2004; Giacomini et al. 2011). As the lakes of the studied system have few native predators, we expected lakes with non-native predators to show a strong reduction in native fish diversity (Giacomini et al. 2011) and in the abundance of native competitors of H. littorale (i.e., species that feed on invertebrates). We expected reduced antagonistic pressure on H. littorale and thus less biotic resistance to its colonization (e.g., space free of competitors), thus we tested the hypothesis that colonization by H. littorale is facilitated by the prior establishment of non-native fish. Our predictions were as follows: (i) the abundance and biomass of H. littorale are higher in lakes where it co-occurs with P. nattereri or C. kelberi than in lakes where H. littorale is the unique non-native fish; (ii) H. littorale populations co-
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occurring with *P. nattereri* and *C. kelberi* have higher condition factor, (iii) diet breadth is wider in *H. littorale* populations that co-occur with *P. nattereri* and *C. kelberi*.

**Material and Methods**

**Study area**

The Rio Doce Basin is located in southeastern Brazil and drains an area of approximately 83,500 km² (ANA 2013). Its middle portion consists of natural lake systems containing about 140 lakes formed approximately 4,000 to 10,000 years ago through tributary impoundment of the main river (Tundisi & De Meis 1985). This study was conducted at the Dionisio District (meridians 42º38'W and 48º28'W and parallels 19º41'S and 19º30'S) in the state of Minas Gerais, Brazil. The altitude varies between 236 and 515 m above sea level, and the climate is tropical with rainy summer (Nimer 1989). This region is near the Rio Doce State Park, an important protected area of the Atlantic Forest, one of the world’s biodiversity hotspots (Myers et al. 2000).

Twenty-four lakes are located in areas owned by Companhia Agrícola Florestal Santa Barbara (CAF). For this study, we selected six lakes in CAF, which were sampled bimonthly between July 2002 and May 2003, and collected six samples from each lake. Lakes were divided into two groups: (1) where *H. littorale* was the only non-native fish species (Group I, formed by Poço Redondo, Romoalda, and Timburé Lakes), and (2) where *H. littorale* co-occurs with *P. nattereri* and *C. kelberi* (Group II, formed by Águas Claras, Ariranha, and Palmeirinha Lakes). A map of the studied area, including all studied lakes, is presented in Figure 1.

**Fish sampling**

Bimonthly sampling was carried out from July 2002 to May 2003 (a total of 6 samplings, except for Palmeirinha Lake, with only five because the gillnets were stolen). Sampling involved the use of six gillnets, each with a different mesh size (15, 20, 30, 40, 50, and 60 mm between adjacent knots). The six different gillnets represented a set. For each sample at each lake, we used three sets, totaling 18 gillnets per lake (three sets x six mesh size). All the gillnets were 1.6 m in height and 10 m long, except the 60 mm mesh gillnet, which was 2 m in height and 20 m long. Gillnets were deployed near the margin that included different habitat physiognomies, which consequently ensured a representative sample of the environmental heterogeneity. Moreover, nets were deployed for three hours, covering the peak activity of fish, which occurs at approximately 18:00 h (Sunaga & Verani 1985).

Figure 1 – Satellite image of the study area. In the bottom right, the location of the study region in South America. The studied lakes are numbered in the figure as Group I (Tito – Timburé; Po – Poço Redondo, and Ro – Romoalda) in white, where the catfish *H. littorale* is the only non-native fish species, and Group II (Pa – Palmeirinha, Ag – Águas Claras, and Ar – Ariranha) in black, where *H. littorale* co-occurs with *P. nattereri* and/or *C. kelberi*.

Gillnets were set between 16:00 h and 19:00 h (dusk), totaling 3 daily hours of sampling and a total effort of 160 m²h⁻¹ [5 gillnets x 10 m x 1.6 m x 3 sets / 3 h] + (1 gillnet x 20 m x 2 m x 3 sets / 3 h)] per sample, and a sampling effort of 960 m²h⁻¹ for all six samples (160 m²h⁻¹ per each sample x 6 samples). We collected only five samples in Palmeirinha Lake, with a total sampling effort of 800 m²h⁻¹. Our total sampling effort was 5600 m²h⁻¹.

**Diet analysis**

All fish sampled were put in water with ice and later fixed in 10% formalin. Total length and weight were measured in the laboratory of
Parque Estadual do Rio Doce. For the diet analysis, we randomly selected 410 individuals, including 41 of *H. littorale*. Each individual was gutted, and the contents were identified and counted using a stereoscopic microscope. All items were weighted (g) using a precision balance. All analyses were performed at the Laboratory of Museu Zoologia João Moojen, at the Universidade Federal de Viçosa, MG, Brazil.

**Environmental variables**

Differences in the structure and composition between the local assemblages can be the result of local environmental conditions. Therefore, we assessed four environmental variables: the lake area (ha) and lake perimeter (m), both measured using GIS and remote sensing image processing system called Spring (available on: http://www.dpi.inpe.br/spring/english/) and a satellite image of the study region; and oxygen concentration (mgL\(^{-1}\)) and water turbidity (ntu – nephelometric turbidity units) obtained using specific electronic portable equipment.

**Statistical analysis**

We used a repeated measures ANOVA (Zar 1999) to test differences in abundance and biomass of *H. littorale* populations in the lakes where was the only non-native fish species (Group I) and compared to lakes where co-occurred with *P. nattereri* or *C. kelberi* (Group II) and the control temporal effects. In this analysis, the total abundance and biomass of *H. littorale* in each lake at each sampling were the dependent variables, and the lake group was the independent variable with two levels (with and without *P. nattereri* and *C. kelberi*). The homogeneity of variance was tested; and whenever necessary, we used log transformation to meet the assumptions required for the use of parametric statistics.

The condition factor is an estimator of the physiological status of fish and the relative well-being of fish populations (Bolger & Connoly 1989; Pope & Kruse 2007). We estimated the alpha and beta parameters by fitting linear regressions between logarithmic transformations of the standard length and weight (continuous predictor) to assess whether the *H. littorale* populations between the lake groups (categorical predictor) show differences in their condition factor. We then checked for differences in the condition factor between the lake groups using an ANCOVA (Zar 1999).

We used the Smith’s measure (Smith 1982) to obtain the *H. littorale* diet breadth in the two groups:

\[ FT = \sum_{j=1}^{R} \left( \frac{p_j}{a_j} \right) \]

where *FT* is the Smith’s measure of diet breadth, *p*\(_j\) is the proportion of individuals found in or using resource state *j*, *a*\(_j\) is the fraction of total resources constituted by resource *j* (expressed in weight), and *R* is the total number of possible resource states.

We used a 95% confidence interval, as suggested by Krebs (1999), to compare the *H. littorale* diet breadth between the two groups:

\[ CI_{95\%} = \sin \left( x \pm \frac{1.96}{\sqrt{y}} \right) \]

where *x* is the arcsine (*FT*) and *y* is the total number of individuals studied \((\sum N_j)\). Ontogenetic development is an important factor that influences the diet of fish (Gerking 1994). Therefore, we performed a *t*-test to assess whether the *H. littorale* individuals used for the diet characterization have different body sizes (standard length) between the groups of lakes. Lastly, we tested whether the environmental conditions were different between the lake groups using a non-parametric multivariate analysis of variance (MANOVA) (Anderson 2001). For all the statistical tests, the significance level was set at *α=0.05*, and the statistical analyses were performed in the software R (R Development Core Team 2008).

**Results**

We sampled 893 individuals belonging to 18 fish species, with a total biomass of 103.37 kg. The abundance and biomass of *Hoplosternum littorale* was 125 individuals and 14.145 kg, respectively, showing no homogeneity of variance (Levene’s test: *p<0.05*). Thus, data were log transformed. We removed sampling months was heteroscedastic from our dataset which corresponded to *H. littorale* biomass in the first sample and *H. littorale* abundance in the fourth sample. Only
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one individual of *H. littorale* was sampled in Águas Claras Lake during our study; then we decided to remove this lake from our analysis. Table 1 shows the values of biomass and abundance of non-native and native fish sampled in the lakes.

Table 1 – Fish species sampled in six lakes of the middle Doce River Lake system in Dionisio District, Minas Gerais State, southeastern Brazil. We used gillnets to sample fish bimonthly from July 2002 through May 2003. Body size range (standard length), total abundance, and biomass (kg) are presented. Non-native species are identified by an X.

| Species | Non-native | Standard length (cm) | Sample size | Total fish biomass |
|---------|------------|----------------------|-------------|-------------------|
| **Order Characiformes** |
| Family Anostomidae |
| *Leporinus steindachneri* Eigenmann, 1907 | 8.6-34.0 | 44 | 7.191 |
| Family Characidae |
| *Astyanax* sp. | 4.5-14.0 | 168 | 2.315 |
| *Moenkhausia doceana* (Steindachner, 1877) | 5.0-8.6 | 15 | 0.128 |
| *Oligosarcus solitarius* Menezes, 1987 | 8.2-19 | 115 | 2.620 |
| *Pygocentrus nattereri* Kner, 1858 | X | 7.5-23.5 | 110 | 15.950 |
| Family Curimatidae |
| *Cyphocharax gilberti* (Quoy & Gaimard, 1824) | 6.8-18.0 | 47 | 2.598 |
| Family Erythrinidae |
| *Hoplias malabaricus* (Bloch, 1794) | 10.5-37.0 | 115 | 23.450 |
| Family Prochilodontidae |
| *Prochilodus vimboides* Kner, 1859 | 7.5-41.0 | 58 | 23.380 |
| **Order Siluriformes** |
| Family Auchenipteridae |
| *Trachelyopterus striatulus* (Steindachner, 1877) | 10.0-19.7 | 26 | 2.396 |
| Family Callichthyidae |
| *Hoplosternum littorale* (Hancock, 1828) | X | 9.4-19.7 | 125 | 14.145 |
| Family Claridae |
| *Clarias gariepinus* (Burchell, 1822) | X | 30.5-55.0 | 3 | 3.165 |
| **Order Gymnotiformes** |
| Family Gymnototidae |
| *Gymnotus carapo* Linnaeus, 1758 | 6.2-31.0 | 9 | 0.854 |
| **Order Perciformes** |
| Family Cichlidae |
| *Astronotus ocellatus* (Agassiz, 1831) | X | 13.5 | 1 | 0.15 |
| *Cichla kelberi* Kulander & Ferreira, 2006 | X | 14.5-37.5 | 8 | 2.175 |
| Crenicichla lacustris (Castelnau, 1855) | 11.3-22.0 | 5 | 0.489 |
| *Geophagus brasiliensis* (Quoy & Gaimard, 1824) | 5.4-18.0 | 28 | 1.993 |
| Family Sciaenidae |
| *Pachyurus adspersus* Steindachner, 1879 | 21.5-22.5 | 2 | 0.405 |
| **Order Clupeiformes** |
| Family Engraulidae |
| *Lycengraulis* sp. | 6.5-15.0 | 13 | 0.115 |
Hoplosternum littorale biomass was greater in the Group II (F=41.192; df=1; p=0.023, Figure 2) and not affected by time (F=0.583; df=4; p=0.683) or by interactions between the groups of lakes and time (F=0.130; df=4; p=0.966). In Group II, we also found higher abundances of H. littorale (F=28.029; df=1; p=0.013, Figure 3). Again, the effect of time was not significant (F=1.345; df=4; p=0.309) as well as the interaction between the lake group and time (F=0.215; df=4; p=0.354). The condition factor of the two groups of lakes were not significantly different (F=1.3; df=1; p=0.25). Figure 4 illustrates the relationship between the logarithm of weight (Log W (g)) and logarithm of standard length (Log SL(cm)) in the Groups I and II lakes.

A total of 34 (83%) out of 41 H. littorale guts examined contained some measurable content, indicating the high feeding activity of this species in the lakes under study. In the absence of P. nattereri and C. kelberi (Group I), H. littorale used five different food resources (including one unidentified; Figure 5A), whereas the number of food items increased to ten (including unidentified items; Figure 5B) in the presence of these species (Group II). Smith’s measure of the diet breadth of H. littorale was also high in the Group II (Figure 6). These individuals presented a body size of about 15 cm, whose standard length values were not significantly different between the groups of lakes (t=-0.66; df=40; p=0.50). Therefore, we can reject any effect of ontogenetic development on the diet of H. littorale between lake groups. Lastly, no differences in environmental conditions were found between lake groups (F=1.127; p=0.40).
Discussion

Predation pressure by non-native species on native fish is the main driver of reduction in abundance and richness of native species and increase in the temporal variability in species composition in lakes (Latini et al. 2004; Giacomini et al. 2011). It may affect native fish assemblages and potentially provide resources to non-native fish, such as *H. littorale*. These effects may explain the higher abundance and biomass of *H. littorale* and the broader diet of this species in environments where it co-occurs with *P. nattereri* and *C. kelberi*. However, some issues need to be clarified. There is evidence that species of *Cichla* and *Pygocentrus* prey upon *H. littorale* in its native habitats (Nico & Taphorn 1988). Thus, it is possible that *C. kelberi* and *P. nattereri* are also preying on *H. littorale* in non-native habitats. Nevertheless, *H. littorale* remains were not found in gut contents of these predators in the studied lakes, which corroborates the hypothesis of facilitation.

There is a marked difference in *H. littorale* body size between lake groups (Figure 4); in other words, *H. littorale* individuals are smaller in lakes where this species is the only non-native fish. This result may indicate a possible spatial segregation between immature and mature sexual classes. Although we have not examined the reproductive biology of this species, we can assume that this type of segregation does not occur: (i) *Hoplosternum littorale* does not present reproductive migration, which can result in a spatial segregation between juvenile and adults; (ii) different studies have shown that *H. littorale* starts its reproductive period at about 8 cm standard length (Winemiller 1987; Hahn et al. 1997). All the individuals sampled in our study showed standard length above 10 cm. Therefore, it is plausible that the sampled individuals were adults.

Another explanation for the observed differences in body size between lake groups could be viewed as an antagonistic rather than facilitative process. Smaller species and/or individuals tend to suffer greater impacts of predation (Woodward & Hildrew 2002; Sinclair et al. 2003; Woodward et al. 2005) and are
frequently the first impacted by an introduced predator. In the same lakes, suggested a similar mechanism to explain a shift in the composition of native fish communities, from small native fish in non-invaded lakes to large native fish in invaded lakes (Giacomini et al. 2011). In this case, the non-native predator can select larger individuals of _H. littorale_ via predator gap limitation. Conversely, differential survival does not explain why _H. littorale_ is more abundant in lakes where it co-occurs with non-native predators; indeed, the opposite was expected.

If predation pressure from _P. nattereri_ and _C. kelberi_ are significant to the point where it reduces or excludes local native species (Latini & Petrere 2004), the question remains as to why it does not negatively affect _H. littorale_ populations. First, _H. littorale_ overlaps home range with _C. kelberi_ and _P. nattereri_ (Reis et al. 2003) and most likely already has mechanisms to avoid predation from these predator species. In contrast, native fish did not develop mechanisms to avoid predation, since predation by the congener species _C. kelberi_ and _P. nattereri_ did not occur in their evolutionary history. The native top predator in lakes of the current study area is _Hoplias malabaricus_, which is phylogenetically distant, morphologically dissimilar, and exhibits a different foraging behavior (ambush predator). Second, _P. nattereri_ and _C. kelberi_ are visually oriented, active predators that ambush their prey in daylight (Lowe-McConnell 1999). On the other hand, _H. littorale_ displays a peak activity at night (Boujard et al. 1990; 1992; Hahn et al. 1997). Thus, it is probable that these differences in activity patterns may promote non-native co-occurrence. In fact, this behavior of _H. littorale_ was reported as a strategy to avoid predation (Boujard et al. 1990). Furthermore, this strategy was also corroborated by the maintenance of native _H. malabaricus_ in lakes where _P. nattereri_ and _C. kelberi_ are also present (Latini 2001); because both species are nocturnal (Machado 2003). At last, _H. littorale_ exhibits parental care and aggressive behavior during its reproductive period (Winemiller 1987), and both biological characteristics impart success to the establishment of non-native species (Holway & Suarez 1999; Drake 2007).

The studied lakes are very similar in environmental conditions and support similar fish communities (with the exception of invaded lakes). This finding was expected because the lakes have similar geological formation and are located in the same landscape (Sugio & Kohler 1992; Perônico & Castro 2008).

Other uncontrolled factor most likely influenced the system and contributed to the observed results. However, we think that indirect facilitation is a plausible mechanism responsible for the differences found in this study. Specifically, the presence of _C. kelberi_ and _P. nattereri_ caused negative impacts on the local communities, mainly with regard to small competitors of _H. littorale_ and an increase in the temporal variability of the invaded communities (release of resources over time). With a decrease in the abundance of competitors, _H. littorale_ was provided with access to additional feeding resources (as reflected in the different diet breadth). This increase in feeding resources is most likely reflected in its greater abundance and biomass in the lakes with co-occurrence of non-native predators.

Non-native invasions cause major ecological, social, and economical problems worldwide (USBC 1998; Pimentel et al. 2001), and detailed information is important for suggesting effective global control practices (Kolar & Lodge 2001; Marchetti et al. 2004) and different Brazilian ecosystems (Pelicice 2009; Zeni & Zillier 2011). Thus, despite earlier studied pointing out to facilitation among non-native species as important for biological invasions (Bruno et al. 2003), evidence found in our study suggest that facilitation may be occurring among non-native fish in the lakes of the Rio Doce Basin, which may intensify negative ecological impacts on the aquatic ecosystem. Potential mechanics responsible for positive interactions among non-native fish species should be further investigated in experimental studies.
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