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Reduction of a native fish fauna by alien species: an example from Brazilian freshwater tropical lakes

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Abstract The consequences of introducing *Cichla* cf. *monoculus* Spix & Agassiz, *Astronotus ocellatus* (Agassiz) and *Pygocentrus nattereri* Kner into lakes in the River Doce basin, Brazil, on richness, diversity and efficiency of aquatic macrophytes as natural refugia to native fishes was investigated. Samples were taken from lakes with and without alien fishes in areas with and without aquatic macrophytes. The presence of alien fishes reduced richness and diversity of the native fish community. The refugia function, which could be attributed to the clustering of aquatic macrophytes, does not exist in these lakes probably because the alien fishes exploit such habitats for reproduction. Since introductions threaten the native fish diversity of the region, studies on regional dispersion and factors that minimise the spread of alien fishes are needed.

KEYWORDS: alien species, Brazil, habitat heterogeneity, River Doce State Park, tropical fish community.

Introduction

Stimulated by increasing food production, generation of economic benefits and recreation (Welcomme 1988), the introduction of alien fishes has caused great changes to the composition of fish fauna in many lakes, e.g. Nile perch, *Lates niloticus* (L.) into Lake Victoria in Africa (Ogutu-Ohwayo 1990). These introductions modify local ecological conditions by altering the reproduction, growth and development of native species, as well as hybridisation and introducing diseases and parasites.

In Brazil, fish translocation was common during the 1960s and 1970s, mainly from the Amazon Basin to the north-east and south-east of the country (Agostinho, Júlio & Petrere 1994; Agostinho 1996; Agostinho & Júlio 1996). The Parque Estadual do Rio Doce, an important reserve within the Atlantic Forest biome, is located in the middle River Doce, southeastern Brazil. The peacock cichlid, *Cichla* cf *monoculus* Spix & Agassiz, oscar, *Astronotus ocellatus* (Agassiz), and red piranha, *Pygocentrus nattereri* Kner, were introduced into lakes neighbouring this Park, later reaching the lakes within the reserve area (Sunaga & Verani 1985, 1987; Godinho & Formagio 1992). The introduction of these species in lakes of the Park affected the native fish community, causing the disappearance of some species and a reduction in the abundance of young individuals of others, coupled with reduction in mean weight of these individuals (Sunaga & Verani 1991; Godinho, Fonseca & Araújo 1994).

The effects of introducing these alien fishes into the lakes of River Doce State Park and the effectiveness of aquatic macrophytes as refugia for native fish species from the alien species was examined. Six lakes were sampled: three with alien fishes (experimental group) and three without (control group) and the following hypotheses were tested: (i) is there a decrease in the native species richness and diversity between these two groups of lakes as a function of the introductions? (ii) do areas with larger heterogeneity (due to the presence of macrophyte mats) serve as refugia for the native species in lakes with the alien species? (iii) are there changes in the total fish biomass and mean weight of

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native species as a function in the presence of alien species?

The hypothesis of differences in mean weight for native populations is suggested as a measure of the impact of alien species on certain native species, since young individuals of the latter could serve as food for the alien piscivorous species. Thus, a reduction in the abundance of young individuals of the native species is expected, which should result in an increase of the mean weight of the individuals in these populations.

Materials and methods

Study area

This study was conducted at River Doce State Park, located in the southeast of the State of Minas Gerais (Fig. 1). The predominant vegetation is Atlantic Forest, a biome that was regarded as the fourth most important hotspot for biodiversity on earth, based on endemism and the density of vertebrates and plants (Myers, Mittermeier, Mittermeier, Fonseca & Kent 2000). The total park area is about 35 000 ha, with altitudes varying between 236 and 515 m (Tundisi & De Meis 1985). The climate is tropical hot and semi-humid, with a rainy season in the summer and a dry season that lasts for 4–5 months in the winter. The park is bound to the east by the River Doce and to the northwest by the River Piracicaba. Some streams cross the park flowing into the River Doce. About 50 lakes make up its lacustrine system (Fig. 1), occupying 6% of its area (Godinho 1996).

Three alien species occur in the lakes of the park: the peacock cichlid, *C.* cf. *monoculus*, the oscar, *A. ocellatus* and the red piranha, *P. nattereri*. The peacock cichlid is a piscivorous species with a generalist diet (Keenleyside 1991). Once introduced, this species has great potential to cause damage to the native fish communities (Fontenele & Peixoto 1979; Welcomme 1988). The oscar is also a cichlid fish, with an omnivorous diet, feeding on fruits, insects, crustaceans and small fish. This species displays parental care and is territorial during the reproductive period (Lowe-McConnell 1999). The red piranha is a piscivorous characid fish that also feeds on shrimps and other aquatic invertebrates (Sazima & Machado 1990; Uetanabaro, Wang

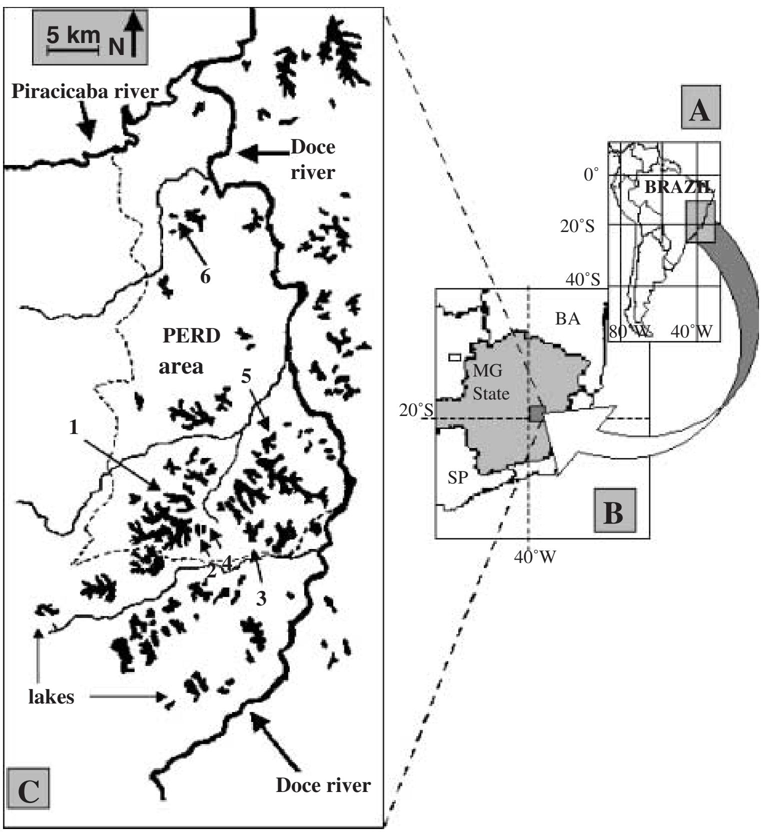

Figure 1. Location of Parque Estadual do Rio Doce in South America (A) and in southeastern Brazil (B). C shows an image of the Park. Dashed lines, River Doce (East) and River Piracicaba (West) determine the Park limits. Numbers 1–6 refer to the sampled lakes of Table 1.

Table 1. Characteristics of the six sampled lakes in River Doce State Park, Brazil. Numbers in parentheses refer to the lake positions of Fig. 1

Type of lake	Lake	Area (ha)	Latitude (S)	Longitude (W)
I. With alien species	Bonita (1)	86.04	19 °48′24″	42 °36′12″
	Gambá (2)	19.91	19 °47′22″	4 2°35′06″
	Águas Claras (3)	76.80	19 °49′05″	42 °34′21″
II. Without alien species	Gambazinho (4)	7.82	19 °49′43″	42 °35′12″
	Azul (5)	65.42	19 °44′20″	42 °31′33″
	Lagoinha (6)	7.11	19 °35′32″	42 °33′34″

& Abe 1993). During the reproductive season, this species displays territorialism as they build and protect nests in the aquatic vegetation (Lowe-McConnell 1999).

Experimental design

Samples were collected in six lakes located inside the park, where fishing is only allowed for scientific purposes. The lakes were divided in two groups: the Gambá, Águas Claras and Bonita lakes with alien fishes, and the Gambazinho, Azul and Lagoinha lakes without, constituting the control group (Table 1). These groups constituted the factor 'type of lakes' used in the factorial analyses.

The ecotype of the littoral zone of these lakes was classified (based on physical aspects) as macrophyte and forest edge areas according to De Marco & Latini (1998). The macrophyte areas are coastal areas with a smooth bathymetric profile and without a pronounced increase in depth. In these areas, the margin consists of grasses and fallen logs rarely being shaded by forest. The bathymetric profile and lack of canopy favour the development of dense clusters of macrophytes, with a dominance of *Eleocharis* sp., followed by *Salvinia* sp. and Nympheaceae.

The forest edge areas correspond to littoral areas where the bathymetric profile is steeper, with an abrupt increase in depth. In these areas, the margin is frequently shadowed by the forest, precluding the development of aquatic macrophytes. Nympheaceae species occur at greater depths. In these areas, the substratum consists of vegetation and dead leaves.

In each lake, six littoral areas were identified: three with macrophytes, regarded as possible refugia, and three as forest edge areas. Each of these areas constituted a sampling unit and these area categories were the factor habitat type. In Águas Claras Lake, three areas with macrophytes and only two forest edge areas were identified.

Fish were sampled between May and August 2000. The order of sampling of the lakes was random. The fishing effort was standardised using 13 gill nets with the same length (10 m) and height (1.6 m), but with meshes varying from 15 to 110 mm, knot to knot. The gill nets were set perpendicularly from the shoreline in a random order, maintaining a spacing of 5 m. Fishing began at 16:00 hrs and finished at 08:00 hrs. Three samples were taken from both areas comprising an effort of 12 480 m h^{-1} in each lake.

Fishes were fixed in 10% formalin. In the laboratory, specimens were identified to species using appropriate identification keys (Géry 1977; Garavello 1979; Britski, Silimon & Lopes 1999). Standard length (L_s in cm), and total weight (W in g) were recorded.

Statistical analysis

To compare species richness between the two groups of lakes, the jackknife procedure was used (Magurran 1988) based on each sample collected. For lakes with alien species, two estimates, total number of species and number of native species were obtained. This procedure presents an advantage over other richness estimators, which normally give an underestimated value for the community's richness. The jackknife procedure gives a more realistic estimate of species richness, by taking into account rare species (Krebs 1999).

Shannon and Berger–Parker diversity indices were calculated for each sampling unit (Magurran 1988). Both indices were computed for the weight data and for the total number of individuals. The Shannon index (H') considers that the individuals were randomly sampled and that all the species were represented in the same sample (Magurran 1988). The Berger–Parker index expresses the proportional importance of the most abundant species (Magurran 1988) and it is one of the more satisfactory diversity measures according to May (1975). The reciprocal of that index ($1/d$) was used so that it reflected a direct relationship with an increase in diversity. These indices were used in the factorial analyses.

To evaluate richness among the lake communities, the variance of the species richness estimated from the jackknife procedure was used, to obtain 95% confidence intervals, according to (Krebs 1999):

$$\mathrm{IC}_{95\%} = \hat{S} \pm t_\alpha \times \sqrt{\mathrm{var}(\hat{S})}, \qquad (1)$$

where $\mathrm{IC}_{95\%}$ is the 95% confidence interval, $\hat{S}$ the jackknife estimate of species richness, t_α is the Student t value for $n - 1$ degrees of freedom for the suggested α value and $\mathrm{var}(\hat{S})$ the variance of the jackknife estimate.

Two-way ANOVA was used to test the hypotheses (i)–(iii). In hypotheses (i) and (ii), one model was used to test the homogeneity of the diversity indices (H' and $1/d$) between lakes with and without alien species, and the refugia effect of macrophytes. In hypothesis (iii), this model was used to test total weight of captured fish among the factors 'type of lakes' (two levels, with and without alien species), and 'type of habitats' (two levels, with and without macrophyte mats). Thus, the additive linear model for the experimental design is:

$$Y_{ijk} = \mu + \pi_i + \gamma_j + (\pi \times \gamma)_{ij} + e_{ijk} \qquad (2)$$

where $Y_{ijk}(H'$ or $1/d)$ is the response variate, μ the overall mean, π_i the factor 'type of lake' with $i = 1, 2$, γ_j the factor 'type of habitats' with $j = 1,2$, $(\pi{\cdot}\gamma)_{ij}$ the interaction term, k the replication, and e_{ijk} a random variate supposed $N\ (0, \sigma^2)$.

Two-way ANCOVA was used to test for differences in weight measurements (W) and the standard length (L_s) of native species among lakes:

$$\ln(W_{ijk}) = \mu + \pi_i + y_j + (\pi \times \gamma)_{ij} + \beta \ln(L_{sijk}) + e_{ijk}, \qquad (3)$$

where W_{ijk} (g) is the total weight, μ the overall mean, π_i the factor 'type of lake' with $i = 1, 2$, γ_j the factor 'type of habitats' with $j = 1, 2$, $(\pi\gamma)_{ij}$ the interaction term, k the replication and L_{sijk} is the covariate coefficient of the covariate standard length, L_s (cm) and e_{ijk} is a random variate supposed $N\ (0, \sigma_2)$.

Independence among the experimental units, normality of the data and homogeneity of the variances are conditions for the use of factorial analyses. For all groups of data, asymmetry (γ_1) and kurtosis (γ_2) of the curve were analysed through comparison of the estimated values of their respective estimators g_1 and g_2 from the residual of the model ((observed value) – (expected value)), with the tabulated values in Snedecor & Cochran (1989) and D'Agostino & Tietjen (1971). Homocedasticity was tested with the Levene test when significant values were detected a square root or logarithmic transformation was applied to the data (Zar 1996). For all tests, a significance level of 5% was used.

Results

Community composition

Fish catches were restricted to the 15–60 mm mesh sizes, gill nets greater than 70 mm mesh did not capture fish. A total of 1301 individuals were caught, with 265 individuals (20.3%) showing signs of predation, as evidenced by mutilations and scars over the body while in the nets. Weights of these fish were not included and the length measurements were only used when the mutilations did not affect determination of L_s The remaining 1036 fish weighed 163 kg and were distributed amongst 14 species belonging to 13 genera and six families (Table 2). Characiformes dominated with eight species in three families.

Table 2. Fish species with diet and reproduction traits (from Godinho 1996; Lowe-McConnell 1999). Codes indicate the presence of vegetable parts (vg); invertebrates (in); sediments (sd) and fish (fs) in the diet; display of nest behaviour (nb); defense of the spawn (ds); defense of juveniles (dj) and internal fecundation (if) in the fishes reproducing in the River Doce Lakes. nr indicates fish that do not reproduce in the lakes

	Diet				Reproduction				
Species	vg	in	sd	fs	nb	ds	dj	if	nr
Family CHARACIDAE									
Astyanax taeniatus (Jenyns)	x	x		x					
Astyanax bimaculatus (Linnaeus)	x	x		x					
Moenkausia doceana (Steindachner)	x	x		x					
Oligosarkus solitarius Menezes		x		x					
Family SERRASALMIDAE									
Pygocentrus nattereri Kner	x	x		x	x	x	x		
Family PROCHILODONTIDAE									
Prochilodus vimboides Kner			x						x
Family ANOSTOMIDAE									
Leporinus steindachneri Eigenmann	x	x	x						
Family ERYTHRINIDAE									
Hoplias malabaricus (Bloch)		x		x	x	x			
Family CICHLIDAE									
Astronotus ocellatus Pellegrin	x	x		x	x	x	x		
Cichla cf. *monoculus* Spix & Agassiz		x		x	x	x	x		
Cichlasoma fascetum (Jenyns)	x	x	x		x	x	x		
Geophagus brasiliensis (Qöuy & Gaimard)	x	x	x		x	x	x		
Family SCIANIDAE									
Pachypops adspersus Steindachner		x	x						
Family AUCHNIPTERIDAE									
Parauchenipterus striatulus (Steindachner)		x		x				x	

Lakes where alien fishes were present had at most, six species of six genera and four families. These lakes always had two alien species, *C.* cf. *monoculus* and *P. nattereri*, while Águas Claras included a third species, *A. ocellatus*. The largest number of native species found in lakes with alien species was three: the trahira, *Hoplias malabaricus* (Bloch), the singing catfish, *Parauchenipterus striatulus* (Steindachner) and the curimbatá, *Prochilodus vimboides* Kner.

Species richness and diversity

Use of the confidence intervals for species richness showed that only Lake Azul had a greater richness

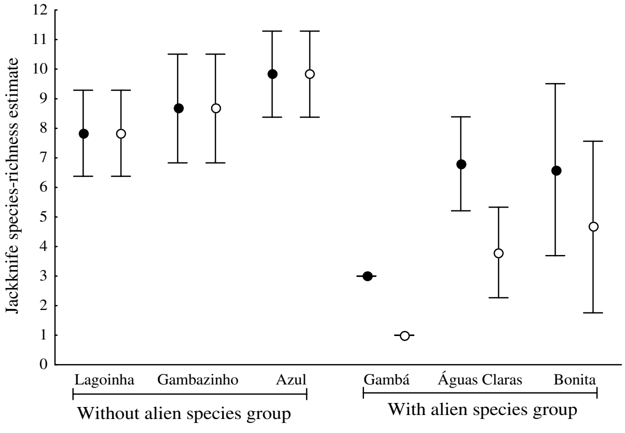

Figure 2. Evaluation of richness estimated values by jackknife between fish communities of the lakes. Full circles indicate total richness estimates and open circles indicate native richness. Bars represent 95% confidence intervals.

than lakes with alien species (Fig. 2) and that there were no differences among lakes Gambazinho, Lagoinha and Bonita. However, comparison of the second richness estimate, only for native species, showed that all the lakes with alien fish species had fewer total species than lakes without alien species. Therefore, the presence of alien species is correlated with decreasing richness of fishes.

For all the diversity indices, the normality and homocedasticity assumptions were not violated. Two-way ANOVA indicated differences between lakes with and without alien species (Table 3). There were no differences among the factors 'type of habitat' ($F_{(1,31)} = 0.060$; $P = 0.808$ for weight and $F_{(1,31)} = 0.006$; $P = 0.940$ for number of individuals) and there was no interaction between the factors 'type of habitat' and 'type of lakes' ($F_{(1,31)} = 2.590$; $P = 0.118$ for weight and $F_{(1,31)} = 2.567$ and $P = 0.119$ for number of individuals). However, for both indices, significant differences for the factor 'type of lakes' were observed ($F_{(1,31)} = 10.512$; $P = 0.003$ for weight and $F_{(1,31)} = 49.631$; $P = 0.003$ for number of individuals). These results confirm that diversity is higher in lakes without alien species, and that areas of higher heterogeneity are apparently not being used as refugia by native species.

The inverse of Berger–Parker index for weight did not reveal differences among the factors 'type of habitats' ($F_{(1,31)} = 0.026$; $P = 0.874$), 'type of lakes' ($F_{(1,31)} = 2.443$; $P = 0.128$), and there was no interaction between these two factors ($F_{(1,31)} = 1.371$; $P = 0.251$). The same index calculated for number of individuals indicated equality among the factors 'type of habitats' ($F_{(1,31)} = 1.358$; $P = 0.253$) and differences among the factors 'type of lakes' ($F_{(1,31)} = 29.980$; $P < 0.001$), as well as a significant interaction between the two factors ($F_{(1,31)} = 7.854$; $P = 0.009$; Fig. 3). These results indicate that diversity is greater in lakes without alien species, but not so in lakes with the presence of aquatic macrophythes. However, the results of the interaction suggest that in the most heterogeneous habitats there is a tendency for lower

Table 3. Results of the two-way ANOVA for the Berger–Parker and Shannon indices calculated for numbers and weight of individual fish. For the factor type of habitat, the first level is the presence and the second the absence of macrophyte mat. For the factor type of lake, the first level is the presence and the second the absence of alien species

Response variable	Source of variation	Mean Level 1	Mean Level 2	Sum of squares	df	Mean squares	F	P
Shannon for weight $r^2 = 0.29$	Habitat	0.625	0.651	0.006	1	0.006	0.060	0.808
	Lakes	0.467	0.809	1.020	1	1.020	10.512	0.003
	Interaction			0.251	1	0.251	2.590	0.118
	Residual			3.009	31	0.097		
Shannon for numbers $r^2 = 0.63$	Habitat	0.924	0.932	0.001	1	0.001	0.006	0.940
	Lakes	0.543	1.313	5.167	1	5.167	49.631	0.003
	Interaction			0.267	1	0.267	2.567	0.119
	Residual			3.227	31	0.104		
Reciprocal of Berger–Parker for weight $r^2 = 0.11$	Habitat	1.425	1.444	0.003	1	0.003	0.026	0.874
	Lakes	1.342	1.528	0.300	1	0.300	2.443	0.128
	Interaction			0.169	1	0.169	1.371	0.251
	Residual			3.813	31	0.123		
Reciprocal of Berger–Parker for numbers $r^2 = 0.56$	Habitat	1.425	1.444	0.337	1	0.337	1.358	0.253
	Lakes	1.398	2.321	7.434	1	7.434	29.980	< 0.001
	Interaction			1.947	1	1.947	7.854	0.009
	Residual			7.687	31	0.248		

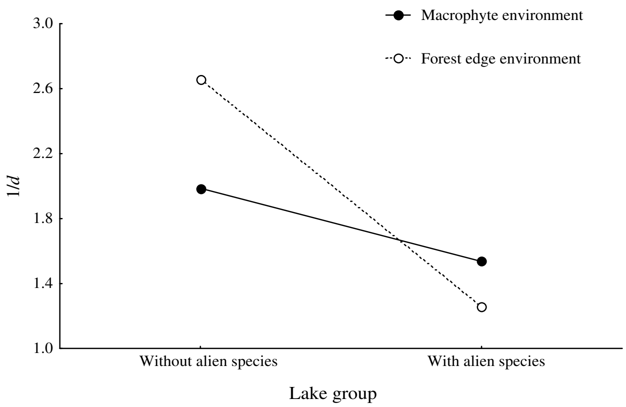

Figure 3. Interaction plot between the factors type of habitat and type of lake by the Berger–Parker index of diversity ($1/d$) calculated for numbers of individuals, compared by two-way ANOVA.

diversity with the presence of alien species, reflecting a characteristic of refugia.

Total weight and mean weight of native populations

Data for total weight of fish captured in the communities were normally distributed but did not meet the test for homoscedasticity (Levene test: $F_{(1,31)} = 4.014$; $P = 0.015$), and were thus log transformed ($F_{(1,31)} = 2.343$; $P = 0.091$).

Two-way ANOVA of transformed data with normal residuals, showed no difference in weight of fish across the factor 'type of habitats' ($F_{(1,31)} = 0.610$; $P = 0.441$). Similarly, no difference was found for the factor 'type of lakes' ($F_{(1,31)} = 0.251$; $P = 0.620$) or for the interaction between these two factors ($F_{(1,31)} = 1.671$; $P = 0.206$; Table 4). The explanation of this model was low ($r^2 = 0.07$).

Only three species of native fish were detected in lakes with alien species: the Brazilian croaker, *Pachypops adspersus* Steindachner, the singing catfish, *P. striatulus* and trahira, *H. malabaricus*. The weight data were insufficient to perform a strong test for *P. adspersus* ($n = 7$) and *P. striatulus* ($n = 14$), leaving comparisons for *H. malabaricus* ($n = 254$) only.

The relationship between weight (W) and standard length (L_s) for *H. malabaricus* was not linear, but it could be made so with a log–log transformation. In the exploratory application of Eq. (2) outliers were detected, even after successive removals. The conclusions, however, remained the same. As there is not a ready equivalent non-parametric test for the ANCOVA, the first result was accepted, treated as a strong one, even though asymmetric results and significant kurtosis were detected.

Two-way ANCOVA revealed that habitat complexity ('type of habitats') did not affect the weight of *H. malabaricus* ($F_{(1,250)} = 0.002$; $P = 0.969$). However, the presence of alien species ('type of lakes') affected it ($F_{(1,250)} = 6.629$; $P = 0.011$), even with a difference of just 6 g. The interaction between the factors 'type of habitats' and 'type of lakes' did not exert an effect on the weight of *H. malabaricus* ($F_{(1,250)} = 1.308$; $P = 0.254$). The covariate L_s was significant, as expected in the weight/length relationship ($F_{(1,250)} = 42{,}499$; $P < 0.001$). The factors and covariate explained 82% of the model (Table 5).

Discussion

Effects of the alien fishes on the local fish community

The presence of alien species in lakes of the River Doce State Park is correlated with reduced richness of the local fish community. This agrees with ecological studies in several parts of the world that focus on the invasion of reservoirs by alien species (Ricciardi, Neves & Rasmussen 1998). Taken together, such studies indicate a non-random pattern in the response of communities faced with invasion by alien species.

Behavioural relationships between native and alien species can be important in explaining the success of biological invasions (Probert & Litvaitis 1996; Holway & Suarez 1999). Parental care and predatory behaviour

Table 4. Results of the two-way ANOVA for total weight of fish caught. For the factor type of habitat, the first level is the presence and the second the absence of macrophyte mat. For the factor type of lake, the first level is the presence and the second the absence of alien species

Response variable	Source of variation	Mean (g) Level 1	Mean (g) Level 2	Mean	df	Mean square	F	P
Total weight $r^2 = 0.07$	Habitat	3810	4586	313.58	1	313.58	0.610	0.441
	Lakes	4442	3944	129.15	1	129.15	0.251	0.620
	Interaction			859.49	1	859.49	1.671	0.206
	Residual			15943.36	31	514.30		

Table 5. Results of the two-way ANCOVA for weight differences ln(W) for the trahira *H. malabaricus* utilising the standard length (L_s) as the covariate. For the factor type of habitat, the first level is the presence and the second the absence of macrophyte mat. For the factor type of lake, the first level is the presence and the second the absence of alien species. The adjusted mean values were back calculated by natural exponentiation

Response variate	Source of variation	Mean (g) Level 1	Mean (g) Level 2	Sum of squares	df	Mean squares	F	P
ln(W), W = individual trahira weight, $r^2 = 0.82$	Habitat	226.5	224.2	< 0.001	1	< 0.001	0.002	0.969
	Lakes	230	224	0.562	1	0.562	6.629	0.011
	L_s			3603.1	1	3603.1	42.499	< 0.001
	Interaction			0.111	1	0.111	1.308	0.254
	Residual			21.195	250	0.085		

are two ecological characteristics of the alien species of this study (Lowe-McConnell 1999). The parental care may increase the competitiveness of these species and the predatory behaviour put the alien fishes on top of the food web in these lakes. The absence of these characteristics in the populations of the native species, indicating insufficient anti-predatory mechanisms as seen in Table 2, where the traits *cn*, *ds*, *dj*, *if*, are not possessed by native species, except *H. malabaricus*, suggesting that the presence of alien species is the precursor of local extinction of the native populations. It is expected that lakes invaded by alien species would have a decrease in richness and diversity of their fish fauna as evident in Figure 2 and Table 3, although in Lake Victoria with a reduction of the stocks of the alien Nile perch the original fauna is resetting itself (Mkumbo, Ezekiel, Budeba & Cowx 2002).

Hoplias malabaricus is the only native species that is still able to persist in the invaded lakes. Its persistence is probably linked to its prey-ambush foraging behaviour and strong territoriality during the reproductive season (Paiva 1974). Its persistence in disturbed habitats is also evident by the similarity in the mean weight of its populations among lakes with and without alien species, an unexpected pattern, if the young were rare in the lakes with the alien species due to its preferential predation. The current analysis indicated a significant difference of just 6 g among the mean weights in lakes with alien species (230 g) and without (224 g). This small difference, albeit statistically significant, has no practical meaning. Furthermore, the log-transformation resulted in a compression of the data, thus decreasing the variance.

Although the alien species reduced richness and the diversity of the native fish community, the total weight of captured fish was not reduced in the lakes with aliens. This reflects a decrease of the energy lost in the food web due to the loss of trophic levels in the community and, consequently, to the reduction of the sum of energy lost in the transfers among the existing levels. This may be exemplified by the Nile perch in Lake Victoria: between the 1980s and 1990s the total catch increased five times and the Nile perch catch contributed over 70% of total landings; but in the mid-1990s this dominant species showed signs of decline, due to the intense fishing pressure and use of illegal gears (Mkumbo *et al.* 2002).

If a native fish population is not competitive or possess an efficient anti-predatory mechanism, its chances of persisting in invaded communities, before the presence of the alien species, can be linked to its ability of using refugia inside the lakes. An area of higher heterogeneity inside aquatic systems often reduces the effectiveness of predators and strong competitors (Power, Marks & Parker 1992) and increases the persistence of prey species and weak competitors (Ross 1991). Although there is a tendency in the presence of alien species, towards a smaller reduction in diversity in areas with macrophytes compared with areas of forest edge (Fig. 3), the diversity and weight of the species is the same between these two areas.

Consequently, in the lakes with alien species, the most heterogeneous habitats do not apparently serve as refugia for the native fish populations. These facts suggest that the importance of macrophyte mats as refugia to native fishes should be related with bionomics and behaviour of native and alien species that comprise the impacted community. If an alien species efficiently uses these mats, e.g. *P. nattereri*, there would be a smaller chance for a native species, e.g. the chameleon cichlid, *Cichlasoma facetum* (Jenyns), to efficiently use the same area as refugia.

Perspectives for the fish community of middle River Doce Basin

The reduction in the regional fish community is still not fully understood: the group of streams that cross the park and the channels that drain excess water during the rainy season, connect the lakes and may allow a temporary connection that may facilitate the dispersion of aquatic organisms. This connection between lotic and lentic habitats seems to be the main factor responsible for the invasion of those lakes by alien species on a regional level. This is evident from the presence of alien species in at least 67% ($n = 45$) of the lakes in the park. Thus, the occurrence of alien species in the lakes of the area has increased and consequently the regional fish diversity has declined. It is concluded that the dispersion of alien species is not only restricted to some lakes of the park and their neighbouring habitats, but it is affecting the maintenance of the whole fish community of the valley of the middle River Doce.

To understand fully how alien species affect the native fish community of the area, information is needed on their dispersion within and between lakes and streams to formulate the necessary measures to conserve the native fish community in areas free of invaders.

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References

Agostinho A.A. (1996) O lado oculto da introdução de peixes. *Boletim Informativo da Abrapoa* **7,** 9–11.

Agostinho A.A. & Júlio H.F. (1996) Ameaça ecológica: peixes de outras águas. *Ciência Hoje* **21,** 36–44.

Agostinho A.A., Julio H.F. & Petrere M. Jr. (1994) Itaipu Reservoir (Brazil): impacts of the impoundment on the fish fauna and fisheries. In: I.G. Cowx (ed.) *Rehabilitation of Freshwater Fisheries*. Oxford: Fishing News Books, Blackwell Science, pp. 171–184.

Britski H.A., Silimon K.Z.S. & Lopes B.S. (1999) *Peixes do Pantanal – Manual de identificação*. Corumbá: Embrapa CPAP.

D'Agostino R.B. & Tietjen G.L. (1971) Simulation probability points of b_2 for small samples. *Biometrika* **58,** 669–672.

De Marco P.J. & Latini A.O. (1998) Estrutura de guildas e riqueza de espécies em uma comunidade de larvas de Anisoptera (Odonata). In: J.L. Nessimian & A.L. Carvalho (eds) *Ecologia de Insetos Aquáticos*. Rio de Janeiro: PPGE-UFRJ, Vol. 5, pp. 101–112.

Fontenele O. & Peixoto J.T. (1979) Apreciação sobre os resultados da introdução do tucunaré comum *Cichla ocellaris* (Bloch & Scheider, 1801), nos açudes do Nordeste Brasileiro, através da pesca comercial. *Boletim Técnico do Departamento Nacional de Obras contra a Seca* **37,** 109–134.

Garavello J.C. (1979) Revisão Taxonômica do Gênero *Leporinus* SPIX, 1829 (Ostariphusi, Anostomidae). MSc Thesis, Instituto de Biociências da Universidade de São Paulo, 102 pp.

Géry J. (1977) *Characoids of the World*. Neptune City: T F H Publication Inc. Ltd, 403 pp.

Godinho A.L. (1996) *Peixes do Parque Estadual do Rio Doce*. Belo Horizonte: Instituto Estadual de Florestas/ Universidade Federal de Minas Gerais, 32 pp.

Godinho A.L. & Formagio P.S. (1992) Efeitos da introdução de *Cichla ocellaris* e *Pygocentrus* sp. sobre a comunidade de peixes da Lagoa Dom Helvécio. *Encontro Anual de Aqüicultura de Minas Gerais* **10,** 93–102.

Godinho A.L., Fonseca M.T. & Araújo M.L. (1994) The ecology of predator fish introductions: the case of Rio Doce valley lakes. In: R.M. Pinto-Coelho, A. Giani & E. von Sperling (eds) *Ecology and Human Impact on Lakes and Reservoirs in Minas Gerais with Special Reference to Future Development and Management Strategies*. Belo Horizonte: SEGRAC, pp. 77–83.

Holway D.A. & Suarez A.V. (1999) Animal behavior: an essential component of invasion biology. *Trends in Ecology and Evolution* **14,** 328–330.

Keenleyside M.H.A. (1991) *Cichlid Fishes, Behaviour, Ecology and Evolution*. London: Chapman & Hall, 378 pp.

Krebs C.J. (1999) *Ecological Methodology*. Menlo Park: Benjamim/Cummings, 620 pp.

Lowe-McConnell R.H. (1999) *Estudos Ecológicos de Comunidades de Peixes Tropicais*. São Paulo: Editora da Universidade de São Paulo, 534 pp.

Magurran A.E. (1988) *Ecological Diversity and its Measurement*. London: Cambridge University Press, 179 pp.

May R.M. (1975) Patterns of species abundance and diversity. In: M.L. Cody & J.M. Diamond (eds) *Ecology and Evolution of Communities*. Cambridge: Harvard University Press, pp. 81–120.

Mkumbo O.C., Ezekiel C., Budeba Y.L. & Cowx I.G. (2002) Analysis of exploitation patterns for Nile perch, *Lates niloticus*, in Lake Victoria. In: I.G. Cowx (ed.) *Management and Ecology of Lake and Reservoir Fisheries*. Oxford: Blackwell Science, pp. 84–95.

Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403,** 853–858.

Ogutu-Ohwayo R. (1990) The reduction in fish species diversity in lakes Victoria and Kyoga (East Africa) following human exploitation and introduction of non-native fishes. *Journal of Fish Biology* **37,** 207–208.

Paiva M.P. (1974) *Crescimento, Reprodução e Alimentação da Traíra Hoplias malabaricus Bloch, no Nordeste Brasileiro*. Fortaleza: Imprensa Universitária da Universidade Federal do Ceará, 32 pp.

Power M.E., Marks J.C. & Parker M.S. (1992) Variation in the vulnerability of prey to different predators – community-level consequences. *Ecology* **73,** 2218–2223.

Probert B.L. & Litvaitis J.A. (1996) Behavioral interactions between invading and endemic lagomorphs: implications for conserving a declining species. *Biological Conservation* **76,** 289–295.

Ricciardi A., Neves R.J. & Rasmussen J.B. (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* **67,** 613–619.

Ross S.T. (1991) Mechanisms structuring stream fish assemblages; are there lessons from introduced species? *Environmental Biology of Fishes* **30,** 359–368.

Sazima I. & Machado F.A. (1990) Underwater observations of piranhas in western Brazil. *Environmental Biology of Fishes* **28,** 7–31.

Snedecor G.W. & Cochran W.G. (1989) *Statistical Methods*. 8th edn. Ames: The Iowa State University Press, 503 pp.

Sunaga T. & Verani J.R. (1985) Preliminary report of comparative study on fish community of the Rio Doce Valley lakes. In: Y. Saijo & J. G. Tundisi (eds) *Limnological Studies in Rio Doce Valley Lakes and Pantanal Wetland, Brazil*. Vol. 1, Nagoya: Nagoya University Press, pp. 167–174.

Sunaga T. & Verani J.R. (1987) Second report of comparative study on fish community of the Rio Doce Valley lakes. In: Y. Saijo & J. G. Tundisi (eds) *Limnological Studies in Rio Doce Valley Lakes and Pantanal Wetland, Brazil*. Vol. 2, Nagoya: Nagoya University Press, pp. 129–135.

Sunaga T. & Verani J.R. (1991) The fish communities of the lakes in Rio Doce Valley, Northeast, Brazil. *Verhandlungen der Internationalen Vereinigung für Theoretiche und Angewandte Limnologie* **24,** 2563–2566.

Tundisi J.G. & De Meis M.R.M. (1985) Geomorphology and limnological processes at the Middle Rio Doce Valley. In: Y. Saijo & J.G. Tundisi (eds) *Limnological Studies in Rio Doce Valley Lakes and Pantanal Wetland, Brazil*. Vol. 1. Nagoya: Nagoya University Press, pp. 11–17.

Uetanabaro M., Wang T. & Abe A.S. (1993) Breeding behavior of the red-bellied piranha *Pygocentrus nattereri* in nature. *Environmental Biology of Fishes* **38,** 369–371.

Welcomme R.L. (1988) International introductions of inland aquatic species. *FAO Fisheries Technical Papers* **294,** 1–318.

Zar J.H. (1996) *Biostatistical Analysis*. 3rd edn. New Jersey: Prentice Hall Inc, 662 pp.