

## Habitat preference of freshwater snails in relation to environmental factors and the presence of the competitor snail *Melanoides tuberculatus* (Müller, 1774)

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*Our objective is to evaluate the habitat preference of freshwater snails in relation to environmental factors and the presence of the competitor snail Melanoides tuberculatus. In the first phase, snails were collected at 12 sites. This sampling sites presented a degree of organic input. In the second phase 33 sampling sites were chosen, covering a variety of lotic and lentic environments. The snail species found at Guapimirim, state of Rio de Janeiro, displayed a marked habitat preference, specially in relation to the physical characteristics of each environment. Other limiting factors for snail distribution at the studied lotic environments were the water current velocity and the amount of organic matter, mainly to Physa marmorata, M. tuberculatus, and Biomphalaria tenagophila. The absence of interactions between M. tuberculatus and another snails could be associated to the distinct spatial distribution of those species and the instability of habitats. This later factor may favor the coexistence of M. tuberculatus with B. glabrata by reduction of population density. In areas of schistosomiasis transmission some habitat modification may add to the instability of the environment, which would make room for the coexistence of M. tuberculatus and Biomphalaria spp. In this way, some of the usual measures for the control of snail hosts would prevent the extinction of populations of Biomphalaria spp. by M. tuberculatus in particular habitats.*

Key words: *Melanoides tuberculatus* - *Melanoides tuberculata* - *Biomphalaria* - habitat preference - schistosomiasis - competition

The thiarid snail *Melanoides tuberculatus* Müller, 1774 (syn = *Melanoides tuberculata*) is now distributed in all Neotropical region. It was reported for the first time in Brazil in 1984 (Vaz et al. 1986). Several biological control programmes using *M. tuberculatus* as competitor of the snail intermediate hosts of *Schistosoma mansoni* (Sambon 1907) have been performed in the Caribbean area (Pointier & Jourdan 2000). The mechanisms of competition between *M. tuberculatus* and *Biomphalaria* spp. are not yet understood, but the competition for food probably occurs because these snails have a similar diet, including fine detritus and epiphytic algae (Madsen 1992). *M. tuberculatus* is capable to reach high densities, hence competition for space is also possible (Freitas & Santos 1995). However, the outcome of the interactions between *M. tuberculatus* and *Biomphalaria* spp. seems to be related to the habitat type where both species occur. In a former study in Kenya (Mkoji et al. 1992), no evidence was found of negative effects due to the presence of *M. tuberculatus* on *Biomphalaria* spp. populations. In Brazil, *M. tuberculatus* has spread over several localities as a result of successive accidental introduction associated with fishfarms (Vaz et al. 1986). However, there are few reports of interaction between *M. tuberculatus* and *Biomphalaria* spp. In Sumidouro, state of Rio de Janeiro, Brazil, popula-

tions of *B. glabrata* (Say 1818) naturally infected by *S. mansoni* have been monitored in several habitats, as part of an eco-epidemiological study of schistosomiasis (Giovanelli et al. 2001). After the invasion of *M. tuberculatus* in an irrigation channel, the population of *B. glabrata* suffered the greatest and more permanent impact observed during the five years of monitoring (Giovanelli et al. 2004).

The impact of *M. tuberculatus* on other aquatic macroinvertebrate species is also unknown. In French Antilles, Pointier and Delay (1995) did not observe any type of impact of that species on the native molluscan fauna.

So, the study of the biology of *M. tuberculatus* and its interaction with the native molluscan fauna is essential for the evaluation of the potential and risks of the use of *M. tuberculatus* in biological control programs of intermediate host snails of medical and veterinary importance.

Surveys of macroinvertebrate assemblages on Guapimirim, state of Rio de Janeiro, Brazil revealed that there is a large variety of aquatic environments in that municipality, displaying different degrees of anthropic impact (Buss 2002). Besides, a survey of the molluscan fauna of Guapimirim revealed a high species diversity, including two species acting as intermediate hosts for *S. mansoni* and one species acting as intermediate host for *Fasciola hepatica* (Linnaeus 1758) (Thiengo et al. 1998).

The start point of this study was the observation that *M. tuberculatus* occurred most frequently in lotic habitats. Based on that finding, a search for possible factors

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that could explain the distribution of *M. tuberculosis* and other snail species in lotic environments was made. At first, chemical and environmental factors of the water in lotic areas were analyzed. Then, an analysis of the distribution of snails in different habitats was made, in order to evaluate if the mollusk species in each habitat would be susceptible to some kind of interaction with *M. tuberculosis*.

#### MATERIALS AND METHODS

**Study area** - Guapimirim (22°32'S, 42°58'W) is a municipality on the border of the Serra dos Órgãos, a mountain chain in the state of Rio de Janeiro, Brazil. This area is influenced by orographic rains and mean annual rainfall averages 2500 mm. A wet season occurs from October to March (more than 200 mm month<sup>-1</sup>), and a dry season occurs from June to August (less than 100 mm month<sup>-1</sup>). Its most important water body is Guapimirim river, whose drainage basin is also formed by Corujas, Bananal, Soberbo, and Iconha streams. At the stream portions near the mountain base, the border vegetation is dense with predominance of Atlantic Forest species. In contrast, at low altitude portions, the landscape is composed by the inundation plains of the Guapimirim river, occupied by grazing land, agricultural areas, and human settlements.

**Relative abundance of freshwater snails in lotic habitats – First phase** - The sampling sites were chosen based on the preliminary observation that *M. tuberculosis* was most frequently encountered in lotic environments. The

study included 12 sites on five tributaries of the Guapimirim river (Fig. 1). The following sampling sites were chosen: three in Soberbo stream (S1, S2, S3), three in Bananal stream (B1, B2, B3), two in Caneca Fina stream (CF1, CF2), two in Iconha stream (I1, I2), one in Corujas stream (CJ), and one in an urban portion of a stream subjected to high anthropic impact (CV). The sampling sites were chosen to represent an environmental gradient related to land use, input of organic sewage, and hydrological characteristics. The sites S1, B1, CF1, and I1 are located in areas of high environmental integrity, with the presence of woods along the stream border and few or no sewage inflow. The remaining sites present a gradient of environmental integrity, with the occurrence of sewage inflow and accentuated deforestation along the stream margins. The site CV has rectified margins and receives a great amount of organic sewage input.

Relative abundance of snails was estimated for the 12 sites using the method of Olivier and Schneidermann (1956). In each site snails were captured with a long metallic scoop with 4 mm mesh, moving one step every scoop, covering the length of 30 m for a 20 min period. In the laboratory the larger snails of each sample were dissected under a stereomicroscope for identification.

The samples were made at the dry period (June 2001), the beginning of rainy period (October 2001) and at the end of the rainy period (February 2002).

**Qualitative analyses of freshwater snails communities – Second phase** - Thirty three sampling points were

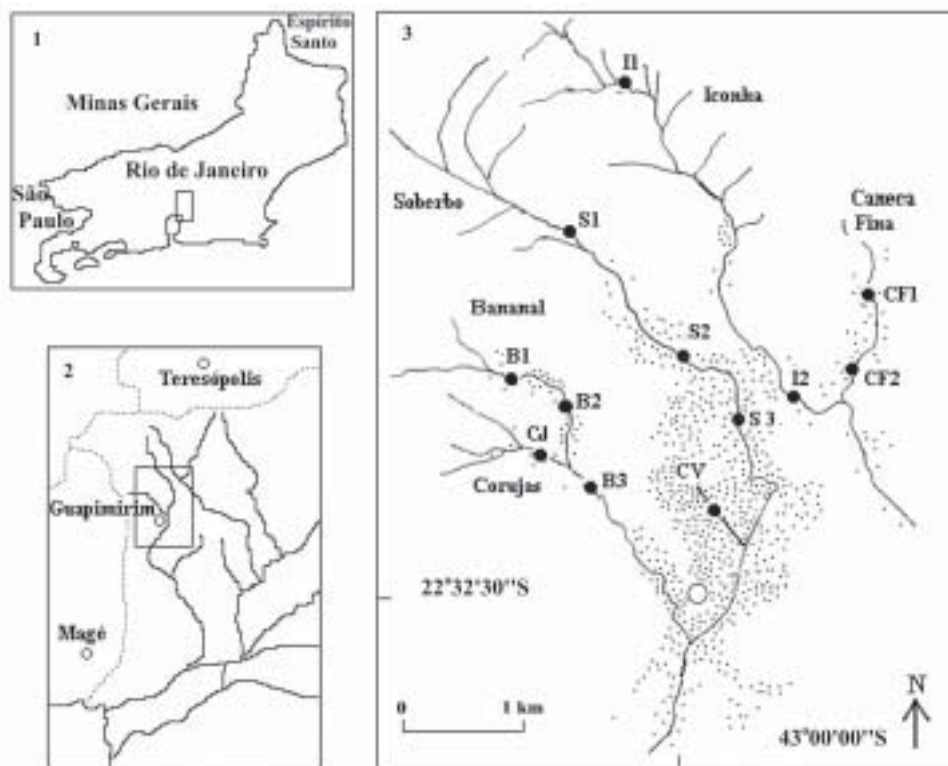


Fig. 1: section of the Guapimirim river basin, state of Rio de Janeiro, indicating the sampling sites of the first phase. The open circle indicate the downtown of Guapimirim. Dots represent buildings. The sampling sites of the second phase were mainly distributed along the Guapimirim river basin, in the lowland and near to the urban area (downtown). Map adapted from Buss et al. (2004).

chosen, covering a variety of lotic and lentic environments. The sampling sites presented variation in relation to sewage input and physical characteristics. However, most of the selected habitats presented high to intermediate degrees of anthropic impact. The number of sampling sites at each of the available habitats was chosen in order to represent the proportion of each habitat in the locality: channels (15 stations), streams (8 stations), artificial ponds (4 stations), marshes (4 stations), lake (1 station), and pool (1 station). One sampling was made in each site at the dry period of 2003. The sampling sites were mainly distributed along the Guapimirim river basin, in the lowland and near to the urban area (Fig. 1).

In each site, the snails were captured using the same methodology applied in the first phase. Only qualitative sampling were made at this stage. The snails were identified at the higher taxonomic level possible for each taxon: species for *Biomphalaria* Preston, 1910, *Melanooides* Olivier, 1804, *Physa* Draparnaud, 1801, and *Lymnaea* Lamarck, 1799; genus for Pomacea Perry, 1810 and *Drepanotrema* Crosse & Fischer, 1880; and family for Ancyliidae.

**Environmental variables** - In the first phase, water was sampled and frozen in order to measure physical and chemical variables in laboratory:  $\text{NH}_4\text{-N}$ ,  $\text{NO}_2\text{-N}$ ,  $\text{Cl}^-$ , Mg, Ca, pH, alkalinity and hardness. Further samples of water were performed to measure bacteriological parameters (total coliforms and faecal coliforms) using the filter membrane method (Standard Methods Organization 1985). In lotic habitats, channel morphology was evaluated by measuring cross-sectional widths and depths. Current velocity was taken by timing a floating object over a 2 m stretch of the stream with a chronometer. Canopy cover and the percentage of emergent, submerged and floating aquatic vegetation were estimated visually in each sampling site. In the second phase the same variables were taken, except the current velocity and nitrate series. At this phase, width and depths were associated by multiplying one by another.

**Data analysis** - In the first phase, the snail abundance and environmental parameters were the mean value estimated for the three sampling period. A principal component analysis (PCA) was performed with a variance-covariance matrix, to evaluate the relationship between the sampling stations and the variation of the hydrological and physico-chemical parameters of the stream stretch. The effects on snails of hydrological and chemical parameters were tested by stepwise multiple regression. The dependent variables were the mean abundance of snails estimated by the Olivier and Schneidermann method.

The canopy cover and aquatic vegetation were a percentage, hence it was arcsin-square root transformed before the analyses. The other variables were log-transformed to reduce discrepancies between variances and non-linear relationships between variables (Sokal & Rohlf 1995).

In the second phase, a canonical correspondence analysis (CCA) was performed between the hydrological and chemical factors in the sampling station matrix and the qualitative data of snail species. The association between pairs of species was tested through a chi-square

test at 0.05% significance level. In this later analysis only samples with at least one snail was considered.

## RESULTS

**Relative abundance of freshwater snails in lotic habitats – First phase** - At the samplings made in lotic environments during the first phase, the following species were found: *M. tuberculatus*, *P. marmorata* Guilding, 1828, and *B. tenagophila* (Orbigny 1835). The highest abundance of *M. tuberculatus* was found in the Corujas stream (209 specimens) and in the CV site (159 specimens), both at the beginning of the rainy period. *P. marmorata* presented its higher abundance in the CV site during the dry season (326 specimens). In all other sampling periods and sites, the abundance of *P. marmorata* was always bellow 68 individuals. The mean abundance of this species at the 12 sites was also small (Fig. 2). *B. tenagophila* presented its higher abundance in the CV site during the dry season (June 2001). The mean abundance of *B. tenagophila* was very small (Fig. 2). *M. tuberculatus* and *P. marmorata* were found in eight of the 12 sampling sites, at least in one of the sampling periods. *B. tenagophila* was found in only three sampling sites. The mean abundance of all three species was drastically reduced during the rainy season in February 2002 (Fig. 2).

The results from PCA for sites are presented in Fig. 3A. The first axis (79.2% of the variance explained; eigenvalue = 5.80) separated the sampling sites in relation to their degree of environmental integrity. It was possible to recognize three groups: the first group was formed by the sites with high environmental integrity (I1, B1, CF1, S1); the second group was formed by the sites with intermediate degrees of environmental integrity (CJ, B2, I2, B3, S3, CF2, S2), and the third group was formed only by the site CV, whose environmental integrity is very low. In the first group, no snails were found; in the second group, the snail abundance was variable and the third group displayed the higher snail abundance (Fig. 3A). The first eigenvalue was significant according to the broken-stick model. The eigenvalue associated to the second axis (13.8% of the variance explained; eigenvalue = 1.01) was not significant according to the broken-stick model.

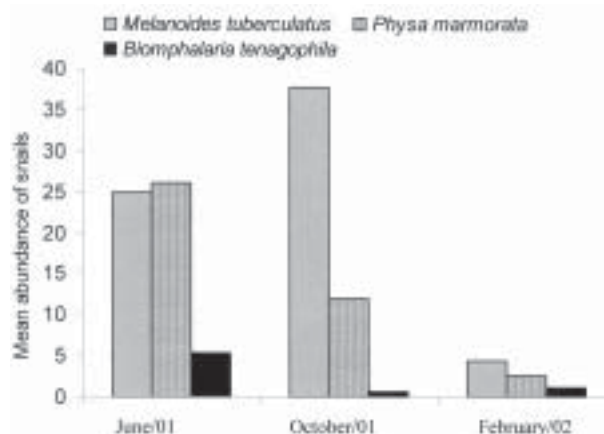


Fig. 2: mean abundance of snails collected at 12 sites in Guapimirim river basin.

The results from PCA for environmental variables are presented in Fig. 3B. The first axis (92.9% of the variance explained; eigenvalue = 77.2) separated the environmental variables in relation to the degree of organic pollution and channel morphology (mean width and mean velocity). The proportion of variance explained by second axis was low (5.3%) and the eigenvalue for this axis (4.4) was not significant according to the broken-stick model. In the site plot, the environmental variables associated with organic pollution were mainly located at the left side. The opposite was observed for the variables associated with channel morphology. This matched the sites distribution related to pristine and polluted groups (Figs 3A, B).

The regression model selected in the stepwise regression using the abundance of *M. tuberculatus* included the chlorid concentration and faecal coliforms (75.8% of variance explained). The regression model using the density of *P. marmorata* included the total alkalinity and mean velocity (78.8% of variance explained). The other variables were excluded in both stepwise regressions (Tables I, II).

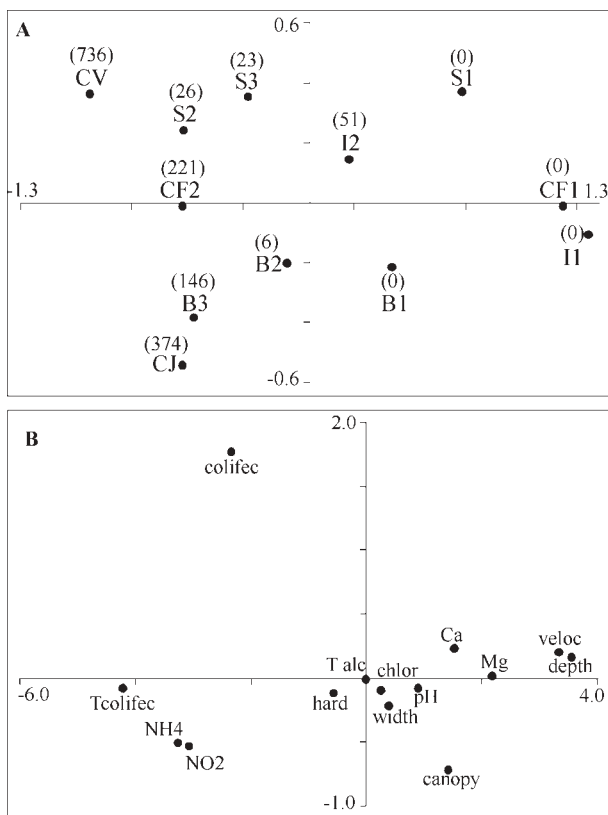


Fig. 3: diagram of principal component analysis. A: sites sampled in relation to physical and chemical variables. The number above the site plots show the total abundance of snails collected in the study area; B: ordination of environmental variables at 12 sampling sites. B: Bananal stream; S: Soberbo stream; CV: Canal da Veterinária stream; CF: Caneca Fina stream; I: Iconha stream; CJ: Corujas stream. Environmental variables: canopy: canopy cover; tcolifec: total coliforms; colifec: fecal coliforms; Talc: total alkalinity; Mg: Mg concentration; Ca: Ca concentration; Hard: hardness; Chlor: chloride concentration; NH4: ammonia; NO2: nitrite; width: mean width; depth: mean depth; veloc: mean velocity

*Qualitative analyses of freshwater snail communities – Second phase* - The ordination results of the CCA on the relative importance of macroinvertebrate-environment variation are given in Table III. The data gathered in the second sampling phase show a separation of species by habitat type. At CCA (Fig. 4), the sampling sites were separated by the physical characteristics of the habitats (relation between depth and width), the presence of canopy cover, and the percentage of aquatic vegetation. Those factors allowed the discrimination between lentic environments (marshes and tanks/lake) and lotic environments (channels and streams). The most important factors associated with the differentiation of the streams and channels were the quantity of faecal coliforms, pH, hardness, calcium and chloride concentrations (Fig. 4). The two types of lentic habitats show different characteristics. The marsh habitat had high percentage of aquatic vegetation and high percentage of canopy cover (Fig. 4). Lakes and tanks presented higher depth, as well as higher concentration of total coliforms (Fig. 4).

The snail species displayed distinct preferences for each type of habitat (Fig. 4). Thus, *Lymnaea* was most frequently encountered in lakes and tanks; *Drepanotrema*, *Pomacea* and *Ancylidae* in marshes; and *P. marmorata*, *M. tuberculatus*, and *Biomphalaria* spp. in streams and channels. The first three axis of the CCA accounted for 46.8% of the total variance explained (21.1 % for first axis and 15% for second axis).

The snails *M. tuberculatus*, *P. marmorata*, and *B. tenagophila* were found in similar habitat conditions, according to the CCA. However there were some differences in habitat preference among those species. *M. tuberculatus* was more tolerant to streams than the other two species (Table IV). *B. straminea* (Dunker, 1848) was encountered only on a water pool found in the margin of Soberbo stream (Table IV). *M. tuberculatus* and *P. marmorata* were the most frequent species at the whole study area. They were found in three or four different types of habitats, respectively, but most specimens were sampled from channels (Table IV).

The test of association between pairs of species did not show any type of significant result (Table V).

## DISCUSSION

The snail species found at Guapimirim displayed a marked habitat preference, specially in relation to the physical characteristics of each environment. *P. marmorata*, *B. tenagophila*, and *M. tuberculatus* were associated to lotic environments, with a low percentage of aquatic vegetation and variable degrees of domestic sewage input. The multiple regression analysis show that the high concentration of faecal coliforms and chloride were the most important factors for explaining the abundance of *M. tuberculatus* in lotic environments. The increase of the chloride concentration is expected in environments contaminated by sewage, due to the inflow of urea-rich effluents (Feema 1981). In lotic environments, the abundance of *P. marmorata* was correlated with the alkalinity and the mean velocity. High alkalinity values may be related to organic pollution, due to the increase in phosphate and ammonium salts (Feema 1981). Ndifon and Ukoli

TABLE I  
Stepwise multiple regression (backward) with the mean abundance of *Melanoides tuberculatus* as the dependent variable (in the last step,  $R^2 = 0.758$ )

Independent variables in the initial model	Variables in the selected model	Coefficient	Df	F	P
Chloride concentration (mg <sup>l</sup> <sup>-1</sup> )	In	7.931	1	5.238	0.048
Faecal coliforms (CFU)	In	0.730	1	10.673	0.010
Total hardness (mg <sup>l</sup> <sup>-1</sup> )	Out	-0.115	1	0.107	0.752
Ca concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	-0.363	1	1.212	0.303
Mg concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.079	1	0.050	0.828
pH	Out	0.510	1	2.810	0.132
Total alkalinity (mg <sup>l</sup> <sup>-1</sup> )	Out	0.126	1	0.129	0.728
Ammonia concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.301	1	0.799	0.398
Nitrit concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	-0.374	1	1.304	0.287
Mean velocity (m/s)	Out	-0.162	1	0.216	0.655
Canopy cover (%)	Out	0.250	1	0.535	0.485
Total coliforms (CFU)	Out	0.249	1	0.527	0.488
Mean width (m)	Out	0.104	1	0.087	0.776
Mean depth (m)	Out	0.583	1	4.119	0.077

Df: degrees of freedom; P: probability; CFU: colony formers unity

TABLE II  
Stepwise multiple regression (backward) with the mean abundance of *Physa marmorata* as the dependent variable (in the last step,  $R^2 = 0.788$ )

Independent variables in the initial model	Variables in the selected model	Coefficient	Df	F	P
Total alkalinity (mg <sup>l</sup> <sup>-1</sup> )	In	7.420	1	23.470	
Mean velocity (m/s)	In	13.961	1	8.359	
Total hardness (mg <sup>l</sup> <sup>-1</sup> )	Out	0.094	1	0.071	
Ca concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	-0.216	1	0.392	
Mg concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.234	1	0.463	
Chloride concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.140	1	0.160	
pH	Out	-0.266	1	0.609	
Ammonia concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.473	1	2.304	
Nitrit concentration (mg <sup>l</sup> <sup>-1</sup> )	Out	0.395	1	1.480	
Canopy cover (%)	Out	-0.493	1	2.566	
Total coliforms (CFU)	Out	-0.370	1	1.266	
Faecal coliforms (CFU)	Out	-0.537	1	3.246	
Mean width (m)	Out	-0.035	1	0.010	
Mean depth (m)	Out	-0.163	1	0.217	

Df: degrees of freedom; P: probability; CFU: colony formers unity

(1989) verified that *M. tuberculatus* and *P. waterloti* (Germain 1911) were most frequently encountered in water bodies polluted by high amounts of human and animal excrements, as well as domestic sewage. The abundance of organic matter increases the concentration of detritus

TABLE III  
Axis summary statistics of the canonical correspondence analysis

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.719	0.512	0.369
Percentage of variance explained (%)	21.1	15.0	10.8
Cumulative percentage of variance explained (%)	21.1	36.0	46.8
Species-environment Pearson correlation coefficients	0.872	0.906	0.816

Total variance (inertia) in the species data: 3.417

and possibly aids in the proliferation of epiphytic algae. The diet of both planorbid and prosobranch snails includes those items (Madsen 1992, Lombardo & Cooke 2002).

Another limiting factor for snail distribution in the studied lotic environments was the water current velocity and the occurrence of spates. All the three species encountered at those environments were found mostly on drainage channels, which have slower water flow than those from streams. In streams, *B. tenagophila* abundance was extremely low. In the state of Minas Gerais, Brazil, the populations of *B. glabrata* and *B. straminea* were also more abundant in channels than in streams (Kloos et al. 2001). In the rainy period (summer), the populations of *M. tuberculatus*, *B. tenagophila*, and *P. marmorata* in streams of Guapimirim presented a drastic reduction. A study made by Buss et al. (2004) in streams of that region demonstrated that the density of macroinvertebrates were negatively influenced by spates. The influence of rainfall on

populations of *Biomphalaria* has been demonstrated in several studies (Baptista & Jurberg 1993, Ernould & Sellin 1999, Teles et al. 2002). Water flow in lotic environments is the most important factor for explaining the longitudinal distribution of the snails that are the intermediate hosts of *Schistosoma* spp. (Appleton 1978). During the present study, the populations of *P. marmorata* and *M. tuberculatus* were also strongly affected by water flow and rain distribution.

The snails *L. columella* (Say 1817), *Pomacea* sp., *Drepanotrema* sp., and Ancyliidae were most frequently encountered in lentic environments. *L. columella* preferred lentic environments with relatively high water column (dams, tanks, and lake). This finding corroborates the literature data, which associate the presence of Lymnaeidae to environments with slow flow or stagnant water (Lima 1995, Hanley & Ultsch 1999). In a snail survey made in the state of São Paulo, Brazil, *L. columella* was more abundant in lentic environments (Vaz et al. 1987).

*Pomacea* sp., *Drepanotrema* sp., and Ancyliidae occurred exclusively in low-depth marshes with plenty of floating, emergent, and submerged vegetation. After Santos (2003), ancylids live on aquatic plants or on rotten leaves found in lentic environments, or in water bodies

with slow water flow and low pollution degree. In the present study, representatives of the family Ancyliidae were found in only one habitat, displaying characteristics similar to those cited by Santos (2003). The small amount of data does not allow any generalization on habitat preference by the Ancyliidae species found in the present study. *Drepanotrema* sp. was also found in only one type of habitat. The species of the genus *Pomacea* are distributed throughout the Neotropical region, occupying environments with slow flow or stagnant water (Thiengo 1995). *P. paludosa* (Say 1829) is associated to different kinds of substrata with aquatic vegetation (Pain 1972).

In the present study, there was no evidence of competition between *M. tuberculatus* and the other species of freshwater snails found in the same habitats. In the same way, chi-square analysis did not provide any evidence in favour of competition between any of the species encountered. The absence of interactions between *M. tuberculatus* and *Pomacea* sp., *L. columella*, *Drepanotrema* sp., and Ancyliidae is associated to the distinct spatial distribution of those species. While *M. tuberculatus* inhabits mostly lotic environments, the other species are found in lentic environments. Due to this habitat segrega-

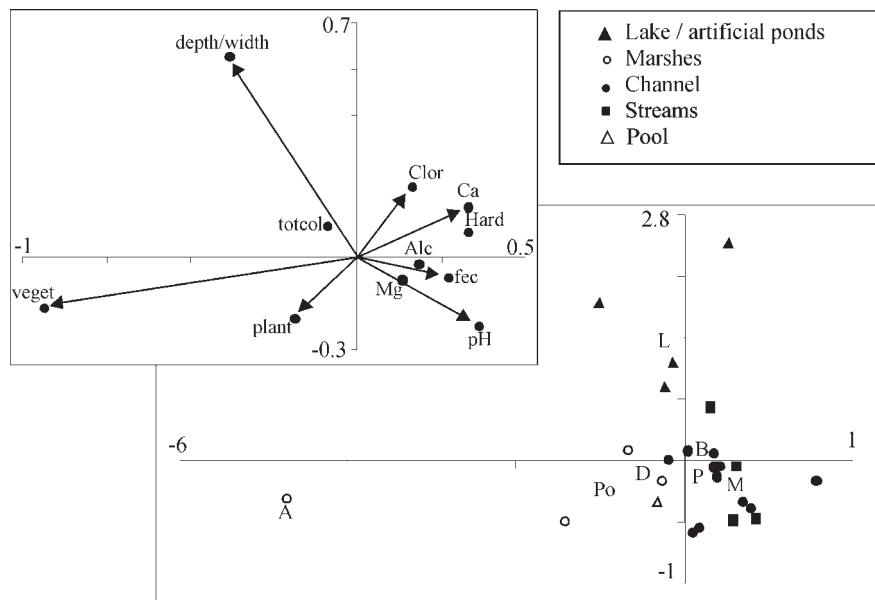


Fig. 4: canonical correspondence analysis of sites sampled in relation to snails and environmental factors. Species of snail L: *Lymnaea columella*; B: *Biomphalaria* spp.; P: *Physa marmorata*; M: *Melanoides tuberculatus*; Po: *Pomacea* sp.; D: *Drepanotrema* sp.; A: Ancyliidae. Environmental variables: plant: canopy cover; veget: percentage of aquatic vegetation; totcol: total coliforms; fec: fecal coliforms; alc: total alkalinity; Mg: Mg concentration; Ca: Ca concentration; Hard: hardness; Chlor: chloride concentration

TABLE IV

Number of habitat types where snails were found. Under habitat type is indicated the correspondent sampling number

	Channel (15)	Stream (8)	Lake/tank (5)	Marsh (4)	Pool (1)
<i>Physa marmorata</i>	7	1	0	2	1
<i>Lymnaea columella</i>	1	0	4	0	0
<i>Pomacea</i> sp.	0	0	0	3	0
<i>Drepanotrema</i> sp.	0	0	0	1	0
Ancyliidae	0	0	0	1	0
<i>Biomphalaria straminea</i>	0	0	0	0	1
<i>Biomphalaria tenagophila</i>	4	0	1	0	0
<i>Melanoides tuberculatus</i>	7	3	1	0	0

TABLE V

Test of association ( $\chi^2$ ) between pairs of species of snails collected in the second phase. Only samples with at least one snail was considered (N = 24)

Pairs of species	$\chi^2$	df	p
<i>Melanoides</i> × <i>Biomphalaria</i>	0.02	1	0.9024
<i>Melanoides</i> × <i>Physa</i>	0.27	1	0.6015
<i>Melanoides</i> × <i>Lymnaea</i>	0.12	1	0.7314
<i>Biomphalaria</i> × <i>Physa</i>	3.67	1	0.0555
<i>Biomphalaria</i> × <i>Lymnaea</i>	0.01	1	0.9089
<i>Physa</i> × <i>Lymnaea</i>	0.47	1	0.4923
<i>Melanoides</i> × others	0.55	1	0.4583
<i>Biomphalaria</i> × others	2.75	1	0.0973
<i>Physa</i> × others	0.59	1	0.4427
<i>Lymnaea</i> × others	0.12	1	0.7314

Df: degree of freedom; P: probability

tion, the potential impact of *M. tuberculatus* on the species associated with lentic environments at the study area is limited. In Martinica, the local freshwater snails, including *P. glauca* (Linnaeus 1758), *D. lucidum* (Pfeiffer 1839), *D. depressissimum* (Moricand 1839), and *D. cimex* (Moricand 1839) do not seem to be threatened by extinction after the invasion of *M. tuberculatus* (Pointier & Delay 1995).

No association was observed between *M. tuberculatus* and *P. marmorata* or *B. tenagophila*, although all three species were most frequently encountered on the same type of habitat. In French Antilles, the competitive interaction between *M. tuberculatus* and *Biomphalaria* spp. has been an important factor for the success of biologic control programs (Pointier & Jourdan 2000). In other places, however, a wide range of outcomes were obtained. In Venezuela, biological control experiments using *M. tuberculatus* generally failed (Pointier et al. 1991). In Kenya there was no evidence of negative influence of *M. tuberculatus* on *Biomphalaria* spp. (Mkoji et al. 1992). In Nigeria, Ndifon and Ukoli (1989) observed that *M. tuberculatus* was positively associated with *Physa waterloti* and *B. pfeifferi*.

The occurrence of competitive interaction between *M. tuberculatus* and *Biomphalaria* spp. only in some specific environments is related to the different life strategies adopted by those species. As opposed to *Biomphalaria* spp., *M. tuberculatus* has low reproduction rates, low mortality rates, and a long life span (Pointier et al. 1991). Such life history traits indicate that in permanent and stable habitats, *M. tuberculatus* theoretically has a competitive advantage over *Biomphalaria* spp. (Pointier & Guyard 1992).

In Guapimirim, the frequent occurrence of spates may be considered as a factor of instability, specially in lotic environments (Buss et al. 2004). In this case, the drastic reduction of the populations of *M. tuberculatus* and *Biomphalaria* spp. may lead to the coexistence of those species, as it keeps both populations at low densities. In the present study, the higher abundance of *B. tenagophila* was found in a rectified stream with high inflow of organic effluents. However, that environment

was also subjected to occasional spates, which prevented that the populations of *B. tenagophila* and *M. tuberculatus* reached high densities. Besides the effect of environmental instability (flooding variations), other factors limited the efficiency of *M. tuberculatus* as a competitor for *Biomphalaria* spp. The presence of diverse microhabitats in heterogeneous environments may favor the coexistence of *M. tuberculatus* with *B. glabrata*, as it may allow both species to avoid competition (Pointier et al. 1993). In Venezuela, the quantity of food was associated to the limited competitive effect of *M. tuberculatus* on *B. glabrata*. The large amount of food in a pond allowed the installation of dense populations of *M. tuberculatus* and *B. glabrata* (Pointier et al. 1991). In Guapimirim, the occurrence of spates, allied to the intense pollution by sewage, specially in channels and streams, probably allowed the coexistence of *M. tuberculatus*, *B. tenagophila*, and *P. marmorata*. However, in other regions of Brazil a competitive interaction was observed between *M. tuberculatus* and *B. glabrata*. In the state of Minas Gerais, *M. tuberculatus* was able to exclude populations of *B. glabrata* and *B. straminea* after its introduction in a lake (Guimarães et al. 2001). In the state of Rio de Janeiro, *M. tuberculatus* invaded an irrigation channel and reduced the population of *B. glabrata* in an area of schistosomiasis transmission (Giovanelli et al. 2004). The evidence found in the latter cited study emphasizes the need for studies on the biology and ecology of *M. tuberculatus*, as well as its interaction with snail hosts encountered in Brazil. These studies are specially important because *M. tuberculatus* is rapidly spreading through many Brazilian regions, including areas where schistosomiasis is endemic. In those areas, it is common the occurrence of attempts of human intervention aiming to control the population of snail hosts. In some circumstances, such interventions may have an adverse effect on the efforts to control populations of *Biomphalaria* spp., in areas where they co-occurs with *M. tuberculatus*. The application of molluscicide must be reevaluated where *M. tuberculatus* and *Biomphalaria* are found together. The possibility that *M. tuberculatus* be more sensitive to the molluscicide than *Biomphalaria* spp. may lead to a reduction of the competitive interaction between those species, thus indirectly stimulating the increase in the population of *Biomphalaria* spp. (Giovanelli et al. 2002). On the other hand, some environmental modifications may add to the instability of the environment, what would make room for the coexistence of *M. tuberculatus* and *Biomphalaria* spp. In this way, some of the usual measures for the control of intermediate hosts would prevent the extinction of populations of *Biomphalaria* spp. by *M. tuberculatus* in particular habitats.

Thus, the increase knowledge on the ecological aspects of the interactions between *M. tuberculatus* and *Biomphalaria* spp. is essential for the adoption of efficient measures for the control of *Biomphalaria* spp. populations in endemic areas of schistosomiasis, where the competitor snail, *M. tuberculatus*, is also found.

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