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INFLUÊNCIA DE FATORES AMBIENTAIS DE AMPLA ESCALA NA DISTRIBUIÇÃO ESPACIAL DE MOLUSCOS LÍMNICOS

DISSERTAÇÃO DE MESTRADO

Aline Monique Blank do Amaral

Santa Maria, RS, Brasil

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INFLUÊNCIA DE FATORES AMBIENTAIS DE AMPLA ESCALA NA DISTRIBUIÇÃO ESPACIAL DE MOLUSCOS LÍMNICOS

Aline Monique Blank do Amaral

Dissertação apresentada ao Curso de Mestrado do Programa de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Bioecologia de Invertebrados Aquáticos, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do grau de **Mestre em Biodiversidade Animal**

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INFLUÊNCIA DE FATORES AMBIENTAIS DE AMPLA ESCALA NA DISTRIBUIÇÃO ESPACIAL DE MOLUSCOS LÍMNICOS

elaborada por
Aline Monique Blank do Amaral

como requisito parcial para obtenção do grau de **Mestre em Biodiversidade Animal**

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Santa Maria, 14 de fevereiro de 2014

The way of life can be free and beautiful, but we have lost the way. Greed has poisoned men's souls, has barricaded the world with hate, has goose-stepped us into misery and bloodshed. We have developed speed, but we have shut ourselves in. Machinery that gives abundance has left us in want. Our knowledge has made us cynical; our cleverness, hard and unkind. We think too much and feel too little. More than machinery, we need humanity. More than cleverness, we need kindness and gentleness. Without these qualities, life will be violent and all will be lost.

(Charlie Chaplin)

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“Always remember: Two things are infinite: the universe and human stupidity; and I'm not sure about the universe.”

RESUMO

Dissertação de Mestrado
Programa de Pós-Graduação em Biodiversidade Animal
Universidade Federal de Santa Maria

INFLUÊNCIA DE FATORES AMBIENTAIS DE AMPLA ESCALA NA DISTRIBUIÇÃO ESPACIAL DE MOLUSCOS LÍMNICOS

AUTORA: ALINE MONIQUE BLANK DO AMARAL
ORIENTADOR(A): CARLA BENDER KOTZIAN
Data e Local da Defesa: Santa Maria, 14 de fevereiro de 2014.

A presente dissertação apresenta abordagens singulares acerca da influência de variáveis ambientais em diferentes escalas espaciais (temperatura, precipitação e altitude meso e macro regionais) (1) e de fatores terrestres e aquáticos em escala ampla (2) na distribuição espacial da malacofauna límnica brasileira. O estudo foi realizado através de meta-análise, a partir de dados de distribuição de comunidades de gastrópodes e bivalves existentes na literatura. Baseado na composição taxonômica, 35 localidades estudadas em 33 trabalhos foram selecionadas, utilizando-se critérios para minimizar especialmente divergências amostrais. Como alguns trabalhos concentraram-se exclusivamente em uma das classes de moluscos, do total de localidades, 27 foram utilizadas para análises das comunidades de gastrópodes e 22 para as de bivalves. As informações ambientais foram obtidas de dados geoespaciais. A similaridade entre as comunidades de gastrópodes e de bivalves foi representada por uma análise de Cluster (WPGMA) e possíveis distorções gráficas foram avaliadas pelo Coeficiente de Correlação Cofenética (r). Através do teste de Mantel foi verificada a existência de autocorrelação espacial para ambas as comunidades ($r = 0.21$, $P = 0.02$ para gastrópodes, e $r = 0.425$, $P = 0.0002$ para bivalves). Deste modo, um teste de Mantel parcial foi utilizado, comparando as matrizes de similaridade com as ambientais, removendo o efeito da distância geográfica. A correção de Bonferroni foi considerada devido a possíveis vieses da variabilidade amostral. Os dendrogramas evidenciaram a formação de 4 e 6 pequenos grupos para bivalves e gastrópodes, respectivamente, com similaridade maior do que 50%. A região climática de Köppen teve uma correlação significativa positiva com ambas as comunidades nas duas abordagens (1) (2) apesar da questão espacial. Variáveis ambientais em escala macro (região climática de Köppen e intervalos de precipitação) mostraram-se importantes na distribuição de gastrópodes e bivalves. Em escala meso, apenas a altitude teve forte relação com as comunidades de bivalves. Em contrapartida, apesar da evidente influência do espaço, variáveis terrestres (região climática de Köppen, bioma e formação vegetal) tiveram uma correlação mais forte com as comunidades de bivalves do que variáveis aquáticas (região hidrográfica e ecossistema aquático). Além disso, o ecossistema aquático (e.g., lago, rio), neste caso, não foi afetado pelo espaço. Para as comunidades de gastrópodes, além da forte correlação com a região de Köppen, houve relação com a região hidrográfica, mas esta deixou de existir quando o efeito da distância foi removido. Os resultados obtidos neste estudo indicam que a elaboração de estratégias de proteção (i.e., áreas de conservação) para a malacofauna límnica deve considerar macrovariáveis como região de Köppen, bioma e ainda altitude, e a integridade dos ecossistemas límnicos também deve ser incluída nos programas de conservação.

ABSTRACT

Master Dissertation
Post-Graduation in Animal Biodiversity
Federal University of Santa Maria

INFLUENCE OF LARGE SCALE ENVIRONMENTAL FACTORS ON THE SPATIAL DISTRIBUTION OF FRESHWATER MOLLUSKS

AUTHOR: ALINE MONIQUE BLANK DO AMARAL
ADVISOR: CARLA BENDER KOTZIAN
Date and Local of defense: Santa Maria, February 14th 2014.

This dissertation presents unique approaches about the influence of environmental variables at different spatial scales (meso and macro regional temperature, rainfall and altitude) (1), and aquatic and terrestrial factors on a large scale (2) on the spatial distribution of Brazilian freshwater malacofauna. The study was conducted through meta-analysis, based on distribution data of gastropods and bivalves communities from the existing literature. According to the taxonomic composition, 35 localities from 33 previous studies were selected under certain criteria to minimize specifically sampling deviations. As some studies had focused exclusively on one mollusk class, from all the localities, 27 were used for gastropods communities' analysis and 22 for bivalves. Environmental information was obtained from geospatial data. The similarity between gastropods and bivalves communities was represented by a Cluster analysis (WPGMA) and possible graphic distortions were evaluated by Coefficient of Cophenetic Correlation (r). Through a Mantel test, spatial autocorrelation was observed for both communities ($r = 0.21$, $P = 0.02$ for gastropods, and $r = 0.425$, $P = 0.0002$ for bivalves). Thus, a partial Mantel test was used, comparing the similarity matrixes and the environmental ones removing the geographic distance effect. The Bonferroni's correction was considered due to possible biases arising from sample variability. The dendrogram demonstrated the formation of 4 and 6 small groups, of bivalves and gastropods, respectively, with similarity greater than 50%. The Köppen's climate region had a significant positive correlation with both communities in both approaches (1) (2) despite the space issue. Environmental variables in macro scale (Köppen's climate region and rainfall range) were important in the distribution of gastropods and bivalves. At meso-scale, only altitude had a strong relationship with the bivalves' communities. However, despite the obvious influence of the space, terrestrial variables (Köppen's climate region, biome and vegetal formation) had a stronger correlation with the bivalves' communities than aquatic ones (hydrographic region and aquatic ecosystem). In addition, the aquatic ecosystem (e.g., lake, river), in this case, was not affected by space. For gastropods communities, in addition to strong correlation with Köppen's climate region, there was some relationship with hydrographic region, but this vanished when the effect of distance was removed. The results of this study indicate that the development of protection strategies for the freshwater malacofauna should consider macrovariables as Köppen's climate region, biome and even altitude, and the integrity of limnic ecosystems should also be included in conservation programs.

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INTRODUÇÃO

A identificação dos fatores que determinam os padrões de diversidade constitui uma questão central em ecologia (BROSSE et al., 2003) e depende da escala espacial de investigação (LEVIN, 1992). Muitas vezes, em consequência da heterogeneidade ambiental e peculiaridades das comunidades, variáveis mensuradas em diferentes escalas espaciais podem imprimir diferentes respostas nos organismos (SANDIN & JOHNSON, 2004). Geralmente padrões observados em uma escala ampla podem não existir em escala menor para um mesmo fator (BONADA et al., 2008). Além disso, existe uma intrínseca e controversa conexão entre as diferentes escalas de observação. De acordo com teoria da hierarquia, fatores ambientais mais amplos parecem governar fatores locais (ALLEN & STARR, 1982). Clima, geologia, vegetação, uso da terra e topografia de bacias hidrográficas influenciam características químicas locais da água, com efeito direto sobre as comunidades (veja referências em COOPER et al., 1998).

Estudos sobre fatores que influenciam os padrões de distribuição de comunidades em escalas espaciais amplas são um enfoque ecológico em ascensão (WIENS, 1989), fornecendo informações mais adequadas à escolha de áreas de preservação, do que aqueles em escalas locais (DINIZ-FILHO et al., 2009). Porém, a maioria ainda concentra-se em ecossistemas terrestres e/ou vertebrados (e.g. RODRÍGUEZ et al., 2005; RAHBEK et al., 2007; DINIZ-FILHO et al., 2008; SANTOS et al., 2009; VASCONCELOS et al., 2010). Tais estudos indicam que altitude, precipitação anual total, temperatura média anual e bioma são importantes preditores em macro-escala de riqueza e composição das espécies analisadas.

Contudo, nos últimos anos, pesquisas têm sido direcionadas a explorar a forma como as comunidades de água doce estão organizadas, especialmente em escalas mais amplas (STENDERA et al., 2012). Isto se deve a crescente preocupação com as modificações impostas aos habitats de água doce. Adicionalmente, sistemas límnicos são interessantes para abordar questões de escala, pois apresentam aspectos bióticos e abióticos que variam em diferentes escalas espaciais (DOWNES et al., 2000). Na estrutura espacial natural de rios, variadas escalas também podem ser reconhecidas (LIGEIRO et al., 2010). Entretanto, especialmente para macroinvertebrados, estudos conduzidos em escalas amplas ainda são pouco numerosos (e.g., LI et al., 2001; WEIGEL et al., 2003; SANDIN & JOHNSON, 2004; FELD & HERING, 2007; BONADA et al., 2008). Isto acaba impossibilitando a definição de áreas de preservação que atendam às reais necessidades dos organismos aquáticos (MOULTON, 2009).

Dentre os diversos ecossistemas, ambientes límnicos estão amplamente ameaçados, principalmente devido a sua posição na paisagem, que os tornam receptores de resíduos, sedimentos e poluentes por escoamento (DUDGEON et al., 2006), e pela superexploração humana de seus recursos e serviços. Intervenções humanas nos ecossistemas aquáticos, cada vez mais impactantes à medida que a demanda aumenta, acabam alterando o fluxo e/ou as características químicas e físicas da água, com consequências variáveis para os organismos que ali habitam (STRAYER & DUDGEON, 2010). Ecossistemas de água doce apresentam maior riqueza em espécies/área do que ecossistemas terrestres e marinhos, porém a perda de biodiversidade em ambientes de água doce é muito maior (LOH et al., 2005).

Dos diversos grupos que compõem a fauna de água doce e que tem apresentado elevadas taxas de extinção nos últimos anos estão os moluscos (RICCIARDI & RASMUSSEN, 1999; LYDEARD et al., 2004). A influência de fatores ambientais ‘de’ ou ‘em’ ampla escala sobre a estruturação e distribuição espacial de moluscos límnicos é pouco conhecida, especialmente na região Neotropical. Além disso, o conhecimento existente sobre a influência de macrovariáveis sobre macroinvertebrados de água doce dificilmente pode ser estendido para moluscos, uma vez que estes são, geralmente, subamostrados nestes estudos. Porém, um pequeno número de estudos tem mostrado que certos fatores típicos de ecossistemas terrestres, como relevo e/ou altitude podem ser bons preditores da estrutura dessas comunidades (JACOBSEN, 2004; STURM, 2007; MALTCHIK et al., 2010). Em relação a fatores típicos de ecossistemas límnicos, mais conhecidos, sabe-se que a ordem do rio pode influenciar a riqueza das comunidades (MOUTHON, 1999), bem como o tipo de substrato (macrófitas e granulometria do sedimento) (BRÖNMARK, 1985; SÁ et al., 2013) e também a condição hidráulica (MCMAHON & BOGAN, 2001).

Nesse contexto, o presente estudo tem como objetivo principal testar se e como a estrutura das comunidades de moluscos de água doce é afetada por fatores ambientais em escala espacial ampla, de modo a contribuir para políticas de conservação.

Especificamente, o estudo procura responder as seguintes questões:

a) ARTIGO 1 - Como fatores que podem ser observados em diferentes escalas espaciais (e.g., altitude, precipitação e temperatura) influenciam a estrutura das comunidades de moluscos, se analisados em diferentes escalas (e.g., local de coleta, pontual ou zonas, faixas)?

b) ARTIGO 2 - Fatores em macro-escala, que comumente afetam a distribuição das comunidades terrestres (e.g., clima, bioma, vegetação) também seriam importantes preditores de composição das comunidades de moluscos límnicos?; Ou seriam essas comunidades mais influenciadas por fatores intimamente relacionados a ecossistemas límnicos, como regiões hidrográficas, habitat e tipo de sistema aquático (lêntico, lótico, reservatório)?

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ARTIGO 1

THE INFLUENCE OF TEMPERATURE, RAINFALL AND ALTITUDE, AT MESO AND MACRO REGIONAL SPATIAL SCALES, ON THE STRUCTURE OF COMMUNITIES OF THE BRAZILIAN MALACOFAUNA

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ABSTRACT

Freshwater mollusks are among the most threatened aquatic animals. In Brazil, some freshwater ecosystems still maintain their integrity, but usually they are being affected, especially by water drainage and diversion. Thus, comprehending which environmental factors drive the spatial distribution of mollusk communities may help to determine the best areas for their preservation. The influence of temperature, rainfall and altitude on the distribution of gastropod and bivalve communities from 35 previously studied localities in the country was analyzed based on their taxonomic composition. Meta-analyses were conducted at meso and macro scales, using continuous (meso-environmental variables) and categoric (macro-environmental variables) data respectively. The macro variable Köppen's climatic region was the most important driver for gastropod and bivalve communities, in part because of the coincidence of some climatic regions with portions of certain large hydrographic basins; while rainfall range showed less influence. The macro variable relief did not affect the communities, but the meso variable mean altitude was related to bivalve communities, due their strictly relationship with grain size and food availability, especially Unionoida, in low-altitude areas. To preserve the diversity of Brazilian freshwater mollusks, conservation programs should protect areas in different climatic regions, especially those at low altitudes, including montane areas with streams.

KEYWORDS: Neotropics, Bivalves, Gastropods, Conservation, Ecology

INTRODUCTION

Identifying processes that affect the patterns of spatial distribution of biodiversity in ecosystems is a central issue in ecology (BROSSE et al., 2003), and the results may depend on the spatial scale of observation (BONADA et al., 2008). Spatial scales used in studies of community structure vary widely. They can range from small, restricted areas, i.e., local scale of study to a wide array of larger scales, also including very large geographic scales (LEVIN, 1992; SANDIN & JOHNSON, 2004). The environmental factors that drive the structure of communities according to these scales can be interdependent, exhibiting a hierarchical relationship. Macro-environmental variables can regulate meso-environmental and micro-environmental variables (FELD & HERING, 2007). For instance, geology and climate can modulate local hydrological and thermal traits of limnetic environments (WILEY et al., 1997). The biome in which a watershed is located influences the vegetation type at smaller spatial scales and consequently the type of organic matter entering in the streams (CORKUM, 1990).

The hierarchical influence of large scale factors on smaller ones is not a general rule. A macro variable can affect the community structure, but meso or micro variables that it modulates may not. Vegetation can be, but not always, more important than water chemistry for terrestrial and aquatic mollusks (HORSÁK & HÁJEK, 2003). Micro variables such as local riparian vegetation can influence the structure of the communities more than macro spatial variables such as climate or geology (WEIGEL et al., 2003). Indeed, some studies have found that a certain variable may or may not affect a community according to the scale of analysis adopted. For instance, vegetation cover may have no influence on macroinvertebrate communities at the stream-basin scale, but the riparian vegetation influences the communities at the reach scale (RIOS & BAILEY, 2006).

From all the ecosystems, freshwater environments are the most endangered worldwide due its relevancy to life maintenance (DUDGEON et al., 2006). The use of water for power generation and irrigation for agriculture (MOULTON & SOUZA, 2006) have destroyed or altered streams, lakes and wetlands, affecting the water characteristics and inhabitants (STENDERA et al., 2012). As evidenced for terrestrial environments, large-scale factors can be good or better predictors of the distribution of communities, essential to the establishment of conservation areas (DINIZ-FILHO et al., 2009). However, there is little information on how macro and meso variables drive animal communities, especially macroinvertebrates (e.g., BONADA et al., 2007; CÉRÉGHINO et al., 2012), across wide spatial scales (e.g., RAHBEK et al., 2007; DINIZ-FILHO et al., 2008; VASCONCELOS et al., 2010). The lack of knowledge on how macro and meso-environmental variables affect freshwater communities hinders the development of appropriate mitigating actions to preserve these environments (DUDGEON et al., 2006; HERBERT et al., 2010; STRAYER & DUDGEON, 2010). Bias like this have been causing problems in preserving freshwater settings, especially streams, because conservation areas rarely include downstream stretches and both streambanks, or because they preserve fragmented areas with no connectivity to the main course (MOULTON, 1999; see discussion in HERBERT et al., 2010).

Among the freshwater fauna, mollusks are in a constant and an increasing danger, all over the world (LYDEARD et al., 2004; BOGAN, 2008; LYSNE et al., 2008). However, studies focusing on their conservation are concentrated in the northern hemisphere, and have analyzed the biology of certain species (VAUGHN & TAYLOR, 1999; WATSON & ORMEROD, 2005) or the spatial distribution of communities locally, at micro (e.g. JURKIEWICZ-KARNKOWSKA, 2006) and meso (e.g. PÉREZ-QUINTERO, 2012) spatial scales. Although important factors structuring mollusk communities are well known (e.g., grain size, presence of macrophytes, hydraulic conditions; see discussion in BROWN, 2001 and MCMAHON & BOGAN, 2001), the relationships of these factors have been studied only as micro variables, in a local scale (e.g., BRÖNMARK, 1985; HORSÁK & HÁJEK, 2003; JURKIEWICZ-KARNKOWSKA, 2006; STURM, 2007; PYRON et al., 2009). Furthermore, even the existing knowledge about the influence of macro variables on freshwater macroinvertebrates of the north hemisphere (TOWNSEND et al., 2003; SANDIN & JOHNSON, 2004; FELD & HERING, 2007; BONADA et al., 2008) can hardly be extended to mollusks, because the malacofauna is usually a subsample in these studies, comprising a less-numerous and less-diverse group (DORÁZIO, 1999). On the other hand, studies conducted at a meso spatial scale (e.g., STURM, 2007; PÉREZ-QUINTERO, 2012) have suggested, indirectly, that some macro variables, such as climate and relief, may be important predictors of the community composition of freshwater mollusks.

The Neotropical region still contains large areas that have been little affected by human activities. In Brazil, some portions of the Amazon Rainforest, Caatinga and Cerrado biomes are uninhabited or not used for agricultural activities, and their freshwater ecosystems can be considered little modified (COURA et al., 2011) if compared to those from other Brazilian biomes. Even in more populated areas, forest fragments and preservation areas still ensure some degree of environmental integrity for streams and lakes (AGOSTINHO et al., 2005). However, the economic growth and agricultural expansion in recent decades are increasing the rate of alteration of many formerly untouched streams and lakes, including in Amazon Rainforest, Caatinga and Cerrado (SAWYER, 2008; CASTELLO et al., 2013). Besides, dam construction is one of the most common projects throughout Brazil (AGOSTINHO et al., 2005; ROLAND et al., 2012). Consequently, many Brazilian freshwater animals are now under threat (AGOSTINHO et al., 2005), but the anthropogenic impacts on the freshwater mollusks are rarely documented (MANSUR et al., 2003; ERTHAL et al., 2011). The vulnerability of this group to environmental changes and degradation (LYDEARD et al., 2004) increases the urgency of studies on environmental factors that can ensure their preservation in the country.

This study provides new information on how temperature, rainfall and altitude influence the structure of Brazilian freshwater mollusk communities, at meso (local mean minimum temperature, local mean annual rainfall and altitude) and macro (Köppen’s climatic regions, rainfall intervals and relief) spatial scales, evaluated through a meta-analysis. Knowing that variables on a local scale exert a more direct influence on freshwater communities (BOYERO, 2003), our initial hypothesis is that temperature, precipitation and altitude at meso scale exert greater influence on the communities of freshwater mollusks than those at macro scale.

MATERIAL AND METHODS

Community selection

Thirty five localities (Figure 1a, Table 1) distributed throughout the Brazilian country were selected from thirty three studies published about freshwater gastropods and bivalves communities structure. Certain criteria were used to select the studies because both richness and composition are influenced by differences in sampling effort (e.g., see discussions by SANTOS et al., 2009 and KORICHEVA et al., 2013). Thus, the studies selected should focus both on the community structure and on the environments (inventories and species lists for geographic areas, such as municipalities or states, were not considered), and be devoted exclusively to mollusks, preferably published in reviewed journals or book chapters (except for those by ALVARENGA et al., 1979; MANSUR et al., 2007; FERNANDEZ, 2011; KOTZIAN & AMARAL, 2013). Furthermore, knowing the bias arising from a meta-analysis, we tried to select studies with more than one type of sampler and several replicates or subsamples.

Other procedures were also adopted to analyze tha data from the studies selected. Cases of nomenclatural synonymy among the species were evaluated using specialized literature for each taxon (e.g., MANSUR & PEREIRA, 2006), and alien species and taxa with undetermined species identification (sp.) were excluded from the analyses. Some studies whose authors provided a species list by subarea (i.e., river stretches larger than 20 km or individual lakes apart from each other by less than 10 km) were divided in more than one locality (e.g., MANSUR & PEREIRA, 2006; LANZER, 2001; FRANÇA et al., 2007; SURIANI et al., 2007). Also, from those studies dealing with samples conducted in nearby localities, showing a species list by localities (e.g., LANZER, 2001), we chose only that containing the highest richness.

Based on geographic coordinates (i.e., localization) of the sampling sites provided by the studies, a medium geographical point was defined to represent each locality to thereafter obtain environmental information (Table 1). Thereby in this meta-analysis our sampling unit is each locality regardless of the number of sampling sites, if they are separated by at least 10 km.

As many studies on Brazilian freshwater mollusk communities deal exclusively with either gastropod or bivalve communities (e.g., PEREIRA et al., 2000a; PIMPÃO & MANSUR, 2009), mollusks classes were analyzed separately. Thus, based in the criteria adopted, 35 localities from 33 studies were included in the analyses (a total of 109 species, see Suplementary data = [Apêndice]), where 27 were used for gastropod community analyses (39 species), and 22 for bivalve community analyses (70 species).

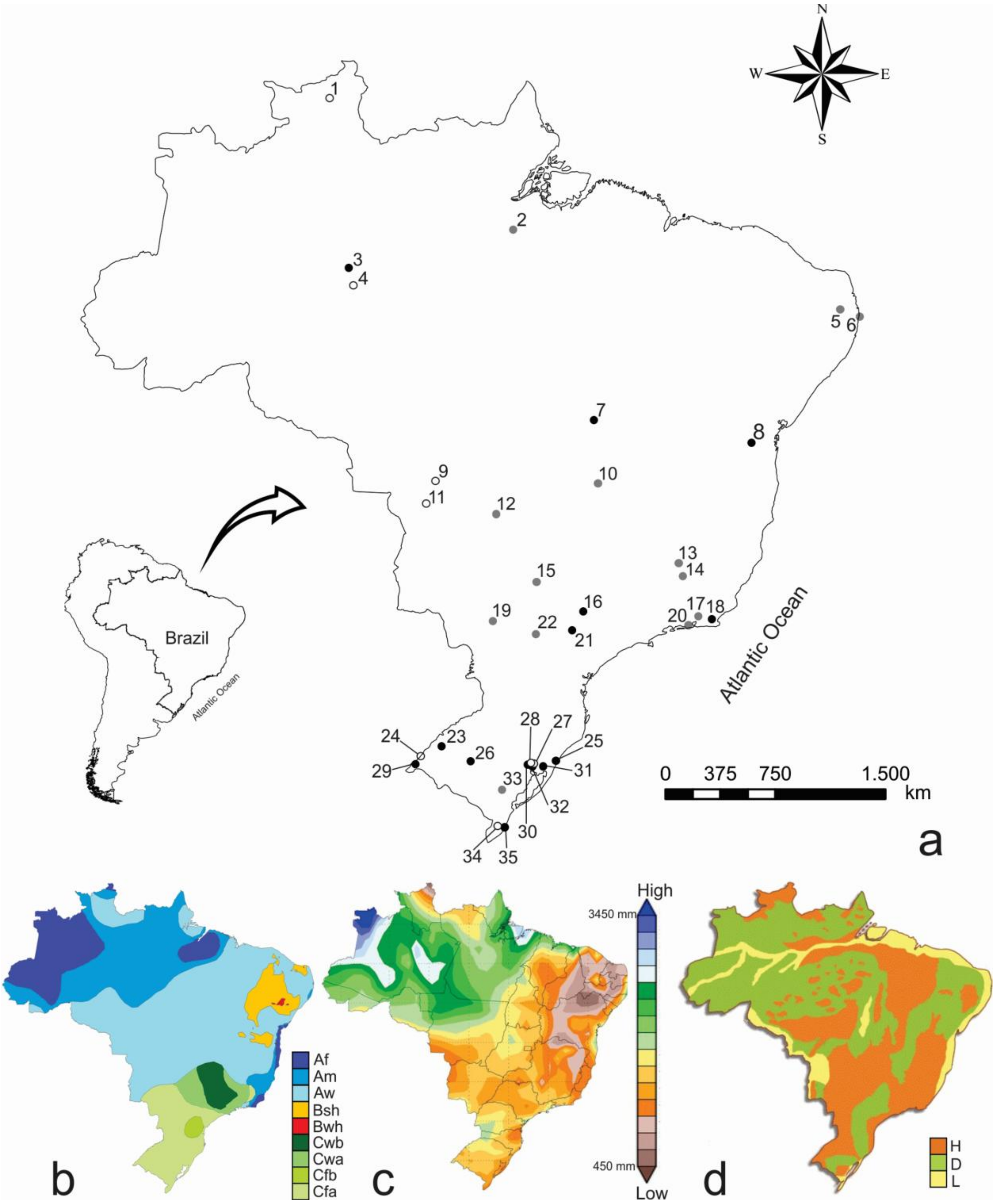

Figure 1 - a) Locations of the 35 localities selected for studying Brazilian gastropod and bivalve communities. Black dots: localities with both gastropod and bivalve communities; Gray dots: localities with only gastropod communities; Empty dots: localities with only bivalve communities. b-c) simplified maps showing b) Köppen's climatic regions (Af: Tropical forest; Am: Tropical monsoon; Aw: Wet and dry tropical climate or savanna; Bsh: Medium latitude steppe and desert; Cwa: Humid temperate climate with dry winters and warm summers; Cfa: Humid temperate climate with warm summers; c) rainfall ranges; d) relief (H: highlands; L: lowlands; D: depressions). The number and abbreviation for each locality are listed in Table 1. Maps C and D were adapted from INMET (1992) and Ross (1990), respectively.

Table 1. Location, environmental characterization and sampling method of the 35 Brazilian localities analyzed (Samplers: 1 – manual; 2 – analysis of rocks/logs; 3 – analysis of macrophytes; 4 – artificial substrate; 5 – free diving; 6 – sieve; 7 – Surber; 8 – D-frame net; 9 – trawl net; 10 – Van Veen grab; 11 – Ekman grab; 12 – Metalic scoop. For Rainfall intervals, Köppen's climatic regions and Relief see explanations in Material and Methods and Figure 1).

Loc.	Localities studied	Geogr. Coordinates	Geogr. region	Samples by year	Samples by sites	Sampler	Temp. (ºC)	Rainfall (mm/y)	Alt. (m)	Climate	Rainfall Interval	Relief	Richness
1	Uraricoera, Branco and Parimé rivers (Mansur & Valer 1992)	03°21'33"N 61°20'15"W	North	1	10	1	21,2	1590	84	Am	D	D	10
2	Middle Xingu River (Jesus et al., 2007)	03°13'49"S 52°12'38"W	North	4	8?	1, 7	20,5	1853	97	Am	D	D	3
3	Aripuanã and Madeira rivers (Pimpão 2007)	05°07'13"S 60°24'06"W	North	1	51	1, 2, 3, 5, 8, 9	21,4	1450	25	Am	F	L	9
4	Aripuanã and Juma rivers (Pimpão & Mansur, 2009)	06°00'00"S 60°11'00"W	North	1	1?	1, 2, 3	20,4	1429	35	Am	F	L	10
5	Bodocongó Reservoir (Abílio et al., 2006)	07°12'50"S 35°54'57"W	Northeast	3 to 6	3	3, 6, 10	17,2	692	518	Aw	A	H	4
6	Stream of Distrito Carne de Vaca (Souza et al., 2010)	07°34'29"S 34°50'00"W	Northeast	2 to 10	9	6	19,1	2131	7	Aw	E	L	5
7	Reservoirs on Tocantins River (Fernandez, 2011)	12°47'36"S4 8°14'37"W	North	4 to 12	90	1, 12	16,8	1436	290	Aw	D	D	19
8	Contas River basin (Kotzian & Amaral,2013)	13°51'23"S 40°20'32"W	Northeast	2	20	7	17,2	574	232	BSh	A	H	8
9	Cuiabá River (Mansur et al., 2007)	15°45'27"S 56°07'43"W	Midwest	-	18	-	16,1	1247	151	Aw	C	D	19
10	Lake Paranoá and Riacho Fundo stream (Martins-Silva & Barros, 2001)	15°52'15"S 47°58'38"W	Midwest	1 to 5	5	8	12,3	1813	1062	Aw	D	H	1
11	Lakes along the Cuiabá River (Colle & Callil, 2012)	16°50'05"S 56°34'35"W	Midwest	2	20	1	16,5	1243	119	Aw	B	D	5
12	Alto Araguaia – Lake (Teles et al., 1991)	17°24'07"S 53°03'16"W	Midwest	2	1	-	12,8	1671	711	Aw	E	H	3
13	Pampulha Lake (Marco JR et al., 2001)	19°51'05"S 43°58'42"W	Southeast	9	3	3	11,2	1394	818	Aw	D	H	3
14	Soledade Lake and streams (Silva et al., 1994)	20°30'31"S 43°45'46"W	Southeast	?	29	12	9,3	1435	964	Cwa	D	H	4
15	Três Irmãos Reservoir – lower Tietê River (França et al., 2007)	20°46'22"S 51°02'15"W	Southeast	2	3	10	11,7	1556	327	Cwa	B	H	1
16	Bariri Reservoir - middle Tietê River (Suriani et al., 2007)	22°16'01"S 48°43'36"W	Southeast	2	3	10	10,6	1209	453	Cwa	B	H	5
17	Guapimirim River basin (Giovanelli et al., 2005)	22°29'49"S 42°59'37"W	Southeast	4?	45?	12	12,3	1709	372	Aw	E	H	4
18	Juturnaíba Lake (Alvarenga et al., 1979)	22°38'02"S 42°18'17"W	Southeast	1 to 3	10	1, 6, 11	16,2	1069	11	Af	B	L	3

Loc.	Localities studied	Geogr. Coordinates	Geogr. region	Samples by year	Samples by sites	Sampler	Temp. (ºC)	Rainfall (mm/y)	Alt. (m)	Climate	Rainfall Interval	Relief	Richness
19	Upper Paraná River (Rangel e Souza et al., 2008)	22°44'02"S 53°13'54"W	South	4 to 8	3	3	12,1	1272	239	Cfa	C	L	1
20	Engenho Novo, Grande and Pequeno rivers (Santos et al., 2003)	22°56'26"S 43°28'50"W	Southeast	2 to 3	6	4	10	1655	790	Aw	C	H	4
21	Piraju Reservoir - Paranapanema River (Henry & Simão, 1986)	23°11'18"S 49°16'32"W	Southeast	1	6	1	10,1	1199	540	Cfa	B	H	7
22	Reservoir abandoned (Chieffi & Moretti, 1979)	23°23'09"S 51°04'39"W	South	12	2	12	10,9	1364	403	Cfa	B	H	2
23	Iguariaçá River wetland (Martello et al., 2008)	28°58'44"S 55°46'10"W	South	3	20	3	8,8	1635	89	Cfa	D	H	6
24	Middle Uruguai River (Castillo et al., 2007)	29°30'20"S 56°50'41"W	South	1 to 11	3	1, 6	8,9	1314	44	Cfa	C	H	10
25	Quadros Lake (Lanzer, 2001)	29°41'31"S 50°05'05"W	South	4	1	1, 6, 11	11,1	1485	3	Cfa	C	L	10
26	Ibucuí-Mirim River (Indrusiak, 1983)	29°43'16"S 54°19'20"W	South	6	4	1, 2, 3, 6	9,3	1667	107	Cfa	D	L	20
27	Sinos River basin – lower course (Mansur & Pereira, 2006)	29°50'34"S 51°08'46"W	South	REVIEW	REVIEW	REVIEW	10,2	1440	32	Cfa	D	L	21
28	Channel of a reservoir – COPESUL (Mansur et al., 1994)	29°52'00"S 51°21'59"W	South	4 to 10	3	1, 6	10,4	1394	10	Cfa	D	D	8
29	Touro Passo River – Uruguai River basin (Martello et al., 2006)	29°52'05"S 57°03'33"W	South	1 to 2	10	3, 6	8,7	1180	59	Cfa	C	H	6
30	Capivara stream – tributary of Jacuí River (Pereira et al., 2000b)	29°53'38"S 51°28'40"W	South	1to 3	8	3, 6, 11	10,5	1373	7	Cfa	D	L	27
31	Banhado Grande wetland– Gravataí River (Veitenheimer-Mendes et al., 1992)	29°57'36"S 50°42'46"W	South	3	8	3, 6, 11	9,6	1498	11	Cfa	C	L	19
32	Jacuí delta (Pfeifer & Pitoni, 2003)	29°58'21"S 51°14'30"W	South	1 to 4	3	3, 11	10,3	1397	2	Cfa	C	L	21
33	Camaquã River basin (Pereira et al., 2000a)	31°07'39"S 52°44'58"W	South	X	35	1, 3, 6	8,9	1449	211	Cfa	C	H	12
34	Taim Ecological Station (Mansur et al., 1991)	32°58'13"S 52°57'07"W	South	1 to 3	35	1, 3, 6, 11	8,6	1199	0	Cfa	C	L	13
35	Mangueira Lake (Lanzer, 2001)	33°00'39"S 52°38'04"W	South	4	1	1, 6, 11	8,8	1194	1	Cfa	C	L	10

Environmental data

Macro and meso spatial scales were defined arbitrarily. Macro scale variables were considered those occupying large areas (Köppen's climatic regions, rainfall intervals and relief; Figure 1), while meso scale variables occupy smaller areas and were included in the large areas, although not having hierarchical relationship (*s. s.)* with the formers (mean minimum temperature, mean annual rainfall and altitude).

Environmental data used for analyzing the influence of temperature, rainfall and altitude at macro spatial scales were qualitative (categorical) macro variables (Table 1). According to geographical localization of the localities, the Köppen's climatic regions analyzed were Af (Tropical forest), Am (Tropical monsoon), Aw (Tropical wet and dry or savanna), Bsh (Medium latitude steppe and desert), Cwa (Humid temperate climate with dry winters and warm summers), Cfa (Humid temperate climate with warm summers) (Figure 1b). The 250 mm rainfall intervals considered were 750-1000 (A), 1000-1250 (B), 1250-1500 (C), 1500-1750 (D), 1750-2000 (E), and 2500-2750 mm (F) (Figure 1c) based on INMET data (1992). This range involves more-striking variations in rainfall than do smaller ranges, and therefore must exert a greater influence on aquatic ecosystems and consequently on the mollusk communities. Relief was classified as H (highland), L (lowland), and D (depression, i.e., geographic regions lower than the areas around them), according to ROSS (1989) (Figure 1d). Environmental data at meso spatial scale were quantitative (continuous) meso variables (Table 1). Mean minimum temperature, mean annual rainfall and altitude data were obtained considering smaller areas around the mean point of each locality studied. For localities covering large basins or lakes, with sparse samples, mean values of the meso variables were obtained from a point localized in the center of the sampling area.

Information of meso and macro environmental variables (Table 1) were obtained from Worldclim climate database (<http://www.worldclim.org>) and geospatial vector data (*shapefile*) of Brazilian institutes (IBAMA, 2012; IBGE, 2012). All geoprocessing was conducted in the geographic information system software ArcGIS (ESRI, 2012).

Data Analysis

The similarity between pairs of communities was calculated using the Coefficient of Geographic Resemblance (CGR) (DUELLMAN, 1990), where: CGR = 2NS/NA + NB (NS:

species number in both areas; NA: species number in area A, NB: species number in area B). This ratio is equivalent to the Sørensen, Dice and Czekanowski indexes (WOLDA, 1981; KREBS, 1999; MAGURRAN, 2004), and ranges from 0 (maximum dissimilarity) to 1 (maximum similarity). The similarity matrices (CGR) were represented by cluster analysis (Clustering) on a weighted arithmetic mean method (WPGMA; SOKAL & MICHENER, 1958) to avoid the effect of sample size (species richness in different communities) on the analysis (VALENTIN, 1995). Possible distortions in the graphical representation of the similarity matrices caused by the cluster analysis method were evaluated by the cophenetic correlation coefficient (*r*) (ROMERSBURG, 1984). The closer the *r* value is to 1, the less is the distortion of the cluster dendrogram (ROHLF, 2000). Clusters were considered as groups if they showed similarity higher than 50%.

In order to analyze the existence of spatial autocorrelation (LEGENDRE & LEGENDRE, 1998), a geographic distance matrix of the locations was correlated with a similarity matrix of gastropod or bivalve composition, using the Mantel test (MANLY, 2000). This test performs correlations between matrices based on the Z statistic, where Z depends on the number of elements in the matrix to be compared (VALENTIN, 1995). Thus, a normalization is necessary to transform Z into a coefficient (*r*) ranging from 1 to -1 (VALENTIN, 2000). The significance of Z was determined by the Monte Carlo permutation test (SMOUSE et al., 1986), using 5000 permutations.

Both gastropod and bivalve communities showed spatial autocorrelation ($r = 0.21$, $P = 0.02$, and $r = 0.425$, $P = 0.0002$, respectively). Thus, the partial Mantel test (SMOUSE et al., 1986) was used in both communities to test the correlation between the similarity matrix and the environmental matrices, using the geographical distance matrix as a covariate. This test compares two matrices (A and B) by removing the effect of a third matrix (C in this study corresponds to the geographic distance matrix) using C regression on A and B. Thus, a residual matrix is obtained which represents the variations in A and B matrices that are not explained by the C matrix (SMOUSE et al., 1986). Therefore, the two residual matrices can be compared normally.

Although the use of Bonferroni's correction is questioned in ecological studies (MORAN, 2003), in the partial Mantel test performed here it was adopted in order to minimize the bias arising from the variability of samplers, sampling effort, etc.

The similarity in composition obtained for the bivalve and gastropod communities was correlated with the environmental matrices at meso and macro scales by the Mantel test.

Environmental matrices based on regional macro variables (qualitative data) were generated by assigning 1 to pairs of localities with the same environmental conditions, and 0 for pairs with different conditions. Matrices based on meso variables (quantitative data) were generated by Euclidean distance (MAGURRAN, 2004). Analyses were performed using the NTSYS PC 2.10S software (ROHLF, 2000).

RESULTS

Gastropods

The cluster analysis indicated low similarity among the gastropod communities of most localities selected for study. The dendrogram formed six groups (I to VI) with similarity higher than 50% (Figure 2), represented mainly by communities from localities that share the same climatic region and relief (Table 1 and Figure 2).

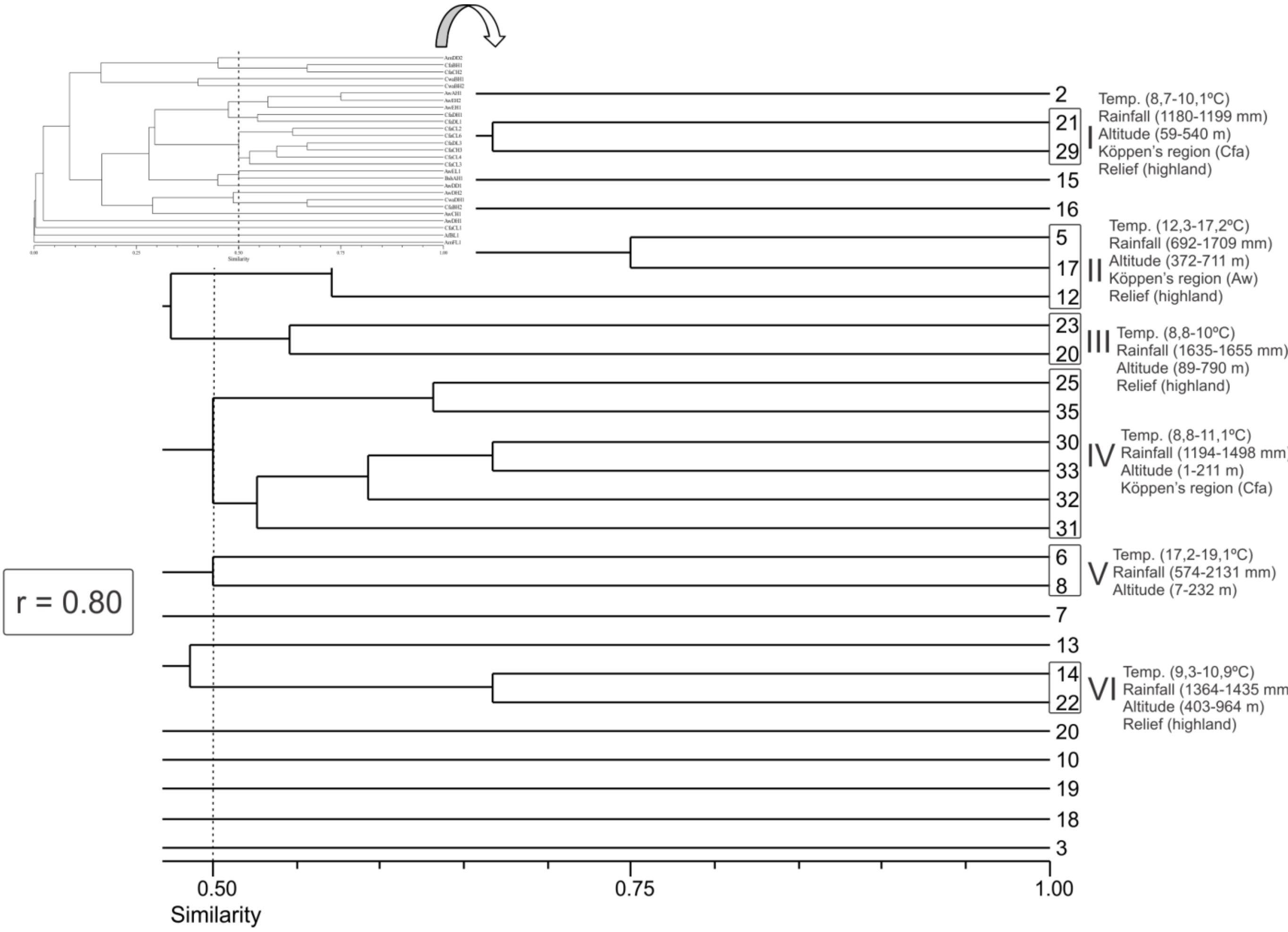

Figure 2 - Similarity (Coefficient of Geographic Resemblance; CGR) in the taxonomic composition of gastropods in five geographic regions of Brazil. *r* represents the Cophenetic Correlation Coefficient. The six groups formed with similarity higher than 50% are highlighted (I to VI) as well as the meso and macro scale variables shared by the localities on each group.

'I' grouped communities from two localities in highlands with Cfa climate, although these localities are located in different geographic regions and with different rainfall intervals; 'II' grouped communities of three highland localities with Aw climate, located in different geographic regions and with different rainfall intervals; 'III' grouped communities from two southern localities with Cfa climate and the same rainfall interval (1500-1750 mm), but located in terrain of different relief; 'IV' grouped communities from six southern localities with Cfa climate, located mainly in lowlands and with a 1250-1500 mm rainfall interval; 'V' grouped communities from two localities that share only the same geographic region (northeast); and 'VI' grouped communities from two southeast highland localities, located in different climatic regions and different rainfall intervals.

The gastropod species shared by all the localities contributing for each group are shown in Table 2. Other species are shown in Suplementary Data.

Table 2. Gastropod species shared by all the localities of each group (I to VI) exibting similarity higher than 50%, which were formed in the cluster analysis based on 27 localities. Group I (Loc. 21 and 29), group II (Loc. 5, 12, 17), group III (Loc. 20 and 23), group IV (Loc. 25, 30, 31, 32, 33, 35), group V (Loc. 6 and 8) and group VI (Loc. 14 and 22). The numbers in parenteses correspond to the number of localities, according to Table 1).

Species	**Groups (number of localities forming each group)**					
	I (2)	**II (3)**	**III (2)**	**IV (6)**	**V (2)**	**VI (2)**
Pomacea canaliculata (Lamarck, 1801)	X			X		
Lymnaea columella Say, 1817		X	X			
Aplexa marmorata (Guilding, 1828)		X	X			
Biomphalaria glabrata (Say, 1818)						X
Biomphalaria tenagophila (Orbigny, 1835)				X		X
Drepanotrema anatinum (Orbigny, 1835)					X	
Drepanotrema cimex (Moricand, 1839)					X	
Drepanotrema lucidum (Pfeiffer, 1839)					X	
Hebetancylus moricandi (Orbigny, 1837)			X			

Bivalves

The cluster analysis performed for bivalve communities indicated four small groups (I to IV) with similarity higher than 50% (Figure 3). The clusters represented mainly communities from localities with the same climatic region and rainfall range (Table 1 and Figure 3).

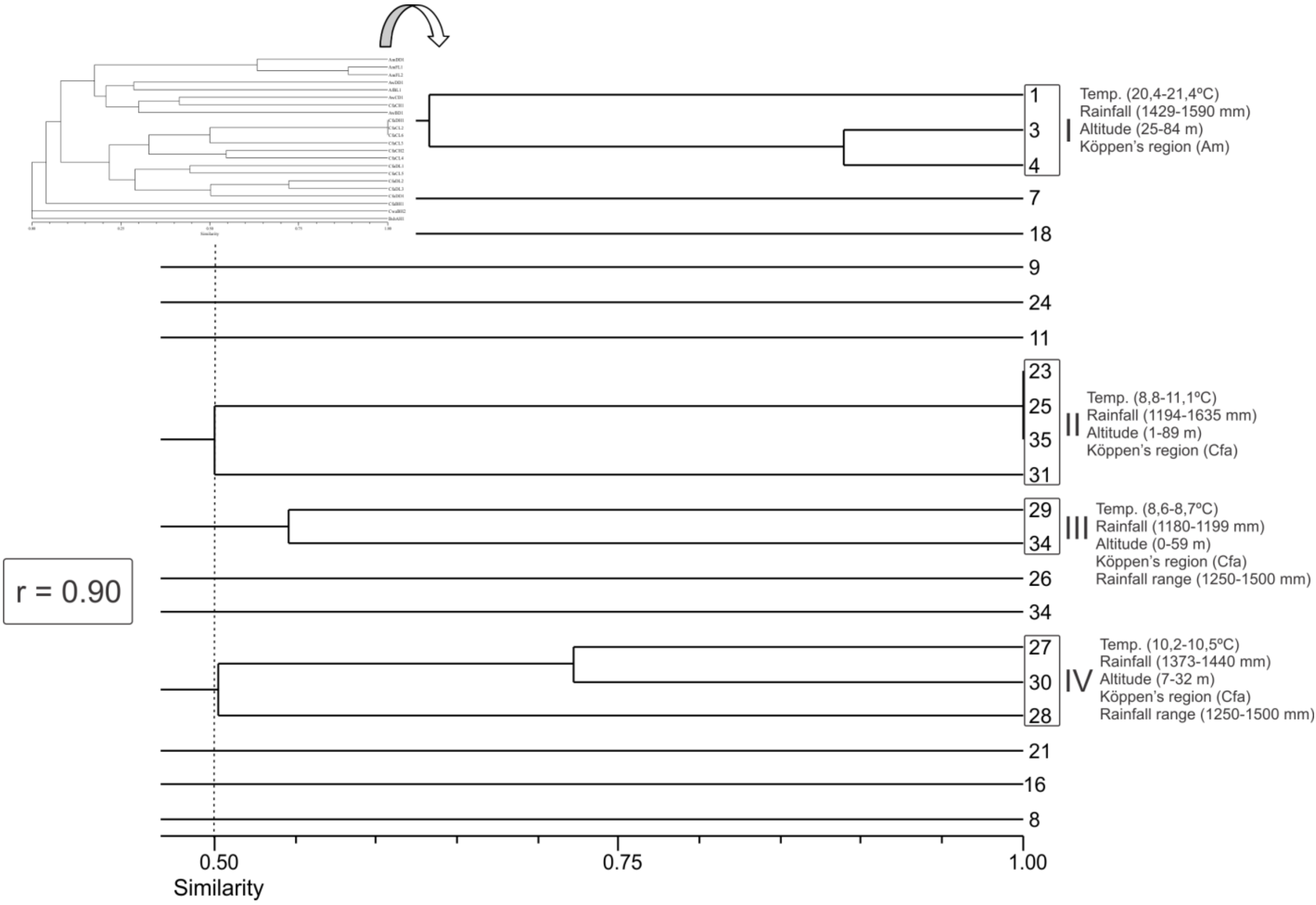

Figure 3 - Similarity (Coefficient of Geographic Resemblance; CGR) in the taxonomic composition of bivalves in five geographic regions of Brazil. *r* represents the Cophenetic Correlation Coefficient. The four groups formed with similarity higher than 50% are highlighted as well as the meso and macro scale variables shared by the localities on each group.

Thus, 'I' grouped communities from three northern Am climate localities with a rainfall interval of 2500 to 2750 mm, mainly situated in lowlands; 'II' grouped communities from four southern Cfa climate localities, mostly located in lowlands, but with different rainfall intervals; 'III' grouped communities from two southern localities with Cfa climate and a rainfall interval of 1250-1500 mm, but in terrain with different relief; and 'IV' grouped communities from three southern localities with Cfa climate and a rainfall interval of 1500-1750 mm, but again in terrain with different relief.

The bivalve species shared by all the localities contributing for each group are shown in Table 3. Other species are shown in Suplementary Data.

Table 3. Bivalve species shared by all the localities forming each group (I to IV) with similarity higher than 50%, which were formed from cluster analysis based on 22 locations. Group I (Loc. 1, 3, 4), group II (Loc. 23, 25, 31, 35), group III (Loc. 29, 34) and group IV (Loc. 27, 28, 30). The numbers in parenteses correspond to the number of localities, according to Table 1).

Species	**Groups (number of localities forming each group)**			
	I (3)	**II (4)**	**III (2)**	**IV (3)**
Castalia ambigua Lamarck, 1819	X			
Castalia martensi (Ihering, 1891)				X
Diplodon martensi (Ihering, 1893)				X
Diplodon obsolescens F. Baker, 1914	X			
Diplodon suavidicus (Lea, 1856)	X			
Prisodon obliquus Schumacher, 1817	X			
Triplodon corrugatus (Lamarck, 1819)	X			
Anodontites trapesialis (Lamarck, 1819)				X
Anodontites trapezeus (Spix, 1827)				X
Monocondylaea minuana Orbigny, 1835				X
Eupera klappenbachi Mansur & Veitenheimer, 1975		X	X	X
Eupera simoni (Jousseaume, 1889)	X			
Pisidium punctiferum (Guppy, 1867)			X	
Pisidium sterkianum Pilsbry, 1897			X	

Some of these species were exclusive to certain groups, and did not occur in any other group or locality studied here. *Castalia ambigua* Lamarck, 1819, *Diplodon obsolescens* F. Baker, 1914, *Prisodon obliquus* Schumacher, 1817 and *Triplodon corrugatus* (Lamarck, 1819) were exclusive to group I not occurring in another locality, and *Castalia martensi* (Ihering, 1891) occurred only in group IV.

The results indicated that the macro variable Köppen's climatic regions had a significant positive correlation with the compositions of the gastropod and bivalve communities (Table 4).

Table 4. Correlation values from Partial Mantel tests among meso and macro variables (altitude, rainfall, temperature) and gastropod and bivalve communities, after removing spatial autocorrelation and using Bonferroni's correction ($P < 0.005$). Significant results are in bold.

	Meso variables			Macro variables		
	Altitude	Local rainfall	Local temp.	Relief	Rainfall Range	Köppen
Gastropoda	r = -0.0705	r = -0.03	r = -0.125	r = 0.04	**r = 0.14**	**r = 0.28**
	P = 0.2114	*P* = 0.377	*P* = 0.045	*P* = 0.25	***P* = 0.014**	***P* = 0.0016**
Bivalvia	**r = -0.3601**	r = -0.14	r = -0.017	r = -0.003	**r =0.17**	**r =0.33**
	***P* = 0.0004**	*P* = 0.101	*P* = 0.378	*P* = 0.49	***P* = 0.013**	***P* = 0.0006**

If a marginal significance is considered (FARJI-BRENER, 2006), the rainfall range also had a reasonable positive correlation with the compositions of both mollusk communities.

Among the meso variables, only altitude showed a correlation, but only with bivalve community composition.

DISCUSSION

The macro variable Köppen's climatic region showed good relationships to the spatial distributions of both the gastropod (28%) and bivalve (33%) communities. The influence of climatic zones on the structure of freshwater mollusk communities has not been studied previously. However, the effects of climate were evaluated indirectly, by means of studies conducted across wide altitudinal ranges (e.g., STURM, 2007; PÉREZ-QUINTERO, 2012). The effects of climate on mollusk communities are also evident for terrestrial gastropods that inhabit areas with a wide annual range of climatic conditions (HAUSDORF, 2006). In freshwater ecosystems, air temperature can modulate water temperature, mainly in shallow settings (O'DRISCOLL & DEWALLE, 2006). The many bivalves and gastropods that are common in shallow freshwater environments (HUBENDICK, 1958; VAUGHN & TAYLOR, 1999) can be easily affected by climatic ranges. Water temperature is a very important factor for many mollusk species, affecting biological processes such as reproduction and metabolic rates, including filtering rates in bivalves (VAUGHN & HAKENKAMP, 2001). Extreme temperatures can affect the behavior such as burrowing and dispersal (MCMAHON & BOGAN, 2001; KAPPES & HAASE, 2012). In the Neotropics studies on the biology of species are rare, focused especially for mollusks with medical importance and to their reproduction (e.g., MANSUR et al., 2012).

The compositional similarity of 13 of the 27 gastropod communities and 12 of the 22 bivalve communities studied here was correlated to the Köppen's climatic regions. *Pomacea canaliculata* (Lamarck, 1801), *Biomphalaria tenagophila* (Orbigny, 1835) and *Hebetancylus moricandi* (Orbigny, 1837) were shared by groups I, III and IV, which were related to Cfa climate; while *Lymnaea columella* Say, 1817 and *Aplexa marmorata* (Guilding, 1828) were shared by group II, related to Aw climate. For bivalves, the Köppen's climatic regions were markable related to all groups formed (Figure 3). Species such as *C. ambigua*, *D. obsolescens*, *Diplodon suavidicus* (Lea, 1856), *P. obliquus*, *T. corrugatus* and *Eupera simoni* (Jousseaume, 1889) were related to Am climate; while *C. martensi*, *Diplodon martensi* (Ihering, 1893), *Anodontites trapesialis* (Lamarck, 1819), *Anodontites trapezeus* (Spix, 1827), *Monocondylaea minuana* Orbigny, 1835, *Eupera klappenbachi* Mansur and Veitenheimer, 1975, *Pisidium* *punctiferum* (Guppy, 1867) and *Pisidium sterkianum* Pilsbry, 1897 were related to Cfa climate.

Rainfall range were also associeted to the spatial distribution of both communities, but with lower correlations (14%, gastropods; 17%, bivalves) than those obtained for Köppen's climatic regions, and with only marginal significance. The hydroperiod of continental water bodies can be strongly related to variations in annual cumulative precipitation (LEWIS JR, 2008), mainly in environments that depend on rainfall to recharge (BONADA et al., 2007; ROLAND et al., 2012). Hydroperiod is an important factor for the development of aquatic communities because it is commonly related to the size (area) and stability of water bodies (STENDERA et al., 2012). Floods and droughts are important to the system productivity and habitats availability (LAKE, 2000). The influence of hydroperiod on mollusk community composition has been observed in previous studies (MALTCHIK et al., 2010; HOVERMAN et al., 2011, PÉREZ-QUINTERO, 2011). Some communities studied here were influenced not only to Köppen's climatic regions, but also to rainfall intervals. For example, the gastropod *H. moricandi* was related to localities with rainfall intervals of 1500-1750 mm, as were the bivalves *C. martensi*, *D. martensi*, *A. trapesialis*, *A. trapezeus* and *M. minuana*. The bivalve *E. klappenbachi* occurred predominantly in localities in areas with rainfall intervals of 1250-1500 mm, as did the group containing *P. punctiferum* and *P. sterkianum*, and the gastropods *P. canaliculata* and *B. tenagophila*. In fact, Köppen's climatic regions are based on a combination of both mean temperature and rainfall factors (KÖPPEN, 1918).

Temperature and rainfall commonly affect gastropod and bivalve communities at local spatial scale (PÉREZ-QUINTERO, 2011; KOTZIAN & AMARAL, 2013). Thus the negative result obtained here, at meso spatial scale analysis, may reflect the capacity of the Brazilian freshwater malacofauna to adapt to environmental adversity (see review in KOTZIAN & SIMÕES, 2006). Many species of pulmonate gastropods can tolerate extreme variations in temperature and hydroperiod (BROWN, 2001). For example, planorbids have secondary gills and respiratory pigment (hemoglobin) that allow them to survive in low-oxygen environments (STRONG et al., 2008). Ancylids can develop a septum related to the conservation of body water (FERNÁNDEZ, 1981). Non-pulmonate gastropods, such as ampullarids, can also tolerate long periods of exposure to air, having both gills and lungs (STRONG et al., 2008). Some bivalves (Sphaeriidae) are also able to tolerate periods of drought, surviving to long exposures to air (MCMAHON & BOGAN, 2001). However, variations among the local temperature and rainfall of many localities within a certain Köppen's climatic region were small. For example, localities in the Cfa region had mean temperatures ranging from 8.6º to 12.1ºC and rainfall from 1180 to 1667 mm (Table 1).

Altitude was the only environmental factor that showed a relationship with the spatial distribution of mollusk communities at the meso spatial scale but just with bivalve communities. Bivalves are filter-feeders and depend on suspended organic matter to survive (VAUGHN & HAKENKAMP, 2001). Fine particles are available especially in middle-to high-order streams, which are commonly located in flat areas where the water velocity decreases and particles can settle (VANNOTE et al., 1980); as well as in lentic settings. These conditions also facilitate the occurrence of macrophytes (HASLAM, 1978), an important factor in the establishment of some species of bivalves (WATSON & ORMEROD, 2005). However, lowlands and depressions per se do not guarantee the presence of fine particles in many Brazilian streams located in lowlands, because they may be low-order and/or intermittent. Some Brazilian plateaus contain high-order streams (5th, 6th) that flow between mountains, at low altitudes, in straight valleys (e.g., localities 24, 29 and 33). Although many watersheds are included in areas of plateau relief, the riverbeds themselves may be at low altitudes, forming suitable conditions for bivalves.

The influence of altitude on bivalve community composition has been observed previously (e.g., STURM, 2007; MALTCHIK et al., 2010; DUDGEON, 2012). Almost all bivalve community groups formed from the cluster analysis are constituted by communities from localities with local altitude of 100 m or less. Unionoida was the main bivalve taxon shared by these groups (Table 3). The strong relationship between the downstream/upstream gradient and the diversity of mussels is a well-known distributional feature of freshwater mollusk communities (e.g., MOUTHON, 1999; STURM, 2007; DUDGEON, 2012). The Unionoida represent about 60% of the diversity of the Brazilian freshwater bivalve genera (MANSUR et al., 2012) and 65% of their species diversity (SIMONE, 2006).

Gastropod communities from 10 localities showed less than 50% similarity (Figure 2). This could be explained, besides variables not assessed, by the inclusion of artificial environments in the analysis (e.g., reservoirs; 7, 15, 16) or localities containing exclusive species (e.g., 2: *Doryssa heathi* (Baker, 1914), *Doryssa starksi* (Baker, 1913); 3: *Pomacea papyracea* (Spix, 1827); 7: *Biomphalaria schrammi* (Crosse, 1864); 20: *Pomacea sordida* (Swainson, 1823) (see Suplementary data = [Apêndice]) or a low richness (Table 1). Likewise, bivalve communities from 10 localities did not form groups. In some cases, the type of sampler may have precluded a reliable sampling of endofaunal bivalves; at 16 (Van

Veen grab) and 8 (Surber) localities only one species each was recorded, *Diplodon expansus* (Kuster, 1856) and *Pisidium pulchellum* (Orbigny, 1835), respectively. Most of the 22 localities analyzed contained one or more bivalve species that were found exclusively in that locality. The use of only one sampler to collect freshwater gastropods in some localities (10, 13, 15, 16, 18, 19, 20) possibly prevented the formation of clusters because of the wide range of habitats used by these mollusks within the ecosystem and their aggregate distribution. However, there is no evidence that the sampler may have affected the bivalve species recorded, because even localities where only one type of sampler was used showed a large number of species (11, 21).

The Mantel test also indicated strong spatial autocorrelation, especially for the bivalve communities. The spatial autocorrelation hypothesis states that elements of an ecosystem closer to each other in space are likely to be influenced by the same environmental factors (LEGENDRE & FORTIN, 1989). This effect arises from differences in the responses of organisms to local environmental conditions that vary in space, and is closely related to the organisms' dispersal capabilities. This implies that even if the environment changes in space, the chance of finding the same or similar communities is higher if both are spatially close to each another. Mollusks show active 'slow and steady' dispersal, through crawling (KAPPES & HAASE, 2012), but they can also disperse passively, through water flow or vectors (KAPPES & HAASE, 2012, see discussion in MCMAHON & BOGAN, 2001). Dispersal with fish is a well-known strategy used by bivalves (VAUGHN & TAYLOR, 1999; VAUGHN, 2005), especially by some Unionoida (KAT, 1984; VAUGHN, 2005). Some gastropods can also survive passage through the fish gut and establish a new population in different suitable environments (BROWN, 2007). Although fishes can assist mollusks to disperse over wide areas, their distribution will be restricted by the limits of hydrographic basins. Consequently, spatial proximity is an important factor affecting the similarity of mollusk communities. In Brazil, Köppen's climatic regions have a mosaic distribution, but in general, they are geographically well separated, and correspond somewhat to the hydrographic regions. Thus, the slow and limited dispersal ability of mollusks explains the observed spatial autocorrelation and the stronger influence of climatic regions on bivalve communities than on gastropod communities.

CONCLUSION

Although this meta-analysis may involve some bias in the results, the relationships observed among the environmental factors and the communities analyzed are consistent with existing knowledge of mollusk ecology. The spatial distribution of both gastropod and bivalve communities of Brazilian freshwater systems is related to the regional macro variable Köppen’s climatic regions, which are characterized not only by ranges of mean annual temperatures, but also by ranges of rainfall. Temperature and rainfall range are related to the biology of many mollusk species, and consequently affect the taxonomic composition and also the overall spatial distribution patterns of these communities. Köppen’s climatic regions especially influence the composition of bivalve communities because they are related to certain Brazilian hydrographic basins, which can limit the dispersal of some species. On the other hand, geographical relief does not influence community composition, but its effect on bivalve communities becomes apparent when analyzed at the meso-spatial scale (mean altitude). More than 60% of the Brazilian freshwater bivalvia diversity is comprised by Unionoids and they are closely related to lowland areas, even though these areas may be located in regions of rugged relief. In other words, the perceived influence of temperature, rainfall and altitude on the Brazilian freshwater mollusk communities depends on the scale of the analysis. Therefore, conservation programs for this malacofauna must take into account the different climatic and hydrographic regions, and give priority to low-altitude areas, including some streams in montane regions.

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ARTIGO 2

MACROVARIABLES PREDICTING THE COMPOSITION OF BRAZILIAN FRESHWATER MOLLUSK COMMUNITIES: THE INFLUENCE OF TERRESTRIAL AND AQUATIC FACTORS

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ABSTRACT

Freshwater mollusks, especially mussels, have been presenting the highest extinction rates in the last decades specially due to the impact of human activities on the freshwater environment. However, preservation areas have been determined based on terrestrial ecosystems data, failing to adequately protect freshwater organisms. In this study the influence of terrestrial (Köppen's climatic region, Biome, and Vegetal Formation) and aquatic macrovariables (Hydrographic region, Freshwater Habitat and Freshwater Ecosystem) on the Brazilian freshwater mollusk communities were analyzed. Meta-analyses based on data from 35 localities in the country were conducted, in order to determine the influence of these drivers on the taxonomic composition of gastropod and bivalve communities separately. Despite the spatial autocorrelation, terrestrial variables showed greater influence on the communities, mainly bivalves. Although the Köppen's region has presented the strongest correlation with both classes, the Biome and the Forest formation correlated only with bivalves. Among aquatic macrovariables, just the Hydrographic region had some relationship to both communities. The greater influence of terrestrial macrovariables may reflect the intrinsic connection between aquatic and terrestrial environments. Different terrestrial profiles may impose different physical, chemical and biological traits on the freshwater environments. Additionally, bivalves may be more dependent of suitable terrestrial and aquatic conditions to survive and reproduce than gastropods, because they are sedentary, bad dispersers and more sensitive to habitat changes.

KEYWORDS: Neotropical Region, Ecology, Gastropods, Bivalves, Biomes.

INTRODUCTION

Although freshwater ecosystems comprise about 12% of the global animal diversity and many terrestrial species depend indirectly of aquatic environments (ABRAMOVITZ, 1996), determination of priority areas for biodiversity conservation has been based often on terrestrial data, primarily on vertebrate communities (MYERS et al., 2000; STRAYER, 2006). As freshwater ecosystems are strongly influenced by terrestrial ecosystems, land conservation measures can still provide some protection to rivers and lakes (SAUNDERS et al., 2002; MANCINI et al., 2005). However, these protection areas may not adequately address the needs of aquatic organisms, especially those inhabiting rivers. The conservation areas are commonly established downstream of degraded areas and usually located in only one bank or in small fragmented areas, thus lacking the connectivity necessary to sustain a broad range of aquatic habitats and processes (see discussion in HERBERT et al., 2010). Additionally, conservation areas designed specifically for aquatic environments may not guarantee effective protection to their inhabitants. Disturbance in land use and hydrology, and also the introduction of exotic species may occur beyond their limits, compromising the integrity of the reserves (SAUNDERS et al., 2002).

Another important question concerning preservation of freshwater ecosystems is the scarcity of studies available about the importance of wide spatial scale environmental factors, especially qualitative macrovariables driving the distribution and structure of their communities. For example, the influence of biomes and other ecoregions (to aquatic ecosystems see HARDING & WINTERBOURN, 1997) on animal spatial distribution is best comprehended in the case of terrestrial vertebrates (RODRÍGUEZ et al., 2005; SANTOS et al., 2009; HERNÁNDEZ-SALINAS & RAMÍREZ-BAUTISTA, 2012), and provides useful information for protecting terrestrial ecosystems. This knowledge is especially important for the conservation policy of large-area countries, because it allows to concentrate preservation efforts in ecoregions sustaining different communities, and to protect the overall biodiversity.

Studies dealing with aquatic macrovariables and their influence in freshwater communities are scarce (SANDIN & JOHNSON, 2004), and focus mainly on fish communities (BROSSE et al., 2013). Recently, a model of segregation of watersheds into smaller units (see further information at *www.feow.org*) was proposed for the establishment of protection areas. These "freshwater ecoregions" (ABELL et al., 2008) were based on fish data, the most studied freshwater group on a global scale. These freshwater ecoregions are defined as large areas encompassing one or more freshwater systems, containing distinct aquatic assemblages and similar environmental conditions. Thus, they were classified within biogeographic regions, considering the climate and major habitat types (e.g., tropical and subtropical upland rivers).

Freshwater mollusks are among the most endangered invertebrate group in the world. Human activities such as pollution and mainly hydrologic modifications (NEVES et al., 1997; BOGAN, 2008; PÉREZ-QUINTERO, 2011; PEREIRA et al., 2013) have determined the extinction or extirpation of many species over the world, especially freshwater mussels (RAHEL, 2002; LYDEARD et al., 2004; PEREIRA et al., 2013). The degree of the threat facing these animals is not being accompanied by studies dealing with wide spatial scale distribution (but see PEREIRA et al., 2013 for an exception), as well as with the ecological macrovariables driving the structure of their communities. An ongoing research conducted by the authors of the present study shows that Köppen's climatic regions are important factors controlling the spatial distribution and structure of the communities, according to their composition. However, the influence of wide scale aquatic macrovariables on freshwater mollusk communities remains unknown, precluding the adequacy of strategies for their preservation.

Understanding the role of terrestrial and aquatic environmental factors on the spatial distribution and structure of freshwater mollusk communities constitute an important and indispensable piece of information for mollusk conservation programs. It may allow the choice of areas containing different communities, enabling protection of the overall taxonomical diversity in large-area countries. This study analyzes the influence of certain terrestrial and aquatic macrovariables on the spatial distribution of Brazilian freshwater mollusk communities. Due to the strictly aquatic life habit of gastropods and bivalves, our hypothesis is that the Köppen's climatic region, biome and vegetal formation, here considered terrestrial macrovariables, should be drivers of less importance than macrovariables directly related to freshwater environments, such as hydrographic region, freshwater habitat and freshwater ecosystem.

MATERIAL AND METHODS

Community Selection

A thorough review of the current literature on freshwater Brazilian mollusks was performed. Certain criteria were used to select the studies because both richness and composition are influenced by differences in sampling effort (e.g., see discussions by SANTOS et al., 2009 and KORICHEVA et al., 2013). These studies should focus on community structure and the environments (so not including inventories and species lists by geographic areas, such as municipalities or states), studies exclusively dedicated to mollusks and preferentially published in peer-reviewed journals or book chapters (with the exception of those by ALVARENGA et al., 1979; MANSUR et al., 2007; FERNANDEZ, 2011; KOTZIAN & AMARAL, 2013).

Studies conducted in very large and neighbouring areas (rivers comprising distances greater than 20 km or lakes with less than 10 km of distance from each other; e.g., MANSUR & PEREIRA, 2006; LANZER, 2001; FRANÇA et al., 2007; SURIANI et al., 2007) whose subareas presented a species list were analyzed individually (stream stretches or individual lakes or ponds). For example, to each study regarding a river of great extension with a species list to each stretch (e.g., superior, medium and inferior regions), such division was maintained and each stretch was considered a locality. However, from these studies with samples in nearby areas and a species list by subarea (e.g., LANZER, 2001) we chose only localities with the highest richness.

To avoid the influence of sampling effort of each study in the meta-analysis were prioritized those having more than one kind of sampler and with several repetitions or subsamples. Cases of nomenclatural synonymy among the species lists were evaluated using the specialized literature for each taxon (for instance, MANSUR & PEREIRA, 2006). Exotic species and taxa with indeterminate identification of their species (sp.) were excluded from the analyses (i.e., only the species native list that was considered).

Based on geographic coordinates (i.e., localization) of the sampling sites provided by the studies, a medium geographical point was defined to represent each locality to thereafter obtain environmental information (Table 1). Thereby in this meta-analysis our sampling unit is each locality regardless of the number of sample points.

Thirty five localities were selected from thirty three studies. As some studies on freshwater mollusk communities deal exclusively with either gastropod or bivalve communities (e.g., PEREIRA et al., 2000a, PIMPÃO & MANSUR, 2009), the mollusks classes were analyzed separately. So, from 35 localities (a total of 109 species), 27 were used for gastropod community analyses (39 species), and 22 for bivalve community analyses (70 species).

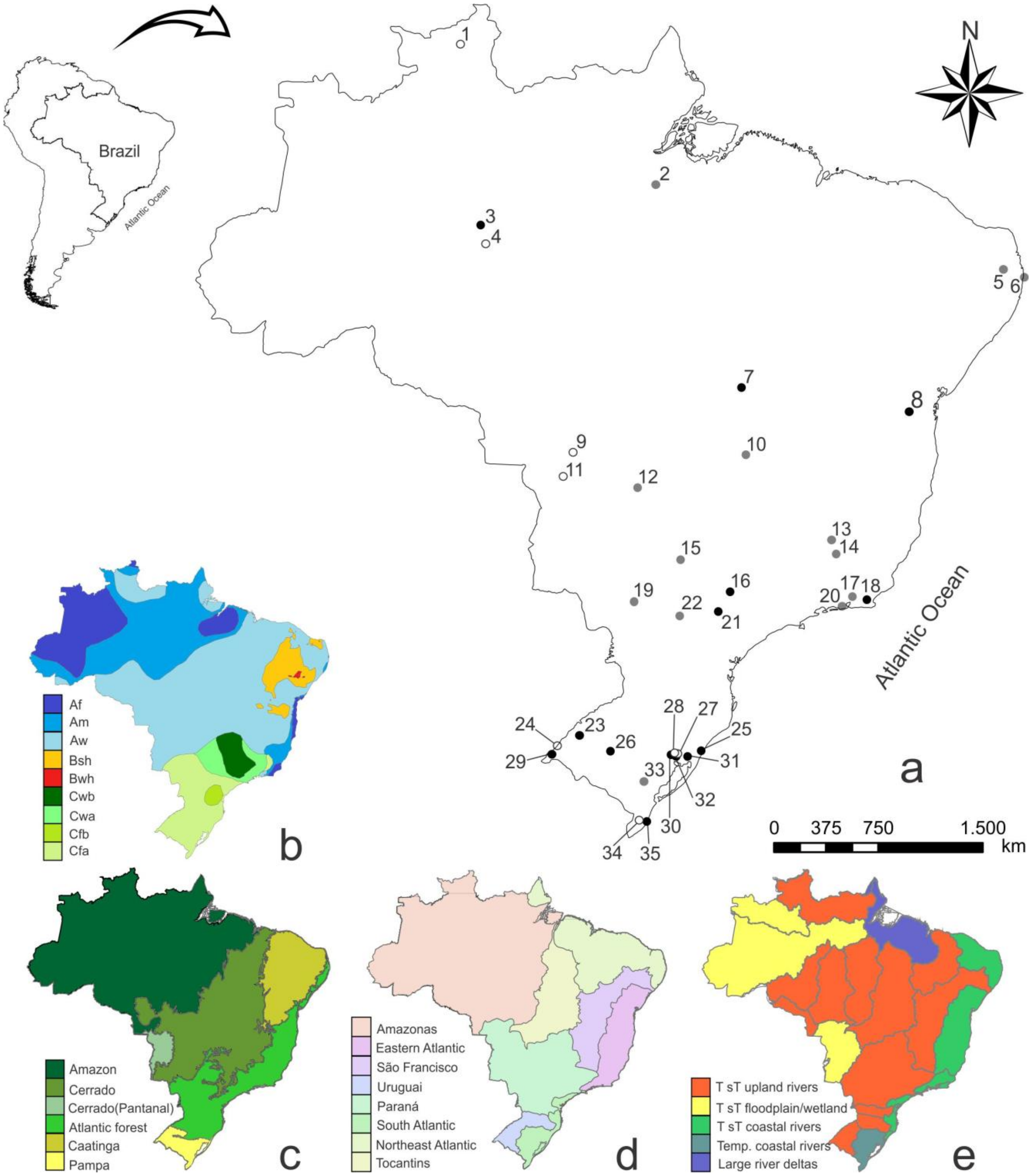

Figure 1 - a) Locations of the 35 localities selected for studying Brazilian gastropod and bivalve communities. Black dots: localities with both gastropod and bivalve communities; Gray dots: localities with only gastropod communities; Empty dots: localities with only bivalve communities. b-e) simplified maps showing b) Köppen's climatic regions; c) Biomes; d) Hydrographic regions; e) Freshwater habitat (T sT: Tropical and Subtropical; Temp.: Temperate). The number and abbreviation for each locality are listed in Table 1. Map "e" was adapted from Freshwater Ecoregions of the World (*www.feow.org*).

Table 1. Location, environmental characterization and sampling method of the 35 Brazilian localities analyzed (Samplers: 1 – manual; 2 – analysis of rocks/logs; 3 – analysis of macrophytes; 4 – artificial substrate; 5 – free diving; 6 – sieve; 7 – Surber; 8 – D-frame net; 9 – trawl net; 10 – Van Veen grab; 11 – Ekman grab; 12 – Metallic scoop). Köppen’s region: Am – Tropical monsoon; Aw – Wet and dry tropical climate or savanna; Bsh – Medium latitude steppe and desert; Cwa – Humid temperate climate with dry winters and warm summers; Af – Tropical forest; Cfa – Humid temperate climate with warm summers. Hydrographic region: Am – Amazonas; NA – Northeast Atlantic; To – Tocantins; EA – East Atlantic; Pa – Paraná; SF – São Francisco; Ur – Uruguay; SA – South Atlantic. Biome: Am – Amazon; Ca – Caatinga; AF – Atlantic Forest; Ce – Cerrado; Pa – Pampa. Freshwater habitat: 1 – Tropical and subtropical upland rivers; 2 – Tropical and subtropical floodplain rivers and wetland complexes; 3 – Tropical and subtropical coastal rivers; 4 – Temperate coastal rivers. Vegetal formation: DOF – Dense Ombrophilous Forest; SDF – Seasonal Deciduous Forest; SSF – Seasonal Semideciduous Forest; St – Steppe; Sa – Savanna; PF – Pioneer Formations. Freshwater Ecosystem: Ri – river; Re – reservoir; St – stream; La – lake; We – wetland.

Loc.	**Localities studied**	**Geogr. Coordinates**	**Geogr. Region**	**Samples by year**	**Samples by sites**	**Sampler**	**Köppen’s region**	**Hydrographic region**	**Biome**	**Freshwater habitat**	**Forest formation**	**Freshwater ecosystem**	**Richness**
1	Uraricoera, Branco and Parimé rivers (Mansur & Valer 1992)	03°21'33"N 61°20'15"W	North	1	10	1	Am	Am	Am	1	DOF	Ri	10
2	Middle Xingu River (Jesus et al. 2007)	03°13'49"S 52°12'38"W	North	4	8?	1, 7	Am	Am	Am	1	DOF	Ri	3
3	Aripuanã and Madeira rivers (Pimpão 2007)	05°07'13"S 60°24'06"W	North	1	51	1, 2, 3, 5, 8, 9	Am	Am	Am	2	DOF	Ri	9
4	Aripuanã and Juma rivers (Pimpão & Mansur 2009)	06°00'00"S 60°11'00"W	North	1	1?	1, 2, 3	Am	Am	Am	2	DOF	Ri	10
5	Bodocongó Reservoir (Abílio et al. 2006)	07°12'50"S 35°54'57"W	Northeast	3 to 6	3	3, 6, 10	Aw	NA	Ca	3	St/SDF	Re	4
6	Stream of Distrito Carne de Vaca (Souza et al. 2010)	07°34'29"S 34°50'00"W	Northeast	2 to 10	9	6	Aw	NA	AF	3	PF	St	5
7	Reservoirs on Tocantins River (Fernandez 2011)	12°47'36"S4 8°14'37"W	North	4 to 12	90	1, 12	Aw	To	Ce	1	St	Re	19
8	Contas River basin (Kotzian & Amaral, 2013)	13°51'23"S 40°20'32"W	Northeast	2	20	7	BSh	EA	Ca	3	Sa	Ri	8
9	Cuiabá River (Mansur et al. 2007)	15°45'27"S 56°07'43"W	Midwest	-	18	-	Aw	Pa	Ce	2	Sa	Ri	19
10	Lake Paranoá and Riacho Fundo stream (Martins-Silva & Barros 2001)	15°52'15"S 47°58'38"W	Midwest	1 to 5	5	8	Aw	Pa	Ce	1	Sa	La/st	1
11	Lakes along the Cuiabá River (Colle & Callil 2012)	16°50'05"S 56°34'35"W	Midwest	2	20	1	Aw	Pa	Ce	2	Sa/SSF	Ri	5
12	Alto Araguaia – Lake (Teles et al. 1991)	17°24'07"S 53°03'16"W	Midwest	2	1	-	Aw	To	Ce	1	Sa	La	3
13	Pampulha Lake (Marco JR et al. 2001)	19°51'05"S 43°58'42"W	South	9	3	3	Aw	SF	Ce	1	Sa/SSF	La	3
14	Soledade Lake and streams (Silva et al. 1994)	20°30'31"S 43°45'46"W	South	?	29	12	Cwa	EA	AF	1	SSF	La/St	4
15	Três Irmãos Reservoir – lower Tietê River (França et al. 2007)	20°46'22"S 51°02'15"W	South	2	3	10	Cwa	Pa	AF	1	SSF	Re	1
16	Bariri Reservoir - middle Tietê River (Suriani et al. 2007)	22°16'01"S 48°43'36"W	South	2	3	10	Cwa	Pa	AF	1	SSF	Re	5

Loc.	Localities studied	Geogr. Coordinates	Geogr. Region	Samples by year	Samples by sites	Sampler	Köppen’s region	Hydrographic region	Biome	Freshwater habitat	Forest formation	Freshwater ecosystem	Richness
17	Guapimirim River basin (Giovanelli et al. 2005)	22°29'49"S 42°59'37"W	South	4?	45?	12	Aw	EA	AF	3	DOF	St	4
18	Juturnaíba Lake (Alvarenga et al. 1979)	22°38'02"S 42°18'17"W	South	1 to 3	10	1, 6, 11	Af	EA	AF	3	DOF	Re	3
19	Upper Paraná River (Rangel e Souza et al. 2008)	22°44'02"S 53°13'54"W	South	4 to 8	3	3	Cfa	Pa	AF	1	SSF	Ri	1
20	Engenho Novo, Grande and Pequeno rivers (Santos et al. 2003)	22°56'26"S 43°28'50"W	South	2 to 3	6	4	Aw	EA	AF	3	DOF	Ri	4
21	Piraju Reservoir - Paranapanema River (Henry & Simão 1986)	23°11'18"S 49°16'32"W	South	1	6	1	Cfa	Pa	Ce	1	Sa	Re	7
22	Abandoned reservoir (Chieffi & Moretti 1979)	23°23'09"S 51°04'39"W	South	12	2	12	Cfa	Pa	AF	1	SSF	Re	2
23	Iguariaçá River wetland (Martello et al. 2008)	28°58'44"S 55°46'10"W	South	3	20	3	Cfa	Ur	Pa	1	Sa/St	We	6
24	Middle Uruguai River (Castillo et al. 2007)	29°30'20"S 56°50'41"W	South	1 to 11	3	1, 6	Cfa	Ur	Pa	1	St	Ri	10
25	Quadros Lake (Lanzer 2001)	29°41'31"S 50°05'05"W	South	4	1	1, 6, 11	Cfa	SA	AF	3	DOF	La	10
26	Ibicuí-Mirim River (Indrusiak 1983)	29°43'16"S 54°19'20"W	South	6	4	1, 2, 3, 6	Cfa	Ur	Pa	1	Sa	St	20
27	Sinos River basin – lower course (Mansur & Pereira 2006)	29°50'34"S 51°08'46"W	South	REVIEW	REVIEW	REVIEW	Cfa	SA	Pa	4	Sa/SDF	Ri	21
28	Channel of a reservoir – COPESUL (Mansur et al. 1994)	29°52'00"S 51°21'59"W	South	4 to 10	3	1, 6	Cfa	SA	Pa	4	Sa/SDF	St	8
29	Touro Passo River – Uruguai River basin (Martello et al. 2006)	29°52'05"S 57°03'33"W	South	1 to 2	10	3, 6	Cfa	Ur	Pa	1	St	Ri	6
30	Capivara stream – tributary of Jacuí River (Pereira et al. 2000b)	29°53'38"S 51°28'40"W	South	1to 3	8	3, 6, 11	Cfa	SA	Pa	4	Sa/SDF	St	27
31	Banhado Grande wetland– Gravataí River (Veitenheimer-Mendes et al. 1992)	29°57'36"S 50°42'46"W	South	3	8	3, 6, 11	Cfa	SA	Pa	4	Sa/SDF	We	19
32	Jacuí delta (Pfeifer & Pitoni 2003)	29°58'21"S 51°14'30"W	South	1 to 4	3	3, 11	Cfa	SA	Pa	4	Sa/SDF	Ri	21
33	Camaquã River basin (Pereira et al. 2000a)	31°07'39"S 52°44'58"W	South	X	35	1, 3, 6	Cfa	SA	Pa	4	Sa	Ri	12
34	Taim Ecological Station (Mansur et al. 1991)	32°58'13"S 52°57'07"W	South	1 to 3	35	1, 3, 6, 11	Cfa	SA	Pa	4	PF	La/St	13
35	Mangueira Lake (Lanzer 2001)	33°00'39"S 52°38'04"W	South	4	1	1, 6, 11	Cfa	SA	Pa	4	PF	La	10

Environmental Data

All of the environmental data was obtained through geospatial vectors (*shapefile*) from Brazilian institutes (ANA, 2012; IBAMA, 2012; IBGE, 2012) and freshwater habitats, according to the Freshwater Ecoregions of the World information map (FEOW, 2013; available at *http://www.feow.org*). The ArcGIS geographical information software system was utilized to manage the geoprocessing (ESRI, 2012). The terrestrial macrovariables considered were Köppen's climatic region, Biome and Vegetal formation. Regarding the localities distribution, the climatic regions included were Af (tropical forest), Am (tropical monsoon), Aw (wet and dry tropical climate or savanna), Bsh (medium latitude steppe and desert), Cwa (humid temperate climate with dry winters and warm summers) and Cfa (humid temperate climate with warm summers) (Figure 1b); whilst the biomes analyzed were the Amazon, the Cerrado, the Atlantic Forest, the Caatinga and the Pampa (Figure 1c); and the vegetal formations Ombrophilous Dense Forest, Seasonal Deciduous Forest, Seasonal Semideciduous Forest, Steppe, Savanna and Pioneer Formations (*restinga*).

In contrast with the terrestrial macrovariables, the aquatic macrovariables analyzed were Hydrographic region, Freshwater habitat (based on the FEOW classification) and Freshwater ecosystem (according to the information provided by the authors of each study or locality analyzed). Thereby, the hydrographic regions included in the analysis were Amazonas, Eastern Atlantic, São Francisco, Uruguay, Paraná, Southern Atlantic, Northeastern Atlantic and Tocantins (Figure 1d); whilst the freshwater habitats utilized were tropical and subtropical upland rivers, tropical and subtropical floodplain rivers and wetland complexes, tropical and subtropical coastal rivers, and temperate coastal rivers (Figure 1e); and the freshwater ecosystems were rivers, streams, lakes, wetlands and reservoirs.

Data Analysis

The Coefficient of Geographical Similarity (CGR) was used to calculate the similarity amongst the community pairs (DUELLMAN, 1990), where: $CGR = 2NS/NA + NB$ (NS: number of species in both areas; NA: number of species in area A, NB: number of species in area B). This ratio is equivalent to the indexes calculated by Sørensen, Dice and Czekanowski (WOLDA, 1981; KREBS, 1999; MAGURRAN, 2004), and ranges from 0 (maximum dissimilarity) to 1 (maximum similarity). The similarity matrices (CGR) were represented by the cluster analysis (Clustering), using a weighted arithmetic mean method (WMGMA; SOKAL & MICHENER, 1958) in order to avoid the effect of sample size (species richness in different communities) in the analysis (VALENTIN, 1995). Possible distortions in the graphic representations of the similarity matrices caused by the cluster analysis method were evaluated by the coefficient of cophenetic correlation (*r*) (ROMERSBURG, 1984). The closer the value of *r* to 1, the lower will be the distortion of the cluster dendrogram (ROHLF, 2000). Groups which presented a similarity higher than 50% were considered clusters.

The similarity in the composition obtained for the bivalve and gastropod communities was correlated with the terrestrial and aquatic matrices by the Mantel test (MANLY, 2000). This test performs correlations amongst the matrices based on the Z statistic, where Z depends on the number of elements in the matrix to be compared (VALENTIN, 1995). Thus, a normalization is necessary to transform Z into a coefficient (*r*) ranging from 1 to -1 (VALENTIN, 2000). The meaning of Z was determined by the permutation test of Monte Carlo (SMOUSE et al., 1986), using 5000 permutations. Environmental matrices were generated assigning 1 to pairs of localities with the same environmental conditions and 0 to pairs with different conditions. A transitory value (0.5) was used in cases of Forest formations ecotone (Steppe/Seasonal Deciduous forest; Savanna/Seasonal Semideciduous Forest) and localities with samples in more than one freshwater habitat (lake/river).

With the aim of analyzing the existence of spatial autocorrelation (LEGENDRE & LEGENDRE, 1998), a geographic distance matrix of the localities was correlated with a gastropod composition similarity matrix ($r = 0.80$) and a bivalve one ($r = 0.90$), also using the Mantel test (MANLY, 2000). Both the gastropod and the bivalve communities presented spatial autocorrelation ($r = 0.21$, P = 0.02, and $r = 0.425$, P = 0.0002, respectively). Thereby, a partial Mantel test (SMOUSE et al., 1986) was used in both communities to test the correlation between the similarity matrix and the environmental matrices, utilizing the geographic distance matrix as a covariate. This test compares two matrices (A and B), removing the effect of a third matrix (C in this study corresponds to the geographic distance matrix) utilizing the regression of C in A and B. Thus, a residual matrix is obtained, representing the variations in the matrices A and B which are not explained by matrix C (SMOUSE et al., 1986). Therefore, the two residual matrices may be compared normally. Even though the utilization of the Bonferroni correction is questioned in ecological studies

(MORAN, 2003), in the partial Mantel test carried out herein it was adopted with the aim of minimizing the bias derived from the variability of samplers, sampling effort, etc. All the analyses were performed with the utilization of the NTSYS PC 2.10 S software (ROHLF, 2000).

RESULTS

Bivalves

The cluster analysis performed for bivalve communities led to the formation of four small groups (I to IV) with similarity higher than 50% (Figure 2). The clusters represented mainly communities from localities with the same climatic region and biome (Table 1 and Figure 2).

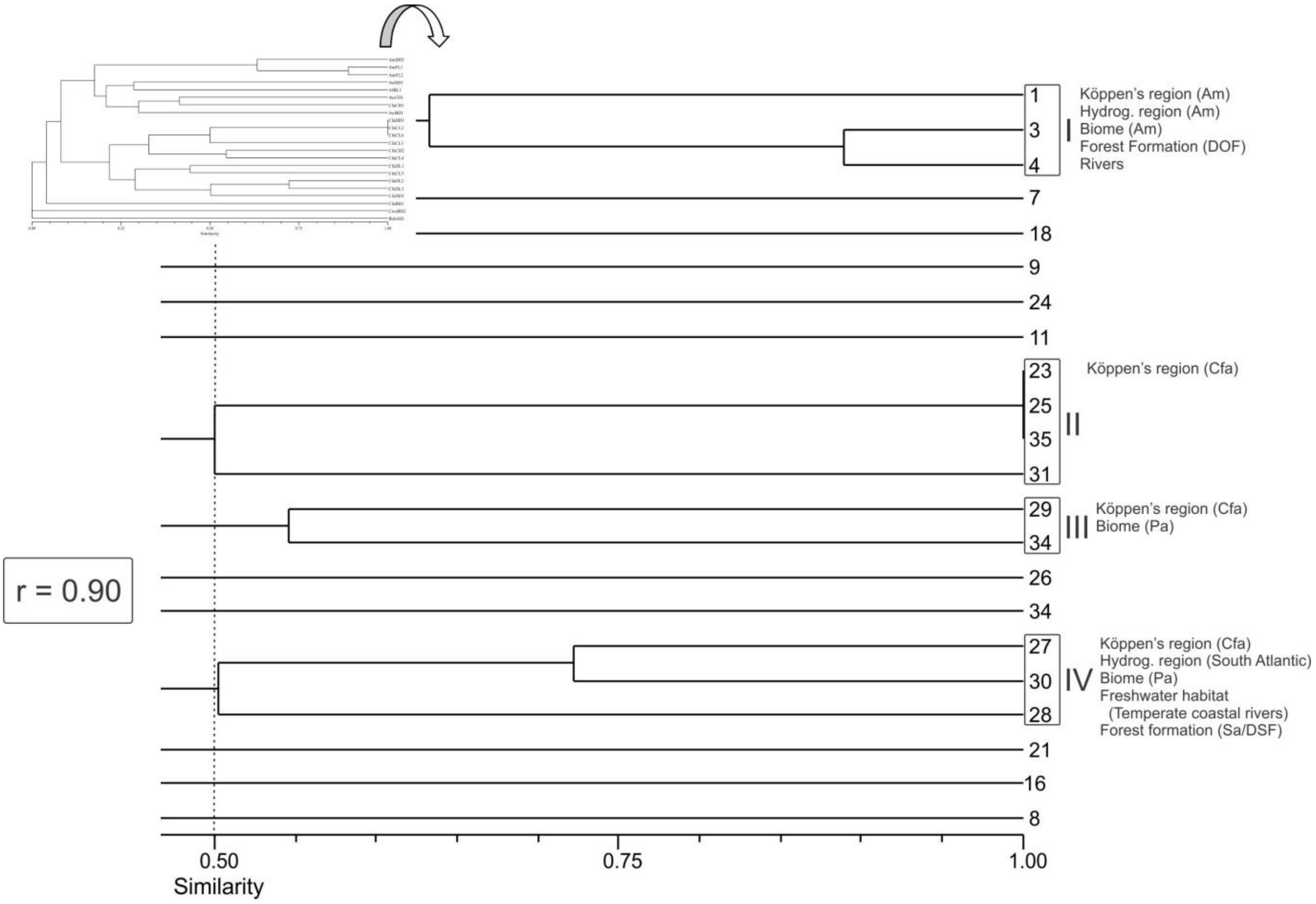

Figure 2 - Similarity (Coefficient of Geographic Resemblance; CGR) in the taxonomic composition of bivalves in five geographic regions of Brazil. *r* represents the Cophenetic Correlation Coefficient. The four groups formed with similarity higher than 50% are highlighted and identified with the terrestrial and/or the aquatic variables shared by the localities from each group.

Group ‘I’ comprises three localities localized in the Tropical monsoon (Am) region in the Amazon biome with Dense Ombrophilous Forest formation belonging to the Amazonas hydrographic region, representing floodplains of big rivers. Freshwater habitat varied among the localities (“Tropical and subtropical upland rivers” and “Tropical and subtropical floodplain rivers and wetland complexes”). Group ‘II’ was formed by four localities with Cfa climate, localized predominantly in the Atlantic Forest biome but with different forest formations (Savanna/Steppe, Dense Ombrophilous Forest, Savanna/Seasonal Deciduous Forest and Pioneer Formations) and comprehending both wetlands and lakes inserted predominantly in the South Atlantic hydrographic region and diverse freshwater habitats (“Tropical and subtropical upland rivers”, “Tropical and subtropical coastal rivers”, and “Temperate coastal rivers”). Group ‘III’ was represented by two Cfa climate localities in the Pampa biome but with different forest formations (Steppe and Pioneer Formations), a lake/stream and a river embedded in different hydrographic regions (Uruguay and South Atlantic) and freshwater habitats (“Tropical and subtropical upland Rivers” and “Temperate coastal rivers”). Group ‘IV’ comprises three Cfa climate localities in the Pampa biome within an Savanna/Seasonal Deciduous Forest ecotone; comprising a river and two streams inserted in the South Atlantic hydrographic region within the same freshwater habitat (“Temperate coastal rivers”).

The bivalve species typical of the groups are presented in Table 2.

Table 2. Bivalve species shared by all the localities forming each group (I to IV) with similarity higher than 50%, which were formed from cluster analysis based on 22 locations. Group I (Loc. 1, 3, 4), group II (Loc. 23, 25, 31, 35), group III (Loc. 29, 34) and group IV (Loc. 27, 28, 30). The numbers in parenteses correspond to the number of localities, according to Table 1).

Species	Group (number of localities forming each group)			
	I (3)	**II (4)**	**III (2)**	**IV (3)**
Castalia ambigua Lamarck, 1819	X			
Castalia martensi (Ihering, 1891)				X
Diplodon martensi (Ihering, 1893)				X
Diplodon obsolescens F. Baker, 1914	X			
Diplodon suavidicus (Lea, 1856)	X			
Prisodon obliquus Schumacher, 1817	X			
Tripodon corrugatus (Lamarck, 1819)	X			
Anodontites trapesialis (Lamarck, 1819)				X
Anodontites trapezeus (Spix, 1827)				X
Monocondylaea minuana Orbigny, 1835				X
Eupera klappenbachi Mansur and Veitenheimer, 1975		X	X	X
Eupera simoni (Jousseaume, 1889)	X			
Pisidium punctiferum (Guppy, 1867)			X	
Pisidium sterkianum Pilsbry, 1897			X	

Gastropods

The cluster analysis performed for gastropod communities formed six groups (I to VI) with similarity higher than 50% (Figure 3). The clusters represented mainly communities from localities with the same climatic region and freshwater habitat (Table 1 and Figure 3).

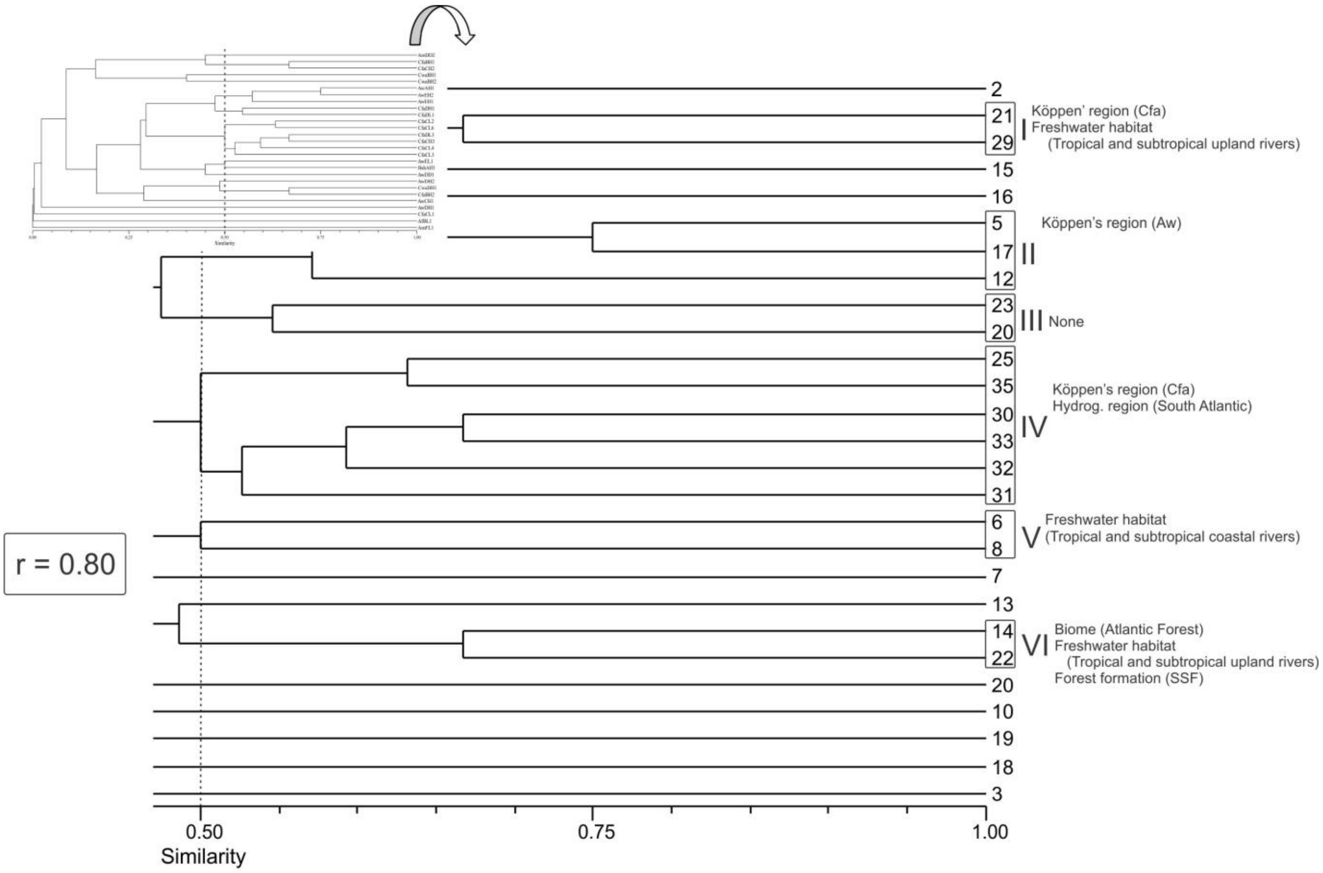

Figure 3 - Similarity (Coefficient of Geographic Resemblance; CGR) in the taxonomic composition of gastropods in five geographic regions of Brazil. *r* represents the Cophenetic Correlation Coefficient. The six groups formed with similarity higher than 50% are highlighted (I to VI) and identified with the terrestrial and/or the aquatic variables shared by the localities from each group.

Group 'I' was formed by two Cfa climate localities, one in the Cerrado biome with Savanna vegetation and another in the Pampa biome with Steppe vegetation comprehending a reservoir inserted in the Paraná hydrographic region and a river in the Uruguay hydrographic region, both within the "Tropical and subtropical upland rivers" freshwater habitat. Group 'II' was represented by three Aw climate localities, a reservoir, a lake and a stream with no other similar terrestrial or aquatic environmental variable (Caatinga, Cerrado and Atlantic Forest biomes; Steppe/Seasonal Deciduous Forest, Savanna and Dense Ombrophilous Forest; Northeast Atlantic, Tocantins and East Atlantic hydrographic regions; two in the same freshwater habitat – "Tropical and subtropical coastal Rivers" – and another in the "Tropical and subtropical upland Rivers"). Group 'III' was formed by two localities, a river and a wetland with no similar terrestrial or aquatic environmental variable (Köppen's region: Aw, Cfa; biome: Atlantic Forest, Pampa; forest formation: Dense Ombrophilous Forest, Steppe; hydrographic regions: East Atlantic, Uruguay; freshwater habitats: "Tropical and subtropical upland Rivers" and "Tropical and subtropical coastal Rivers"). Group 'IV', the largest one, was represented by six Cfa climate localities predominantly located in the Pampa biome (only one lake in the Atlantic Forest) not sharing the same type of vegetation (Dense Ombrophilous Forest, Savanna/Seasonal Deciduous Forest, Savanna and Pioneer Formations), comprehending diverse aquatic ecosystems (lakes, stream, wetland, rivers) embedded in the South Atlantic hydrographic region mainly in the "Temperate coastal Rivers" freshwater habitat (only one lake in "Tropical and subtropical coastal rivers"). Group 'V' comprises two localities, a stream and a river, inserted in the same freshwater habitat ("Tropical and subtropical coastal rivers") but with no similar Köppen's region (Aw, BSh), biome (Atlantic Forest, Caatinga), forest formation (Pioneer Formations, Savanna) or hydrographic region (Northeast, East Atlantic). Finally, group 'VI' was formed by two localities in different Köppen's regions (Cwa, Cfa) in the Atlantic Forest biome with Seasonal Semideciduous Forest, comprising a lake/stream inserted in the East Atlantic and a reservoir inserted in the Paraná hydrographic region both in the "Tropical and subtropical upland rivers" freshwater habitat.

The gastropod species typical of the groups are presented in Table 3.

Table 3. Gastropod species shared by all the localities of each group (I to VI) with similarity higher than 50%, which were formed in the cluster analysis based on 27 localities. Group I (Loc. 21 and 29), group II (Loc. 5, 12, 17), group III (Loc. 20 and 23), group IV (Loc. 25, 30, 31, 32, 33, 35), group V (Loc. 6 and 8) and group VI (Loc. 14 and 22). The numbers in parenteses correspond to the number of localities, according to Table 1).

Species	Groups (number of localities forming each group)					
	I (2)	**II (3)**	**III (2)**	**IV (6)**	**V (2)**	**VI (2)**
Pomacea canaliculata (Lamarck, 1801)	X			X		
Lymnaea columella Say, 1817		X	X			
Aplexa marmorata (Guilding, 1828)		X	X			
Biomphalaria glabrata (Say, 1818)						X
Biomphalaria tenagophila (Orbigny, 1835)				X		X
Drepanotrema anatinum (Orbigny, 1835)					X	
Drepanotrema cimex (Moricand, 1839)					X	
Drepanotrema lucidum (Pfeiffer, 1839)					X	
Hebetancylus moricandi (Orbigny, 1837)			X			

Relationship with the macrovariables

The Köppen's region showed the highest, and also positive, significant correlation to both communities (Gastropoda and Bivalvia), regardless of the spatial situation (Table 4). Notwithstanding, the spatial effect was evident, reducing most of the correlation values, and highlighting the importance of the spatial autocorrelation mainly in the influence of the Köppen's region on both communities. Biome had a positive correlation with bivalve communities regardless of the spatial circumstance, but had only a very weak relationship with gastropod communities, when considering the distance effect and the marginal significance. The Vegetal formation also had a positive correlation with bivalve communities, but was influenced by the distance in light of the statistical significance decrease (marginal value) when the spatial effect is removed.

Table 4. Correlation values from Partial Mantel tests among terrestrial (Köppen's region, Biome and Vegetal formation) and aquatic variables (Hydrographic region, Freshwater habitat and Freshwater ecosystem), and gastropod and bivalve communities, with and without the influence of the distance (spatial autocorrelation). Bonferroni's correction considered P < 0.005. Significant results are in bold and marginal results are in italics.

Variable	Bivalvia		Gastropoda	
Influence of the Distance	With	No	With	No
Terrestrial				
Köppen's region	**r = 0.51533**	**r = 0.32973**	**r = 0.33909**	**r = 0.27823**
	p = 0.0002	**p = 0.0006**	**p = 0.0002**	**p = 0.0016**
Biome	**r = 0.30693**	**r = 0.24553**	*r = 0.16189*	r = 0.08141
	p = 0.0008	**p = 0.0022**	*p = 0.0108*	p = 0.0940
Vegetal formation	**r = 0.19460**	*r = 0.14191*	r = 0.09509	r = 0.06770
	p = 0.0078	*p = 0.0364*	p = 0.0580	p = 0.1132
Aquatic				
Hydrographic region	**r = 0.36514**	*r = 0.18264*	**r = 0.18182**	*r = 0.10116*
	p = 0.0002	*p = 0.0132*	**p = 0.0028**	*p = 0.0430*
Freshwater habitat	r = 0.06093	r = -0.01986	r = 0.09022	r = 0.04698
	p = 0.1682	p = 0.4099	p = 0.1166	p = 0.2639
Freshwater ecosystem	*r = 0.17633*	**r = 0.22194**	r = -0.07330	r = -0.06561
	p = 0.0172	**p = 0.0058**	p = 0.0622	p = 0.0918

Based on the results, the aquatic macrovariables had a lower influence on both communities. In contrast to terrestrial macrovariables and also to the Hydrographic region and Freshwater habitat, the influence on the Freshwater ecosystem was not affected by the spatial autocorrelation. In fact it had the strongest positive relationship with bivalve communities when distance was removed from the analysis. The influence of the Hydrographic region on both gastropod and bivalve communities was also affected by the distance, showing the same marginal pattern as the Vegetal formation, while the Freshwater habitat presented no relationship with gastropod or bivalve communities even considering marginal significance values.

DISCUSSION

In general, the terrestrial macrovariables (TM) had a greater influence than the aquatic ones (AM) on the similarity of the taxonomic composition of the communities studied, especially on the bivalves'. Furthermore, it seems that the larger the spatial scale of the TM, the greater the influence on the similarity between bivalve communities. The influence of the TM "Köppen's region" on mollusks communities had already been observed in an ongoing study conducted by the authors of this work. Köppen's climatic regions are based on a combination of both annual mean temperature and accumulated rainfall (KÖPPEN, 1918). Air temperature, which modulates water temperature mainly in shallow settings (O'DRISCOLL & DEWALLE, 2006) and precipitation exert a great influence on the freshwater mollusks' distribution, directly or indirectly (PÉREZ-QUINTERO, 2012). These factors affect physiological (filtration, reproduction, resistance to desiccation; VAUGHN & HAKENKAMP, 2001) and behavioral (burrowing and dispersal; MCMAHON & BOGAN, 2001; KAPPES & HAASE, 2012) processes, as well as biotic (establishment of aquatic macrophytes and periphyton colonization; BRÖNMARK, 1985) and abiotic (hydroperiod, size of the area; CLEMENTS et al., 2006; HOVERMAN et al., 2011) processes important for mollusks.

Thirteen of the 27 gastropod communities and 12 of the 22 bivalve communities studied herein were influenced by Köppen's climatic regions. For gastropods, species such as *Pomacea canaliculata* (Lamarck, 1801), *Biomphalaria tenagophila* (Orbigny, 1835) and *Hebetancylus moricandi* (Orbigny, 1837), shared by groups I, III and IV, were related to Cfa climate. This climate region is characterized by average temperature below 18ºC in the coldest month, and above 22ºC in the warmest month, and also by hot summers, infrequent frosts and a tendency of concentration of rainfall in the summer months, but with no defined dry season (SAMPAIO et al., 2011). *Lymnaea columella* Say, 1817 and *Aplexa marmorata* (Guilding, 1828), shared by group II, were related to Aw climate. This savanna climate, with average monthly temperature above 18ºC, is defined by two seasons, dry and rainy, and at least one of the months of the year has a total precipitation average lower than 60 mm (SAMPAIO et al., 2011). Brazilian gastropods are well adapted to temperature variations and hydroperiod oscillations. For instance, *P. canaliculata* has both tropical and subtropical distribution, but is able to survive in regions with lower temperatures (MARTÍN et al., 2001; COWIE, 2002), such as the Cfa region. *Biomphalaria tenagophila* and *H. moricandi* also have tropical and subtropical distribution, but the former is more sensitive to desiccation than other *Biomphalaria* species, occurring preferentially in regions with regular rainfall (BRASIL, 2007). The latter can develop a calcarious septum that ensures the preservation of the water body during hibernation (FERNÁNDEZ, 1981). The pulmonate *L. columella* thrives in a wide range of temperatures and needs a small amount of water, living in wetland habitats (HARRIS & CHARLESTON, 1977; PREPELITCHI et al., 2011). Although the biology of *A. marmorata* is poorly known, there is some unknown relationship of this species with climate characteristics. It was introduced in Africa by the end of the 19th century and now is well established in countries with Aw climate (Benin, Togo, Ghana, Nigeria, Ivory Coast) (BONY et al., 2007). Even in Brazilian subtropical regions, colder periods are not enough to threaten the integrity of malacological populations, only limiting reproduction and/or growth, which recover its usual functioning with increasing temperatures.

For bivalves, the Köppen’s climatic regions were related to all groups formed (Figure 2), and some species were related to Am climate, while others to Cfa climate. In order to disperse, most bivalves require some live vector (terrestrial or aquatic vertebrates, but see exception in PEREIRA et al., 2013 for *Rhipidodonta*), and if they survive the path undertaken by their disperser, they may be released into new habitats (VAUGHN & TAYLOR, 2000; KAPPES & HAASE, 2012). This locomotion limitation could be the reason for the high endemism of some bivalve species, such as those located on Am climate, specifically in the Amazon region. It’s interesting to note that the Am Köppen’s region is inserted in the Amazonas hydrographic region and comprehends the largest portion of it, which is mainly comprised of big river courses and floodplains. These environments are appropriate to bigger bivalves species such as *Castalia ambigua* Lamarck, 1819, *Diplodon obsolescens* F. Baker, 1914, *Diplodon suavidicus* (Lea, 1856), *Prisodon obliquus* Schumacher, 1817, *Triplodon corrugatus (*Lamarck, 1819*)* that were related to Am climate. The Cfa Köppen’s region comprises the southernmost part of Brazil, which is considered to have a subtropical climate encompassing about three Brazilian hydrographic regions. *Castalia martensi* (Ihering, 1891), *Diplodon martensi* (Ihering, 1893), *Anodontites trapesialis* (Lamarck, 1819), *Anodontites trapezeus* (Spix, 1827), *Monocondylaea minuana* Orbigny, 1835, *Eupera klappenbachi* Mansur and Veitenheimer, 1975, *Pisidium punctiferum* (Guppy, 1867) and *Pisidium sterkianum* Pilsbry, 1897 were related to the Cfa climate. But most of these "Cfa" species have a wider distribution, making it difficult to understand their real relationship with the climatic zones. For both Am and Cfa Köppen's regions, there is possibly species-preference to a set of suitable factors in certain climatic regions. However, studies on the biology of Brazilian bivalve species are very scarce, and it is not possible to explain this relationship.

Both terrestrial and aquatic macrovariables used in the analyses performed here present a somewhat hierarchical relationship (Köppen's region > Biome > Vegetal formation; Hydrographic region> Freshwater habitat > Freshwater ecosystem). Thus, the TM Biome and Vegetal formation present a spatial relationship, and their influence on communities decreases according to their spatial scale. These macrovariables also influenced the composition of bivalve communities when the effect of the geographical distance was removed, but with lower and less significant value. According to hierarchy theory (ALLEN & STARR, 1982), variables on smaller scales are governed by those at larger ones. Biome can be defined as large regions with relatively uniform climate and vegetation (BROWN & MAURER, 1989), i.e., the vegetation in the biomes tends to be more similar than that one between biomes. The type and density of terrestrial vegetation adjacent to aquatic systems directly influence the processes of structural and functional communities (MINSHALL et al., 1985; CORKUM, 1992). This is mainly due to different characteristics of plant material (composition and structure) because the largest source of particulate organic matter for aquatic ecosystems has an allochthonous origin (plant material from the riparian vegetation) (GIMENES et al., 2010). Bivalves are filter feeders removing particulate organic matter, algae and bacteria in the water column (VAUGHN, 2005). Thus, the type of vegetation can have some indirect effect on bivalves by influencing trophic relationships (i.e., modifying the composition of microorganisms). In addition, riparian vegetation can affect the biological patterns of bivalves, since shading influences physical and chemical characteristics of aquatic environments (MORRIS & CORKUM, 1999). Riparian zones are also responsible for mitigating excessive intake of sediment, nutrients and other contaminants of aquatic environments (CORKUM, 1992), which influences the bivalve filtration efficiency and/or their survival (MORRIS & CORKUM, 1996; NEVES et al. 1997; VAUGHN & HAKENKAMP, 2001). The biology of freshwater bivalves is not sufficiently well known (PEREIRA et al., 2013), which makes it difficult to detail the relationship found among the species related to specific biomes and forest formations.

The aquatic macrovariable (AM) Hydrographic region had a strong influence on the similarity of the bivalve communities, but its influence decreased when the effect of distance was removed from the analysis. As mentioned above, bivalves are greatly influenced by space, since their dispersion process is very dependent on aquatic vertebrates (KAPPES & HAASE, 2012), and since they have a sedentary life habit (VAUGHN, 2005). Thus, species like *C. ambigua*, *D. obsolescens*, *D. suavidicus*, *P. obliquus*, *T. corrugatus*, apparently dependent on dispersers limited by the hydrographic regions (e.g. fish), were related to the Amazon hydrographic region, while *C. martensi*, *D. martensi*, *A. trapesialis*, *A. trapezeus* and *M. minuana*, to the South Atlantic hydrographic region. In fact, species such as *P. obliquus* and *T. corrugatus* are endemic to the Amazon basin (PEREIRA et al., 2013).

Only Freshwater ecosystem exhibited an increased influence on bivalve communities when the distance effect was removed from the analysis, overcoming the influence of the Hydrographic region. Freshwater ecosystems (e.g., lakes, rivers, streams) do not have a hierarchical relationship with the other aquatic macrovariables analyzed nor a spatial design. This variable is very important to bivalves. They have an intrinsic relationship to water level and hydraulic conditions (MCMAHON & BOGAN, 2001), and most species are more frequently found in floodplains, big rivers, standing waters, and river banks (PFEIFER & PITONI, 2003; PIMPÃO, 2007; COLLE & CALLIL, 2012). For instance, *Eupera simoni* (Jousesseaume, 1889) is the only Sphaeriidae occurring in the Amazon hydrographic region, being adapted to the water level fluctuations and long drought periods (PEREIRA et al., 2013).

The apparent no influence of Freshwater habitat on the distribution of gastropods and bivalves may be due a scale bias. The Freshwater Ecorregions of the World proposed by Abell et al. (2008) may have concealed important local aspects to mollusks by covering large spatial areas. The habitat (coastal/highland rivers with different temperature) is primordial in structuring freshwater mollusks, specially by the water temperature variance and upstream to downstream sediment granulometry modifications.

Only larger spatial scale TM and AM influenced the similarity of the composition among gastropod communities, and the Köppen's region had greater influence than the Hydrographic region. This divergence is due, presumably, to the greater importance of environmental variables related to the Köppen's region (e.g., temperature and rainfall) than those related to the Hydrographic region (e.g., geology and relief) for the survival of these communities. Furthermore, as observed to bivalves, the influence of both macrovariables decreased when the distance effect was removed from the analysis. Temperature and rainfall, therefore, seem to have a greater influence on the gastropod communities than on the bivalve communities. Biomes had little relationship with the gastropod community structure due to geographical proximity, and when the distance was removed, the relationship no longer existed.

CONCLUSION

Environmental macrovariables can be drivers as important as some local or small spatial scale factors, such as grain size, presence of macrophytes and river order (BROWN, 2001; MCMAHON & BOGAN, 2001), in structuring the taxonomical composition of freshwater mollusk communities. The influence of ancient hydrographic basins in the spatial distribution of the Neotropical freshwater bivalve diversity was demonstrated by Pereira et al. (2013), a study conducted with data of specimens deposited in many museums of the world. Our study, although performed by means of meta-analysis, corroborates the effect of macrovariables on freshwater mollusk communities as a whole. It shows that, at least in the Brazilian territory, the present day 'terrestrial' macrovariables such as Köppen's climatic regions and biomes can be more important than one of the aquatic macrovariables, the hydrographic region especially for the bivalve communities. This influence occurs even when the effect of distance (autocorrelation) is removed from the statistical analyses. The strongest influence of the terrestrial macrovariables on the structure of animal communities with a strictly aquatic life habit can be explained by the close association between aquatic and terrestrial ecosystems. Energy and nutrients flow, and also biogeochemical processes are related to both systems (CORKUM, 1992). However, the scarcity of studies on the biology of most Brazilian mollusks species makes it difficult to understand how the effects of climate and biome on the aquatic ecosystem act on each species, and consequently affecting the composition of mollusk communities.

Brazil has a large and dense freshwater network throughout its whole territory (ANA, 2013), and also the richest freshwater malacofauna of the Neotropics (PEREIRA et al., 2013). Our study shows that both gastropod and bivalve communities have a spatially structured distribution, thus allowing the choice of ecoregions for their preservation. Areas located in different Köppen's regions (such as Am, Aw, Cfa) and also in different biomes (Amazon, Atlantic Forest, and Pampa) will ensure the preservation of different mollusk communities across the country, and the preservation of the overall Brazilian mollusk diversity. Fortunately, many of these terrestrial ecoregions encompass some hydrographic regions (or part of them), which are also important for maintaining mollusk diversity. However, other environmental factors must be considered also when choosing preservation areas, such as freshwater systems, substrate characteristics, river order, etc. However few Brazilian preservation units encompass the integrity of aquatic ecosystems (mostly located in the North region or RAMSAR wetlands of international importance (ICMBIO, 2013)). Thus, if we wish to preserve freshwater mollusk diversity, we should also preserve the integrity of freshwater ecosystems as a whole.

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CONCLUSÕES

- Apesar dos vieses que emergem de uma abordagem realizada com metadados, este estudo possibilitou verificar de forma direta o efeito de fatores geralmente não analisados em ecossistemas de água doce (aqueles estritamente terrestres, ou em escalas mais amplas, etc), especialmente para moluscos.

- Muitos estudos demonstram que variáveis ambientais locais exercem uma influência mais direta sobre as comunidades, inclusive em ambientes límnicos. Porém, evidenciou-se que fatores analisados em ampla escala e/ou macrovariáveis podem ser tão bons ou melhores preditores da estrutura da malacofauna dulcícola, principalmente das comunidades de bivalves. As faixas de precipitação e especialmente a região climática de Köppen foram importantes tanto para as comunidades de gastrópodes quanto de bivalves, independente da questão espacial. Contudo, a altitude, a única meso-variável significativa, teve efeito ainda maior do que a região climática de Köppen para os bivalves.

- Comparando a relação das variáveis aquáticas e terrestres na estruturação das comunidades de moluscos, constatou-se que fatores relacionados aos ecossistemas terrestres (regiões climáticas de Köppen, biomas e formações florestais) tiveram uma forte relação com as comunidades de bivalves, não sendo observada essa afinidade com as comunidades de gastrópodes. Porém, esta correlação significativa não pôde ser totalmente explicada devido à carência de informações acerca dos processos biológicos (e.g., dispersão, alimentação, reprodução) das espécies de moluscos de água doce do Brasil. As regiões hidrográficas foram altamente influenciadas pelo espaço, pois o efeito que as mesmas imprimiam sob ambas as comunidades desapareceu após a remoção da distância. Apenas o ecossistema aquático não sofreu influência espacial já que não possui uma relação hierárquica com as demais variáveis tampouco uma estrutura espacial.

- Os bivalves, em especial, parecem mais sensíveis a fatores ambientais do que os gastrópodes por apresentarem um hábito mais sedentário (com dispersão lenta), pelo modo de obtenção de nutrientes (filtração), pela especificidade reprodutiva (especialmente em Unionoida, através de larvas geralmente parasitas de peixes). São restritos a locais com substratos adequados (principalmente arenoso), onde a velocidade da água permita o fluxo constante de nutrientes e gases.

- Com base nos dois estudos aqui realizados, é possível propor estratégias para o estabelecimento de áreas de preservação baseadas nas necessidades das comunidades de água doce em contracorrente às atuais políticas de conservação estritamente terrestres. Sugere-se que áreas destinadas a preservação e conservação de moluscos, ao menos em território brasileiro, contemplem diferentes regiões climáticas, biomas, e regiões hidrográficas, ou seja, uma sobreposição das variáveis em escala mais ampla significativas. Além disso, especialmente para bivalves, deve-se optar por locais com diferentes fisionomias (lagos, rios), em áreas mais baixas (planícies), considerando também aspectos importantes já conhecidos para o grupo (ordem do rio, substrato, etc).

- Finalmente, é imprescindível estimular a realização de estudos em áreas como norte e nordeste do Brasil que carecem de informações sobre diversidade de moluscos de água doce e estrutura das comunidades. As bacias hidrográficas inseridas nestas regiões vêm sofrendo modificações ecológicas significativas em decorrência, principalmente, da implementação de usinas hidrelétricas e transformação da paisagem natural em áreas de cultivo. Além disso, para melhor compreender o efeito dos fatores ambientais sobre as comunidades e idealizar áreas de preservação, são necessários mais estudos biológicos espécie-específicos especialmente a respeito das características tróficas (e.g., itens alimentares) e de dispersão (e.g., provável relação entre peixes e a maioria das espécies de Unionoida) da malacofauna.

Apêndice

Apêndice A – Lista de espécies de gastrópodes de água doce registradas em 27 das 35 localidades selecionadas para análise.

Espécies/localidade	2	3	5	6	7	8	10	12	13	14	15	16	17	18	19	20	21	22	23	25	26	29	30	31	32	33	35
Asolene spixi (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Pomacea archimedis Spix, 1827	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomacea canaliculata (Lamarck, 1801)	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1	1	1
Pomacea lineata (Spix, 1827)	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomacea papyracea (Spix, 1827)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomacea sordida (Swainson, 1823)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Doryssa heathi (Baker, 1914)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Doryssa starksi (Baker, 1913)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aylacostoma behni (Reeve, 1860)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Aylacostoma tenuilabris (Reeve, 1860)	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Heleobia** (= Littoridina) *bertoniana* (Pilsbry, 1911)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
*Heleobia** (= Littoridina) *cuzcoensis* (Pilsbry, 1911)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
*Heleobia** (= Littoridina) *piscium* (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Potamolithus catharinae Pilsbry, 1911	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Potamolithus ribeirensis Pilsbry, 1911	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Chilina fluminea (Maton, 1809)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1
Lymnaea columella Say, 1817	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	0	1	0
*Aplexa marmorata** (Guilding, 1828)	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0
Antillorbis nordestensis (Lucena, 1954)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
Biomphalaria glabrata (Say, 1818)	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Biomphalaria intermedia (Paraense e Deslandes, 1962)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biomphalaria oligoza Paraense, 1974	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0
Biomphalaria peregrina (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Biomphalaria schrammi (Crosse, 1864)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biomphalaria straminea (Dunker, 1848)	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biomphalaria tenagophila (Orbigny, 1835)	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	1	1	1	0	0	1	1	1	1	1
Drepanotrema anatinum (Orbigny, 1835)	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Drepanotrema cimex (Moricand, 1839)	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Drepanotrema depressissimum (Moricand, 1839)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Drepanotrema heloicum (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Drepanotrema kermatoides (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Drepanotrema lucidum (Pfeiffer, 1839)	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Burnupia ingae Lanzer, 1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Ferrissia gentilis Lanzer, 1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Gundlachia radiata (Guilding, 1828)	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gundlachia ticaga (Marcus e Marcus, 1962)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Hebetancylus moricandi (Orbigny, 1837)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	1
Uncancylus concentricus (Orbigny, 1835)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1
Omalonyx unguis (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0

Apêndice B – Lista de espécies de bivalves de água doce registradas em 22 das 35 localidades selecionadas para análise.

Espécies/localidade	1	3	4	7	8	9	11	16	18	21	23	24	25	26	27	28	29	30	31	32	34	35
Castalia ambigua Lamarck, 1819	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Castalia duprei Récluz, 1842	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castalia inflata Orbigny, 1835	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castalia quadrata Sowerby, 1867	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castalia martensi (Ihering, 1891)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Castalia schombergiana Sowerby, 1869	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castalia sulcata Krauss, 1849	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Castalia undosa Martens,1885	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Diplodon aethiops (Lea, 1860)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Diplodon berthae Ortmann, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0
Diplodon besckeanus (Dunker, 1849)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplodon charruanus Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Diplodon deceptus Simpson, 1914	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Diplodon delodontus (Lamarck, 1819)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Diplodon expansus (Kuster, 1856)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplodon granosus (Lea, 1851)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Diplodon hylaeus (Orbigny, 1835)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplodon hildae Ortmann, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Diplodon iheringi (Simpson, 1900)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diplodon imitator Ortmann, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Diplodon koseritzi (Clessin, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Diplodon martensi (Ihering, 1893)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Diplodon obsolescens F. Baker, 1914	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplodon parallelopipedon (Lea, 1834)	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon piceus (Lea, 1860)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon pilsbryi (Marshall, 1928)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Diplodon rhuacoicus (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Diplodon suavidicus (Lea, 1856)	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon uruguayensis (Lea, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Paxyodon syrmatophorus (Meuschen, 1781)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continua)

(continuação)

Espécies/localidade	1	3	4	7	8	9	11	16	18	21	23	24	25	26	27	28	29	30	31	32	34	35
Prisodon obliquus Schumacher, 1817	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triplodon chodo Mansur e Pimpão, 2008	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triplodon corrugatus (Lamarck, 1819)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites crispatus Bruguière, 1792	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites elongatus (Swainson, 1823)	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites ensiformis (Spix, 1827)	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites felix (Pilsbry, 1896)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Anodontites iheringi (Clessin, 1882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Anodontites lucidus (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anodontites patagonicus (Lamarck, 1819)	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
Anodontites schomburgianus (Sowerby, 1870)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites soleniformes (Orbigny, 1835)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites trapesialis (Lamarck, 1819)	1	0	0	1	0	1	1	0	1	0	0	1	0	1	1	1	1	1	0	0	1	0
Anodontites trapezeus (Spix, 1827)	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0
Anodontites trigonus (Spix, 1827)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Fossula fossiculifera (Orbigny, 1835)	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Haasica balzani (Ihering, 1893)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leila blainvilliana (Lea, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Leila esula Orbigny, 1835	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monocondylaea corrientesensis Orbigny, 1835	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Monocondylaea minuana Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0
Monocondylaea paraguayana Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Monocondylaea parchappi Orbigny, 1835	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mycetopoda legumen (Martens, 1888)	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Mycetopoda siliquosa (Spix, 1827)	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mycetopoda soleniformes Orbigny, 1835	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupera klappenbachi Mansur e Veitenheimer, 1975	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1
Eupera platensis Doello-Jurado, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Eupera simoni (Jousseaume, 1889)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Musculium argentinum (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pisidium forensis Meier-Brook, 1967	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

(conclusão)

Espécies/localidade	1	3	4	7	8	9	11	16	18	21	23	24	25	26	27	28	29	30	31	32	34	35
Pisidium globulus Clessin, 1888	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium pulchellum (Orbigny, 1835)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium punctiferum (Guppy, 1867)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
Pisidium sterkianum Pilsbry, 1897	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Pisidium vile Pilsbry, 1897	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sphaerium observationis (Pilsbry, 1911)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cyanocyclas limosa (Maton, 1809)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Tamziella schroeteriana (Lea, 1852)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bartlettia stefanensis (Moricand, 1856)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0