

Bivalve distribution in hydrographic regions in South America: historical overview and conservation

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Abstract Based on literature review and malacological collections, 168 native freshwater bivalve and five invasive species have been recorded for 52 hydrographic regions in South America. The higher species richness has been detected in the South Atlantic, Uruguay, Paraguay, and Amazon Brazilian hydrographic regions. Presence or absence data were analysed by Principal Coordinate for Phylogeny-Weighted. The lineage Veneroidea was more representative in hydrographic regions that are poorer in species and located West of South America. The

Mycetopodidae and Hyriidae lineages were predominant in regions that are richest in species toward the East of the continent. The distribution of invasive species *Limnoperna fortunei* is not related to species richness in different hydrographic regions there. The species richness and its distribution patterns are closely associated with the geological history of the continent. The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance. A plan to the management of this fauna according to

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particular ecological characteristics and human uses of hydrographic regions is needed.

Keywords Bivalve · South America · Literature review · Scientific collections · Phylogenetic composition

Literature review

Earlier works on the freshwater bivalves of South America (from ~1800 to ~1890) are descriptive and consist of illustrated catalogs of species collected by naturalists during exploratory expeditions along river basins (Spix, 1827; Orbigny, 1835, 1846; Hupé, 1857). Shells acquired from travelers or merchants, or through exchange with colleagues or amateurs, have been described and cataloged by collectors and naturalists such as Maton (1811), Lamarck (1819), Lea (1834, 1838, 1852, 1857, 1860, 1863, 1869, 1874), Philippi (1847), Küster (1842), Sowerby (1864, 1867, 1868, 1869a, b), among others. Most scientific collections were private and would be eventually sold or donated to European museums (Dance, 1966; Olazarri, 1975; Haag, 2012). At that time, descriptions of new species were extremely poor, largely vague, and based on outdated concepts containing few illustrations and mostly from single specimens. Some of these catalogs were more iconographic than descriptive. In some cases, with the intent of showing the beauty shells, some conchological features were overlooked by designers. This fact led to misunderstandings and wrong identification at the genus or species levels. Very often, collecting localities were

unknown or poorly documented, consisting of vague references such as the continent or country name where a species was collected. Sometimes, old local names of rivers and lakes are no longer used, making the collection site difficult to locate.

In a subsequent period (~1890–1960), special attention was given to the works of Simpson (1900, 1914) who published a summary and a catalog of World Unionoida, including South American species. This publication includes redescrptions, lists of synonyms, and significant taxonomic comments, with many species being labeled as *incertae sedis*. Hermann von Ihering emigrated from Germany to Brazil and lived there for many years, where he studied and collected bivalve mollusks, starting in the State of Rio Grande do Sul. Some years later, he moved to São Paulo to open the Museu de Zoologia da Universidade de São Paulo in 1895. Ihering organized the malacological collection and published over 35 articles on mollusks (Vaz, 1986), including checklists and identification keys of taxa from several drainages from Brazil and neighboring countries (Ihering, 1890, 1893, 1910). He also revisited the bivalve species described by Spix and Lamarck (Ihering, 1890, 1910) by examining the types. He was the first researcher to see and describe the lasidium (Ihering, 1891) larvae of Mycetopodidae, which is very similar to the haustorium of African species of the same Etherioidea superfamily (Wächtler et al., 2001). Unfortunately, due to political problems during WWI, Ihering was forced to leave both the museum and the country, and ended up selling his collection to European museums. In the early twentieth century, a pioneering initiative by local researchers attempted to catalog bivalves.

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Among them, we can mention Formica-Corsi (1900) who looked at Uruguayan bivalves, as well as Morretes (1949, 1953) who worked with the mollusks from Brazil. Ortmann (1921) was the first researcher to include anatomical traits of the soft parts of adults and the glochidia larvae in the descriptions of his species. He proposed the first studies on phylogenetic relationships among Unionoida. However, his studies were not given the right recognition by his future fellow scholars.

Many Unionoida and Veneroida species were described for hydrographic basins located in Patagonia, Venezuela, Colombia, and Uruguay by Marshall (1916, 1922, 1924, 1927a, b, 1928, 1930) and Pilsbry (1896, 1897). Many new species were described (Baker, 1914, 1930) after conducting North American expeditions in the Amazon region, Brazil, and Venezuela. The 433 species of Unionoida described from South America were reduced by Haas (1930, 1931a, b, 1969) to 124, based primarily on shell characteristics. He mentioned 70 species and subspecies of Hyriidae and 54 Mycetopodidae.

With Argentino Bonetto and his team from Argentina, a new period (from ~1960 to present) pioneered by South American morphologists and taxonomists began. A series of morphological and taxonomic studies were published including the description of many species of glochidia and lasidia of South American freshwater bivalves (Bonetto, 1961a, b, 1962, 1963, 1964, 1965, 1966, 1967a, b, 1972, 1997); Bonetto & Ezcurra-de-Drago, 1966; Bonetto et al., 1986).

At the end of the last century, malacology was consolidated in many South American universities, mainly Argentina, Brazil, Chile, Uruguay, and in other research institutions like: Instituto Miguel Lillo at Tucuman and Instituto Nacional de Limnología at Santa Fé (both in Argentina), Plataforma de Investigación en Ecohidrología y Ecohidráulica at Santiago (Chile), Museo Nacional de Historia Natural de Montevideo (Uruguay), and Fundação Zoobotânica do Rio Grande do Sul at Porto Alegre (Brazil). From there, the study of freshwater bivalve became more consolidated resulting in several important scientific publications (Olazarri, 1963, 1966, 1975; Mansur, 1970, 1972, 1974, 1999; Veitenheimer, 1973a, b; Hebling & Penteadó, 1974; Mansur & Veitenheimer, 1975; Hebling, 1976; Veitenheimer & Mansur, 1978a, b; Mansur & Veitenheimer-Mendes, 1979; Alvarenga & Ricci, 1979a, b, 1989; Mansur & Anflor, 1981; Mansur et al., 1987, 1988, 1991, 1994;; Mansur & Garces, 1988; Mansur & Campos-

Velho, 1990, 2000; Mansur & Silva, 1990, 1999; Ricci et al., 1990; Mansur & Valer, 1992; Simone, 1994, 1997, 1999, 2006; Mansur & Olazarri, 1995; Avelar & Mendonça, 1998; Serrano et al., 1998; Pereira et al., 2000, 2011, 2012; Callil & Mansur, 2002, 2005, 2007; Mansur & Pereira, 2006; Scarabino & Mansur, 2007; Mansur & Pimpão, 2008; Pimpão et al., 2008, 2012; Lasso et al., 2009; Pimpão & Mansur, 2009). Chilean researchers carried out multiple studies on *Diplodon chilensis* documenting its ecology (Lara & Parada, 1991, 2009; Lara & Moreno, 1995; Lara et al., 2002a, b; Grandón et al., 2008), taxonomy (Parada & Peredo, 2002), morphology (Parada et al., 1989a; Valdovinos & Pedreros, 2007), reproduction (Peredo & Parada, 1984, 1986, Parada et al., 1987, 1990; Peredo et al., 1990), life history (Parada et al., 1989b, Parada & Peredo, 1994), genetics (Jara-Seguel et al., 2000; Peredo et al., 2003), distribution (Lara & Parada, 1988, 2008; Parada et al., 2007), and relocation (Parada & Peredo, 2005; Peredo et al., 2005). This intensive effort propelled *D. chilensis* as the best known species of Hyriidae in the continent.

Considering the order Veneroida, Spix (1827), Orbigny (1835, 1846), Anton (1837), Baker (1930), Clessin (1879, 1888), Josseaume (1889), Pilsbry (1897, 1911), described the first species of Sphaeriidae from South America. Later, South American researchers described and cataloged several species for that continent: Doello-Jurado (1921), Meier-Brook (1967), Ituarte (1989, 1994a, 1995, 1996, 1999, 2000, 2001, 2004, 2005, 2007), Ituarte & Mansur (1993), Ituarte & Korniuschin (2006), Klappenbach (1962), Mansur & Meier-Brook, (2000), and Mansur et al. (2008).

Parodiz & Hennings (1965) reviewed the 30 species of Corbiculidae described for the Paraná/Paraguay and Uruguay basins. The authors concluded that only *Cyanocyclus* (= *Necorbicula*) *limosa* (Maton, 1811) and *Cyanocyclus paranensis* (Orbigny, 1835) would be valid species, whereas the others would be synonymized. Nevertheless, the species cited for the Amazon [*Cyanocyclus amazonica* (Prime, 1870) and *Cyanocyclus brasiliiana* (Deshayes, 1854)], and more to the North of South America [*Cyanocyclus bavayi* (Ancey, 1880); *Cyanocyclus cuneata* (Jonas, 1844); *Cyanocyclus rotunda* (Prime, 1860) and *Cyanocyclus surinamica* (Clessin, 1879)] need revision. Later, Ituarte (1994b) presented important publications that provided diagnostic morphological and reproductive data of invasive species *Corbicula fluminea* (Müller,

1774) and *Corbicula largillierti* (Philippi, 1884) compared to native species *C. limosa*. Martins et al. (2004) reviewed the Corbiculidae invasive species in Southern Brazil looking at morphological and conchological characters. Two known Dreissenidae species and *Anticorbula fluviatilis* (Adams, 1860), the last placed with doubts inside Myoida, requires taxonomic revisions. Darrigran & Damborenea (2009) and Mansur et al. (2012c) compiled a series of studies on *Limnoperna fortunei* (Dunker, 1857) after the invasion in South America since 1991.

Recently, Simone (2006) has published an illustrated catalog of the continental mollusks of Brazil and neighboring countries, which cited 120 species of freshwater bivalves. Despite this massive effort, many genera and species were listed without the proper taxonomic revision. Furthermore, synonyms of different species were brought together without considering advances in the study of the larvae.

Biological characterization

In South America, there are three lineages of freshwaters Bivalvia: Mytiloidea, Unionoidea, and Veneroidea. According to Simone (1999), the systematic definition of *A. fluviatilis* into Lyonsiidae and Myoida was used as a temporary suggestion.

Mytiloidea is represented by the invasive species *L. fortunei* commonly known as golden mussel. *L. fortunei* is native from Asia, and was probably brought to South America via ballast water in 1991 (Darrigran & Pastorino, 1995; Mansur et al., 2003b, 2004a, b; Santos et al., 2012). With morphological characteristics similar to marine mussels (Mansur, 2012), it presents the complete larval cycle in the plankton (Mansur et al., 2012a) and after recruitment forms macroclusters. *L. fortunei* is very aggressive to the environment since it modifies the landscape, the flora, and benthic fauna as an “ecosystem engineer” (Darrigran & Damborenea, 2011). In built environments that use untreated water for cooling, the golden mussel causes clogging with considerable economic losses (Darrigran et al., 2007).

The Unionoidea are commonly known as freshwater mussels or only mussels, without marine members. They can be found all over the world except for Antarctica. In South America, this order is represented by two families, Hyriidae and Mycetopodidae,

comprising of only native species. They normally have from 2 to 10 cm in length though they can be longer, but according to Castellanos & Landoni (1990), *Mycetopoda soleniformis* (Orbigny, 1835) can reach up to 22 cm in length. They are considered to be good biological (Pereira et al., 2011) and paleoenvironment (Wesselingh, 2006) indicators. During geological time, these bivalves were the first to adapt to freshwater. Fossil record of freshwater bivalve *Anthraconauta Pruvost*, 1930, from the Carboniferous and Permian (late Paleozoic era) (Pellant, 1996), hold many similarities to the current species (Parodiz, personal communication). The unionids are very biodiverse. They have an amazing life cycle and strategies allowing survival in extreme situations, such as waterfalls, drought, and flood pulses. In the larval stage, most are temporary fish parasites. The larvae form cysts on the gills, scales, and fish fins. After 1 month, the larvae evolve to the juvenile stage breaking the cysts and falling to the substrate. This strategy helps the bivalves to overcome the problems of dispersion in upstream rivers. The South American unionoids show two basic larval types: the lasidium of Mycetopodidae, and glochidium of Hyriidae (Mansur et al., 2012a). Both the larval types are modified veligers and act as temporary ectoparasites on fish. As fish parasites, the lasidium triples in size and sends haustorium that penetrates the host tissues and remove its nutrients. The larval shell consists of a single helmet-shaped piece which involves the dorsal part of a body. This is formed by an anterior tongue-shaped ciliated lobe or a bilobated one, a central body with ventral lobes, a bilobated posterior tail with terminal hooks, and an anterior transparent adhesive organ. Depending on the species, this can be either strip-shaped (genus *Monocondylaea* Orbigny, 1835), scourge-shaped (*Leila blainvilliana* Lea, 1834), or flower-shaped with a micro hook at one end, as *Anodontites* Bruguière, 1792, *Mycetopoda* Orbigny, 1835 and *Acostea rivolii* Deshayes, 1827) (Bonetto, 1997). The lasidia of other species and genera of the family, as *Mycetopodella* Marshall, 1927, *Diplodontites* Marshall, 1922, *Fossula* Lea, 1870, *Haasica* Strand, 1932, *Bartlettia* A. Adams, 1866, and *Tamsiella* Haas, 1931 are unknown.

The larval body of glochidia is protected by two valves with an edge on the ventral border, a hook and a basal callus on the internal side of the ventral edge. Internally, there is an adhesive flagellum (absent in

Castalia Lamarck, 1819), sensory cilia, cirrus, a central adductor muscle, a very rudimentary velum, and phagocytic cells lining inside the valves. With the flagellum and hooks, the glochidium is enabled to get attached to the gills, fins, or scales of the fish that develop a cyst covering the larva. However, there are exceptions among species of the genus *Diplodon* Spix (1827). Hook and adhesive filament are absent on glochidia of the subgenus *Rhipidodonta* Morch, 1853. So the respective species are not fish parasites. Larval development until the juvenile stage is complete inside parental marsupium. In general, the glochidia of Hyriidae does not present spinules at the edges of the valves and on the base of the hook like other species of Unionoidea (Unionidae and Margaritiferidae) (Mansur et al., 2012a). Bonetto (1961b) described glochidia of several species of *Diplodon* genus. Based on morphological studies, Pimpão et al. (2012) reviewed and standardized the terminology of glochidia shells from South American Hyriidae, thus facilitating the differentiation between several species of Amazonian Basin.

The order Veneroidea includes the following families: Corbiculidae, Sphaeriidae, and Dreissenidae. They are too considered to be good biological indicators (Lanzer & Schäfer, 1987; Pereira et al., 2011). The Corbiculidae native genera are represented by *Cyanocyclus* Blainville, 1818, and *Polymesoda* Rafinesque, 1828 with pallial sinus. The invasive Corbiculidae are represented by four species of the genus *Corbicula* Mergele von Muehlfeld, 1811. The incubation of larvae is complete in *Cyanocyclus* until it reaches an advanced stage inside the marsupium, a case of euviipary. The number of embryos is small, ranging from 25 to 45 per gill, and the release is not synchronized. Two species of *Polymesoda* occur in brackish waters in the Northern part of the continent. The pallial sinus is absent in the invasive species of Corbiculidae. Only *C. fluminea* and *C. largillierti* have their larval and life cycles known; their embryos are incubated in marsupial gills until the end of stage veliger or pediveliger, and liberated synchronously (Mansur, 2012; Mansur et al., 2012a, b).

In Sphaeriidae, species of the genera *Sphaerium* Scopoli, 1777 and *Musculium* Link, 1807 show sequential development of broods into independent marsupial brood sacs. In *Pisidium* Pfeiffer, 1821 a synchronized development in a single marsupial brood sac occurs (Cooley & Ó Foighil, 2000). An exception

was observed in *Pisidium punctiferum* (Guppy, 1867) which form one brood at a time, but with different sizes of embryos which suggest unsynchronized release (Anflor & Mansur, 2001). *Eupera* Bourguignat, 1854 has the most primitive system of reproduction. Embryos have synchronized development, but there is no brood sac inside the marsupium (Cooley & Ó Foighil, 2000). The species of this genus produce delicate byssus threads that facilitate adherence to pebbles, plants, or floating aquatic vegetation. The great expansion of its excretory sac may explain its adaptation and resistance to prolonged periods of drought. Among Dreissenidae, we only know of the biology of *Mytilopsis lopezi* Alvarenga & Ricci, 1989. In this species, the embryos grow attached to the mantle in the pallial cavity until the juvenile stage, with no synchronous release (Mansur et al., 2012a). *A. fluviatilis* is known from the Amazon River in Brazil and Peru (Simone, 1999). It is a nestling bivalve that lives attached to sandy grains and litter underneath (Beasley, pers. communication). Simone (1999) described its morphology for the first time including it with doubts in Lyonsiidae (Pandoroidea). According to him, this species has been reported by various authors also in Corbulidae (Myoida), sharing some similarities with Myidae, Hiatelloidea, and Thraciidae as well.

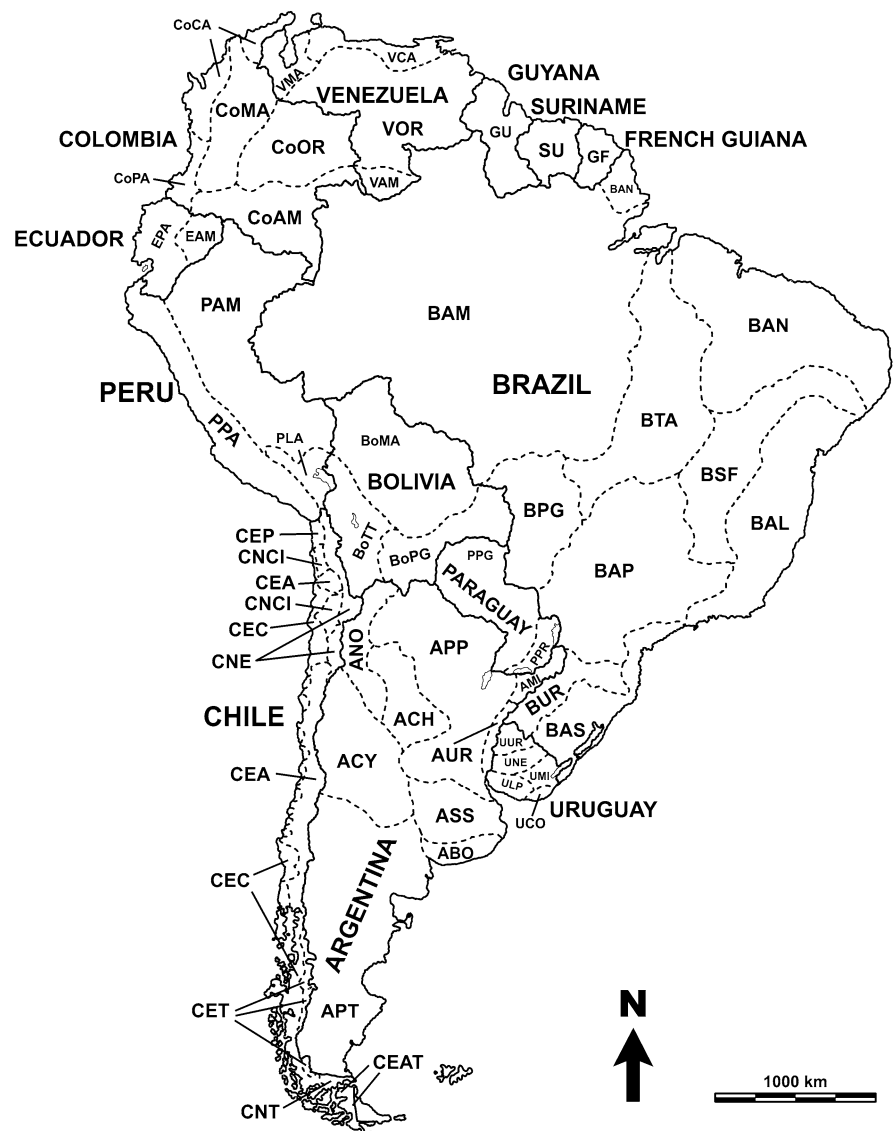
The purpose of this paper is to survey freshwater bivalve species from South America, to classify and rank hydrographic regions based on species richness, composition, and phylogenetic lineages in order to facilitate the identification of region-specific conservation needs of this highly threatened fauna.

Compilation of species records and analysis

South America, with an area of 17,819.100 km², represents 12% of the world land area and is home to 6% of the world population. It has several major river systems such as the Amazon, Orinoco, Parana, and La Plata River basins, with a total drainage area of 9,583.000 km². Both these systems and other smaller ones show areas of endemism, diversity hotspots, and unique landscapes.

Data on the occurrence of bivalve species in hydrographic regions in South America (Fig. 1; Table 1) were compiled from the scientific literature and examinations of the following scientific collections: Academy of Natural Sciences of Philadelphia (ANSP; Philadelphia, USA); Carnegie Museum of

Fig. 1 Hydrographic regions in South American countries and territory. Respective codes shown in Table 1



Natural History (CM; Pittsburgh, USA); Coleção de Moluscos da Universidade do Estado do Rio de Janeiro (UERJ; Rio de Janeiro, Brazil); Coleção de Moluscos da Universidade Federal do Mato Grosso (UFMT; Cuiabá, Brazil); Fundación Miguel Lillo (FML; Tucumán, Argentina); Instituto Nacional de Pesquisas da Amazônia (INPA; Manaus, Brazil); Musée d'Histoire Naturelle Bâle (MHNB; Basel, Switzerland); Musée de Zoologie (ZML; Lausanne, Switzerland); Musée d'Histoire Naturelle de la Ville de Genève (MHNG; Geneva, Switzerland); Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" (MACN; Buenos Aires, Argentina); Museo de La

Plata (MLP; La Plata, Argentina); Museo Nacional de Historia Natural de Chile (MNHNC; Santiago, Chile); Museo Nacional de Historia Natural de Montevideo (MNHM; Montevideo, Uruguay); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP; Porto Alegre, Brazil); Museu de Ciências Naturais Fundação Zoobotânica do Rio Grande do Sul (MCN; Porto Alegre, Brazil); Museu de Zoologia da UNISINOS (MZU; São Leopoldo, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP; São Paulo, Brazil); Museo Nacional da Universidade Federal do Rio de Janeiro (MNRJ; Rio de Janeiro, Brazil); Museu Paraense

Table 1 Hydrographic regions in South America

Countries	Hydrographic regions	Codes
Argentina (AR) ^a	Patagonico System	APT
	Endorreico Central System	ACH
	Cuyano Subandino System	ACY
	Bonaerense	ABO
	Paranoplatense System	APP
	Misionero System	AMI
	Uruguay River System	AUR
	Salado del Sur System	ASS
	Noa System	ANO
Brazil (BR) ^b	Amazonas River	BAM
	Tocantins/Araguaia River	BTA
	Rivers of the North and Northeast Atlantic	BAN
	São Francisco River	BSF
	Rivers of the East Atlantic	BAL
	Upper Paraná River	BAP
	Paraguay River	BPG
	Uruguay River	BUR
	Rivers of the south and southeast Atlantic	BAS
Bolivia (BO) ^c	Madeira River	BoMA
	Titicaca Lake—endorheic basins	BoTT
Chile (CH) ^d	Paraguay River	BoPG
	Atlantic exorheic basins	CEAT
	Trans-Andean exorheic basins	CET
	Andean exorheic basins	CEA
	Pre-Andean exorheic basins	CEP
	Coastal exorheic basins	CEC
	Endorheic Basins of Alta Puna	CNE
	Endorheic basins of intermediate elevations	CNCI
Colombia (CO) ^e	Rivers that flow into the Caribbean Sea	CoCA
	Magdalena River	CoMA
	Orinoco River	CoOR
	Rivers that flow into the Pacific Ocean	CoPA
	Amazon River	CoAM
Guyana (GU) ^f	Rivers that flow into the Atlantic Ocean	GUA
French Guiana (GF) ^g	Rivers that flow into the Atlantic Ocean	GFA
Ecuador (EQ) ^h	Rivers that flow into the Pacific Ocean	EPA
	Amazon River	EAM

Table 1 continued

Countries	Hydrographic regions	Codes
Paraguay (PY) ⁱ	Paraguay River	PPG
	Paraná River	PPR
Peru (PE) ^j	Rivers that flow into the Pacific Ocean	PPA
	Andine Lakes	PLA
Suriname (SU) ^k	Amazon River	PAM
	Rivers that flow into the Atlantic Ocean	SUA
Venezuela (VE) ^l	Rivers that flow into Caribbean Sea	VCA
	Maracaibo Lake	VMA
	Orinoco River	VOR
Uruguay (UY) ^m	Amazon River	VAM
	Uruguay River	UUR
	Negro River	UNE
	La Plata River	ULP
	Mirim Lake	UMI
	Coastal Lagoons	UCO

The hydrographic regions were delimited and adapted according to the following sources:

^a IADIZA—Instituto Argentino de Investigaciones de las Zonas Áridas (www.cricyt.edu.ar/ladyot/lava_carto/mapas/argentina_cuencas/index.html)

^b ANEEL—Agência Nacional de Energia Elétrica (www.aneel.gov.br/area.cfm?id_area=104)

^c Mondaca (2011)

^d IGM—Instituto Geografico Militar del Chile (www.igm.cl/)

^e IGAC—Instituto Geográfico Agustín Codazzi (www.igac.gov.co)

^{f,g,k} Each country is one Hydrographic region considering that all rivers flow into the Atlantic Ocean

^h IGM—Instituto Geográfico Militar del Ecuador (www.igm.gob.ec)

ⁱ Paraguay Biodiversidad (www.pybio.org/)

^j MINEM—Ministerio de Energia Y Minas del Peru (www.minem.gob.pe/minem/archivos/file/DGAAM/mapas/mapas_cuencas.htm)

^l IGVS—Instituto Geográfico de Venezuela Simón Bolívar (www.igvsb.gob.ve/#)

^m IA—Instituto de Agrimensura Facultad de Ingeniería UdelaR (www.fing.edu.uy/ia/deptogeom/libro/capitulo8/hidrografia.htm)

Emilio Goeldi (MPEG; Belém, Brazil); Museum für Naturkunde (ZMB; Berlin, Germany); Museum National d'Histoire Naturelle (MNHN; Paris, France); National Museum of Natural History, Smithsonian Institution (USNM; Washington D.C., USA); Natural

History Museum of United Kingdom (NHMUK; London, United Kingdom); Naturhistorisches Museum (NMW; Wien, Austria); Senckenberg Forschungsinstitut und Naturmuseum (SMF; Frankfurt a.M., Germany); Staatliches Museum für Naturkunde (SMNS; Stuttgart, Germany); and Zoologische Staatssammlung München (ZSM; Munich, Germany). Part of the data on the occurrence of species in Peru, Ecuador, and Colombia were extracted from Mussel Project (mussel-project.uwsp.edu/). All records of species (presence or absence) were tabulated for each country according to the main hydrographic regions.

In order to recognize the phylogenetic composition of Bivalvia in the main hydrographic regions in South America (Fig. 1; Table 1), the following phylogenetic relationships were looked at (Mytilidae ((Hyriidae + Mycetopodidae) ((Sphaeriidae + Corbiculidae) Dreissenidae) *Anticorbula fluviatilis*))) and supported by the molecular and morphological analyses according to Walker et al. (2006) and Giribet & Wheeler (2002).

A pairwise phylogenetic distance matrix (D_P) for the presence or absence of bivalve species in hydrographic regions included in the dataset was generated using Mesquite software (available at <http://mesquiteproject.org/mesquite/mesquite.html>). Hence, tree branch lengths were fixed to 1.0, as clade age estimates for bivalves were not available, and patristic distances between species were computed. The phylogenetic composition of each hydrographic regions was addressed using the phylogenetic fuzzy-weighting method developed by Pillar & Duarte (2010), and implemented in the software SYNCSA v. 2.5.22 (Debastiani & Pillar, 2012, available at <http://www.cran.org>). Pairwise phylogenetic distances in D_P were transformed into a phylogenetic similarity matrix ($S_P = 1 - D_P$). Then, phylogenetic similarities in S_P were used to weigh species composition in hydrographic regions, using a fuzzy set algorithm (see Pillar & Duarte, 2010 for details). This procedure generates a matrix describing the phylogeny-weighted species composition for each hydrographic region in South America in the dataset. That is, the presence of each species i in a given hydrographic region is shared with each species j occurring in the array of hydrographic regions, taking into account the phylogenetic similarity between i and j . Accordingly, those species j that are more phylogenetically related to i (e.g., from the same genus) will receive a proportionally higher fraction of the presence

of i in those hydrographic regions than more phylogenetically distant species (e.g., from a different family), which will receive a proportionally lower fraction, and so on. Note that the sum of species presences (i.e., species richness) in each hydrographic region will remain exactly the same after phylogenetic fuzzy-weighting. After defining a multivariate matrix describing phylogenetic composition of hydrographic regions, we conducted a principal coordinates analysis (Gower, 1966; Legendre & Legendre, 1998) on that matrix to generate principal coordinates of phylogenetic structure (PCPS) for each hydrographic regions (Duarte, 2011; Duarte et al., 2012). This analysis was conducted on square-rooted Bray–Curtis dissimilarities between hydrographic regions. Then, we plotted the two first PCPS in a scatter plot to evaluate the association between the hydrographic regions and major bivalve lineages. PCPS analysis was conducted using the PCO statistical software (by M. Anderson, available at <http://www.stat.auckland.ac.nz/~mja/Programs.htm>). The Mantel test was used to assess the possible relationship of the distribution of invasive species with species richness in hydrographic regions. The test verified the possible correlation between two arrays: presence and absence of *L. fortunei* or *Corbicula* species (obtained from Jaccard index) and richness species of freshwater bivalves (chord distance).

Species richness and distribution

Based on the survey of presence and absence, 168 native limnic bivalves and 5 invasive species were recorded for the 52 hydrographic regions of 12 South American countries, and one territory (Table 2).

Hyriidae (36.42%) accounts for the highest percentage of species, followed by Mycetopodidae (27.75%) and Sphaeriidae (24.86%), Corbiculidae (8.09%), Dreissenidae (1.73%), and Mytilidae and Lyonsiidae (0.58%). The Unionoida represents 64.18% of the species richness of freshwater bivalves in South America while Veneroida 35.26% and Mytilioida 0.58%.

The country that has the highest species richness is Brazil (117 species), followed by Argentina (60), Venezuela (49), and Uruguay (46) (Table 2). Hydrographic regions with the greatest species richness (Fig. 2) are in Brazil followed by Argentina and Uruguay, Venezuela and Peru. In Brazil, the richest hydrographic regions are in the South and Southeast

Table 2 Freshwater bivalves species of South American countries and territory

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Mytiloidea													
Mytilidae													
<i>Limnoperna fortunei</i> (Dunker, 1857)	1	1	1	1	1	0	0	0	0	0	0	0	0
Unionoidea													
Mycetopodidae													
<i>Anodontites (Anodontites) aroanus</i> H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anodontites (A.) carinatus</i> (Dunker, 1858)	0	0	0	0	0	0	1	1	1	0	0	0	1
<i>Anodontites (A.) colombiensis</i> Marshall, 1922	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Anodontites (A.) crispatus</i> Bruguière, 1792	0	1	0	0	1	0	1	1	1	1	1	1	1
<i>Anodontites (A.) elongatus</i> (Swainson, 1823)	1	1	1	1	1	0	1	1	1	0	0	0	1
<i>Anodontites (A.) ferrarisii</i> (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) guanarensis</i> Marshall, 1927	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anodontites (A.) iheringi</i> (Clessin, 1882)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) infossus</i> H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anodontites (A.) irisans</i> Marshall, 1926	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anodontites (A.) lucidus</i> (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) moricandii</i> (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) obtusus</i> (Spix 1827)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) patagonicus</i> (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) puelchanus</i> (Orbigny, 1835)	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anodontites (A.) pittieri</i> Marshall, 1922	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anodontites (A.) schomburgianus</i> (Sowerby, 1870)	0	1	0	0	0	0	0	0	1	1	0	0	1
<i>Anodontites (A.) soleniformis</i> (Orbigny, 1835)	1	1	0	1	1	0	0	0	1	0	0	0	0
<i>Anodontites (A.) tenebricosus</i> (Lea, 1834)	1	1	1	1	1	0	0	0	1	0	0	0	1
<i>Anodontites (A.) tortilis</i> (Lea, 1852)	0	0	0	0	0	0	1	1	1	0	0	0	1
<i>Anodontites (A.) trapesialis</i> (Lamarck, 1819)	1	1	1	1	1	0	1	1	1	0	0	0	1
<i>Anodontites (A.) trapezeus</i> (Spix, 1827)	1	1	1	1	1	0	0	0	0	0	0	0	1
<i>Anodontites (Lamproscapha) ensiformis</i> (Spix, 1827)	1	1	1	1	1	0	0	1	1	1	0	0	1
<i>Anodontites (L.) falsus</i> (Simpson, 1900)	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Mycetopoda legumen</i> (Martens, 1888)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Mycetopoda siliquosa</i> (Spix, 1827)	1	1	1	1	1	0	1	1	1	0	1	0	1
<i>Mycetopoda soleniformis</i> Orbigny, 1835	1	1	1	1	1	0	1	0	1	0	0	0	1
<i>Mycetopodella falcata</i> (Higgins, 1868)	0	1	0	0	0	0	1	0	1	0	0	0	0
<i>Monocondylaea corrientesensis</i> (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Monocondylaea costulata</i> (Moricand, 1858)	0	1	0	0	1	0	0	0	1	0	0	0	0
<i>Monocondylaea franciscana</i> (Moricand, 1837)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Monocondylaea guarayana</i> (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>Monocondylaea jaspidea</i> (Hupé, 1857)	0	1	0	0	0	0	0	0	0	1	0	0	1
<i>Monocondylaea minuana</i> (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Monocondylaea paraguayana</i> (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Monocondylaea parchappii</i> (Orbigny, 1835)	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Fossula fossiculifera</i> (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Tamsiella amazonica</i> Bonetto, 1972	0	1	0	0	1	0	0	0	1	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
<i>Tamsiella schroeteriana</i> (Lea, 1852)	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Tamsiella tamsiana</i> (Dunker, 1858)	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Diplodontites cookei</i> Marshall, 1922	0	0	0	0	0	0	1	1	1	0	0	0	0
<i>Diplodontites olssoni</i> Pilsbry, 1933	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Diplodontites pilsbryana</i> Olsson & Wurtz, 1951	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Haasica balzani</i> (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Leila blainvilliana</i> (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Leila esula</i> (Orbigny, 1835)	0	1	0	1	1	0	1	0	1	1	0	0	1
<i>Acostaea rivolii</i> (Deshayes, 1827)	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Bartlettia stefanensis</i> (Moricand, 1856)	0	1	0	1	1	0	0	1	1	0	0	0	0
Hyriidae													
<i>Diplodon (Australis) solidulus</i> (Philippi, 1869)	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Diplodon (Diplodon) aethiops</i> (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) berthae</i> Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) besckeanus</i> (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) caipira</i> (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) chilensis</i> (Gray, 1828)	1	0	0	0	0	1	0	0	1	0	0	0	0
<i>Diplodon (D.) delodontus</i> (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) dunkerianus</i> (Lea, 1856)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) ellipticus</i> Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) expansus</i> (Küster, 1856)	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) granosus</i> (Bruguère, 1792)	0	1	0	0	0	0	0	0	0	1	1	1	1
<i>Diplodon (D.) guaranianus</i> (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>Diplodon (D.) imitator</i> Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) martensi</i> (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) multistriatus</i> (Lea, 1831)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) obsolescens</i> Baker, 1913	0	1	0	0	0	0	0	0	0	1	0	0	1
<i>Diplodon (D.) parallelopipedon</i> (Lea, 1834)	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Diplodon (D.) parodizi</i> Bonetto, 1960	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) paulista</i> (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) piceus</i> (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) rhombeus</i> Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) rhuacoicus</i> (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) suavidicus</i> (Lea, 1856)	0	1	0	0	0	0	1	0	0	1	0	0	1
<i>Diplodon (D.) vicarius</i> Ortmann, 1821	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (D.) wymanii</i> (Lea, 1860)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (Rhipidodonta) burroughianus</i> (Lea, 1834)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) charruanus</i> (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) deceptus</i> Simpson, 1914 sensu Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) funebris</i> (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) koseritzi</i> (Clessin, 1888)	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) hildae</i> Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Diplodon (R.) hylaeus</i> (Orbigny, 1835)	1	1	1	0	1	0	0	1	1	0	0	0	0

Table 2 continued

Species	South American countries													
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE	
<i>Diplodon (R.) iheringi</i> Simpson, 1914	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon (R.) peraeformis</i> (Lea, 1860)	1	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon (R.) variabilis</i> (Maton, 1811)	1	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon fontainianus</i> (Orbigny, 1835)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon greeffeanus</i> (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon paranensis</i> (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0	
<i>Diplodon pfeifferi</i> (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon rotundus</i> Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon solisianus</i> (Orbigny, 1835)	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon uruguayensis</i> (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0	
<i>Diplodon voltzi</i> Vernhout, 1914	0	0	0	0	0	0	0	0	0	0	1	1	1	
<i>Castalia ambigua</i> Lamarck, 1819	0	1	0	0	1	0	1	1	1	1	1	0	1	
<i>Castalia cordata</i> Swainson, 1840	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Castalia crosseana</i> Hidalgo, 1865	0	0	0	0	0	0	0	1	0	0	0	0	0	
<i>Castalia duprei</i> (Récluz, 1842)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Castalia ecarinata</i> Mousson, 1869	0	0	0	0	0	0	1	1	0	0	0	0	0	
<i>Castalia inflata</i> Orbigny, 1835	1	1	1	1	1	0	0	0	0	0	0	0	0	
<i>Castalia martensi</i> (Ihering, 1891)	0	1	1	0	0	0	0	0	0	0	0	0	0	
<i>Castalia multisulcata</i> Hupé, 1857	0	0	0	0	0	0	1	0	0	0	0	0	1	
<i>Castalia nehringi</i> (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0	
<i>Castalia orbignyi</i> (Deville & Hupé, 1850)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Castalia orinocensis</i> Morrison, 1943	0	0	0	0	0	0	1	0	0	0	0	0	1	
<i>Castalia psammoica</i> (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0	
<i>Castalia quadrata</i> (Sowerby, 1869)	0	1	0	0	0	0	0	0	0	1	0	0	1	
<i>Castalia schombergiana</i> Sowerby, 1869	0	1	0	0	0	0	0	0	0	0	0	0	1	
<i>Castalia stevensi</i> (Baker, 1930)	0	0	0	0	0	0	1	0	0	1	0	0	1	
<i>Castalia sulcata</i> (Krauss, 1849)	0	1	0	0	0	0	0	0	0	1	1	1	1	
<i>Castalia undosa</i> Martens, 1885	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Paxyodon symmathophorus</i> (Meuschen, 1781)	0	1	0	0	1	0	1	0	1	1	0	0	1	
<i>Prisodon obliquus</i> Schumacher, 1817	0	1	0	0	0	0	1	1	1	1	0	0	1	
<i>Triplodon corrugatus</i> (Lamarck, 1819)	0	1	0	0	0	0	1	1	1	0	0	0	1	
<i>Triplodon chodo</i> Mansur & Pimpão, 2008	0	1	0	0	0	0	0	0	0	0	0	0	0	
Veneroida														
Dreissenidae														
<i>Mytilopsis lopesi</i> Alvarenga & Ricci, 1989	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Mytilopsis trautwineana</i> (Tryon, 1866)	0	0	0	0	0	0	1	1	0	0	0	0	0	
<i>Congeria hoeblichii</i> Schütt, 1991	0	0	0	0	0	0	1	0	0	1	0	0	1	
Corbiculidae														
<i>Cyanocyclus amazonica</i> (Prime, 1870)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Cyanocyclus bavayi</i> (Ancey, 1880)	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Cyanocyclus brasiliiana</i> (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Cyanocyclus cuneata</i> (Jonas, 1844)	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Cyanocyclus limosa</i> (Maton, 1811)	1	1	1	0	0	0	0	0	0	0	0	0	0	

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
<i>Cyanocyclas paranaensis</i> (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Cyanocyclas rotunda</i> (Prime, 1860)	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>Cyanocyclas surinamica</i> (Clessin, 1879)	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Corbicula fluminalis</i> (Müller, 1774)	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Corbicula fluminea</i> (Müller, 1774)	1	1	1	0	0	0	1	0	1	0	0	0	1
<i>Corbicula largillierti</i> (Philippi, 1844)	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Corbicula</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Polymesoda solida</i> (Philippi, 1846)	0	1	0	0	0	0	1	0	0	0	0	0	1
<i>Polymesoda aequilatera</i> (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	1	1	1	1
Sphaeriidae													
<i>Byssanodonta paranensis</i> Orbigny, 1846	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Eupera bahiensis</i> (Spix, 1827)	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Eupera doellojuradoi</i> Klappenbach, 1962	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Eupera elliptica</i> Ituarte & Dreher-Mansur, 1993	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Eupera guaraniana</i> Ituarte, 1994	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Eupera iguazuensis</i> Ituarte, 1989	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Eupera klappenbachi</i> Mansur & Veitenheimer, 1975	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Eupera modioliforme</i> (Anton, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eupera platensis</i> Doello-Jurado, 1921	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Eupera primei</i> Klappenbach, 1967	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Eupera simoni</i> (Jousseume, 1889)	0	1	0	0	0	0	0	0	1	0	0	0	1
<i>Eupera tumida</i> (Clessin, 1879)	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Musculium argentinum</i> (Orbigny, 1835)	1	1	1	0	0	1	0	0	0	0	0	0	0
<i>Musculium patagonicum</i> Pilsbry, 1911	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium bejuma</i> Baker, 1930	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Pisidium boliviense</i> Sturany, 1900	0	1	0	0	0	0	0	1	1	0	0	0	0
<i>Pisidium chicha</i> Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium chilense</i> (Orbigny, 1846)	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium chiquitanum</i> Ituarte, 2001	1	0	0	0	1	0	0	0	0	0	0	0	0
<i>Pisidium dorbignyi</i> Clessin, 1879	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Pisidium forense</i> Meier-Brook, 1967	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium globulus</i> Clessin, 1888	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium huillichum</i> Ituarte, 1999	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium inacayali</i> Ituarte, 1996	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium iquito</i> Ituarte, 2004	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pisidium lebruni</i> Mabilie, 1884	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium llanquihuense</i> Ituarte, 1999	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium magellanicum</i> (Dall, 1908)	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pisidium meierbrooki</i> Kuiper & Hinz, 1984	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>Pisidium ocloya</i> Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium omaguaca</i> Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium patagonicum</i> Pilsbry, 1911	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium pipoense</i> Ituarte, 2000	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
<i>Pisidium plenilunium</i> (Melvill & Standen, 1907)	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pisidium punctiferum</i> (Guppy, 1867)	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Pisidium sterkianum</i> Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Pisidium taraguyense</i> Ituarte, 2000	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Pisidium vile</i> Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Sphaerium aequatoriale</i> Clessin, 1879	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Sphaerium cambaraense</i> Mansur et al., 2008	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Sphaerium forbesi</i> (Philippi, 1869)	0	0	0	0	1	1	1	0	1	0	0	0	0
<i>Sphaerium lauricochae</i> (Philippi, 1869)	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Sphaerium titicacense</i> (Pilsbry, 1924)	0	0	0	0	1	0	0	0	1	0	0	0	0
Myoida (?)													
Lyonsiidae (?)													
<i>Anticorbula fluviatilis</i> (Adams, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Species richness (S)	60	117	46	31	27	12	29	18	33	17	9	6	49

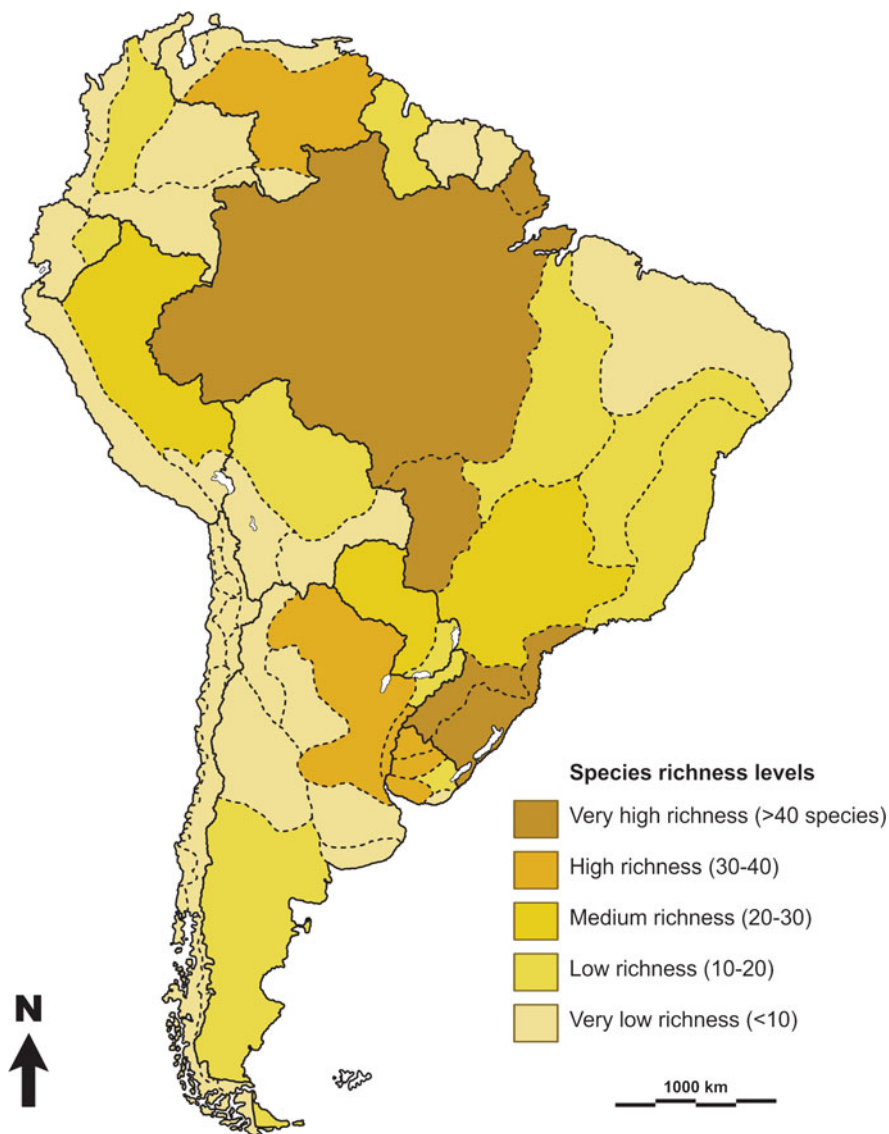
Atlantic, Uruguay, Paraguay, and Amazon Rivers (>40 species). In Uruguay, the continuation of the Uruguay River basin presents the greatest wealth, followed by the basin of the La Plata River. In Argentina, the Uruguay River and the rivers of Paranoplatense System are the richest in species. Further North of this continent, the Orinoco River in Venezuela and Amazon River, in Peru are quite relevant. In rivers, generally there is a greater species richness in the middle and lower zones (Mansur & Pereira, 2006; Pereira et al., 2011), where the primary production is higher. Moreover, in these areas, a floodplain with oxbow lakes containing many species of bivalves (Colle & Callil, 2012) is very common. Very low richness is probably related to small Pacific drainages, to arid domains from the Andes, to the semiarid at Brazilian Northeast Atlantic or salty endorheic systems in Argentina (Fig. 2).

Only 43 native species occur in more than 10% of the hydrographic regions inventoried, while the other species occur in only 5 of 131 hydrographic regions inventoried (<10%) (Fig. 3). It means that there is an expressive and large zone of endemisms forming mosaics with different richness levels and taxocenosis compositions. *Anodontites* (A). *trapesialis* (Lamarck, 1819) and *C. fluminea* are widely distributed in South American hydrographic regions. The respective frequency of occurrence figures for these species in the basins analyzed are 59.6 and 53.8%. The following

species should also be mentioned: *M. siliquosa* (Spix, 1827) (44.2%); *Anodontites* (A). *elongatus* (Swainson, 1823); *Anodontites* (A). *trapezeus* (Spix, 1827) and *C. largillierti* (32.7%); *Anodontites* (A). *patagonicus* (Lamarck, 1819) (28.8%); *Anodontites* (L). *ensifformes* (Spix, 1827) (26.9%); *L. fortunei* (25.7%); *Anodontites* (A). *crispatus* Bruguière, 1792; *Anodontites* (A). *tenebricosus* (Lea, 1834) and *Pisidium sterkianum* Pilsbry, 1897 (25.0%); *M. soleniformis* and *Castalia ambigua* Lamarck, 1819 (21.1%).

A. trapesialis is widely spread in hydrographic regions of the South America, occurring in sandy/muddy or muddy-only sediment, with deposits of silt and clay, in regions of lower water velocity as side channels or in marginal lakes, where it finds food (phytoplankton) in abundance (Bonetto & Di Persia, 1975; Hebling, 1976; Simone, 1994; Pereira et al., 2011; Colle & Callil, 2012). The species had dispersed further due to fish farming. The lasidia of this species appear not to show specificity with hosts (Callil et al., 2012), facilitating the dispersion in the fish farms, causing damage on fish production (Guardia-Felipi & Silva-Souza, 2008). *C. fluminea*, which has been reported in South America since the 70s has invaded all the large basins of the continent from Colombia to the North of Patagonia where it became quickly dominant (Santos et al., 2012). *M. siliquosa* is not abundant but present in most of the South American basins living in small aggregate populations that prefer

Fig. 2 Species richness (S) zonation of freshwater bivalves in the hydrographic regions in South America



compacted substrate of marginal areas. *A. (A). elongatus* is present in many basins from the North at the Magdalena, Orinoco, and Amazon basins to the South in the Uruguay River. It usually occurs together with *A. (A). trapesialis* and *Castalia* spp. sharing the same habitat in areas of marginal lakes and side channels, especially in the region of the Pantanal on the upper Paraguay River (Colle & Callil, 2012). *A. (A). trapezeus* is very common in the basins of the Eastern and Southern Atlantic, Paraná, Paraguay, and Uruguay, and is rare in Tocantins, Amazonas, and Orinoco.

The distribution of two *Corbicula* species does show no significant ($P < 0.01$) correlation with species

richness in the different hydrographic regions in South America: *C. fluminea* ($r = 0.11$; $P = 0.012$) and *C. fluminalis* ($r = 0.07$; $P = 0.31$). However, *C. largillierti* demonstrates significant and poor positive correlation ($r = 0.32$; $P = 0.0001$) with species richness. *C. largillierti* was the first species of the genus to invade South America through the La Plata River. Subsequently, *C. largillierti* decreased in density and distribution after the arrival of another invasive species, *C. fluminea*. *A. (A). patagonicus* is very common in the Southern American hydrographic regions as Paraná, Uruguay, and South Atlantic River basins. *A. (L). ensiformis* is common in the middle Paraná in Argentina,

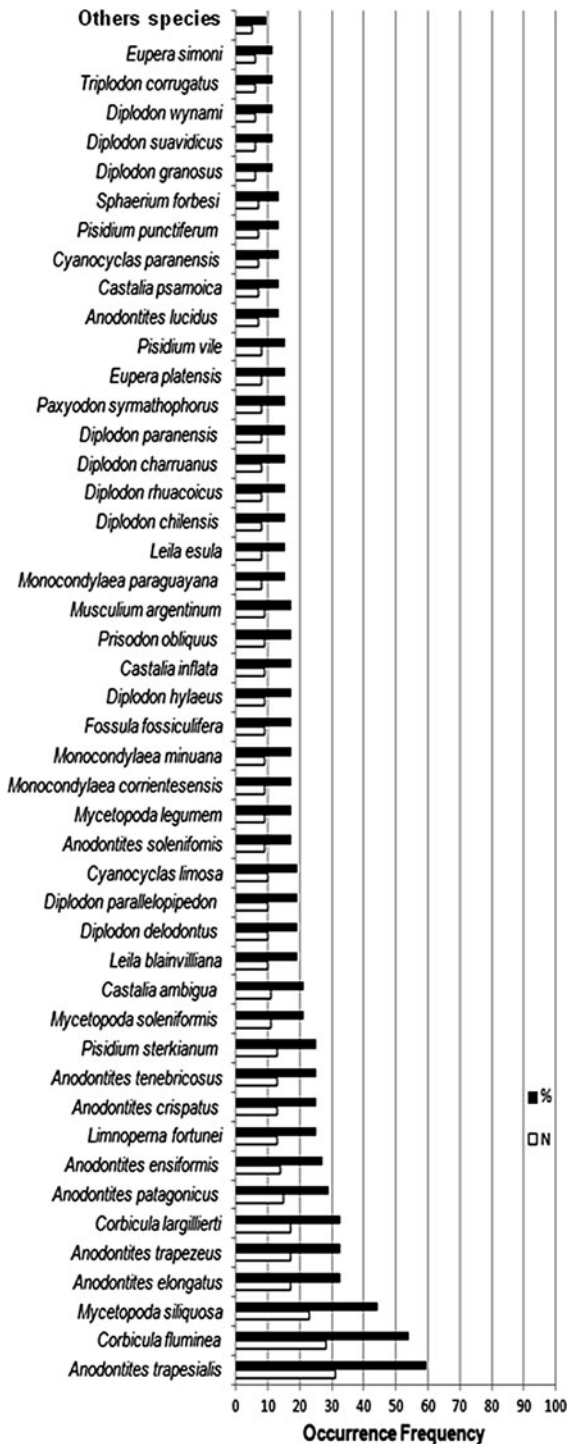


Fig. 3 Occurrence frequency (N and %) of freshwater bivalves in hydrographic regions of South America

in Paraguay River of Brazil and Paraguay and in a small part of middle Uruguay River bordering Argentina and Brazil. Northwards, it is observed in the Madeira River in Bolivia, in the Amazon, Tocantins, and Orinoco basins. Like *M. siliquosa*, it lives in small populations on muddy river margins.

The distribution of *L. fortunei* does show no significant correlation ($r = 0.02$; $P = 0.69$) with species richness in different hydrographic regions in South America. After the first record of *L. fortunei* in the La Plata River near Buenos Aires, the species was rapidly dispersed with the help of the boats that flow through waterways of the Uruguay, Paraná, and Paraguay rivers invading Argentina, Brazil, Uruguay, Paraguay, and Bolivia. So far it has not been reported in the Amazon River Basin despite the proximity. It has been recorded in the upper Paraná River, downstream of the dam of St. Simon at Paranaíba River, bordering the state of Goiás, Brazil. This region is very close to the headwaters of the Tocantins River which flows in the delta of the Amazon River (Santos et al., 2012).

A. (A). crispatus is more frequent in the basins of the Northern part of the continent, and the upper tributaries of the Paraguay river. *A. (A). tenebricosus* is very common on the lower part of the Uruguay river, where it appears in a very robust form. It also occurs in the south Atlantic drainage of Brazil but at a lower extent, and in the basins of Plata and Paraná becoming more scarce to the north. The record of this species for the Orinoco must be revised because it may have been confused with the related species *A. (A). crispatus* or *A. elongatus*.

Pisidium sterkianum is often present and abundant in sandy bottoms of lakes and lower parts of the rivers of Paraguay, Paraná, upper Paraná in Brazil, and Uruguay basins. It has also been reported for the Amazon Basin in Brazil and Bolivia.

Mycetopoda soleniformis just like the other species of this genus, lives in clusters forming small populations. It is most frequently found in the basin of the Paraná River, and much less common in the Uruguay River. As for the Amazonas River, there are records for Peru, Bolivia near the Madeira River, and in the state of Acre in Brazil. *C. ambigua* is common in large parts of the Orinoco and the Amazon Rivers even along the Andes in Peru and Ecuador, and has been reported for the Pacific basin in Ecuador. It occurs also in the rivers

of Suriname and Guyana. The citations of *C. ambigua* to La Plata, Paraná and Paraguay rivers, and the lower reach of the Uruguay River must be carefully studied with the support of genetics considering the similarities to *Castalia inflata* Orbigny, 1835 which predominates in these Southern hydrographic regions. It is possible that both species could be considered as synonyms.

Endemisms can be easily observed in some species that live on stones in running waters like: *A. rivolii* (Magdalena River at Colombia), *Bartlettia stefanensis* (Moricand, 1856) (High Amazon and Paraguay rivers), *Byssanodonta* (Ihering, 1893) (Middle Paraná River), and *M. lopesi* (lower part of Amazon and Tocantins rivers). *Tripodion*, *Paxyodon* Schumacher, 1817 and *Prisodon* Schumacher, 1817 only appear in the Amazon and Orinoco rivers. *H. balzani* lives in very restricted areas of the Paraguay River that present calcareous water. Endemisms are even more evident among Sphaeriidae. *Eupera iguazuensis* Ituarte, 1989 is restricted to Iguazú falls (area bordering Brazil and Argentina) and *Pisidium pipoensis* Ituarte, 2000 found only in the region of Misiones (Argentina). In the region of Patagonia in Argentina and Chile, there are many proper species of *Pisidium* and at Lake Titicaca (area bordering between Peru and Bolivia) some endemic species of *Sphaerium* can be found.

Regarding Dreissenidae, the native *M. lopesi*, from the lower part of the Amazon River and Tocantins/ Araguaia Rivers is adapted to freshwater forming small and low clusters on submerged rocks (Alvarenga & Ricci, 1989). Embryos and larvae develop outside the gills, inside the pallial cavity, fixed to the mantle of parental individuals, and are released as they are young (Mansur, 2012). They differ considerably from estuarine dreissenids as *Mytilopsis sallei* (Recluz, 1849) and *Mytilopsis leucophaeata* (Conrad, 1831) with planktonic larvae. Both species are from North America: the former was detected in Venezuela and the latter has been most recently collected in the mangroves of Recife (Souza et al., 2005). *A. fluviatilis* is an endemic species of Amazonas River occurring from Peru to river mouth on the main channel (Simone, 1999, 2006).

Phylogenetic composition and origin of the hydrographic regions

The principal coordinate's analysis for phylogeny-weighted species composition generated 51 PCPS.

The first two PCPS contained, respectively, 53.6 and 33.8% of the total variation in the phylogenetic composition matrix. The ordination scatter plot (Fig. 4) shows that the first PCPS was positively related to hydrographic regions characterized by the predominant occurrence of Veneroida + *A. fluviatilis*, and negatively related to predominant occurrence of Mycetopodidae and Hyriidae. On the other hand, the second PCPS split hydrographic regions characterized by predominant occurrence of Hyriidae (positive values) and Mycetopodidae (negative values).

The Veneroida had higher species richness in the hydrographic regions located in the Andes Mountains on the far Southwest, and coastal areas of the continent. This order is represented basically by several species of *Pisidium* genus concentrated mainly in Andean area. These are cooler regions, where rivers are born in mountainous areas. These are very similar environments to the frozen rivers of the Palearctic Region, where many species of *Pisidium* are sympatric. However, the species of *Pisidium* are rarely sympatric in South America and show a great variation within populations (Kuiper, 1983). In streams and lakes of the Andean highlands, they are more numerous and concentrated (Kuiper & Hinz, 1984; Ituarte, 2007). Species of *Sphaerium*, are practically only present in the Andean highlands. An exception is *Sphaerium cambaraense* Mansur et al., 2008, which occurs in the highlands (above 800 m) in Southern Brazil at the *Araucaria angustifolia* forest (Mansur et al., 2008). Fitkau (1981) mentioned that the Amazon does not have habitats suitable for the occurrence of Sphaeriidae except for *E. simoni*, which is adapted to the fluctuations of the water level and long drought periods. In the coastal environment of Northern Brazil and Venezuela, species of *Cyanocyclas* and *Polymesoda* genus are predominant.

Parodiz & Bonetto (1963) presented distribution maps of Hyriidae and Mycetopodiade in South America which coincide with the distribution of species observed in this study. Some species of Hyriidae and Mycetopodidae have also been reported in rivers located in mountainous areas which are not so elevated like Andes area. *D. chilensis* is the only species of Unionoida inhabiting Andine Rivers and lakes in the Patagonian region found in Chile, Argentina, and Peru. This is the most frequent species in lakes near the cities of Temuco, Valdivia, and Puerto Montt at Chile (Parada & Peredo, 2002; Parada et al., 2007).

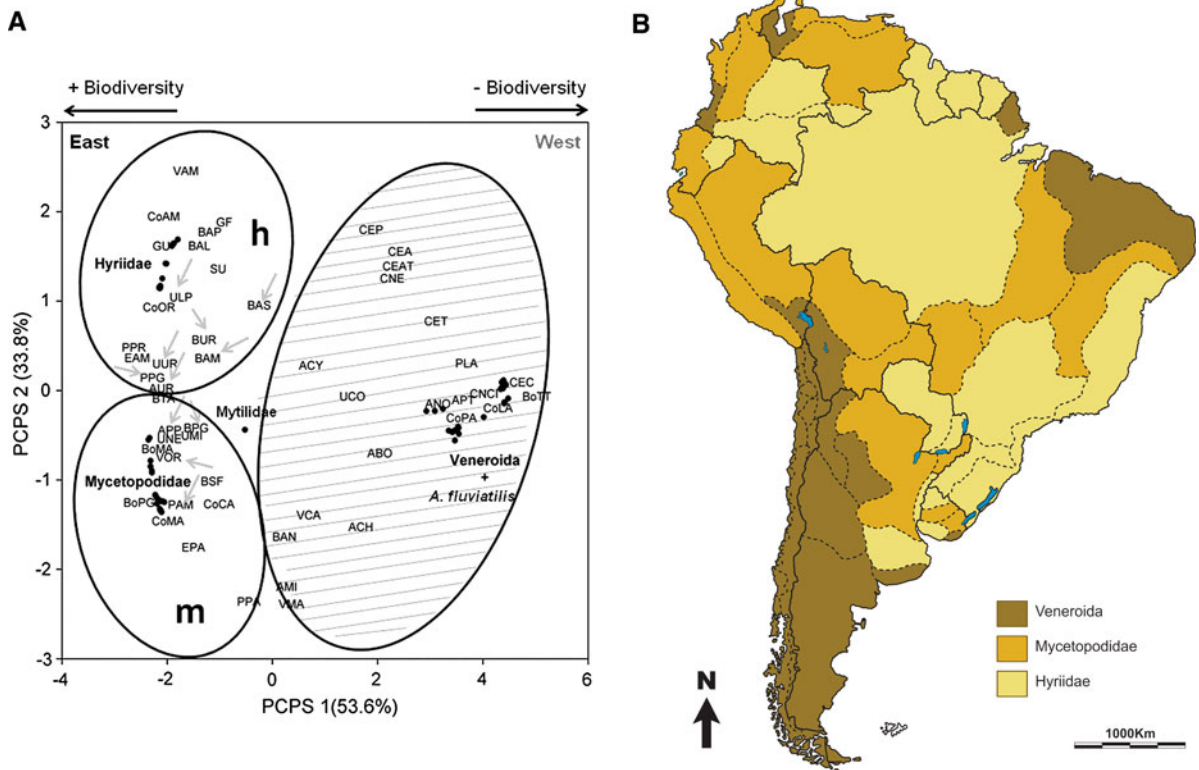


Fig. 4 Principal coordinates analysis of phylogenetic structure (PCPS) for each hydrographic regions of South America. **A** Ordination scatter plot. **B** Phylogenetic structure of hydrographic regions. *Arrow* indicates very high richness. Hyrriidae (*h*) and Mycetopodidae (*m*)

A. (A). tenebricosus, *B. stefanensis*, and *A. rivoli* are typical waterfall species. However, the highest richness of Mycetopodidae and Hyrriidae is to be found in lowland rivers, oxbow lakes, lakes, and costal lakes. Very inflated species, such as *Castalia inflata*, float over the mud of river margins and lakes. The elongated forms like *Mycetopoda*, *Mycetopodella falcata* (Higgins, 1868), *A. (L). ensiformis* bury themselves in the compacted substrate of wet river banks.

To understand the patterns of distribution of species, it is necessary to know the geological events that gave rise to the current configuration of the landscape and hydrographic regions in South America. According to Leal (2011), during the breakup of the Gondwana Paleococontinent in the Mesozoic (Cretaceous period, ~100 Ma), the main drainage of the South American plate was directed to the West. This pattern changed due to geotectonic episodes like: separation of South America from Africa with the opening of the South Atlantic Ocean, the Andean

uplift, and the closure of the Panamanian Isthmus. Since the upper Mesozoic era (83–67 Ma), three separate large river basins were present, two located at the current Amazon River Basin (one part which flowed East and another West), and another drainage which flowed South and originated the Paraná–Paraguay river system.

According to Hubert & Renno (2006), successive geological events determined the genesis of the current South American basins in the Cenozoic era (Tertiary period) as follows: (1) 15 and 10 Ma: the last event of great marine incursion, before the final establishment of the Amazon, previously dated between and was postulated to lead to a 150-m marine highstand forming a big sea called Pebas. At least one continental sea, the Paranean Sea between Southern Brazil and Northern Argentina, was formed. The Magdalena basin was isolated after the uplift of the Northwestern Andes changing the direction of river flow to the west; (2) 10 and 8 Ma: marine regressions and Andean foreland dynamics are associated with the

final establishment of the Amazon basin. The Paraná–Paraguay split from the protoAmazon at 10 Ma; (3) 8 and 5 Ma: separation of the Orinoco occurred on the Vaupes arch. The modern course of Amazon River appeared with the final uplift of the central Andean cordillera related to the rise of the Purus arch. The Maracaibo Lake was formed after the final uplift of the Northwestern Andes. The Upper Amazon was isolated from the remainders of the Orinoco and Paraná rivers; and (4) 4 Ma: after marine regressions and Andean dynamics, the Upper Amazon was fragmented. The formation of the Pebas sea got several rivers isolated and consequently got their populations of freshwater bivalves isolated, too. According to Wesselingh (2006), the Western Amazonian became a mosaic of lakes, swamps, and meander belts splitting the main river in different subsystems. According to Wares & Turner (2003), the freshwater habitats are typically connected in a hierarchical, fractal geometric fashion with low-order streams draining into larger streams and rivers. This physical configuration offers a great diversity of habitats for freshwater clams. The compartmentation of hydrographic regions in South American basins promoted different ways to diversification of both invertebrate and vertebrate fauna like fishes, and this fact is closely associated with hydrogeological history of the continent (Hubert & Renno, 2006). According to the same authors, “the patchy nature of freshwater habitats, may in some respects account for the high species diversity encountered there considering that opportunity for geographic isolation (and presumably allopatric speciation) is greater than in marine habitats”. For million years in the Miocene, there was also probably sufficient time for diversification of freshwater bivalves. By virtue of the formation of Pebas, the Andean uplift and erosion changed the fluvial landscapes of South America again resulting in more intensive diversification of freshwater bivalves. Events similar to the formation of Pebas occurred in the Southern part of the continent in the Paraná–Paraguay with formation of Paranean Sea. Events like these probably promoted the fauna diversification in water courses as Rivers of the South and Southeast Atlantic, and coastal lakes. Lanzer (2001) verified that the distribution of freshwater clams in lake systems of the coast of Rio Grande do Sul, in Southern Brazil, is related to the genesis of those systems that resulted from the processes of marine transgressions and regressions.

In addition to the geological events, other factors are important for the distribution of bivalves. Freshwater clams cited for South America can also be scattered across the stomach contents of fish, but are limited to the distribution areas of these vectors. They can also be transported over long distances by birds, crossing geographical barriers. These birds eat large bivalves, but normally they break the shell eating only the soft part. However, smaller bivalves can remain unscattered through the gut, mainly Corbiculidae, and Mytilidae, or transported fixed on feathers, mainly Corbiculidae and Sphaeriidae.

Knowledge gaps

The lack of basic knowledge on freshwater clams is a reality that hinders the categorization of species conservation status in South America. This paucity is in part due to the lack of organized and representative collections of the freshwater bivalves species of the main hydrographic regions in South America, difficulties in obtaining type material or respective good illustrations, lack of identification keys and publications on the reproduction, ecology, morphology, and on the affinity of the species with the host fish of glochidia and lasidia, besides the scarcity of limnological institutions or biological stations dealing with mussels. Many hydrographic regions are underrepresented in scientific collections, especially those located in the Northern part of the continent.

By comparing the study of freshwater bivalves in South America with the one developed in other continents, especially Europe and North America, we can see that in the period of the early naturalists (Haag, 2012), the difficulties encountered there, such as the scarcity of morphological data and the lack of sampling locality of the species, were similar to ours. But in South America, we have aggravating circumstances that type material and additional collections were donated or sold to museums in Europe or North America. In the subsequent periods, the first museums and scientific collections were formed in the countries of the Northern hemisphere. At that time, studies on mussels compared morphologies, ecology, and phylogeny saw a period of major development (Haag, 2012). In South America, the studies leave something to be desired by the lack of comparative material, and again, important collections as the one from Ihering

were still sold to Europe. Ortmann (1921), who started and strongly encouraged malacology and mussel ecology in North America (Haag, 2012), did not collect in our watersheds. He described relatively few species from some basins, mainly those mussels collected by his colleague Ichthyologist J. D. Hase-mann, with their testimonies reported at the Carnegie Museum, Pittsburgh, again outside South America.

In recent decades, genetic studies have shed light on the phylogenetic and evolutionary relationships inside Unionoidea. However, the presence of unionoidean doubly uniparental inheritance of mtDNA (DUI) make evolutionary interpretations difficult mainly by the South American Hyriidae that are scarcely evaluated. Genetic studies are also necessary in order to differentiate similar or cryptic species of Mycetopodidae as, *Anodontites (A.) iheringi* (Clessin, 1882), and *Anodontites ferrarisii* (Orbigny, 1835); *A. tenebricosus* and *A. soleniformis*; and of Hyriidae as, *D. granosus* and *D. multistriatus*; *C. ambigua*, and *C. inflata*. Many species are morphologically unknown and rare in scientific collections like, *Anodontites (A.) aroanus* Baker, 1930; *Anodontites (A.) carinatus* (Dunker, 1858); *Anodontites (A.) colombienses* Marshall, 1922; *Anodontites (A.) guanarensis* Marshall, 1927; *Anodontites (A.) puelchanus* Orbigny, 1835; *Monocondylaea costulata* (Moricand, 1858); *Monocondylaea franciscana* (Moricand, 1837); *Monocondylaea guarayana* (Orbigny, 1835); *Tamsiella amazonica* Bonetto, 1972 and, *Tamsiella schroeteriana* (Lea, 1852). It would be necessary to conduct new expeditions in the type localities in order to obtain topotypes to support the redescription of these species.

Many species of *Diplodon* genus cited for the basins of the Eastern Atlantic, Upper Paraná River, and North and Northeast Atlantic are hardly differentiated. Until now, the diagnostic criteria are not well established, thus requiring adequate morphological studies for the recognition of their taxonomic status: *Diplodon (D.) caipira* (Ihering, 1893); *Diplodon (D.) expansus* (Kuester, 1856); *Diplodon (D.) ellipticus* (Spix, 1827); *Diplodon (R.) funebris* (Lea, 1860); *Diplodon (D.) multistriatus* (Lea, 1831); *Diplodon (D.) granosus* (Bruguère, 1792); *Diplodon (D.) paulista* (Ihering, 1893), and *Diplodon (D.) rhombeus* (Spix, 1827). In addition, *Diplodon (D.) imitator* Ortmann, 1921 was described from the Jacuí River in the South Atlantic Basin; however, it has not been found ever since. Some species of genus *Diplodon*

were not yet framed within subgenera due to lack of knowledge of glochidia morphology (Table 2).

The species, *C. ambigua*, *C. inflata*, *Castalia quadrata* Sowerby, 1869, *Castalia schomburgiana* Sowerby, 1869 and *Castalia sulcata* (Krauss, 1849) show a wide morphological variation, with a particular shape of the shell for each different basin, which also hampers the recognition of these species by non-specialists. The internal anatomy is unknown for the most part of the species and the glochidium is not a good intraspecific character in this genus.

Prisodon obliquus Schumacher, 1817 and *Paxyodon syrmatophorus* (Gmelin, 1791) are very similar species with winged hinge, no umbonal sculpture and the same color and periostracum brightness. The upper Amazon River sees a predominance of *P. obliquus*, whereas in the low Amazon River, *P. syrmatophorus* prevails. However, intermediate forms occur in sympatry in some parts of the lower Amazon River. Therefore, questions remain to be answered about the identity of both species, raising suspicions of the existence of only one species with a wide morphological variation along the basin. Pimpão et al. (2012) observed that the glochidia of both species are also very similar.

All species of the genus *Cyanocyclus* should be reviewed. Mainly species of northern part of the continent and *C. limosa*, which shows a wide morphological variation and may represent a large number of species.

Considering Sphaeriidae in the Southern hemisphere, Kuiper (1983) emphasizes the fact that the paucity of species with conspicuous interpopulational variation in the same environment is regarded as a rule. This morphological variation makes difficult the definition of diagnostic criteria and consequently the species recognition. The species of the *Pisidium* genus cited for Argentina, Bolivia, Chile, Peru, and Uruguay were reviewed by Ituarte (2007), and all other hydrographic regions in South America require similar revisions and more collections.

Considering the abovementioned amount of gaps of knowledge, we can recognise that *D. chilensis* is one exception and probably the best known species of Hyriidae in the continent.

Risks for the biodiversity of freshwater bivalves

The main threats to the conservation of freshwater bivalves are related to habitat destruction, water

pollution, and the invasion of exotic bivalves (Mansur et al., 2003a; Machado et al., 2008; Pereira et al., 2012). Among the causes of habitat destruction, we can highlight the deforestation of riparian vegetation, damming and channeling rivers, wetland drainage, siltation of rivers and lakes, sand mining, etc. The bivalves are filter feeders that have little or no mobility in adulthood. As a consequence, they are very sensitive to changes in river flow, sediment grain size, water level, slope and shading on the margins. The destruction of the terrestrial environments entails drastic consequences to hydrographic regions. Until today, the practice of burning forests and savannah environments are common in many South American countries and territories despite the restrictions imposed by environmental agencies sponsored by the government. This practice disrupts the soil, facilitating erosion and siltation. Thus, all processes that modify and destroy the vegetation cover also have a negative impact on hydrographic regions, affecting the assemblage of bivalves.

Miyahira et al. (2012a, b) made some comments on the habitat degradation and their effects on freshwater mussels in the state of Rio de Janeiro. Water pollution is an important factor in the population decline of native bivalves. The high organic contamination decreases the oxygen dissolved in the water, keeping these mollusk from surviving. Contamination from industrial effluents and solid waste generates metals that are incorporated by the bivalves and accumulated in the food chain. The agricultural activity also impacts on this fauna which is poisoned by pesticides.

In South America, the main source of energy is provided by hydroelectric plants. In Brazil, the construction of reservoirs to meet the energy demands required for the accelerated development of this country is encouraged by the government. However, when it comes to mollusks, the terms of reference that guide the implementation of the environmental studies for licensing ventures require only a survey of the snails vector of zoonosis. In addition to that, the construction of dams causes environmental changes in making a river into a lake. This fact changes the patterns of connectivity of the wet drainage and affects the structure of the fish fauna (composition and abundance of fish), and their migratory routes. The majority of the Unionoida use fish as dispersal vectors. With the interruption of the migration route of host fishes, the dispersion of mollusks is compromised.

Historical data (Takeda et al., 2005; Pereira et al., 2012) revealed that the construction of 70 reservoirs in a system of waterfalls along the most populated area of Brazil, in high Paraná River, changed the lotic environment to lentic, favoring the colonization of the Corbiculidae invasive species and *L. fortunei*, as well as the gastropod *Melanooides tuberculata* (Müller, 1774). The river segments that allow the survival of native bivalves in their natural habitats are rare. Furthermore, the fish that dispersed bivalve larvae are unable to move upstream along rivers. Consequently, all Unionoida species reported in this area are endangered, though many of them do not appear on official red lists.

The freshwater bivalves have been adapted to drought and flood of the rivers for millions of years. With the construction of reservoirs, the natural flood pulse that occurred in the floodplains of the rivers has become artificially regulated. In many of those rivers, the overflow of the channel during the rainy season is stopped, so there is no more communication with floodplain lakes. This change in water dynamics of rivers impacts the life cycle of bivalves that depend on fish for their dispersal. The disconnection of these environments limits the lasidia and glochidia dispersion through the fish.

Moreover, the bivalves can not keep up with sudden emptying of reservoirs in times of intense rainfall. Two types of impacts are known to be related to that. One occurs in the reservoir when it is quickly emptied by opening the floodgates. The water level decreases dramatically exposing the entire bank, resulting in the death of bivalves that can not keep up with the speed of emptying. The same impact can be observed in the Northeast of Brazil at the times of severe droughts, when reservoirs became empty due the absence of rains. The other impact occurs downstream the reservoir when the water is released at high speed dragging all the marginal fauna and flora, often throwing the bivalves out of the system.

The dispersion of the invasive bivalve species in several hydrographic regions of South America constitutes a threat to the conservation of native clams. The golden mussel produces byssus threads that enable the incrustation on the various types of hard substrates forming macrofouling. This structure of aggregates alter different types of substrate-forming mussel beds on sediment and between rhizomes of the *Schoenoplectus californicus* (C.A. Mey.) Palla

(Cyperaceae), a kind of emergent shoreline vegetation common in South America (Santos et al., 2012). Also, it forms macroclusters over other types of free-floating and amphibious macrophytes, such as species of trees from the banks of rivers and lakes. All these habitats are modified and so is the entire benthic fauna composition. In addition to the habitat loss, the bivalves are choked by the incrustation of mussels on their shells, keeping the valves from opening, and in some cases, from closing, too. So the native bivalves can not perform filtering and become exposed to predators.

The golden mussel occurs predominantly on hard substrates, and to a lesser extent on sandy bottoms. On the other hand, the Corbiculidae invasive species occurs predominantly on sandy bottoms dominating the benthic communities. Thus, the pressure of invasive species on native clams is intense. *L. fortunei* can reach 500,000 ind m⁻² (Bergonci et al., 2009) and *C. fluminea* just to 5,295 ind m⁻² (Mansur & Garces, 1988).

L. fortunei form macrofouling on hard substrate covering great areas of rivers and lake bottoms altering the benthic fauna structure. The great density of *L. fortunei* related to the high filtration rates have an impact on the planktonic community and food chain (Darrigran & Damborenea, 2011). The macrofouling also impact the equipments of hydroelectric and thermoelectric plants. However, until now new designs for power plants do not present solutions to minimize the effects of biofouling.

Conservation strategies

Since the 1990s there has been a great effort from most South American countries for the preparation of their official lists of endangered species of their fauna. However, most of these lists include only vertebrate species. Out of the 12 South American countries and 1 territory, only 4 have published lists of endangered species of mollusks: Brazil, Colombia, Paraguay, and Uruguay. The Brazilian list of threatened fauna (Machado et al., 2008) includes the following species: *Diplodon (R.) koseritzi* (Clessin, 1888) (critically endangered, CEN); *A. (A.) ferrarisi*, *A. (A.) iheringi*, *D. caipira*, *D. (D.) dunkerianus*, *D. fontainianus*, *D. pfeifferi*, *D. rotundus*, *C. undosa*, *A. (A.) trapezeus*, *Fossula fossiculifera* (Orbigny, 1835), *L. blainvilliana*

(endangered, EN); *A. (A.) elongatus*, *A. (L.) ensiformis*, *A. (A.) soleniformis*, *A. (A.) tenebricosus*, *A. (A.) trapesialis*, *M. legumen*, *M. siliquosa*, *Monocondylaea paraguayana* (Orbigny, 1835), *Leila esula* (Orbigny, 1835), *B. stefanensis*, *D. (D.) expansus* (Vulnerable, VU). The species *A. (A.) soleniformis*, *A. (A.) trapezeus*, *F. fossiculifera*, *H. balzani*, *B. stefanensis*, *D. (D.) expansus*, *C. inflata* and *C. nehringi* were considered in the Paraguayan list (Ministerio de Agricultura y Ganaderia, 1998) in only one category defined as “endangered”. *Polymesoda solida* (Philippi, 1946) was considered to be a vulnerable species in the threatened fauna list of Colombia (Ardila et al., 2002). The list of the IUCN (2012) includes only *D. (D.) dunkerianus* and *D. fontainianus* (endangered, EN); *Diplodon (D.) expansus*, *D. pfeifferi*, and *Castalia martensi* (Ihering, 1891) (vulnerable, VU). The National list of priority species (Scarabino & Clavijo, 2009) recognized that 93% of the species of bivalves (37) from the freshwater environments from Uruguay are priority for conservation. Later Clavijo et al. (2010) prioritized three other species for conservation.

Pereira et al. (2012) listed all species of freshwater bivalves from Brazil and their conservations status based on an official list. According to the authors, 1% of species is critically endangered, 10% are endangered, 9% are vulnerable, and 37% need a new evaluation and should be included in the revised list. Many other species need more information for the adequate determination of their conservation status. The quotation of *A. (A.) trapesialis* in the list of Brazilian threatened fauna should be revised because this species has dispersed through aquaculture systems as well as invasive species. *A. (A.) trapesialis* adapts to different environmental conditions and probably does not fit into any category of endangered species.

The lack of basic knowledge on freshwater clams is a general reality that hinders the categorization of the conservation status of the species. There are too many gaps in collection records in Northern South America. These regions are underrepresented in scientific collections; however, in better represented South regions that are many gaps, too.

For the purposes of conservation and management, Parada & Peredo (2005) and Peredo et al. (2005) made an experience with relocation of two populations of *D. chilensis* through a long-term evaluation of survival and recruitment. After 18 years, the relocated

population remained at the same site. At one site, the authors did not find recruits but the individuals were greater than at the original site. At the other site, the recruitment has resulted from the dispersion of larvae by the host fish. The size of the juveniles suggested that recruitment took place in the previous reproductive season.

In Brazil, Beasley et al. (2000) studied the reproductive cycle of the harvested salmon pink mussel *P. syrrhatophorus*, giving strategies for conservation and management of the species in the Tocantins River Basin, in Brazil. Later, Beasley (2001) studied the density, size frequency distribution, the habitat structure, and the impact of exploitation of these bivalves by industries of pearl buttons aiming to define management strategies. Initiatives on relocation, translocation, and repopulation of the freshwater mussels are unknown in Brazil.

There is little information on the conservation status of freshwater bivalves in Uruguay. Scarabino & Mansur (2007) listed the species of bivalves in Uruguay with the intent of supporting the conservation of this fauna. Scarabino (2004) reviewed for the first time the conservation status of Uruguayan malacofauna and highlighted the priority actions to be taken in order to conserve this fauna. Currently, there are several initiatives to improve and disseminate the knowledge base and implement conservation measures for freshwater bivalves in Uruguay (Clavijo et al., 2010). The first and only experience of relocation was held in Uruguay in 2010 based on a private initiative. As a result of this experience, a total of 133 specimens of *D. (R.) charruanus*, *D. (D.) rhuacoicus* (Orbigny, 1835), *A. (A.) trapesimalis* and *A. (A.) patagonicus* ended up endangered by a dam construction were relocated to a natural place (Clavijo et al., 2012).

The concern on bivalve conservation in Argentina begins with the implementation of database systems for the malacological scientific collections. Rumi et al. (2008) evaluated the richness of mollusk species in continental Argentina, and mapped their distribution. The authors offered subsidies for prioritizing areas for conservation.

Final considerations

The number of 111 Uninoid species places South America as a very rich continent, but not richer than

North America. According to Graf & Cummings (2007), North America presents the highest diversity of mussels on Earth (~300 species). Our results came to 63 mussel species of Hyriidae and 48 Mycetopodidae, a number which is a bit higher than the figures presented by Graf & Cummings (2007) for both families (40 and 32 species, respectively) in South America.

The most diverse hydrographic regions in South America are: (1) very high richness, Amazon River, Paraguay River, Uruguay River, and Rivers of the South and Southeast Atlantic in Brazil; (2) high richness, Orinoco River in Venezuela; Paranoplatense System in Argentina; Uruguay River, La Plata River, and Negro River in Uruguay; and (3) medium richness (Amazon River in Peru, Upper Parana River in Brazil, and Paraguay River in Paraguay). These hydrographic areas are located within the two richest South American macroregions identified by Graf & Cummings (2007): Amazon–Orinoco (on the Peba System) and Paraná–Paraguay (on the Paranean System).

The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be as a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance.

The wide distribution of some native species can be attributed to their high tolerance to environmental factors, transposition of geographical barriers, and persistence in face of geological events in the past. Native species with wide distribution, such as *Anodontites trapesimalis*, may have similar properties to invasive species, which would explain its wide distribution along to hydrographic regions and success in its current dispersion in the fish farms. However, more studies are needed on the biology of this species for us to understand their mechanisms of dispersion and whether these mechanisms are related to a certain degree of invasiveness.

Another issue to be considered is that the small number of invasive species seems not to interfere in the patterns of species composition and phylogenetic lineages in the different hydrographic regions looked at. *L. fortunei* does not contribute to the dominance of Mytilidae lineage in none of the hydrographic regions assessed with complex assemblages of native mollusks. On that line, it can be inferred from the

occurrence of Corbiculidae invaders, among the Veneroida, which are widely distributed in South America, that they appear also in areas dominated by Mycetopodidae and Hyriidae. It is also to consider that the number of corbiculid invaders is much smaller than the total number of species of Veneroida recorded in the continent. However, it is important to raise awareness to the potential impact of invasive species that are dispersing by South American water courses. The golden mussel invasion may result in the reduction of the diversity of bivalve mollusks in the different addressed areas with the capacity to modify the patterns of species richness, species composition, and phylogenetic lineages. Considering this possibility, efforts should be made in order to control the dispersion and population growth of invasive species. The control of the spread of invasive species depends primarily on educational actions intended to raise awareness of boatmen, fishermen, and farmers, who use the water for irrigation; their procedures and equipment must be revised in an attempt to minimize the danger of contamination of new bodies of water.

The distribution of invasive species *L. fortunei*, *C. largillierti*, *C. fluminea*, and *C. fluminalis* is not related to species richness in the different hydrographic regions in South America. This distribution does not corroborate to the assumption that the poorest communities in species would be more susceptible to bioinvasion (Wolfe, 2002; Bohn et al., 2004).

However, the Andean region does not seem to be inviting to the invasion of *L. fortunei* according to Darrigran et al. (2011). The same authors identified three environmental parameters that are barriers to invasion in this region: salinity, river flow intermittence (in different sectors of Pilcomayo and Salado del Norte Rivers), and concentration of suspended sediments (in the Bermejo River and in the upper reaches of the Salado del Norte and Pilcomayo Rivers).

Detailed inventories of native bivalve fauna in different hydrographic regions are also needed, as well as the identification of habitats, with the environmental variables that govern the distribution of the species, the patterns of diversity, and the provision of deeper insights into the reproductive cycle and morphological characters which are determinants for species recognition. This is essential for the establishment of management strategies, identification of potential areas for the conservation, breeding and relocation of endangered species. The species composition and

phylogenetic patterns identified in this study will contribute to the definition of priority actions for the conservation of the native mollusks fauna and the control of invasive species. They can also help to direct more studies in order to understand this diversity and to review the lists of endangered species.

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