



Non-native mollusks throughout South America: emergent patterns in an understudied continent

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Received: 4 October 2018 / Accepted: 10 December 2019 / Published online: 3 January 2020
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Abstract Non-native species have been introduced at escalating rates during the last decades, mainly due to the dispersion generated by the increasing trade and transport worldwide. Mollusks, the second largest metazoan phylum in terms of species richness, are no exception to this pattern, but, to date, a comprehensive synthesis of non-native mollusk species (NNMS) in South America was not available. For this purpose, an e-discussion group was formed with malacologists and taxonomists from South America, where we

exchanged and analyzed bibliography, databases and information about NNMS, providing expert opinion to this assessment. The first list of non-native mollusk species for South America, considering terrestrial, freshwater and marine environments, includes 86 NNMS distributed in 152 ecoregions (terrestrial, freshwater and marine) of the 189 recognized for the South American continent. Information on their native region, vectors, first record for South America and distribution, are also provided. In the analysis of the distribution of the NNMS and the entry points of each species (e.g., ports, cargo and passenger airports, cities) and status of conservation of the ecoregions, four hot spots were recognized: Subtropical-Atlantic,

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-019-02178-4>) contains supplementary material, which is available to authorized users.

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Northern Andes, Central Andes and Southern Andes. This work, thus, sets the baseline on NNMS for South America, a key piece of information regarding the development of policies targeting the management of biological invasions and their socio-ecological impacts.

Keywords Invasive · Ecoregions · Freshwater · Marine · Terrestrial · Hot spot

Introduction

Biological invasions have been recognized as one of the greatest threats to biodiversity in the world (Rodríguez 2001; Bellard et al. 2013; Gallardo et al. 2018). When non-native species invade, they can modify the community structure and the ecosystems function (Simberloff et al. 2012), and also represent a serious socio-economic threat (Pejchar and Mooney 2009). Several factors interact in a successful introduction, establishment and dispersal of species in a new environment, such as propagule supply (Johnston et al. 2009), the biology of the invaders, the ecological characteristics of the invaded ecosystems and the type and intensity of human impacts on receptor ecosystems (Pointier and Delay 1995). Reported invasion rates have increased exponentially over the past 200 years as seen for example in coastal marine communities of North America (Ruiz et al. 2000). Possible causes of increasing invasion include the rising number and variety of transport vectors, the

invasibility of recipient ecosystems and the extensive natural and anthropogenic disturbance (Cohen and Carlton 1998).

Mollusca is the second largest Metazoa phylum, being abundant in most aquatic and terrestrial environments. Some species are ecosystem engineers (Gutiérrez et al. 2003; Sousa et al. 2009) and key species in many local communities (Sousa et al. 2014). Further, mollusks constitute 58.8% of the combined production of marine and coastal aquaculture, and ca. 7% of capture fisheries worldwide (FAO 2018). However, mollusk species may damage human health due to their potential as vectors of animal and human pathogens.

In this context, the knowledge of mollusk fauna in South America is heterogeneous. Despite partial efforts in particular regions or environments, in which non-native mollusk species (NNMS) are well known (e.g., Orensanz et al. 2002; Lee et al. 2008; Rumi et al. 2010; dos Santos et al. 2012; Araya 2015), there are still vast regions in which their diversity is unknown. Most studies on invasive species are biased towards those that have attracted attention due to their great potential for dispersion, their strong impact on ecosystems and, mainly, the economic damage they produce [e.g. *Achatina fulica* (Férussac, 1821); *Limnoperna fortunei* (Dunker, 1857); *Crassostrea gigas* (Thunberg, 1793)]. However, most mollusk species introduced in this region have not received due attention. An example is the introduction of *Sinotaia quadrata* (Benson, 1842) in Argentina (Ovando and Cuezco 2012), recorded in 2009, which constitutes the first record of a living viviparous gastropod in South

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America. This species has a high reproductive capacity and has already gone through the introduction and establishment stages, two previous steps of those necessary to be considered an invasive species (Morton 1996, Ferreira et al. 2017). Ignoring the current distribution of NNMS in South America prevents both foreseeing the risks they may present to the socio-ecological system, as well as the development of prevention and control measures on the dispersal of these species (Castilla and Neill 2009).

It is worth mentioning that there is a large amount of literature on non-native species, mostly from North America, Europe and Australia (Byers 2009; Thomsen et al. 2014). South America is among the regions with fewer studies about this topic (Speziale et al. 2012; Thomsen et al. 2014). In particular, the taxonomy of mollusks is constantly being reviewed, and knowledge about the systematic, biogeography and natural history of native mollusks in South America is limited. This biases the estimation of the number and significance of introduced species (Carlton 2009), since many of them cannot be labeled as native or non-native (Geller et al. 2010). This shows a great imbalance in the efforts to study non-native species in South American countries.

In order to overcome these knowledge gaps, this work aims to provide a comprehensive record of the presence of NNMS in South America, and establish their occurrences, native region, vectors and date of introduction using multiple sources (e-discussion group or expert opinion, literature and databases). The information provided is related to the degree of urbanization and conservation status in receptor

ecoregions. In addition, the impact of some of the well-known NNMS is described. The present work is a baseline on the knowledge of NNMS of South America, and also aims to indicate possible entry points to guide prevention and control efforts on the introduction of species in South America.

Materials and methods

Definitions

For this work, a species is considered non-native when it is introduced outside its natural geographical range through human action, and is able to maintain a self-sustaining population (Turbelin et al. 2017). In addition, if this species is dispersed and has an evident environmental and socio-economic impact, it is considered an invasive species. Likewise, a species is considered cryptogenic if its occurrence in a given place cannot be unequivocally attributed to natural processes or human intervention (Carlton 1996).

Compilation and exchange of information on non-native mollusk species (NNMS) of South America

A collaborative effort was made among 23 expert malacologists and taxonomists from different countries of South America (Argentina, Brazil, Chile, Ecuador, Peru, Uruguay and Venezuela) through an e-discussion group or expert opinion, in which bibliography and experiences were exchanged in a virtual forum. The group exchanged published and unpublished information on confirmed and putative NNMS until a consensus was reached on the species status.

Based on the exchange of information and opinions, the group of experts compiled and synthesized taxonomic information, native region, first reference and date of introduction/detection at a continental (South America) and national (country) scale, and current geographical distribution (by country and ecoregion), known vectors, impacts and most relevant publications, many of them gray literature, for each NNMS.

The experts as a group established a criterion for the inclusion and exclusion of species within the South American NNMS. The specific records generated by the e-discussion group were included in two groups of species:

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1. Species whose non-native status is well documented.
2. Cryptogenic species.

In turn, those species transported by anthropogenic sources within their potential natural distribution range (i.e., transfer, translocation or transplantation, both past and present; see Shine et al. 2005; Falk-Petersen et al. 2006) were excluded.

Vectors, first record and native regions of NNMS in South America

This information was obtained from the literature. When there was no information about vectors, these were considered unknown. Linear and exponential models were applied to analyze the rate of settlement of NNMS in South America being y the number of introductions and x the time in 10-year intervals.

Distribution of NNMS in South America

The geographic range of each species was determined based on experience and literature provided by experts. The geographical representation of the distribution of South American NNMS was performed at ecoregional scale. Following Olson and Dinerstein (2002), ecoregions are defined as areas of land or water with a characteristic set of natural communities, ecological dynamics, and environment that share most of their species. Geographic Information System (GIS) layers were based on Olson et al. (2001) for Terrestrial Ecoregions, Spalding et al. (2007) for Marine Ecoregions, and Abell et al. (2008) for Freshwater Ecoregions.

In South America, 109 ecoregions are recognized for terrestrial environments (<http://maps.tnc.org/files/metadata/TerrEcos.xml>; Online Resource 5); 52 ecoregions for freshwater environments (<http://maps.tnc.org/files/metadata/FEOW.xml>; Online Resource 6); and 28 ecoregions for marine environments (<http://maps.tnc.org/files/metadata/MEOW.xml>; Online Resource 7).

Biodiversity database search

In addition to the distribution of species by ecoregions determined by the opinion of experts and the literature, we also searched international databases for

occurrences of NNMS in South America, and compared both sources of information. We used Global Biodiversity Information Facility—GBIF—(<https://www.gbif.org/>) and Global Invasive Species Database—GISD—(<http://www.iucngisd.org/gisd/>) for the terrestrial NNMS; whereas GBIF, GISD and Ocean Biogeographic Information System—OBIS—(<https://www.obis.org/>) were consulted for aquatic NNMS. In these databases, the occurrences of NNMS were generally not georeferenced and thus, countries and not ecoregions were considered as distribution units. Species held in captivity, intercepted and identified at the genus level were not included in the search.

Relationship between NNMS richness and urbanized areas and the conservation status in South America

The degree of urbanization for each ecoregion was assessed according to four variables: (1) number of cities with more than 500,000 inhabitants (SEDAC 2019); (2) airports with more than 7 million passengers/year (LENA 2014); (3) cargo airports (LENA 2014); and (4) ports with TEU value higher than 700,000 (TEU—Twenty-foot Equivalent Unit) (LENA 2014; ECLAC 2016). The number of cities, cargo and passenger airports, and ports were established for each ecoregion. A fifth variable, the conservation status of each ecoregion, was determined according to Dinerstein et al. (1995) who based the conservation status of the ecoregions on five indicators of landscape integrity, being extinct (completely converted), critical, endangered, vulnerable, relatively stable or relatively intact.

For this analysis, the presence of NNMS before and after the 1970s was considered, the estimated date of the beginning of the globalization process that shaped the current worldwide trade patterns (Buriyank 2005; Hulme 2009; Torija Zone and Gottschalk 2018). A multiple linear regression analysis was performed using NNMS richness per ecoregion as a dependent variable, and the five abovementioned key variables as independent variables. In addition, the simple correlation between the NNMS richness by ecoregion and the five variables was performed using the Spearman coefficient (R).

Results

Compilation and exchange of information on non-native mollusk species (NNMS) of South America

Eighty-six species of non-native mollusks (NNMS) established in South America were recognized, 56 of which belong to the terrestrial environment, 16 to freshwater and 14 to the marine environment (Online Resources 1–3). Within the 56 terrestrial species, five were determined as cryptogenic [i.e., *Helix omissa* Pfeiffer, 1856; *Pupisoma dioscoricola* (Adams, 1845); *Beckianum beckianum* (Pfeiffer, 1846); *Opeas goodali* (Miller, 1822); *Sarasinula plebeia* (Fischer, 1868)]. In addition to these 56 species, three others were detected only during importation [i.e., *Candidula intersecta* Poiret, 1801; *Tandonia sowerbyi* (Férussac, 1823); *Opeas hannense* (Rang 1831)]; and three other terrestrial species were only recorded in captivity (commercial, heliciculture and laboratory) and were not found in the natural environment [i.e., *Achatina monochromatica* (Pilsbry, 1904); *Helix lucorum* (Linnaeus, 1758); *Helix pomatia* Linnaeus, 1758].

During the analysis, we also detected poorly known species or with taxonomic problems. This fact forced the group of experts to make a decision about their status as NNMS (Online Resource 4). Among these species are *Physella cubensis* (L. Pfeiffer, 1839), *Perna perna* (Linnaeus, 1758), *Mytilopsis sallei* (Récluz, 1849), *Mytilus* spp. and *Electroma* sp.

Vectors, first records and native regions of NNMS in South America

The vectors of introduction of the NNMS registered in South America are unknown in 40% of the studied cases (Fig. 1). More than 20% of the identified vectors are associated with horticulture, agriculture, and ornamental plants (parks and gardens). Ballast water and ships follow in importance, representing 10% of the introductions in South America.

The first record of a NNMS in South America dates back to 1835, being a terrestrial snail of the family Bradybaenidae [*Bradybaena similaris* (Férussac, 1822)] (Fig. 2a, Online Resource 1). However, and considering terrestrial, freshwater and marine environments, 64% of the species reported here were recorded since the 1970s. Prior to 1970, only terrestrial species were recorded (34% of the total), except for a single freshwater NNMS (*Pseudosuccinea columella* (Say, 1817), Lymnaeidae) (Fig. 2a, Online Resource 2).

The rate of establishment of NNMS in South America since the first record (1835), considering terrestrial, freshwater and marine species, is best described by an exponential function (Fig. 2 b; $r^2 = 0.9519$; $y = 0.9893 e^{0.2495x}$). In contrast, the rate of establishment of NNMS since the first report up to 1969 is best described by a linear function ($r^2 = 0.9426$; $y = 2.3341x - 5.7912$), and the rate from 1970 to 2018 is best described by an exponential function ($r^2 = 0.9973$; $y = 30.968 e^{0.2074x}$). Finally, when analyzing the native region of the 81 NNMS of South America (86 species reported here minus the five cryptogenic ones), most of them come from

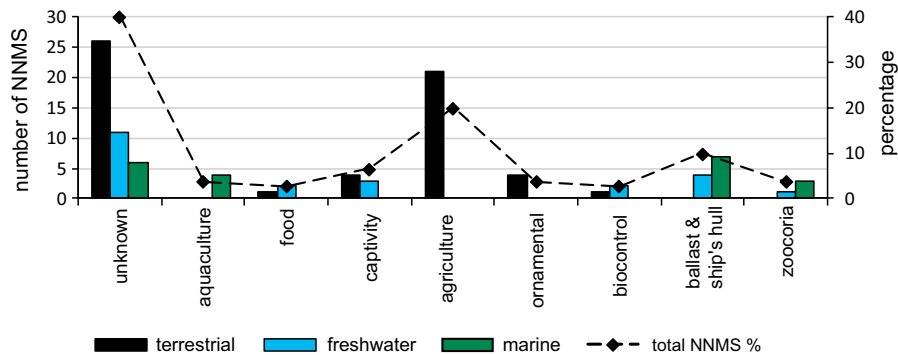
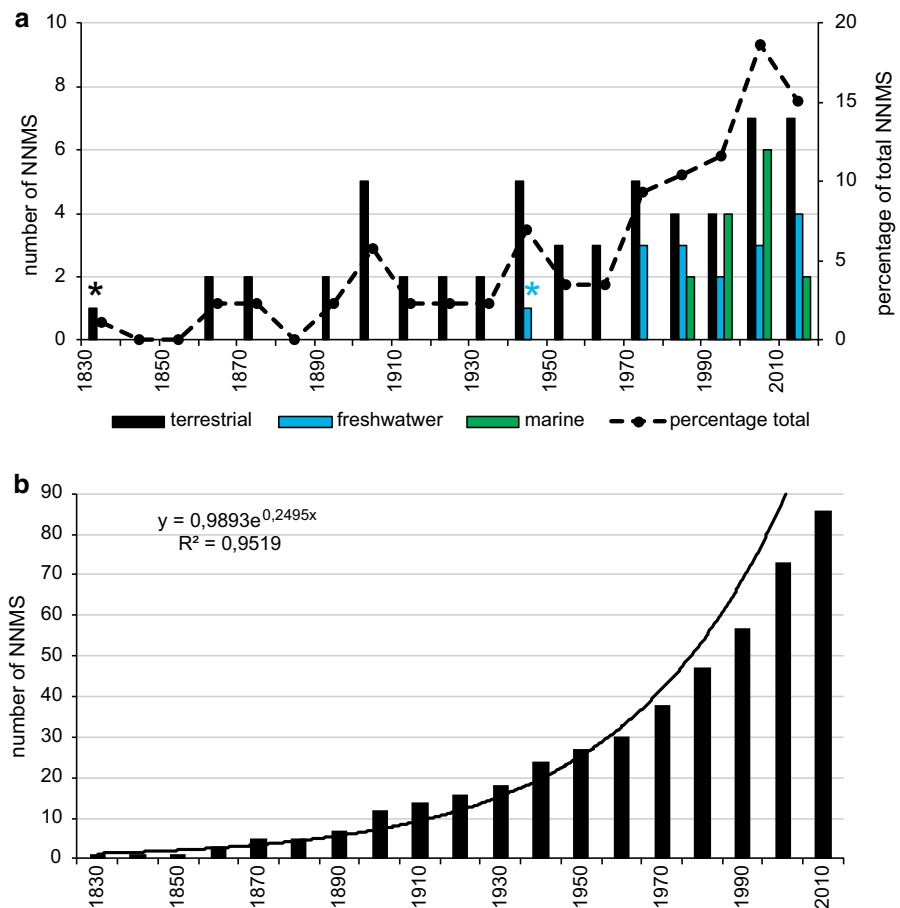


Fig. 1 Number of non-native mollusk species in South America by vector type in terrestrial, freshwater and marine environment (primary axis) and percentage of total number of

non-native mollusk species by vector (secondary axis), in South America. Captivity includes culture, research and ornamental; agriculture includes horticulture and fruticulture

Fig. 2 Non-native mollusk species (NNMS) for South America by date (10-year interval) since first recorded. **a** Number of NNMS from the first reference (1835) until 2018, according to habitat (primary axis) and percentage of NNMS recorded (secondary axis); black asterisk corresponds to the first record in terrestrial environment (*Bradybaena similaris*, Bradybaenidae), and blue asterisk to the first record in freshwater environment (*Pseudosuccinea columella*, Lymnaeidae). **b** Rate of total NNMS reported since 1830 decade, the increase is best described by an exponential function; y: number of NNMS; x: time in 10-years interval



Europe (> 35%), and among them more than 90% belong to the terrestrial environment. The other important native regions are the Asian continent (14% aquatic NNMS and 10% terrestrial), and North America (9% aquatic NNMS and about 5% terrestrial) (Online Resources 1–3). The least frequent native regions are Africa and the Indo-Pacific (Fig. 3).

Distribution of NNMS in South America

Distribution range and number of NNMS in South American ecoregions are heterogeneous. Non-native mollusk species are distributed in 152 ecoregions (89 terrestrial; 46 freshwater, and 17 marine), of the 189 described for South America (80%). The highest number of species is distributed in less than three ecoregions (Fig. 4a–c). In the terrestrial environments, more than 20% of the NNMS are distributed in a single ecoregion and 42% in less than five

ecoregions (Fig. 4a). In both terrestrial and freshwater environments, a few species are widely distributed (Fig. 4a, b). The terrestrial species with the highest distribution range in South America is *Achatina fulica*; 30 years after its invasion, it has been found in 63 (58%) terrestrial ecoregions (Fig. 5a, Online Resource 1). The most widespread freshwater species in South America is *Corbicula fluminea*. More than 35 years after its introduction, it has been recorded in 27 (52%) freshwater ecoregions (Fig. 5b, Online Resource 2). In the marine environment, 57% of the NNMS are found in less than three ecoregions. *Crassostrea gigas* is the species with the greatest distributional range in South America; more than 45 years after its introduction, it has been recorded in six (21%) marine ecoregions (Fig. 5d, Online Resource 3). Other species are distributed in numerous ecoregions, among them, the terrestrial snail *Subulina octona* (Bruguiere, 1789), registered since 1914 in South America, has been

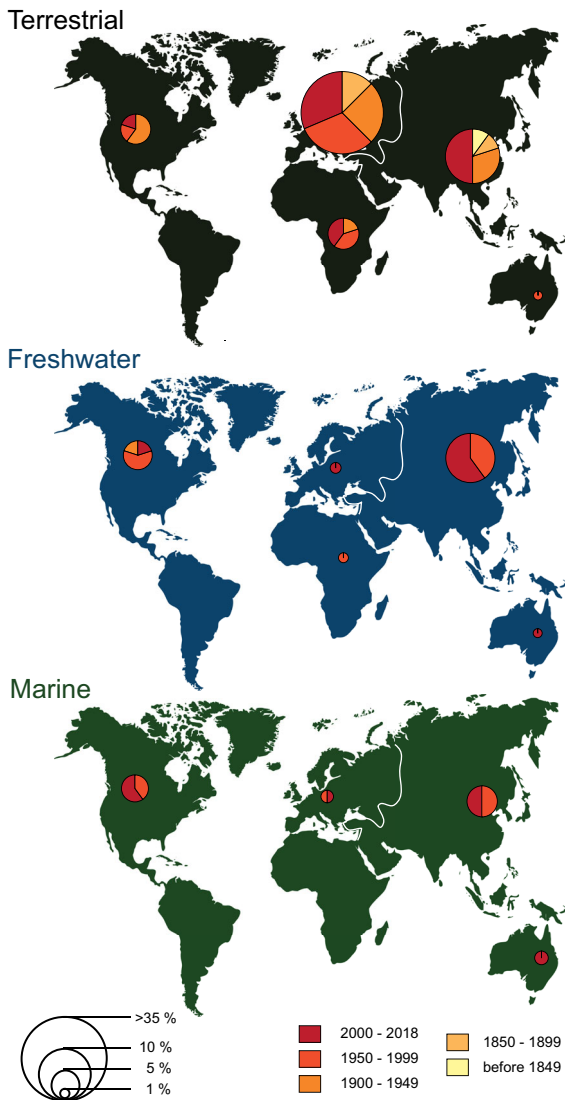


Fig. 3 Percentage of NNMS of South America according to native region and date of first report in South American by environment. Size of circles indicates the percentage of species according to its origin, and colors indicate date of introduction in 50-year interval

found in 23 terrestrial ecoregions, and the snail *Melanoides tuberculata*, registered since 1972, in 25 freshwater ecoregions (Online Resources 1 and 2).

The NNMS richness registered per ecoregion is uneven (Figs. 6, 7, 8). In the terrestrial environment, the ecoregion with the largest number of NNMS is the Uruguayan Savanna (23 species). In the freshwater environment, the Lower Parana, Central Andean

Pacific and San Francisco ecoregions have seven species each, while in the marine environment, the Southeastern Brazil ecoregion has six species.

Biodiversity database search

Biodiversity databases provide less information concerning the occurrence data of NNMS in South America than the literature and the experience of the e-discussion group (Table 1) (Online Resources 1–3). Of the 84 NNMS registered in this study, 24% have no records in the biodiversity database for the South American countries. When comparing the distribution of NNMS by countries between biodiversity databases versus the data from the e-discussion group, there is a coincidence of only 15%.

Relationship between NNMS richness and urbanized areas and the conservation status in South America

Since 1970, the number of NNMS in all environments is related to the presence of large cities, cargo and passenger airports, ports and conservation status of the South American ecoregions. The multiple regression model shows an adjusted R^2 of 0.25 and a critical value of $F\ 2.8621^{-07}$, displaying the relationship between these variables and NNMS richness (Table 2). In this analysis, the presence of cargo airport is the most important predictor, followed by the conservation status and the number of large cities. When analyzing the simple correlations of these variables, the NNMS richness correlates positively and significantly with all the variables (Table 3).

For each environment, four groups of ecoregions with the highest NNMS richness were identified on the basis of the relationships between the NNMS richness since 1970 per ecoregion, and the anthropogenic factors urbanization and trade. These South American zones are: Subtropical Atlantic, Northern Andes, Central Andes, and Southern Andes (Fig. 9).

The Subtropical Atlantic zone displays the highest number of NNMS (30) and the highest number of large cities, passenger airports, and ports. The Southern Andes zone presents 14 NNMS, the Northern Andes zone seven NNMS, and the Central Andes zone five NNMS (Fig. 9).

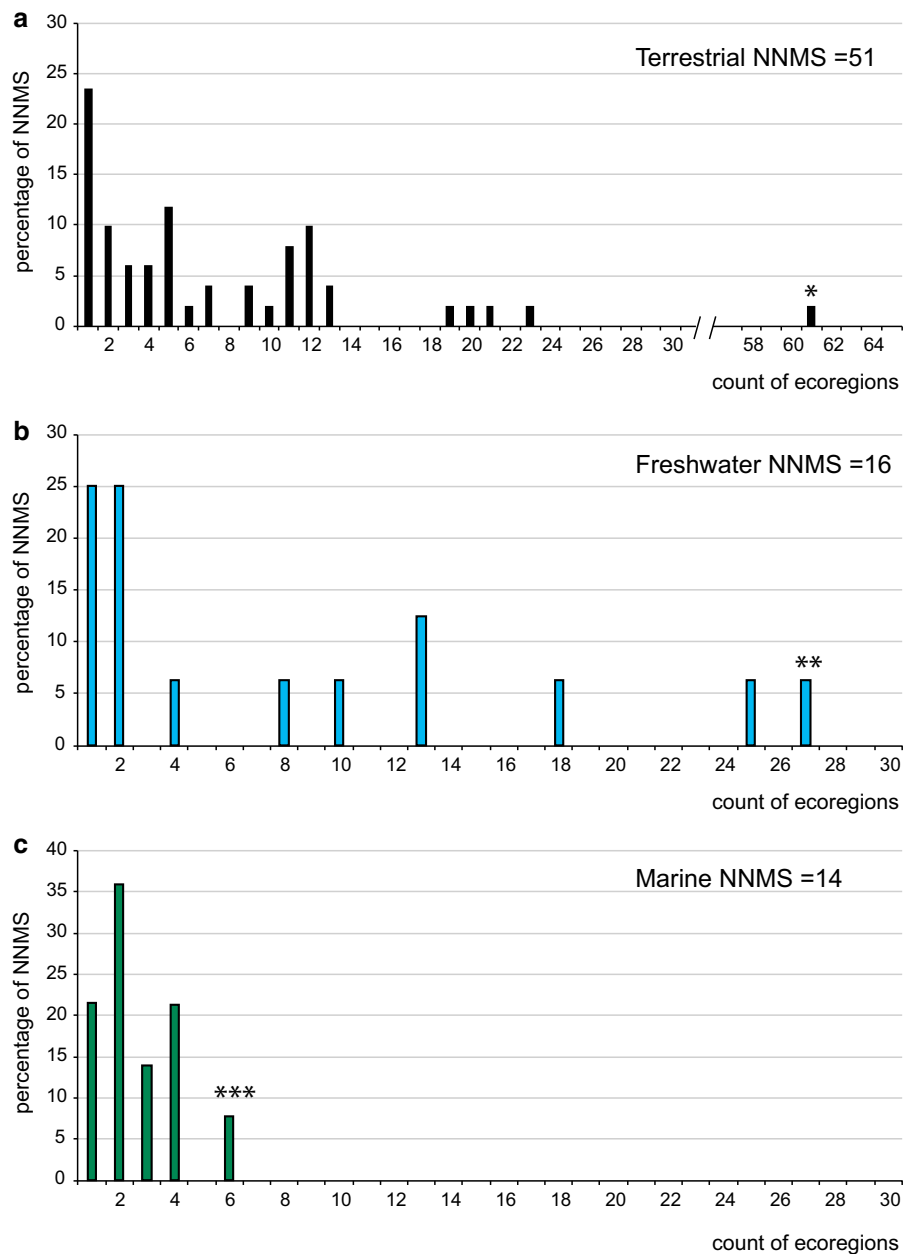


Fig. 4 Histograms showing the percentage of non-native mollusk species in South America according to the number of ecoregions in which they occur, after the present study. **a** Terrestrial, **Achatina fulica* recorded in 61 terrestrial

ecoregions; **b** freshwater, ***Corbicula fluminea* recorded in 27 freshwater ecoregions; **c** marine, ****Crassostrea gigas* recorded in 6 marine ecoregions

Discussion

In relation to the great biodiversity estimated for South America, this continent is still poorly studied. The fauna of native South American mollusks is no exception to this fact. The present work provides

baseline knowledge of non-native mollusk species (NNMS) of South America based on an exhaustive review of information and enhanced by the contribution of the e-discussion group of 23 malacologists and taxonomists from South America. The insufficient knowledge of native species, and the absence of

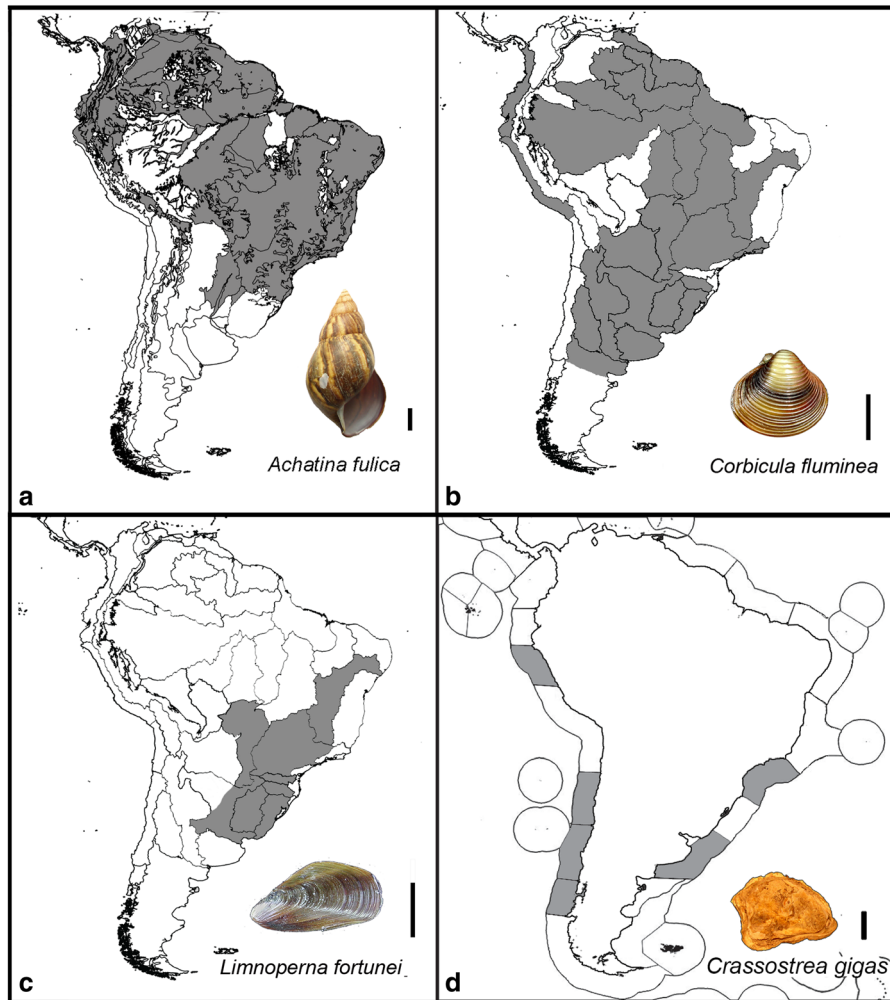


Fig. 5 Distribution of four emblematic non-native mollusk species due to their wide distribution and impact in South America. **a** *Achatina fulica*; **b** *Corbicula fluminea*; **c** *Limnoperna fortunei*; **d** *Crassostrea gigas*. **a, d** According to

the occurrence in the ecoregions; **b** distribution in Patagonia ecoregion limited to the known records; **c** after CBEIH (2014). Scale bar: 1 cm

species inventories in many regions, were the main difficulties in establishing their status as NNMS. This is particularly evident in the terrestrial environment, where studies on mollusk biodiversity are scarce, from the 56 NNMS identified, five are cryptogenic. Furthermore, information is often in gray literature.

The great extension of the South American continent and the diversity of its environments and climates slant the knowledge of the distribution of mollusks, mainly due to (1) the presence of research centers; and (2) malacologists interested in a particular environment. The NNMS distribution patterns arise from the reports generated in this context and, therefore, do not

necessarily coincide with their total distribution. Thomsen et al. (2014) said that the generalization and prediction of the capabilities of the NNMS are limited by the degree of knowledge of their attributes of non-native species, since their research is carried out, in general, according to the degree and type of impact they cause on the invaded system. This incomplete knowledge coincides with the statements of other authors, such as Orensanz et al. (2002), who obtained the same trend in the introduction of non-native marine species on the southwestern Atlantic coast. Likewise, Schwindt and Bortolus (2017) reported a lack of multinational efforts (financial,

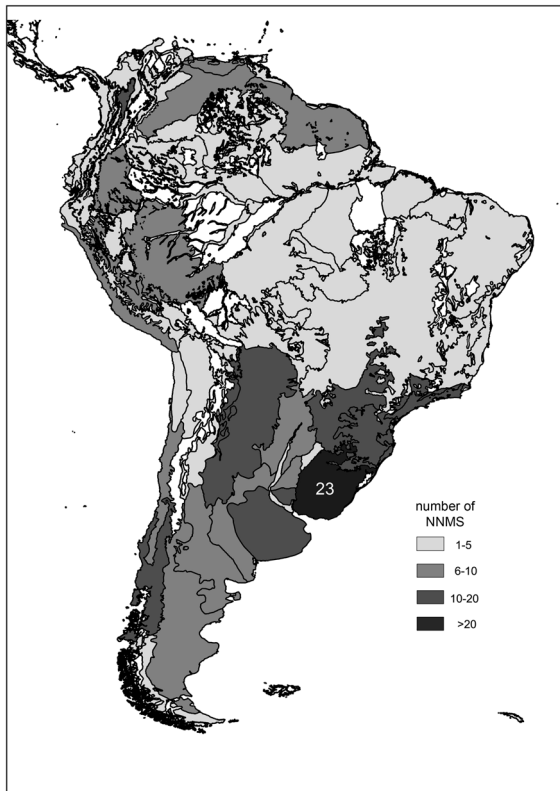


Fig. 6 Number of non-native mollusk species per each terrestrial ecoregion. Number of ecoregions = 109; 23 is the highest number of NNMS recorded

scientific and social aspects) for generating knowledge in aquatic non-native species. Regarding the priority need to prevent the introduction of further non-native species into coastal mainland regions (Dawson et al. 2017), the results reported here highlight the low degree of knowledge about which vectors are related to NNMS in South America. Taking this into account, the vectors for 40% of the NNMS studied could not be established, even though the information on the vectors is basic to prevent and control the introduction of non-native species (Carlton and Ruiz 2005; Simberloff et al. 2013). The vectors identified for terrestrial species were related to cultivation, trade of vegetables and ornamental plants in general, being only a few species introduced in captivity or as food resource. Horticultural and agricultural activities, and ornamental plants in parks and gardens, are also vectors of potential non-native species for South America (Hurrell and Delucchi 2013). Similar to what Gracia et al. (2011) found for Colombia and de Castro

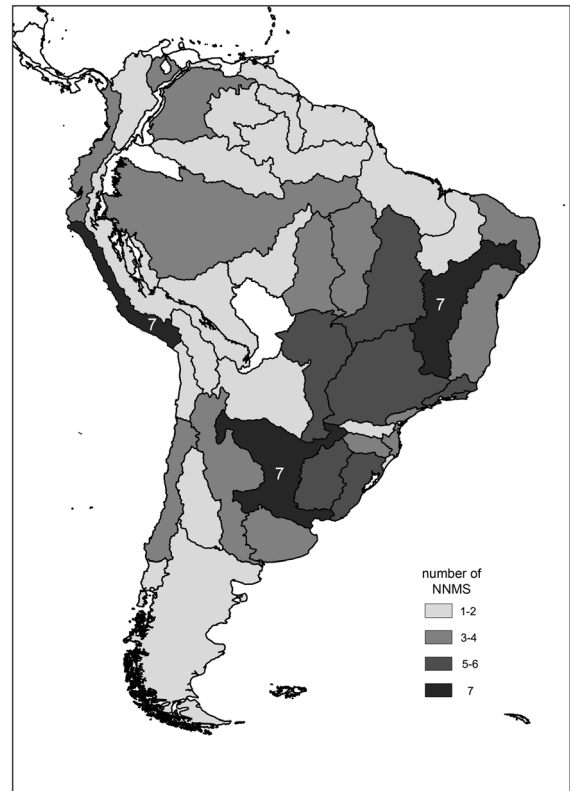


Fig. 7 Number of non-native mollusk species per each freshwater ecoregion. Number of ecoregions = 52; 7 is the highest number of NNMS recorded

et al. (2017) for the southwest Atlantic Ocean, the results of this study indicate that the ballast waters, biofouling and aquaculture are the most frequent vectors for the aquatic environment.

The results reported here reveal that the first record of NNMS in South America corresponds to the terrestrial snail *Bradybaena similaris* and occurred in 1835, related to the European colonial period, when Eurasian species were most successful establishing in America because of the intensity of the propagule. It is estimated that the number of species that moved from Europe to America is 10 times greater than vice versa (Lockwood et al. 2007). Since the middle of the twentieth century there has been a change in economic policy, and the presence of new markets and economic opportunities has broadened the spectrum of source regions for NNMS, including Southeast Asia and North America (Essel et al. 2015). Our results also showed that since the 1970s, freshwater (e.g. *Corbicula fluminea*, *Limnoperna fortunei*) and marine

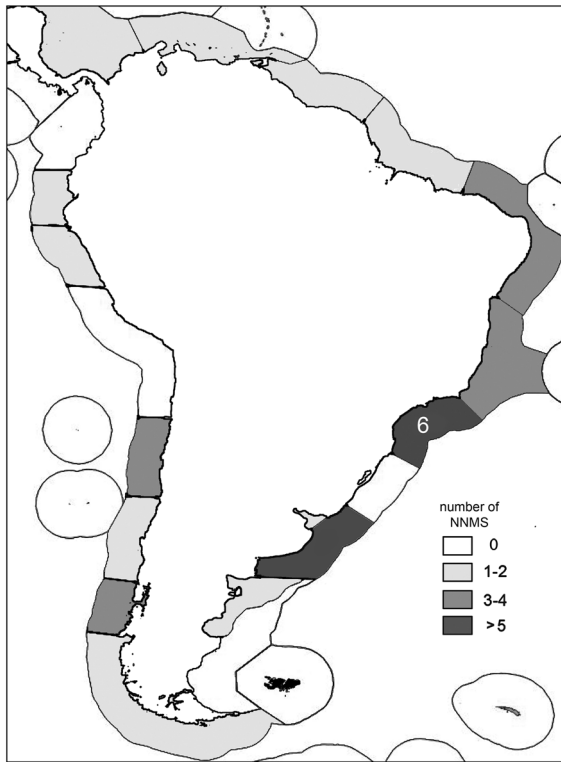


Fig. 8 Number of non-native mollusk species per each marine ecoregion. Number of ecoregions = 28; 6 is the highest number of NNMS recorded

NNMS (e.g., *Crassostrea gigas*) begin to settle in South America, widening the span of native source regions. This period coincides with the commercial process known as globalization, in which the transport of goods and people across international borders causes high propagule pressure (Thomsen et al. 2014). We detected an increase in the rate of introduction since 1970. These facts agree with Seebens et al. (2017) who, considering the records of non-native species introduced by man all over the world in the last 200 years, indicates that 37% were reported between

Table 1 The differences of the number of non-native mollusk species in South America (by environment and total) recorded by two sources: (1) from the bibliographic revision and experts (= e-discussion group), and (2) from biodiversity databases

	Terrestrial	Freshwater	Marine	Total
Total number of species recorded in this research (e-discussion group)	56	15	13	84
Number of species recorded by both sources (e-discussion group and DB)	43	12	9	64
Number of species registered only by the e-discussion group	13	3	4	20

Table 2 Regression summary of non-native mollusk species South America as a dependent variable

	Coefficient	SE	t	P level
Intercept	1.19	0.33	3.56	0.000
Cities > 500,000 inhabitants	0.18	0.11	1.61	0.108
Cargo airports	0.73	0.28	2.57	0.011
Passenger airports	0.28	0.24	1.61	0.247
Ports	0.10	0.27	0.38	0.721
Conservation status	0.18	0.10	1.69	0.092

R = 0.50; R² = 0.25; Adjusted R² = 0.22; F_{5,133} = 8.84; P < 0.000005; SE of estimate: 1.39

1970 and 2014, which also results in an increase of research studies.

Due to its geographical characteristics, South America exhibits a disparity of ecoregions in the terrestrial, freshwater and marine environments. However, each NNMS shows different degree of distribution in South America. The highest number of NNMS is distributed in one or two ecoregions. This could be due to the short time elapsed since their introduction, or because they have restricted (or lack of) invasive capacity (Morton 1996). Marine ecoregions have a greater extension than those from other environments, so marine NNMS can be expected to occupy a smaller number of ecoregions. The results indicated that the majority of marine NNMS are distributed in a few ecoregions, suggesting an interaction between the dispersion capacity of the NNMS and the resistance of the environment to the introduction of foreign species, or the relatively short time of their introduction, since 1970. Byers et al. (2015) stated that, due to the positive relationship between the time of introduction and the range of dispersion, the non-native marine invertebrate species are not in equilibrium, and therefore,

(i.e., GBIF, OBIS, GISD) (= DB). The species kept in captivity, intercepted and identified to genus level (i.e. *Corbicula* sp. and *Saccostrea* sp.) are not included

Table 3 Simple correlation matrix (r) for variables used in the multiple regression analysis reported in Table 2

	Cities > 500,000 habitants	Cargo airports	Passenger airports	Ports	Conservation status
Cargo airports	0.39				
Passenger airports	0.35	0.62			
Ports	0.32	0.39	0.53		
Conservation status	0.29	0.26	0.37	0.25	
NNMS richness	0.32***	0.38***	0.34***	0.25**	0.29**

Significant probability shown for non-native mollusk species (NNMS) richness, * $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$

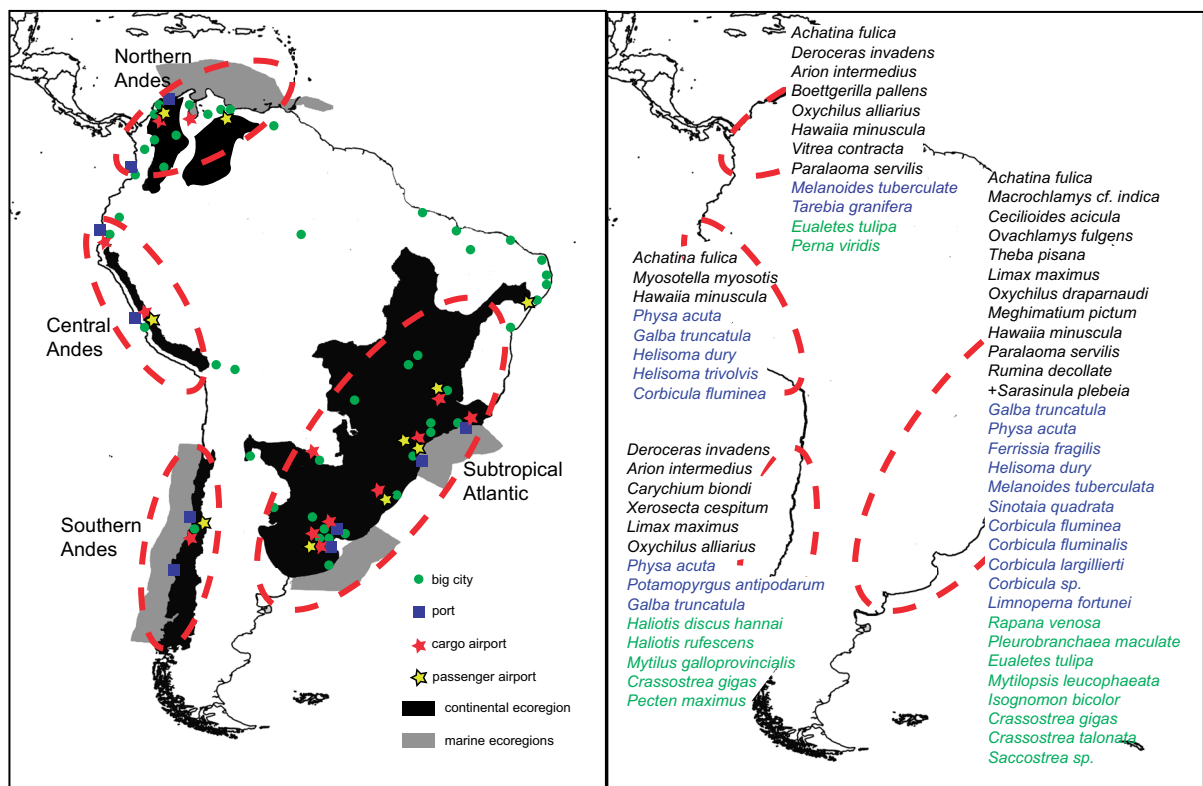


Fig. 9 The four zones of South America with the highest number of non-native mollusk species recorded after 1970. To the left, characteristics of urbanization showing big cities ($\geq 500,000$ citizens) (SEDAC 2019); passenger airports (2012) (> 7 million passenger/year) (LENA 2014); cargo airports (LENA 2014), ports ($> 700,000$ TEU value) (LENA 2014; ECLAC 2016). The *Subtropical Atlantic* zone includes six terrestrial ecoregions (Alto Paraná Atlantic forests*, Serra do Mar coastal forests**, Araucaria moist forests**, Uruguayan savanna, Southern Atlantic mangroves**, Humid Pampas*), seven freshwater (Tocantins-Araguaia*, San Francisco, Upper Paraná*, Paraíba do Sul**, Fluminense**, Laguna dos Patos, Lower Uruguay, Lower Paraná), and two marine (Uruguay-Buenos Aires Shelf*, Southwestern Brazil**). The *Southern Andes* zone includes two terrestrial ecoregions (Chilean

matorral*, Valdivian temperate forests), one freshwater (South Andean Pacific Slopes*) and three marine (Central Chile*, Araucanian*, Chiloense). The *Northern Andes* zone includes one terrestrial ecoregion (Magdalena Valley montane forests*), two freshwater (Magdalena-Sinu*, Orinoco Llanos) and one marine (Southwestern Caribbean*). The *Central Andes* zone includes one terrestrial ecoregion (Ecuadorian dry forest) and one freshwater (Central Andean Pacific Slopes). For details in the extension of the ecoregions see Online Resources 5–7). Asterisks indicate conservation status after Dinerstein et al. (1995) (*endangered and **critical). To the right, the introduced species after 1970 for each zone. In black: terrestrial species, in blue: freshwater species, and in green marine species. For details of the species see Online Resources 1–3). + Cryptogenic species

they are still dispersing. Likewise, the distribution pattern of NNMS in South America may also be due to particular unrelated introduction events.

Invasion impacts have been reported mainly in North America, Europe, and Australasia. Many fewer non-native species have been studied from South America (Thomsen et al. 2014). In turn, non-native species are supposed to compete with native species, affecting them significantly. In general, competition is assumed when there is a success of an invasion; this hypothesis has not been well tested (Byers 2009) and much less for South American NNMS. A few NNMS have a large distribution, occupying many of the ecoregions of South America (Fig. 5), which demonstrates their great dispersal capacity and adaptive potential that allow them to live in regions with different environmental characteristics. For example, *Achatina fulica* (Achatinidae), the giant African snail, that was first introduced in South America in Brazil in the late 1980's to compete with *Cornu aspersum*, the true escargot (Teles and Fontes 2002; Thiengo et al. 2007). Reports suggest that *A. fulica* has expanded its range and has become the most widely distributed terrestrial gastropod in South America (Gutiérrez Gregoric et al. 2011) (Fig. 5a, Online Resource 1). The potential distribution of *A. fulica* shows that it could spread to all South American countries (Vogler et al. 2013). This species is cataloged among the top 100 worst invasive alien species of the world (GISD 2018) and in South America it has caused impact on: (1) agriculture, destructing crops; (2) human health, acting as an intermediate host of several parasites, e.g. nematodes *Angiostrongylus costaricensis* (Morera and Cespedes, 1971), *A. cantonensis* (Chen, 1935), and *Aelurostrongylus abstrusus* (Railliet, 1898); (3) native fauna, via inter-specific competition (Thiengo et al. 2007; Thiengo and Fernández 2016; Valente et al. 2016).

On the other hand, in the freshwater environment, *Corbicula fluminea* (Corbiculidae) or the Asiatic clam, was introduced in South America through the Río de la Plata River between the late 60's and early 70's (Crespo et al. 2015), possibly by the release of living specimens brought as food on-board in vessels or through ballast water (Paschoal et al. 2013). Currently *C. fluminea* is distributed from the Colorado River in the northern limit of the Argentinean Patagonia (39° 01' S–64° 01' W) to Venezuela (10° 10' S–63° 30' W) (Cao et al. 2017; Reshaid et al. 2017) (Fig. 5b, Online

Resource 2). Several impacts on the environment made by this species have been detected in South America (Paschoal et al. 2015; Reyna et al. 2018), including niche overlap and putative negative effects on native *Cyanocyclas* spp. (Clavijo and Carranza 2018). Also, *C. fluminea* occupies a central position in the food chain model, connecting benthic and pelagic systems (Sousa et al. 2008). It feeds on primary producers and in turn is eaten by fish predators (García and Protogino 2005). Additionally, fouling in pipes of refrigeration systems of industries and power plants have been reported in Brazil (dos Santos et al. 2012). *Limnoperna fortunei* (Mytilidae) or golden mussel, was introduced in South America in the Río de la Plata River in 1991 (Pastorino et al. 1993) seemingly through the ballast water in transoceanic ships (Darrigran and Pastorino 1995). Since its first record in the region, the golden mussel has spread significantly (Fig. 5c, Online Resource 2). Its high dispersion ability is associated with its capacity to withstand stressful periods (e.g. starvation and variable temperature; Cordeiro et al. 2016; Andrade et al. 2017). The species is considered an ecosystem engineer in the Río de la Plata basin (Darrigran and Damborenea 2011). Impacts in South America include fouling, easy invasion of water transfer tunnels where they adhere to tunnel walls and structures with high density, resulting in biofouling, pipe clogging (Boltovskoy et al. 2015), and structure corrosion.

In the marine environment, *Crassostrea gigas* (Ostreidae), the pacific or Japanese oyster was introduced in Brazil in 1970 for aquiculture (Melo et al. 2010). Despite being widely distributed on the Atlantic and Pacific coasts of South America (Fig. 5d, Online Resource 3) and its importance for aquaculture (FAO 2005–2018), the information about the species and its impact is scarce. There are not enough studies on the impact over the native communities and ecosystems. However, the alterations of the environment where this species lives produce esthetic changes on the coast that last for a long time (Ruesink et al. 2005). Borges (2005) also reported an increase in the abundance of epifaunal species living at the expense of the oyster, while Escapa et al. (2004) reported an increase in abundance of local and migratory bird species 20 years after the introduction in Bahía Anegada, Argentina. Further, due to its hard shells and sharp edges, as well as the ability to form a hard substrate in former sandy bottoms, *Crassostrea gigas*

impacts artisanal fishing and tourism, preventing both coastal fishing by cutting fishing lines (Zalba et al. 2008) and tourism in highly-invaded areas. *Rapana venosa* (Muricidae) or rapa whelk, was probably introduced in the Río de la Plata River during the late 1980s via larvae transported in ballast water (Pastorino et al. 2000; Orensanz et al. 2002) (Online Resource 3). Reported impacts in South America include probable depletion or reduction of at least some prey population (e.g., mussels) (Carranza et al. 2009) and massive fouling on immature green turtles *Chelonia mydas* (Linnaeus, 1758) (Lezama et al. 2013). On the other hand, the rapa whelk may constitute up to 100% of the diet for immature and mature logger heads, *Caretta caretta* (Linnaeus, 1758), and at least a minor item in the diet of the small shark *Mustelus schmitti* Springer, 1939 (Bonelli et al. 2016).

International online databases of biodiversity (e.g., GBIF, GISD, OBIS), allow quick access to information usually dispersed in different formats and difficult to access (Jiménez and Koleff 2016). When comparing the information provided by these databases with that from the experience of specialists and from the literature on the distribution of non-native mollusks registered in South America, the coincidence between both source of information was low, so our results revealed that the available information in these databases is incomplete concerning the South American NNMS. Large differences between both sources of information have been mentioned by other authors in other areas of knowledge (e.g. Lozano et al. 2017).

When analyzing the distribution of the 56 terrestrial NNMS, the ecoregions with more than five NNMS were areas with a “critical, endangered or vulnerable” status (Dinerstein et al. 1995). According to the International Union for Conservation of Nature (IUCN 2012), in these areas native species face an extremely high to moderate extinction threat, in the state of wildlife. The Uruguayan Savanna (with 23 NNMS) and the Humid Pampas (with 16 NNMS) ecoregions have the highest number of NNMS and their status of terrestrial ecoregions is “vulnerable” and “endangered” (Dinerstein et al. 1995; IUCN 2012). It should be noted that in the Uruguayan Savanna and the Humid Pampas two national capitals are located (Buenos Aires and Montevideo), with an average density of 7.4 million citizens, two cargo airports (IDB 2015), airports with a high number of passengers per

year and two ports with more than 700 thousands TEU (ECLAC 2016). Likewise, the richest agricultural-livestock production area of Argentina is located in the Humid Pampas.

The ecoregions with more species of non-native freshwater mollusks are found on the slopes of the Central Pacific Andes, San Francisco and Lower Parana, with seven species each. The status of these ecoregions is considered as “high biodiversity threat” (Gilbert 2010) or “vulnerable” (Dinerstein et al. 1995). Dams are also regarded as generators of favorable environments for freshwater NNMS (Vörösmarty et al. 2010). For example, in the Brazilian ecoregion of Sao Francisco seven NNMS have been recorded in river channels, concurring with the presence of 50 hydroelectric plants (CBEIH 2014) in this basin.

In the marine environment, the ecoregions of Southeastern Brazil and Uruguay-Buenos Aires Shelf concentrate the largest number (six and five species respectively) of NNMS. Although Battistella et al. (2015) stated that 5–10% of the Southeastern Brazil ecoregion is protected there are 13 ports in the area, of which three, Rio Grande, Paranagua and Santos, are the main ports of the country according to the Olalde (2018). Likewise, for ECLAC (2016), the Port of Santos has the highest container traffic in South America (3,391,593 TEU).

According to Dawson et al. (2017) the hotspots of established non-native species richness are predominantly coastal mainland regions, regardless of the taxonomic group. Our results coincide with Dawson et al. (2017), and in addition, show statistically significant relationships between NNMS richness in ecoregions of South America and the degree of urbanization, commerce and conservation status. Four zones with the highest number of NNMS are recognized, considering only the records since 1970, decade in which global commercial and tourist navigation starts and increases significantly (Hulme 2009). The results confirm the temporal and spatial variation in the introduction of NNMS in South America.

The identified zones with high NNMS richness may be cataloged as entry points of NNMS. These zones also coincide with the bioinvasion hotspots identified by Seebens et al. (2017) globally, as well as with Schwindt and Bortolus (2017) in terms of the most studied freshwater exotic species in biology/ecology per country in South America between 2004 and 2014.

The four zones where the NNMS are established should be regarded with special attention for the conservation of South American biodiversity, not only because they are potential entry points for non-native species, but also because they are considered “hot spots” of high endemism by Johnson et al. (2018). These authors indicate three hot spots areas for South America, which include these four zones. These hot spots are rich in endemic species under significant threat of imminent extinction. This is in agreement with Ziller et al. (2007), who relate the invasion process to the entry points of the species, mainly ports and airports, import and export trade routes, and cargo movement within the country, tourist routes and the main introduction vectors (e.g., agricultural products, ornamental plants, ballast water).

The results open many new questions, including whether taxonomic and geographic biases observed in our background weaken our knowledge base (Pyšek et al. 2008). A future focus on poorly-studied taxa, habitats and regions should improve our understanding and management of impacts associated with non-native species (Thomsen et al. 2014).

Another factor to take into account is climate change. In this scenario, several studies apply distribution models to predict the potential changes in species distribution using current information. In addition, the prediction of potential range of invasive species is key information in the assessment of their risk, monitoring, and management (Byers et al. 2013). As examples in mollusk species, McDowell et al. (2014) and Byers et al. (2013) estimated the potential distribution in North America for *Corbicula fluminea* and *Pomacea insularum* respectively, species widely distributed in South America. In this work, the creation of an e-discussion group of expert opinion of South American malacologists and taxonomists involved in the research on NNMS, was essential to maximize the analysis of existing information in different sources. Therefore, we present here our own database of non-native mollusk species of South America and their distribution patterns by ecoregions. This information is essential for future policies on biodiversity conservation management in South America. These measures can be achieved through distribution models, which could be the next step in the study of South American NNMS. This approach is particularly useful in an understudied place like South America, and the data provided here supply key

information to guide future sampling to where it is predicted that a species is more likely to exist or invade.

Acknowledgements To the Economist Lic. Jorge Darrigran, for his advice on globalization. GD and CD were partially supported by Project No. 11/N795 Universidad Nacional de La Plata, Argentina. Authors thank the reviewers for their comments and suggestions that improve the final manuscript version.

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