



# Species movements within biogeographic regions: exploring the distribution of transplanted mollusc species in South America

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**Abstract** The movement of species is among the most serious environmental threats of the new millennium, as the transplantation of species beyond their native or historical range has intensified in the last five decades. Traditionally, studies on bioinvasions

have focused on species that have been introduced, deliberately or accidentally, to biogeographic regions where they did not previously occur. However, less attention has been given to species movement to novel areas within the same biogeographic region. Our research group, the South America Introduced Molluscs Specialists, analyzed potential cases of native South American mollusc species introduced deliberately or accidentally beyond their natural range within

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South America. To achieve this, it is key to differentiate between anthropogenic processes and passive responses to environmental conditions. We considered the past and current spatial distribution of species, analyzed known or putative vectors, and discuss the impacts of taxonomic and nomenclatural knowledge. Based on the evidence currently available, we propose different scenarios to explain observed changes in mollusc distributions within South America. Seventeen transplanted mollusc species (TMS) were recognized, considering marine, freshwater, and terrestrial environments. Of the 189 South American ecoregions 31 were occupied by transplanted species, but this proportion varied by environment: 10 of 28 marine ecoregions, 12 of 52 freshwater ecoregions, and 9 of 109 terrestrial ecoregions. The ecoregions with TMS are generally located in the peripheral zones of the continent. Those with the highest number of TMS were the Southern Caribbean (three species) in the marine environment, the Central Andean Pacific Slopes (three species) in the freshwater environment, and the Alto Paraná Atlantic forests (two species) in the terrestrial environment. The number of unintentionally moved TMS is greater than those

moved intentionally. The translocation process is similar to the introduction and settlement process of non-native mollusc species, and so is their impact.

**Keywords** Transfer · Translocation · Range expansion · Bioinvasion · Ecoregions

## Introduction

To develop control or eradication measures, the Convention on Biological Diversity (CBD 1992, 2010) prioritizes the identification and study of invasive non-native species, one of the most significant causes of biodiversity loss at a global scale (e.g., Blackburn et al. 2020). This framework led specialists on molluscs and bioinvasions from different regions of South America to establish an expert research group, namely

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the “South America Introduced Molluscs Specialists Group” (eMIAS; <https://alienmolluscsgroup.wixsite.com/saamgroup>). Once established, an initial synthesis of the status and distribution of non-native molluscs in South America at an ecoregional scale was developed (Darrigran et al. 2020). This work targeted introduced species in South America from other continents. However, little attention has been paid to the phenomenon of species movement within the same biogeographic regions. In this context, eMIAS identified species of molluscs, native to South America, that had experienced modifications to their historical distributions within the continent that are not attributable to natural dispersal processes. Cases analyzed ranged from obscure local species, such as the sea slug *Aplysia dactylomela* Rang, 1828, to globally conspicuous species, such as the black-striped mussel, *Mytilopsis sallei* (Récluz, 1849), a brackish-water bivalve native to coastal lagoons and estuaries of Central America and the Caribbean (Fernandes et al. 2018).

In the mainstream literature, the terms ‘transplantation’, ‘transfer’, or ‘translocation’ have been used interchangeably to identify this process. Even though the terms are typically considered synonymous, several authors have pointed out important distinctions and alternative definitions. Currently, it has been argued that the planet is going through a new era, the Anthropocene, in which disturbances are mainly generated from the globalization of trade and climate change (Hobbs et al. 2018). These processes are advancing at unprecedented rates and scales, and have yet to reach their climax. Because of climatic changes, species can access new regions, while others are forced to reduce their ranges (or disappear) in response to altered environments. Hayward et al. (2015) even proposed redefining the IUCN guidelines on the natural range of species to include potential range shifts and subpopulations existing outside the natural range but in broadly similar habitat. In this work, we follow the definition of the IUCN (2022), in which an indigenous species (= native species) is defined based on three criteria: (1) it is intrinsically part of the ecosystem and developed there, (2) it arrived in the area long before records of such matters were kept, (3) it arrived by natural means (unaided by human action). We acknowledge that this definition is only a pragmatic and conventional rule to be used to guide our study (Holguín 2003). Herein, a species

is considered non-native when it is introduced outside its natural geographical range through human action, being able to maintain a self-sustaining population (Turbelin et al. 2017). If a non-native species disperses and has an evident environmental and socio-economic impact, it is considered invasive (Darrigran et al. 2020). Furthermore, we define transplantation (transfer, translocation) as the movement of native species from one locality to another by human action, with successful establishment outside their known historical geographical range (in our case, within South America). Such species movements can be both accidental or deliberate (e.g., for conservation, trade, research). A species is considered to be established in the environment when there are populations with multi-generational reproductive success (Kočovský et al. 2018).

Knowledge of the invertebrate fauna of South America is still fragmented and incomplete (Damborenea et al. 2020; de Barros et al. 2020). Despite the high richness of native molluscs in the continent, there are major knowledge gaps, mostly because of the biased and unequal coverage by the areas studied, errors in identification, and taxonomic uncertainty, all of which can have consequences for conservation (Salvador 2019; de Barros et al. 2020). There are also differences among marine, freshwater and terrestrial environments in terms of species richness, research effort, and vulnerability. In contrast, the socio-economic and ecological impacts of some invasive species have led to a more comprehensive knowledge of these species (Darrigran et al. 2020). As a corollary, in South America, the distribution and biology of economically important invasive mollusc species are better understood than the distribution and biology of native molluscs (Dos Santos et al. 2021). Similarly, some of the knowledge of certain species native to South America has come from studies on other continents where they have become invasive (e.g., Wong et al. 2011; Joshi et al. 2017; Calazans et al. 2018, 2021; Fernandes et al. 2018).

In this context, this work aims to assess native species of molluscs from South America that have been transplanted within the continent, including marine, freshwater, and terrestrial realms. Based on the evidence currently available, we propose different scenarios to explain observed changes in molluscan distribution within the continent.

## Material and methods

A collaborative effort was made by 29 expert malacologists and taxonomists from countries in South America (Argentina, Brazil, Chile, Ecuador, Peru, Uruguay, and Venezuela) and from New Zealand, belonging to the eMIAS group. Scientific and grey literature, databases on the subject were analyzed, and experiences were exchanged through a virtual forum among the group. Then, the group listed the transplanted mollusc species (TMS) and reached a consensus on the status of each species in the 189 ecoregions (marine, freshwater, and terrestrial) recognized in South America (Online Resources 1–3).

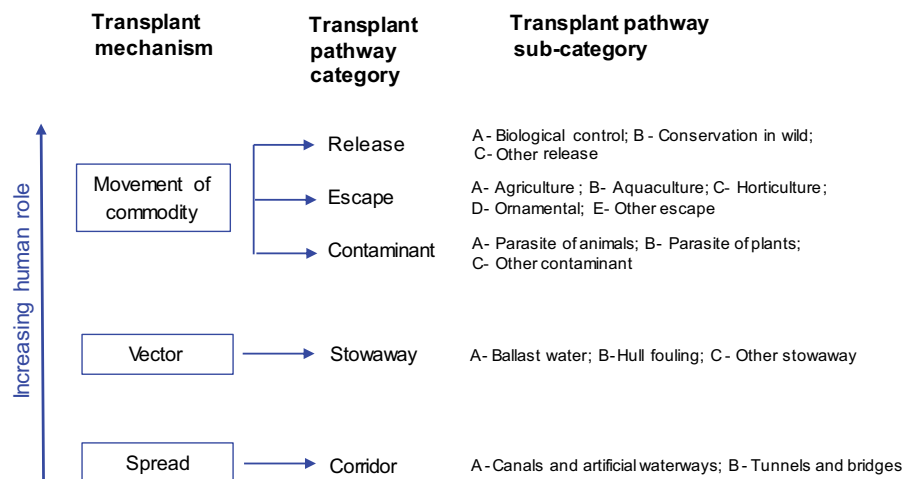
The geographic range of each species was determined based on literature records and expert experience at an ecoregional scale (see also Darrigran et al. 2020). Following Olson and Dinerstein (2002), ecoregions were defined as areas of land or water with a characteristic set of natural communities, ecological 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, 28 ecoregions are recognized for marine environments (<http://maps.tnc.org/files/metadata/MEOW.xml>; Online Resource 1), 52 for freshwater environments (<http://maps.tnc.org/files/metadata/FEOW.xml>; Online Resource 2), and 109 for terrestrial environments (<http://maps.tnc.org/files/metadata/TerrEcos.xml>; Online Resource 3).

The criterion for a species to be considered as a TMS was the existence of documentation of its transplantation within South America. To avoid confusion between the type of species under study and in agreement with the definitions mentioned above, and the description of introduction pathways by Faulkner et al. (2020), we worked on the basis of three premises:

1. The way in which the species are distributed, both in geographic space and in time, responds to historical, ecological, and physiological factors throughout their range (Maciel-Mata et al. 2015).
2. The causes of transplantation of native species are human-related, including conservation, trade, research, and accidental transport.
3. Transplanted species can cause the same problems and potential dangers as introduced species, which leads us to consider the same pathway(s) as those proposed for introduced organisms by the Convention on Biological Diversity (CBD 2014) (as interpreted by IUCN, 2017). The mechanisms and pathways by which TMS may arrive, and enter a new region are detailed in Fig. 1.

Based on these premises, the list of transplanted species was compiled considering known historical distribution, new location(s), ecoregion(s) of the new location(s), pathway(s) of transplantation, and impacts. References are given for each case. Furthermore, mollusc species transported by humans and only found in captivity were mentioned, but are not

**Fig. 1** Classification framework for routes of introduction / transplantation, modified from Faulkner et al. (2020). The nomenclature proposed in IUCN (2017) was partially applied. The mechanisms and pathway categories are based on Hulme et al. (2008)



counted as TMS as they had not been found in the natural environment.

## Results

Seventeen transplanted mollusc species (TMS) were recognized in South America (Online Resources 4, 5): ten bivalves (only one freshwater species) belonging to six families (Fig. 2) and seven gastropods (four freshwater and three terrestrials) belonging to three families (Fig. 3).

Transplanted mollusc species were recorded in 16% (31/189) of the ecoregions, specifically in 36% (10/28) of the marine ecoregions, 23% (12/52) of the freshwater ones, and 8% (9/109) of the terrestrial ones. The ecoregions with TMS (31) are generally located in the peripheral zones of the continent, typically adjacent to other ecoregions with TMS (Figs. 2, 3).

The marine ecoregions with most transplanted species (Table 1) are Southern Caribbean (3 TMS) and Uruguay-Buenos Aires Shelf, Northeastern Brazil and Southeastern Brazil (2 TMS each). In freshwater, Central Andean Pacific Slopes ecoregion has three TMS and Western Amazon Piedmont two TMS, and in the terrestrial environment the only region with more than one TMS is Alto Paraná Atlantic Forest with two. In several localities, certain species were recognized in captivity (Figs. 2, 3). The country with the most TMS is Chile, with five in the wild and three in captivity, followed by Argentina, Brazil and Colombia with four, Ecuador with three, Peru with two, and Uruguay and Venezuela with one each (Online Resources 4 and 5).

The freshwater *Pomacea canaliculata* (Lamarck, 1822) is the transplanted gastropod recorded in the largest number of ecoregions (seven). For bivalves, it is the marine scissor date mussel *Leiosolenus aristatus* (Dillwyn, 1817), present in four ecoregions. The transplantation mechanism (Table 2) was Movement of Commodity for all gastropod species except *P. canaliculata*, while for bivalves this mechanism corresponds to only four of the cases. The remaining bivalve transplants (six) occurred by Vector, as several species are in the two subcategories 'hull fouling' and 'ballast water'.

In South America, TMS are known to cause some type of impact, both on the natural environment

(e.g., modification of the environment, displacement of native fauna), and socio-economic (e.g., agriculture, aquaculture, parasite vector) (Table 3, Online Resources 4 and 5).

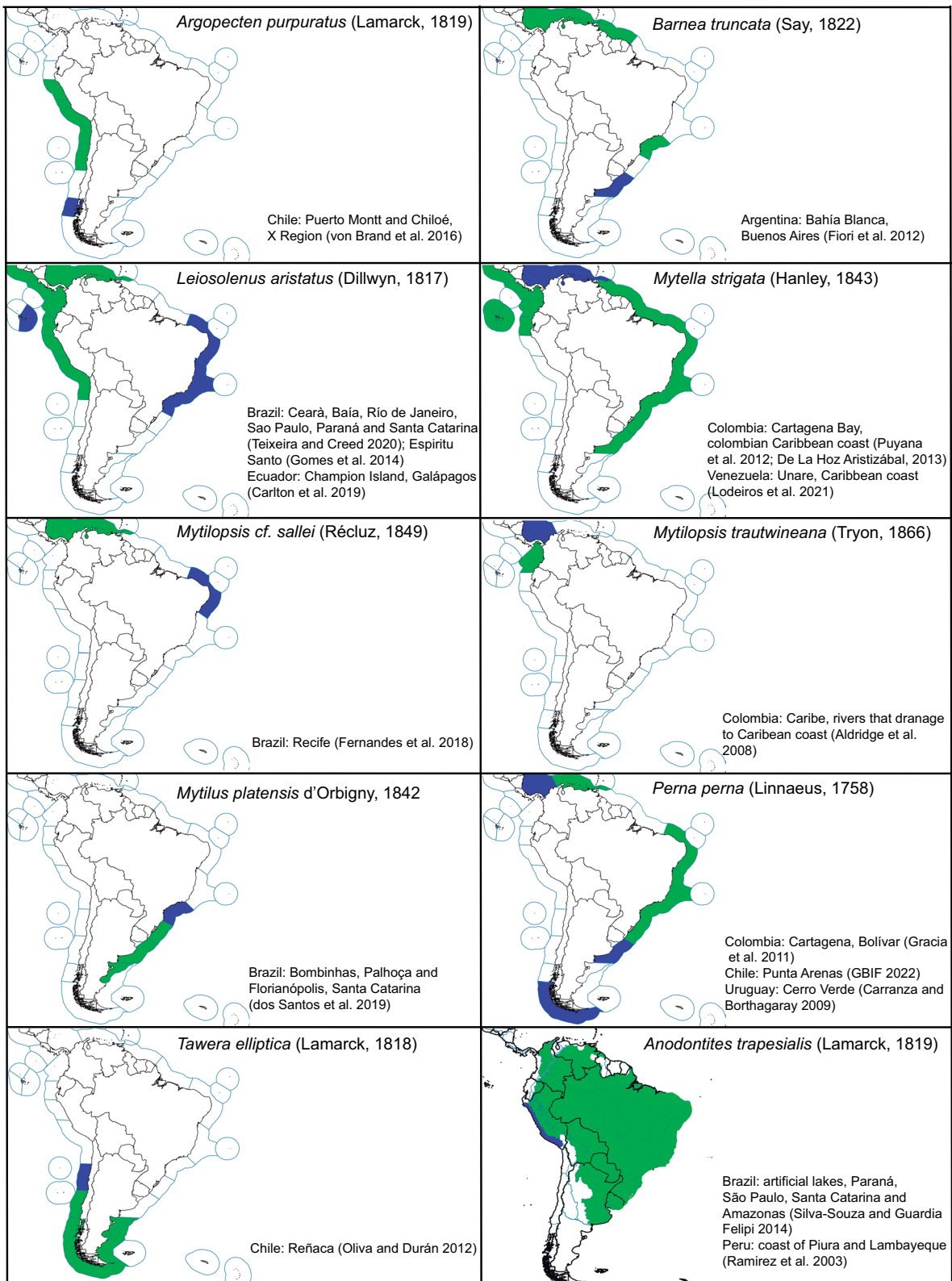
Nine species have undergone modifications in their historical distributions, but do not fit the transplantation definition (Table 4, Online Resource 6). Furthermore, species such as *Mytilus platensis* d'Orbigny, 1842 and *Perna perna* (Linnaeus, 1758) are still undergoing debate regarding their taxonomy and their status as natives (Online Resource 6).

## Discussion

Given our current knowledge of climate change, it is expected that more changes in species distribution and abundance within South America will take place in the coming decades (McDowell et al. 2014; Bárcena et al. 2020). Those changes will be interacting with other stressors, such as habitat loss, change in land use, eutrophication, and impacts of invasive species. To understand the overall impacts of these factors, their interactions must be examined, and probably the first step is to precisely identify the current distributions of species in the continent.

Species are naturally dispersed by different mechanisms, but human activities have become a common means of transport, not only moving species from one geographic region to another, but also expanding their natural distributions. Studies of non-native species are many, particularly biased towards invasive species with noticeable impact on human welfare. However, the transplantation (as here defined) of species is not frequently considered, despite their potential socio-ecological impacts.

Knowledge of the native and non-native mollusc fauna of South America is heterogeneous. Studies on mollusc diversity are incomplete in vast regions of South America (Darrigran et al. 2020) and therefore the number of valid native species is not yet well established (e.g., Salvador 2019; Dos Santos et al. 2021). This lack of knowledge is evidenced in the present study by the number of transplanted mollusc species (TMS) recognized for all of South America. Although there is no up to date record of mollusc species present on the continent, the reported mollusc richness of the largest of the 12 countries in South America, Brazil, is close to 2,950 species considering



◀**Fig. 2** Distribution of transplanted bivalves in South America by ecoregions (limits of ecoregions in light blue). Ecoregions that include the known historical geographic distribution are shown in green; those that include transplant locations are shown in blue. For each species the location and reference of transplants are mentioned. More information is available in Online Resource 4

the freshwater, terrestrial, and marine environments (Amaral and Jablonski 2005; Simone 2006; Salvador 2019); 1800 species have been recorded in Chile (Aldea et al. 2019), while approximately 1300 species are reported from Argentina (Rumi et al. 2008; Bigatti and Signorelli 2018; Dos Santos et al. 2021) and the richness in tropical countries is expected to greatly exceed those numbers. This information allows us to affirm that the 17 TMS identified here for all South America constitute a very conservative estimate. It is likely that our partial knowledge of the distribution and taxonomy of many of the molluscs is masking other potential TMS. Furthermore, there are also species that are mobilized by humans for commercial use, cultivation, or research reasons, but are only found in captivity and have not established themselves in the natural environment (Darrigran et al. 2020); those species can potentially become new transplants in the future.

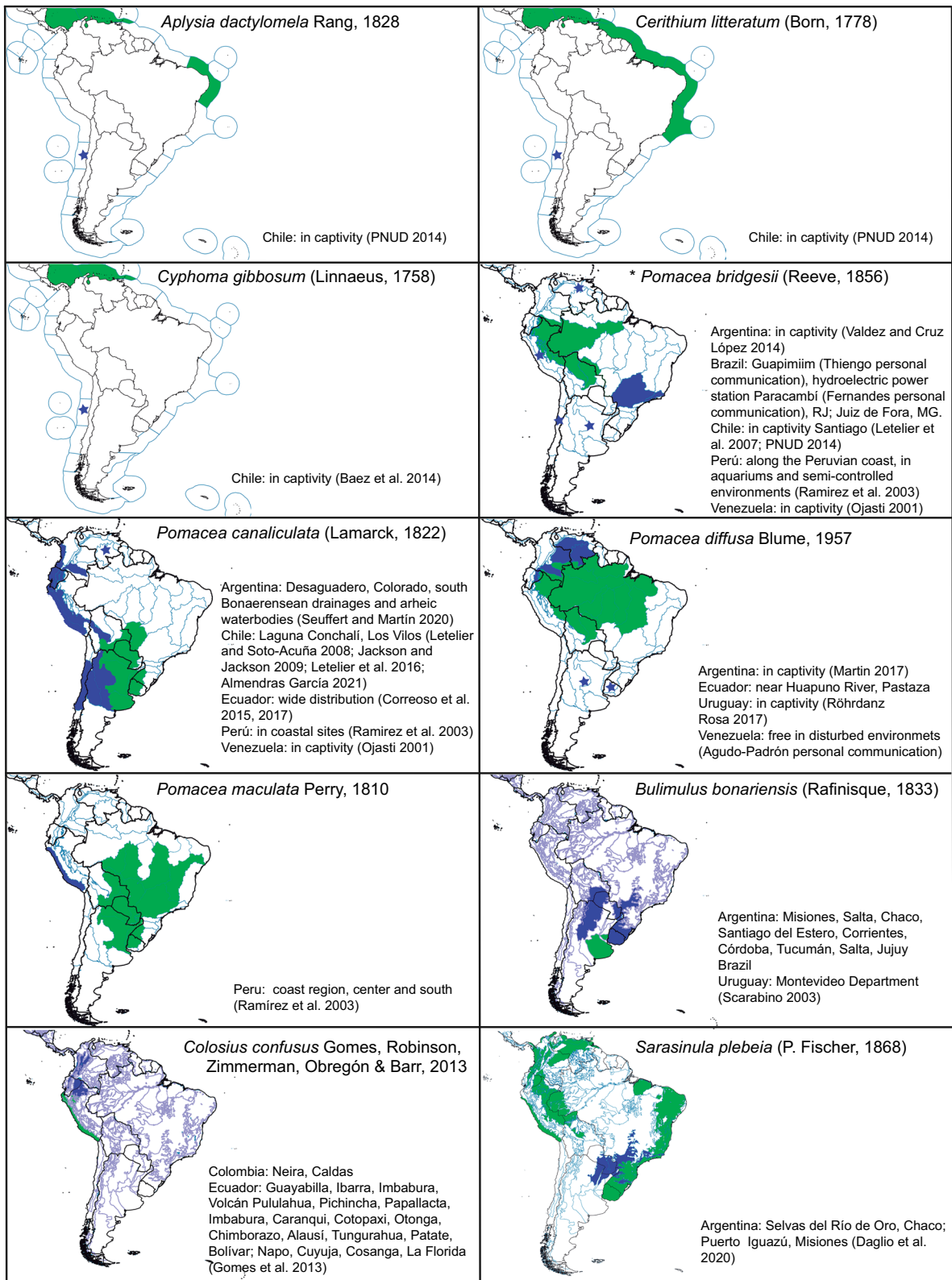
Darrigran et al. (2020) recognized four zones in South America based on the highest number of non-native mollusc species recorded after 1970 and the associated anthropogenic factors (e.g., urbanization and trade). These zones are predominantly peripheral mainland areas (i.e., Subtropical Atlantic, Northern Andes, Central Andes, and Southern Andes) and were recognized as non-native mollusc hot-spots and entry points of non-native mollusc species (Darrigran et al. 2020). Our results show that of the 31 ecoregions with TMS, 14 are included in these four hot-spots of non-native mollusc species. In addition, all terrestrial ecoregions in which transplanted terrestrial molluscs were recognized belong to the category of highest conservation priority at a regional scale (Dinerstein et al. 1995).

Consequently, it can be deduced that the environmental and socioeconomic characteristics that facilitate the introduction and settlement of non-native species of molluscs are also correlated with the transplantation of species within South America (Table 1). This result points to a relationship between the features of the environment (invasibility) and

those of the transplanted mollusc species (invasiveness) (Hicks 2004). Strayer (2022) remarked that the impacts of transplanted species can be predicted from (a) the species traits, (b) how axial the translocation is (i.e., if an existing population is increased, or re-established at a recently occupied site, or introduced to a new site), and (c) the rigor of translocation protocols in cases where the aim is conservation or biocontrol (Novak et al. 2021).

Two highly successful mollusc species transplanted within South America (*Pomacea canaliculata* and *Leiosolenus aristatus*) exhibit behavioral and physiological characteristics that have facilitated their introduction in other continents. *Leiosolenus aristatus* is a boring species from the western Atlantic and the Pacific, which was detected off the coasts of Rio de Janeiro and São Paulo, southeast Brazil (Simone and Gonçalves 2006). It has also been introduced to the Cape Verde Islands (Lopes 2011) and to the Mediterranean coast of Catalonia (López Soriano and Quiñero Salgado 2019). *Pomacea canaliculata* is among 100 of the worst invasive species worldwide (Lowe et al. 2000). This species causes major economic and public health problems in much of Southeast Asia (Joshi et al. 2017), Europe (López et al. 2010), and Africa (Buddie et al. 2021). Trade, maritime routes, and tourism have increased in the twentieth and twenty-first centuries (IUCN 2009; Hobbs et al. 2018), and are the most important factors in the introduction of non-native species globally. This is more pronounced for maritime transport (IUCN 2009) and, accordingly, the majority of TMS in South America have been recorded from marine ecoregions.

Among the terrestrial molluscs, Darrigran et al. (2020) considered the slug *Sarasinula plebeia* (Fischer, 1868) a cryptogenic species. However, Gomes and Thomé (2004) considered there to be a consensus that it was introduced into Australia and the several islands on the Pacific by commerce in the Indian and Pacific Oceans and that it is probably originally from tropical areas of America, as also stated by Cowie et al. (2008). Daglio et al. (2020) noted that *Vaginula behni* Semper, 1885, which is currently a synonym of *S. plebeia* according to Thomé (1993), was originally described based on material from Rio de Janeiro, Brazil, indicating that it has been present in South America for a long time, despite being originally described based on material from New Caledonia, in the Pacific region. According to Daglio et al. (2020), *S. plebeia*





◀**Fig. 3** Distribution of transplanted gastropods in South America by ecoregions (limits of ecoregions in light blue). Ecoregions that include the known historical geographic distribution are shown in green; those that include transplant locations are shown in blue. The blue stars indicate specimens in captivity (not considered TMS). For each species the location and reference of transplants are mentioned. \*The distribution of *Pomacea bidgesii* is difficult to establish because *Pomacea diffusa* was previously considered a subspecies of *P. bridgesii* and, although they are currently recognized as separate species, misidentification of *P. diffusa* as *P. bridgesii* is frequent (Cowie and Thiengo 2003; Hayes et al. 2008, 2009; Cowie et al. 2017). More information is available in Online Resource 5

has been reported in Brazil (since 1885), Colombia (1978), Venezuela (1992), Chile (1993), Ecuador (2008), Peru (2015), and Argentina (2020); they considered its presence in Argentina as a transplanted species.

It is important to note, however, that the geographical origin of some species remains uncertain. Such is the case, as mentioned before, for the brown mussel *Perna perna*, which has been considered native to either South America (Darrigran et al. 2020) or the western coasts of Africa (Oliveira et al. 2017). Calazans et al. (2021) clarified the status of *P. perna* by analyzing the genetic structure of several populations, showing that it is native to both continents: populations in Brazil are derived from natural geographical expansion from the populations in northern Africa, which took place over 2000 years ago. In addition, taxonomic problems often prevent proper assessment of the distribution of species. For example, the geographic range of *Mytilus platensis* is not reliably defined, given its complex identification and diagnosability from other Mytilidae, such as *Mytilus chilensis* Hupé, 1854 from the southeastern Pacific (Zbawicka et al. 2018). Some studies indicate that the distribution of *M. platensis* extends from southern Brazil to southern Argentina (Dellatorre et al. 2007), with the North Patagonian gulfs probably being the southern limit of its distribution. A characteristic of this species is its ecology in the coasts of northern Argentina and southern Uruguay, where in addition to being part of the intertidal and infralittoral community, they form deep banks away from the coast, between 40 and 55 m deep (Penchaszadeh 1980). Adding to the complexity is the introduced Mediterranean *Mytilus galloprovincialis* Lamarck, 1819 in the Puerto Madryn area (42° 51' S, 65° 15' W), where it has hybridized with the local *M. platensis* (Zbawicka et al. 2018).

All these caveats being noted, we found that TMS occur in 18% of the ecoregions in South America, 31% of which are contiguous. Contiguous ecoregions may have similar or at least favorable environmental characteristics for the presence of TMS. Most of these scenarios correspond to contiguous freshwater ecoregions in line with the hypothesis of Bianco (1995), that river basins are the main geographic axes of introduction of non-marine aquatic species. In general, TMS transportation routes in South America are related to economic purposes, namely aquaculture, agriculture, horticulture, and trade of ornamental species. Sindermann (1993) warned about the transplantation and introduction of marine species worldwide in response to the perceived need of expanding aquaculture industries (e.g., fish, shrimp, bivalve molluscs). On the other hand, Bartley et al. (2005) stated that the use of non-native species is a proven means of increasing productivity and value of aquatic ecosystems. Likewise, FAO (2018) promoted practices for the introduction of new species and the responsible movement of live aquatic animals. According to the aforementioned, Álvarez León (2014) pointed out that it is necessary to identify the impacts of transplanting native species and introducing non-native species, in addition to regulating their use in each country. For instance, most of the transplants in Colombia have originated from aquaculture (Restrepo-Santamaría and Álvarez-León 2013) and, as the technological packages of some species were developed, they began to be used in regions different from their basins of origin (“trans-introductions” according to Bianco 1995), highlighting the importance of this type of pathway for the transplantation of species. For example, *Anodontites trapesialis* (Lamarck, 1819) was transplanted to the north coast of Peru for aquaculture purposes in integrated fish and duck cultures (Ramírez et al. 2003). Agudo-Padrón (2019, 2022) reported this species as a contaminant in fish farming tanks, farming areas, and tourist fishing facilities in rivers in southern Brazil. The life cycle of *A. trapesialis* includes an ectoparasitic larval stage that adheres to the gills and fins of host fish. The cycle is completed in the fish rearing tanks, which has a negative impact on the development of this resource. Tanks are mainly contaminated through the inadvertent introduction of infested fish. Likewise, Agudo-Padrón (2005) reported that the Federal Rural University of Pernambuco experimented with freshwater fish farming with

**Table 1** Number of transplanted mollusc species (TMS) according marine, freshwater and terrestrial ecoregions of South America

Ecoregion	TMS	NNMS	Hotspots NNMS
<i>Marine environment</i>			
Southern Caribbean	3	1	Northern Andes
Northeastern Brazil	2	3	*
Uruguay-Buenos Aires Shelf	2	5	Subtropical Atlantic
Southeastern Brazil	2	6	Subtropical Atlantic
Central Chile	1	4	Southern Andes
Chiloense	1	4	Southern Andes
Channels and Fjords of Southern Chile	1	1	*
Eastern Brazil	1	2	*
Eastern Galapagos Islands	1	nc	nc
Southwestern Caribbean	1	1	Northern Andes
Total marine ecoregions with TMS 10/28 = 36%			
<i>Freshwater environment</i>			
Central Andean Pacific Slopes	3	7	Central Andes
Western Amazon Piedmont	2	nc	*
South Andean Pacific Slopes	1	3	Southern Andes
North Andean Pacific Slopes Rio Atrato	1	3	*
Mar Chiquita – Salinas Grandes	1	4	*
Amazonas High Andes	1	2	*
Paraíba do Sul	1	5	Subtropical Atlantic
Fluminense	1	6	Subtropical Atlantic
Cuyan—Desaguadero	1	2	*
Upper Paraná	1	6	Subtropical Atlantic
Orinoco Llanos	1	3	Northern Andes
Orinoco Guiana Shield	1	1	*
Total freshwater ecoregions with TMS 12/52 = 23%			
<i>Terrestrial environment</i>			
Alto Paraná Atlantic forests	2	16	Subtropical Atlantic
Southern Andean Yungas	1	16	*
Magdalena Valley montane forests	1	13	Northern Andes
Napo moist forests	1	6	*
Eastern Cordillera real montane forests	1	5	*
Northwestern Andean montane forests	1	3	*
Dry Chaco	1	12	*
Humid Chaco	1	7	*
Uruguayan savanna	1	22	Subtropical Atlantic
Total terrestrial ecoregions with TMS 9/109 = 8%			

Following Darrigran et al. (2020): NNMS, number of non-native mollusc species (from outside South America); Hotspots of NNMS according to Darrigran et al. (2020)

\*Ecoregions outside the hotspots of non-native mollusc species; nc, ecoregion not considered in Darrigran et al. (2020)

*A. trapesialis* for human consumption, using host fish such as carp, *Cyprinus carpio* (Linnaeus, 1758) and tilapia (*Oreochromis* sp.).

Although no further records of freshwater bivalve culturing were detected in South America, there have been instances of culturing the gastropods *Pomacea bridgesii* (Reeve, 1856) and *Pomacea lineata* (Spix

**Table 2** Pathways of transplanted mollusc species in South America (seven Gastropoda and ten Bivalvia species)

Mechanism of Transplant	Pathway Category	Pathway Sub-category	
Movement of commodity	Escape	Aquaculture	
		1. <i>Anodontites trapesialis</i> **	Ramírez et al. (2003)
		2. <i>Argopecten purpuratus</i> **	von Brand et al. (2016)
		3. <i>Mytilopsis trautwineana</i> **	Albridge et al. (2008)
		4. <i>Pomacea maculata</i> *	Alcantara-Bocanegra and Nakagawa-Valverde (1996)
		5. <i>Tawera elliptica</i> **	Oliva and Durán (2012)
		Ornamental	
		1. <i>Pomacea diffusa</i> *	Scarabino et al. (2012) Martín (2017)
		Horticulture and Agriculture	
		1. <i>Bulimulus bonariensis</i> *	Frana and Massoni (2011)
		2. <i>Colosius confusus</i> *	Gomes et al. (2013)
		Live bait	
		1. <i>Pomacea canaliculata</i> *	Seuffert and Martín (2020)
		Live food	
		1. <i>Pomacea canaliculata</i> *	Seuffert and Martín (2020)
		Other escape	
		1. <i>Pomacea bridgesii</i> *#	Martins and Alves (2008)
		2. <i>Pomacea canaliculata</i> *	Seuffert and Martín (2020)
		3. <i>Sarasinula plebeia</i> *	Daglio et al. (2020)
	Vector	Contaminant	Parasite of animals
		1. <i>Anodontites trapesialis</i> **	dos Santos Silva et al. (2021)
Stowaway		Hull fouling	
		2. <i>Barnea truncata</i> **	Fiori et al. (2012)
		3. <i>Leiosolenus aristatus</i> **	Carlton et al. (2019)
		4. <i>Mytella strigata</i> **	Lodeiros et al. (2021)
		5. <i>Mytilopsis</i> cf. <i>sallei</i> **	Queiroz et al. (2020)
		6. <i>Mytilus platensis</i> **	Cárdenas et al. (2020)
		7. <i>Perna perna</i> **	PNUD (2014)
		8. <i>Pomacea canaliculata</i> *	Seuffert and Martín (2020)
		Ballast water	
		1. <i>Barnea truncata</i> **	Fiori et al. (2012)
		2. <i>Mytella strigata</i> **	Lodeiros et al. (2021)
		3. <i>Mytilopsis</i> cf. <i>sallei</i> **	Queiroz et al. (2020)
		4. <i>Mytilus platensis</i> **	Cárdenas et al. (2020)
		5. <i>Perna perna</i> **	PNUD (2014)

The mechanisms and main categories are based on Faulkner et al. (2020); \*, gastropod species; \*\*, bivalve species. More than one pathway sub-category was recognized for some species

#The identification of *Pomacea bridgesii* is suspect, probably mistaken for *Pomacea diffusa*; *P. diffusa* is widely distributed through much of the Amazon basin and is found around the world in the aquarium trade, while *P. bridgesii* is restricted to Bolivia and the western Amazon basin (Hayes et al. 2008, 2009; Cowie et al. 2017)

in Wagner, 1827). Souza et al. (2013) mentioned that, because of their high rates of reproduction, growth, and early sexual maturity, as well as for having been

previously used as food by settlers in Trinidad, Guyana, French Guiana, and northern Brazil, they were cultivated to evaluate the viability of their use as a

**Table 3** List of mollusc species transplanted in South America and their environmental impacts and positive (+) or negative (–) socioeconomic effects

	Impact on natural environment			Socioeconomic impact		
	Meaningful	Moderate	Null or unknown	Meaningful	Moderate	Null or unknown
Gastropoda						
<i>Bulimulus bonariensis</i> (Rafinisque, 1833)			x	A		
<i>Colosius confusus</i> Gomes et al., 2013			x	A		
# <i>Pomacea bridgesii</i> (Reeve, 1856)		D			AQ	
<i>Pomacea canaliculata</i> (Lamarck, 1822)	D–E				A–V	
<i>Pomacea diffusa</i> Blume, 1957			X		AQ	
<i>Pomacea maculata</i> Perry, 1810		D–E				x
<i>Sarasinula plebeia</i> (Fischer, 1868)			x		A–V	
Bivalvia						
<i>Anodontites trapesia</i> (Lamarck, 1819)			x		F	
<i>Argopecten purpuratus</i> (Lamarck, 1819)			x	P		
<i>Barnea truncata</i> (Say, 1822)		E				x
<i>Leiosolenus aristatus</i> (Dillwyn, 1817)		D				x
<i>Mytella strigata</i> (Hanley, 1843)		D		F		
<i>Mytilopsis</i> cf. <i>sallei</i> (Recluz, 1849)			x			x
<i>Mytilopsis trautwineana</i> (Tryon, 1866)			x		F	
<i>Mytilus platensis</i> d'Orbigny, 1842		D				x
<i>Perna perna</i> (Linnaeus, 1758)			x		P	
<i>Tawera elliptica</i> (Lamarck, 1818)			x		P	

A (–), losses in agriculture; AQ (+), aquarium trade; D (–), species displacement; E (–), environment modification; F (–), losses in aquaculture; P (+), profits from aquaculture; V (–), parasite vector. Details in Online Resource 4 and 5

#The identification of *Pomacea bridgesii* is suspect, probably mistaken for *Pomacea diffusa* (Hayes et al. 2008, 2009; Cowie et al. 2017)

possible new food source. However, concerning the identification and geographical range of both species we highlight that *P. bridgesii* is restricted to Bolivia and the western Amazon basin, whereas *Pomacea diffusa* Blume, 1957 is widely distributed through much of the Amazon basin and it is the one in the aquarium trade that is found around the world now (Cowie et al. 2017). Regarding *P. lineata*, it occurs primarily in the Atlantic drainages of Brazil—the Brazilian Atlantic Forest biogeographic province—and is replaced by its close relative *Pomacea dolioides* (Reeve, 1856) in northern South America (Surinam, French Guiana, Guyana, and Venezuela). Thus, the reference to *P. lineata* is probably a misidentification of *P. dolioides* (Thiengo et al. 2011; Cowie et al. 2017).

In short, the growing circulation of people, the increase in trade, and changes both to the environment and in production practices, give rise to new threats to production systems and to the natural

environment (FAO 2015). In general, non-native species can have negative impacts on recipient environments and so do transplanted species (third premise of Material and Methods). According to Simberloff et al. (2012), when non-native species invade, they can modify community structure and ecosystem function, becoming ecosystem engineers (Jones et al. 1994), increasing the risk of extinction for native species (Collado 2016; Collado et al. 2019), causing negative effects on human health, and becoming a serious socio-economic threat (Pejchar and Mooney 2009). For example, *Colosius confusus* Gomes et al. 2013 occurs in the Andean region, in regions for production of cut flowers and coffee in Colombia and Ecuador (Gomes et al. 2013). In northern Peru it was found attacking coffee in Canchaque. It is also found in two other Departments in Peru (Amazonas and Cajamarca), where it is sympatric with native species in urban areas. Although not causing

**Table 4** Mollusc species with alterations in their known historical distribution, but which are not considered transplantations

	Species	References	Cause of alterations
<i>GASTROPODA</i>			
Terrestrial	<i>Bulimulus apodemetes</i> (d'Orbigny, 1835)	Miquel (1991), Dos Santos et al. (2021)	1
	<i>Gastrocopta servilis</i> (Gould, 1852)	Doering (1874), Pilsbry (1916–1918), Parodiz (1957), Fernández (1973)	1
	<i>Orthalicus pulchellus</i> (Spix, 1827)	Cruz (1995), Simone (1999)	1
	<i>Aplysia juliana</i> Quoy & Gaimard, 1832	Soto (1985), Tomicic (1985), Castilla et al. (2005), Uribe et al. (2013)	2*
Marine	<i>Monoplex keenae</i> (Beu, 1970)	Beu and Cernohorsky (1986), Ashton et al. (2008), Araya (2015)	2*
	<i>Monoplex wiegmanni</i> (Anton, 1838)	Castilla et al. (2005), Ashton et al. (2008)	2*
<i>BIVALVIA</i>			
Marine	<i>Modiolus carvalhoi</i> Klappenbach, 1966	Zaffaroni (2000); Scarabino et al. (2006), Silveira et al. (2006), Borthagaray and Carranza (2007), Huber (2010)	2
	<i>Semimytilus patagonicus</i> (Hanley, 1843) [= <i>S. algosus</i> (Gould, 1850)]	Alamo and Valdivieso (1987, 1997), Coan and Valentich-Scott (2012), Bigatti et al. (2014), Signorelli and Pastorino (2021a, b)	3
Freshwater	<i>Diplodon chilensis</i> (Gray 1928)	Parada and Peredo (2005), Peredo et al. (2005), Valdovinos and Pedreros (2007), Fuentealba et al. (2010)	4

The causes of the alterations were classified as: 1, Nomenclatural and/or taxonomic issues; 2, natural dispersal, without direct human intervention; 3, species intercepted in trade traffic; 4, species mobilized by humans for repopulation in their known historical geographic distribution. Details of the distribution of these species in Online Resource 6

\*Dispersal due to El Niño Southern Oscillation

agricultural damage as in Colombia and Ecuador, and exhibiting a different external coloration in relation to the forms found attacking coffee, no genetic variation was found between them. *Colosius confusus* was first collected in Peru in 1970 and in Ecuador in 1985 (Gomes et al. 2013). In Ecuador, it is the second most commonly found Andean species of Veronicellidae after *Colosius pulcher* (Colosi, 1921). Also, even after Colosi (1921, 1922) examined many specimens from Ecuador, he did not describe *C. confusus*, which lends support to it being a recent transplant. The lack of variation observed in *C. confusus* specimens from Ecuador, Colombia, and Peru using mitochondrial DNA sequences is consistent with recent transplantation between countries. Gomes et al. (2013) indicated thus that the species is probably originally from Peru. In Ecuador, the production of cut flowers began in the late 1970s with exports in the early 1980s (Acción Ecológica 2000), indicating that the spread of *C. confusus* could be related to expanding commercial flower production.

The terrestrial snail *Bulimulus bonariensis* (Rafinesque, 1833) was originally described based on material from Buenos Aires but spread to

northeastern Argentina (Cuezzo et al. 2013), where it is reported as a pest of soybeans (Frana and Massoni 2011). It is also reported from Uruguay (Scarabino 2003) and Brazil, to both of which it was probably transplanted considering its pest status. The case of *Bulimulus* species is remarkable and a good example of how necessary it is to expand taxonomic work based not only on molecular studies but also on morphology. Maintaining taxonomic collections in public institutions is important for understanding historical distribution changes as well as the spread of certain species because of the changes produced by people. *Bulimulus apodemetes* (d'Orbigny, 1835) has an unusually wide distribution for a terrestrial gastropod and the marked intraspecific variability of its shells suggests a complex of species. The advance of agricultural frontiers in some areas of the Yungas (Bolivia, Peru and Argentina) and Dry Chaco (Bolivia, Paraguay and Argentina) ecoregions has produced the appearance of specimens similar to *B. apodemetes* in areas where they did not occur before. However, these abundant specimens in soybean crops and other grains have not yet been correctly identified. New studies are needed that

focus on this malacofauna associated with human environments.

The movement of species is among the most serious environmental threats of the new millennium, as the relocation of species beyond their native or historical geographical range has intensified in the last five decades; however, its general effects on the environment are not yet sufficiently understood (Anton et al. 2019). Since the impacts of TMS may be high, both for natural environments and for socioeconomic systems, we emphasize the need for further studies of transplantations in South America and elsewhere.

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**Code availability** Not applicable.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare.

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