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The Asian clam *Corbicula fluminea* in Ecuador: dispersion and diversity of occupied environments

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Abstract

The Asian clam *Corbicula fluminea* in Ecuador: dispersion and diversity of occupied environments

Populations of invasive species can have a negative impact on the natural environment and socioeconomic effects of artificial systems. The relationship of *Corbicula fluminea* with humans, together with the its great adaptive-reproductive capacity, make it one of the most expansive species of invasive bivalves worldwide. Here we report on the dispersion of *C. fluminea,* and based on genetic analysis we describe the presence and potentially negative effect of this species for the first time in an anthropic environment, an aquaculture facility in Ecuador.

Key words: Bivalve, Invasion, Effects, Impacts, Global distribution, Freshwater

Resumen

La almeja asiática *Corbicula fluminea* en Ecuador: dispersión y diversidad de ambientes ocupados

Las poblaciones de especies invasoras ocasionan impactos sobre el medio natural y efectos socioeconómicos sobre los sistemas artificiales. La relación que tiene la especie *Corbicula fluminea* con el ser humano, sumada a su gran capacidad adaptativa-reproductiva, la convierte en una de las más expansivas entre los bivalvos invasores del planeta. El presente estudio señala no solo la dispersión de *C. fluminea* sino también, a través del análisis genético, la presencia de esta especie por primera vez en un ambiente antrópico en Ecuador, una instalación de acuicultura, y el potencial efecto negativo sobre la misma.

Palabras clave: Bivalvos, Invasión, Efectos, Impactos, Distribución global, Agua dulce

Resum

La cloïssa asiàtica *Corbicula fluminea* a l'Equador: dispersió i diversitat d'ambients ocupats

Les poblacions d'espècies invasores generen impactes en el medi natural i efectes socioeconòmics en els sistemes artificials. La relació que estableix l'espècie *Corbicula lumina* amb l'ésser humà, a més de la gran capacitat adaptativa-reproductiva que té, la converteix en una de les més expansives entre els bivalves invasors del planeta. Aquest estudi no tan sols assenyala la dispersió de *C. fluminea* sinó també, mitjançant l'anàlisi genètica, la presència d'aquesta espècie per primera vegada en un ambient antròpic a l'Equador, una instal·lació d'aqüicultura, i el potencial efecte negatiu en aquesta.

Paraules clau: Bivalves, Invasió, Efectes, Impactes, Distribució global, Aigua dolça

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Introduction

A species is considered invasive when it is detected outside its natural geographic area of dispersal, when it is capable of maintaining a self-sustaining population in that new ecosystem, and when it disperses extensively, causing not only an environmental impact but also having a socioeconomic effect (Diagne et al 2022).

Humans have historically transported species from one place to another, leading to two major increases in the exchange and transportation of non-native species, the first at the end of the Middle Ages and the second with the Industrial Revolution (Collado et al 2020). This trend has increased considerably in recent decades and is currently ongoing at a great magnitude and with great diversity from one point to another on the planet. Two factors favor this third increase in the transportation of non-native species. The first of these is globalization, with worldwide trade causing the 'sending' and 'receiving' of 'non-native species' to other regions of the world. (Hulme et al 2008, Hulme 2009). The second main factor is climate change, which impacts and favors the settlement of non-native species in receiving areas. These two factors act synergistically to increase the potential establishment of non-native species (Hess et al 2024). This phenomenon can have great environmental impact and cause significant economic effects. In aquatic ecosystems, the number of invasive species has increased significantly in in recent decades due to the close relationship of non-native species and human activities (Clusa et al 2017).

The Asian freshwater clam, *Corbicula fluminea* (Müller 1774), is one of the most expansive species of invasive bivalves because its high adaptive-reproductive capacity (Darrigran 2002, Vidinova et al 2021) has allowed it to invade all continents (table 1) except Antarctica (Gama et al 2016), dominating, both lentic and lotic environments worldwide (Darrigran 1992, Lucy et al 2012, Vidinova et al 2021). Given its invasiveness, in South America, its association with human activities (Sousa et al 2008) such as aquaculture, recreational activities such as bait for sports fishing, and transportation for human food, and through various transport vectors (table 2), *C. fluminea* has become the most invasive freshwater bivalve species in the continent (Darrigran et al 2020), causing significant adverse environmental impact. For example, several species of the genus *Corbicula* can impact hydrology, biogeochemical cycling and biotic interactions through wide-ranging mechanisms in individuals and ecosystems (Bespalaya et al 2021), and it may have economic effects such as macrofouling in industrial cooling systems (Darrigran 2002).

The origin of the invasive populations of *C. fluminea* poses a significant challenge due to the low genetic variability of its populations (Gomes et al 2016). In South America, two main invasion lineages have been detected (Gomes et al 2016, Ludwig et al 2024), with the invasive lineage (haplotype) FW5 (morphotype form A/R) showing the greatest distribution in Europe and America. The latter is followed by FW17 (morphotype form C/S), with an intermediate lineage in three sites in Brazil and a population with individuals that presented a new COI haplotype in Brazil (FWBra). Form A has a more trigonal shell, a higher and inflated umbo, thicker and more widely spaced external marginal ribs than form B (present in North America), and a lighter-colored inner shell surface. The form C morphotype has the finest external surface sculpture and the thinnest and least inflated shell of all three New World morphotypes. It is further distinguished from the co-occurring form A morphotype by the latter's prominent umbo, posterior rostrum, and lighter coloration (Ituarte 1994, Lee et al 2005). The FWBra haplotype has shells with flatter umbo than the other morphotypes (Ludwig et al 2024).

In the present study, genetic analysis certified the presence of *C. fluminea* for the first time in an anthropic environment in Ecuador. Here we review the presence and dispersion of the species in South America.

Material and methods

The samples of *C. fluminea* were collected in November 2019 in the province of Manabí, Ecuador, in an aquaculture facility dedicated to the cultivation of the white shrimp *Penaeus vannamei* Boone, 1931 along with the Pacific fat sleeper fish, *Dormitator latifrons* (Richardson, 1844), located at the site La Isla, Pechichal commune, San Isidro parish, Sucre municipality (fig. 1, 0º 18' 05.6'' S 80º 11' 34.9'' W). The shrimp produce is sent to packing facilities that export to various places worldwide, while the Pacific fat sleeper is exported to Asia or meets local demands.

The specimens were identified morphologically following the methodology of in Sabapathy-Allen (2019), and total DNA was extracted from about 20 specimens using the 'E.Z.N.A. Mollusk DNA Kit' (Omega Bio-Tek). Partial COI gene PCR products were obtained using the barcoding primer set LCO1490/HCO2198 (Folmer et al 1994) and the modified primers jgLCO1490/jgHCO2198 (Geller et al 2013), purified with the ExoSAP- It kit (Affimetrix) and sequenced using BigDye. v3.1 X terminator kit on ABI 3500 equipment (Thermo Fisher Scientific).

The resulting sequences were trimmed to remove primers. All sequences correspond to the same haplotype, which was compared to GenBank reference sequences using the BLASTN algorithm (Altschul et al 1990) to identify similarities. One sequence, representing the same haplotype from 20 individuals, was deposited in GenBank under the accession number PP716899.

A phylogenetic analysis was carried out to infer the lineage and possible origin of the samples, using as a basis the sequences published by Lee et al (2005), Gomes et al (2016), and Ludwig et al (2024), both about this species and others of the genus *Corbicula*, and the new genus available in Genbank (as of 30/04/2024) (n = 227). We selected one sequence per haplotype per country (*Corbicula* spp., n = 75; table 1s in supplementary material) with a length of 560 bp

Table 1. Examples of global distribution of the mollusk *Corbicula fluminea*, one of the most invasive bivalve species of the 20th century.

Tabla 1*. Ejemplos de distribución global del molusco* Corbicula fluminea*, una de las especies de bivalvos más invasoras del siglo XX.*

Country	Reference
Native species	
Korea Southeastern Russia	McMahon (1982)
Southeastern China Australia Africa	Lucy et al (2012)
Non-native species	
Asia	
Japan	Yamada et al (2010). Since the early 1980s, *C. fluminea* has been repeatedly introduced into East Asia via Japan
North America	
Canada	The first specimens of *C. fluminea* found in North America were recorded as empty valves on Vancouver Island British Columbia, in 1924 (Counts 1981, McMahon 1982). The low temperature would be a limitation in its dispersions (Simard et al 2012)
United States (Washington 1938-Columbia River)	The first collection of *C. fluminea* in the United States occurred in 1938 in the Columbia River Washington (Counts 1981). Since this first introduction, it has been found in 38 states (Foster et al 2015), the equivalent of 96% of the United States (López-Altarribra et al 2019)
Mexico	According to López-Altarriba et al (2019) it was first recorded in Baja California and Sinaloa (northwestern states, coast of the Pacific Ocean), in 1970. It was later detected in the northeastern state, Gulf Coast of Mexico, from 1981 until 1984. In 1995, it was recorded in both western states and states in the north-central and eastern states
Europe	
France	First citation in La Dordogne (Mouthon 1981)
Belgium	First citation of the genus *Corbicula*, in 1992 (Swinnen et al 1998)
Germany	First citation (Haesloop 1992)
The Netherlands	Live *C. fluminea* were found for the first time in bottom samples taken on 30/09/1988 in the Lek River, near Lekkerkerk (Bij de Vaate and Greijdanus-Klaas 1990)
Portugal	First citation in the Tajo River estuary (Mouthon 1981)
Spain	River Miño in 1989 (Araujo et al 1993)
Luxembourg	In Luxembourg, Corbicula fluminea was first documented by Klaus Groh on 17/06/1996 in the Moselle River in the municipality of Remich (MNHNL 2000, Ries and Pfeiffenschneider 2023)
Austria	It was found in 1997, in a backwater of the Danube River near Bad Deutsch Altenburg (Lower Austria). It is the first discovery of this species in Austria (Fischer and Schultz 1999)
Italy	First citation in 1998 in some sections of the Po River and the River Brenta (Ciutti and Cappelletti 2009)
Czeck Republic	First citation in the Czech Republic in 1999 (Beran 2000). In total, eight specimens were found in four localities on the Elbe River in northern Bohemia
Hungary	It was detected in Hungary in June 1999. From the Danube as the possible reason for their colonization (Csányi 1999)
Switzerland	(Fabbri and Landi 1999)
United Kingdom	In 1997 (Aldridge and Muller 2001)
Romania	First citation, River Danube, in 1999 in the vicinity of Vadu Oii River (km 238) (Bij de Vaate and Hulea 2000).
Slovakia	In 2002, shells and one living adult of Corbicula fluminea were found on the three localities of Danube river and its surroundings, SW and S Slovakia (Vrabec et al 2003)

Table 1. (Cont.)

Country	Reference
Poland	In October 2003, the bivalve was recorded for the first time in Poland. Its first Polish site is the hot water channel of the Dolna Odra power plant in Western Pomerania (Domagata et al 2004)
Serbia	Two species recently introduced into Serbian waters, morphotypes of the Asian clam *Corbicula fluminea* (Müller, 1774) and *C. fluminali*s (Müller, 1774) (Paunović et al 2007)
Republic of Moldavia	First time in the Republic of Moldova (Prut River Basin, November 2009). Perhaps this invasive species entered the Prut River basin from Romanian or Ukrainian territories, where it was previously recorded (Manjiu and Shubernetski 2010)
Ireland	First detection (Sweeney 2010)
South America	
Argentina	Ituarte (1981), in the Río de la Plata (first event for South America). The southernmost event on the continent is in Argentine Patagonia (43º 18' 29.01"S 65º 03' 47.11"W) (Pérez et al 2022)
Brasil	Veitenheimer-Mendes (1981), first citation in Brazil. In 2001, Beasley et al (2003) estimated the arrival of *C. fluminea* between 1997 and 1998 in the lower Brazilian Amazon basin, where individuals were found in parts of the Amazon and Tocantins rivers
Uruguay	Veitenheimer-Mendes and Olazarri (1983)
Colombia	In 1992, on Salamanca Island constitutes the first record of the species and genus in Colombia (De La Hoz Aristizábal 2008)
Ecuador	In 1999 on Pastaza River, Consuelo (Lee et al 2005) In 2000 (Crespo et al 2015) It was concluded that the Guayas estuary most likely corresponds to the introduction of *C. fluminea* in Ecuador. It also exists in the provinces of Manabí and Esmeralda (Lodeiros and Torres 2018). Its occurrence in the upper Amazon basin is attributed to a human-mediated introduction linked to the commercial use of the clam (Conde and Solís-Coello 2017)
Venezuela	Martínez (1987)
Peru	In 2017, first citation in River Mala (Lima) (Torres-Zevallos 2018)
Bolivia	Rico (2009)

was selected. Phylogenetic analyses were performed following sequence alignment with Clustal. The total length of the analyzed matrix was 560 bp. The data were subjected to phylogenetic analysis using the maximum likelihood (ML) method. ML inference was performed using the PhyML program (Guindon and Gascuel 2003), available on the public web server Phylemon2 (http://phylemon.bioinfo.cipf.es). Statistical support for the resulting phylogenies was assessed by bootstrapping with 1,000 replicates (Felsenstein 1985). All trees were edited with FigTree software.

Results

The present findings represent the first report of *C. fluminea* for the province of Manabí, reaffirming its distribution and establishment in the river basins (table 3). We also report the first case in Ecuador of the presence of *C. fluminea* in an artificial culture system of the Pacific white shrimp *Penaeus vannamei* (Boone, 1931) and the Pacific fat sleeper fish *Dormitator latifrons* (Richardson, 1844).

Among the sequences of *C. fluminea* available in Genbank, the Blast carried out revealed 100 % similarity of the sequence obtained in Ecuador with other representatives, mainly from Europe (fig. 2; table 2s in supplementary material), Asia, and America (Argentina, Brazil, Peru, Ecuador, Mexico, Panama, Cuba and USA). In this study, four haplotypes were identified for the genus *Corbicula* in South America. The sequence obtained for Ecuador corresponds to the invasive lineage FW5 (form A/R).

Table 2. Potential vectors capable of dispersing *Corbicula fluminea* in South America.

Tabla 2*. Vectores potenciales capaces de dispersar la especie* Corbicula fluminea *en América del Sur.*

Route	Origin sites	Probability
Natural dispersal	Various	The use of mucous filaments of the ctenidium, considered the main natural dispersal factor in aquatic ecosystems (Minchin and Boelens 2018) Transport by fish (Belz et al 2012) Derived through entanglement with plants and others (Prezant and Chalermwat 1984)
Sport fishing, commercial fishing and fish storage	Fishing in invaded areas	In the bags to store fishing nets and equipment (Minchin 2014) Used as fishing bait (Cao et al 2017, Carranza et al 2023)
Sand transportation for artificial Beaches	Littoral of invaded river	According to Belz et al (2012), although only 6.3% of the sand beaches transported by trucks is used for the development and maintenance of artificial beaches, the density of *C. fluminea* in said transport is 50/m^3
Introduction for local consumption	Various	Asian clams are consumed by the Asian community (Darrigran 2002)
Release of fauna from aquaria	Various, close to human habitats	Not proven, but likely the case (Minchin 2014)

Discussion

Corbicula fluminea is extensively distributed in South America (Darrigran et al 2020) and is found in several countries. In Ecuador, the species has been reported from the provinces of Esmeraldas, Santo Domingo de los Tsachilas, Los Ríos, and Guayas, with this record being the first report for the province of Manabí, and reaffirming its distribution and establishment in the river basins of Ecuador (table 3). Furthermore, it represents the first case of *C. fluminea* in an artificial culture system for the Pacific white shrimp, *P. vannamei*, and the Pacific fat sleeper *D. latifrons*.

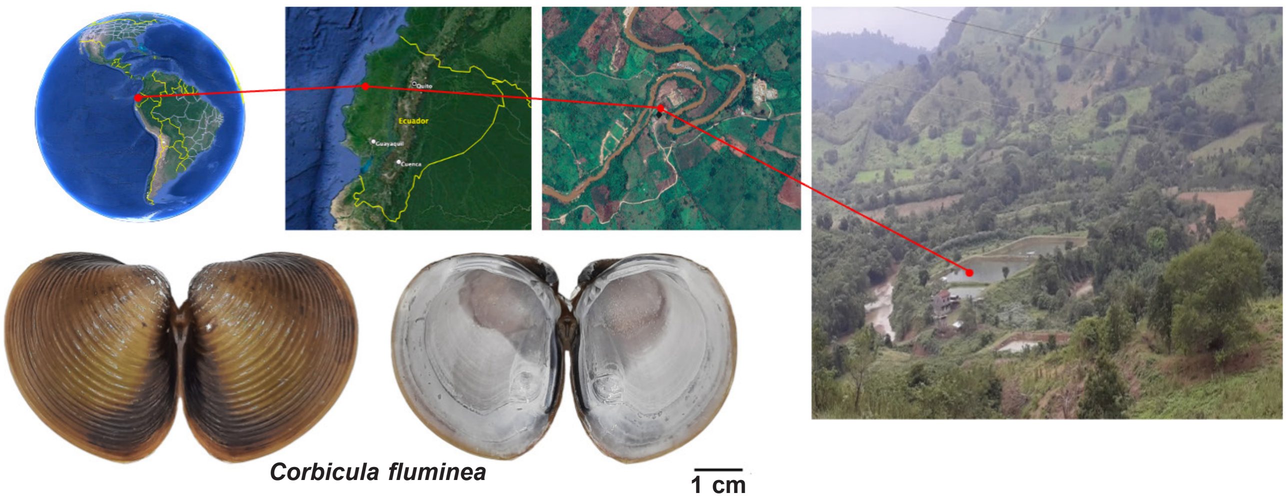

Fig. 1. Extraction site of the invasive species *Corbicula fluminea*. Aquaculture system dedicated to the cultivation of white shrimp *Penaeus vannamei* and Pacific fat sleeper fish *Dormitator latifrons*, in La Isla, Pechichal commune, San Isidro parish, Sucre municipality, Manabí province, Ecuador.

Fig. 1*. Lugar de extracción de la especie invasora* Corbicula fluminea*. Sistema acuícola dedicado al cultivo del camarón patiblanco* Penaeus vannamei*, y del chalaco* Dormitator latifrons *en La Isla, comunidad de Pechichal, parroquia de San Isidro, municipio de Sucre, provincia de Manabí, Ecuador.*

Table 3. Sites where *Corbicula fluminea* has been reported in Ecuador.

***Tabla 3**. Lugares donde se han registrado ejemplares de* Corbicula fluminea *en Ecuador.*

Location, province	Coordinates	Year	References
Pastaza River, Pastaza	2º21'33"S, 77º05'03"W	1999	Willink et al (2005)
Pastaza River, Pastaza	1º55'09"S, 77º48'52"W	1999	Lee et al (2005)
Pastaza River, Pastaza	2º14'09"S, 77º15'10"W	1999	Lee et al (2005)
Esmeraldas River, Esmeraldas	0º55'01"S, 79º39'17"W	2001	INP (2002)
Taura River, Guayas	2º18'00"S, 79º43'60"W	2005	Mora (2005)
Taura River, Guayas	2º15'26"S, 79º22'12"W	2005	Mora (2005)
Baba River, Santo Domingo	0º29'37"S, 79º19'21"W	2010-2011	Cárdenas (2011)
Baba River, Santo Domingo	1º01'02"S, 79º27'49"W	2010-2011	Cárdenas (2011)
El Cristal stream, Los Ríos	1º20'43"S, 79º22'33"W	< 2011	Muzzio (2011)
Montalvo stream, Los Ríos	1º47'43"S, 79º18'05"W	< 2011	Muzzio (2011)
Isla Bejucal River, Los Ríos	1º40'26"S, 79º38'54"W	< 2011	Muzzio (2011)
La Villegas stream, Santo Domingo	0º04'14"S, 79º26'32"W	< 2011	Muzzio (2011)
Río Bua, Santo Domingo	0º04'18"S, 79º30'35"W	< 2011	Muzzio (2011)
Mocoli Island, Babahoyo River, Guayas	2º06'10"S, 79º51'41"W	2017	Conde and Solis-Coello (2017)
Pechichal Island, Manabí	0º18'05"S, 80º11'35"W	2019	This study

The tree shows a topology similar to that of Lee et al (2005), Gomes et al (2016), and Ludwig et al (2024), with several clades with low support or unresolved, identifying four haplotypes for the genus in South America, three published by Lee et al (2005) and the new haplotype mentioned by Ludwig et al (2024) (FWBra, for Brazil).

The sequence obtained for Ecuador corresponds to the invasive lineage FW5 (form A/R), the most widely distributed lineage in America (Lee et al 2005, Gomes et al 2016, Ludwig et al 2024). It corresponds to the morphotype A/ R; and it has also been detected in Colombia (Ludwig et al 2024). The FW17 lineage (form C/S) has been detected outside the native distribution area, although it has not yet been reported from East Asia. In South America, it is found in Brazil, Colombia, and Argentina (Ludwig et al 2024).

The species *C. fluminea* presents several characteristics that indicate a high capacity to colonize different limnological environments, explaining its global distribution. Its life cycle favors the ability to invade other systems due to high growth rates, early maturation (Sousa et al 2008), and capacity for androgenesis and self- fertilization (Pigneur et al 2012), thus causing low genetic variability in their populations. The global phylogenetic analysis performed by Pigneur et al (2011) reveals that sexual lineages of *Corbicula* seem restricted to native areas, while androgenic reproduction is found both in native areas (Pigneur et al 2012) and in all invaded areas (Gomes et al 2016). Androgenic reproduction could have played an important role in the invasive success of *Corbicula* clams as androgenetic clams are generally hermaphroditic and capable of self-fertilization (Pigneur et al 2012).

In summary, androgenesis is the predominant reproductive mode within the hermaphrodite and invasive lineages of the genus *Corbicula*, with its ability to reproduce by cloning being a determining factor in its invasive success, having colonized American and European freshwater systems during the 20th century. However, in clams of *Corbicula* spp. androgenetic genetic mixing between different lineages has also occasionally been observed when the sperm of one lineage fertilizes the oocyte of another. Because of these occasional introgressions, the genetic relationships between *Corbicula* species remain unclear, and the biogeographic origins of invasive androgenetic lineages are difficult to identify. Despite this genetic mixture between invasive *Corbicula* lineages, genetic analyses place one of the invasive forms of *Corbicula* from South America as African (Vastrade et al 2022). However, as previously mentioned, a new COI haplotype (FWBra) was detected in a population from Brazil.

This report is the first to describe the presence of *C. fluminea* in an aquaculture production system with Pacific white shrimp in polyculture with the Pacific fat sleeper fish. Despite *P. vannamei* being a species of marine-estuarine origin, its adaptability to very low salinities allows adequate growth, and profitability can be greater when grown with *D. latifrons*. These production systems have low salinity (2-5‰, JJ Bernal-Zambrano), which allows the existence and proliferation of *C. fluminea*. Despite being a freshwater species, *C. fluminea* can tolerate salinities of up to 10-14‰ (McMahon 2000), allowing it to colonize upstream areas of estuaries (Franco et al 2012, Ilarri et al 2014) where a high number of shrimp

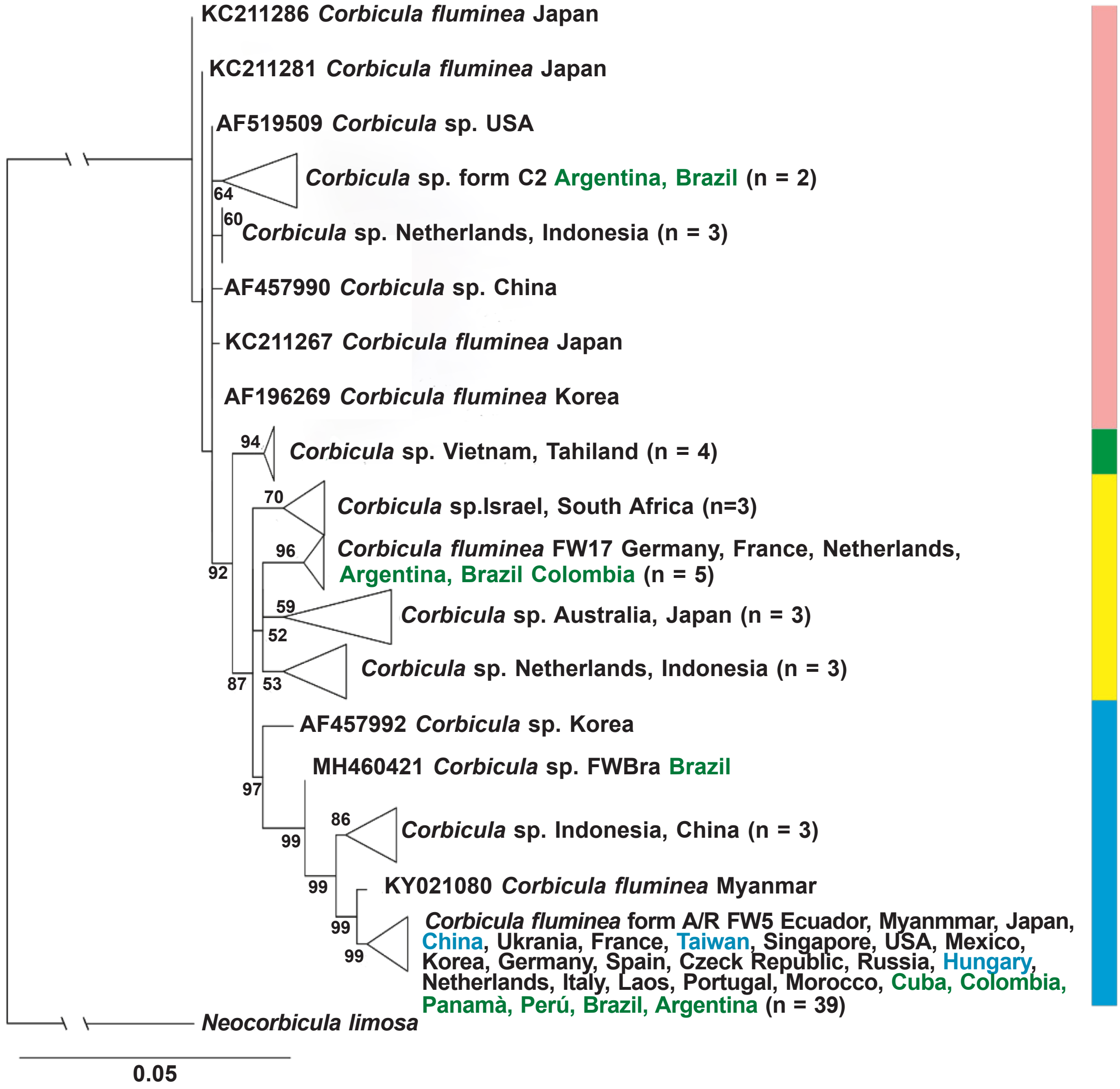

Fig. 2. *Corbicula* spp. phylogenetic tree, based on the COI gene. The sequence from this study was aligned with other sequences from NCBI. Collapsed nodes are indicated by triangles. Values on the tree refer to bootstrap support. The number of sequences per node is shown in parentheses. Nodes with bootstrap values below 50 % were not included. Sequences from Ecuador are shown in red. Other sequences from South and Central America are in green. The text in light blue: sequences from these countries differ in one or two bases of the FW5 haplotype. Color boxes (groups according to Gomes et al (2016): pink: group 1; green: group 2; yellow: group 3; light blue: group 4). In group 3, only one sequence was used for South America (Argentina, Brazil and Colombia) since it is the same haplotype.

***Fig. 2**. Árbol filogenético de la* Corbicula *spp., basado en el gen COI. La secuencia de este estudio se ajustó a otras del National Center for Biotechnology Information (NCBI). Los nodos colapsados se indican con triángulos. Los valores en el árbol se refieren al soporte Bootstrap. Entre paréntesis, se indica el número de secuencias por nodo. Los nodos con valores Bootstrap inferiores al 50 % no se incluyeron. En rojo, se indican las secuencias de Ecuador. En verde, se indican otras secuencias de América del Sur y Central. En azul claro, se indican las secuencias de estos países que difieren en una o dos bases del haplotipo FW5. Los recuadros de color (grupos según Gomes et al (2016): rosa, grupo 1; verde: grupo 2; amarillo: grupo 3; azul claro: grupo 4). En el grupo 3, solo se utilizó una secuencia para América del Sur (Argentina, Brasil y Colombia), ya que se trata del mismo haplotipo.*

farms are established in Ecuador. Although there is no apparent adverse effect on performance with the presence of *C. fluminea*, this species is one of those that have a higher filtration rate than other freshwater filter-feeding mollusks (McMahon 1991). Therefore some of the first impacts that it could cause on production systems would be the decrease in phytoplankton load, and the imbalance in alkalinity, calcium and other essential minerals in the crop, affecting the balance of the system. Furthermore, the consequent water clearing that occurs due to the filtration produced by *C. fluminea* may increase predation by birds (Aldridge et al 2008, Lodeiros and Torres 2018, Lodeiros et al 2019).

Given the potential threat of the invasive species *C. fluminea*, it is crucial to monitor aquaculture systems to prevent its establishment. In systems already invaded by this species, it is equally important to establish the possible effect on said systems and surrounding ecosystems.

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Conflicts of interest

No conflicts declared.

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Supplementary material

Table 1s. *Corbicula* sp. COI gene sequences used in the present work, with Genbank access code and country of origin.

***Tabla 1s**. Secuencias del gen COI de* Corbicula *sp. utilizadas en el presente trabajo, con código de acceso Genbank y país de origen.*

Genbank	Country	Genbank	Country
AF519512	Argentina	KC211289	Japan
AF519507	Argentina	OM912100	Japan
AF519508	Argentina	OM912080	Japan
AF196274	Australia	LC763688	Japan
DQ264393	Brazil	AF196269	Korea
MH460421	Brazil	AF457992	Korea
AF457990	China	ON093199	Laos
KC211251	China	AF519502	Mexico
KT893369	China	AF519501	Mexico
AF519499	Cuba	AF519500	Mexico
MK439902	Czeck Republic	KT006544	Morocco
PP716899	Ecuador	ON908402	Myanmar
AF519505	Ecuador	KY021080	Myanmar
AF519504	Ecuador	AF269096	Netherlands
GU721084	France	GU721082	Netherlands
AF269090	France	GU721083	Netherlands
MF458661	France	AF519503	Panama
AF269094	France	AF519506	Peru
AF269095	France	KJ909515	Portugal
AY097284	Germany	KX192336	Russia
AY097262	Germany	KU318325	Singapore
AY097282	Germany	KC211264-66	South Africa
GQ401362	Hungary	MZ425220	South Korea
GQ401361	Hungary	MF401395	Spain
DQ285579	Indonesia	AF457991	Taiwan
AF457993	Indonesia	OM912053	Taiwan
MN746822	Indonesia	AF196270	Thailand
DQ285594	Indonesia	DQ285578	Thailand
DQ285581	Indonesia	OL441147	Ukrania
DQ285605	Indonesia	AF519509	USA
AY097295	Israel	KU905760	USA
KX231272	Italy	KU906036	USA
KC211267	Japan	AF519495	USA
KC211281	Japan	KC211261-62	Vietnam
KC211286	Japan	AF468018	Vietnam
AF196273	Japan	AF196277	Argentina, *Neocorbicula limosa*
KC211288	Japan		

Table 2s. Pairwise genetic divergence (Kimura two-parameter, %) among individuals of *Corbicula* sp. assessed employing COI gene sequences.

***Tabla 2s**. Divergencia genética por pares (Kimura de dos parámetros, %) entre individuos de* Corbicula *sp. evaluada empleando secuencias del gen COI.*

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	KC211267 Japan																																			
2	**DQ264393 Brazil form C2**	1.52																																		
3	KC211281 Japan	0.43	1.52																																	
4	KC211286 Japan	0.65	1.75	0.21																																
5	GU721084 France	0.43	1.52	0.43	0.65																															
6	KC211261-62 Vietnam	1.09	2.20	1.09	1.30	1.09																														
7	KC211264-66 South Africa	1.99	3.13	1.99	2.21	2.00	1.31																													
8	AF269096 Netherlands	0.43	1.52	0.43	0.65	0.00	1.09	2.00																												
9	DQ285579 Indonesia	0.43	1.52	0.43	0.65	0.00	1.09	2.00	0.00																											
10	**AF519512 Argentina form C2**	0.43	1.08	0.43	0.65	0.43	1.09	2.00	0.43	0.43																										
11	AF519509 USA	0.21	1.30	0.21	0.43	0.21	0.87	1.77	0.21	0.21	0.21																									
12	AF196269 Korea	0.21	1.30	0.21	0.43	0.21	0.87	1.77	0.21	0.21	0.21	0.00																								
13	AF457990 China	0.43	1.52	0.43	0.65	0.43	1.09	2.00	0.43	0.43	0.43	0.21	0.21																							
14	AF196270 Thailand	1.31	2.43	1.31	1.53	1.31	0.21	1.54	1.31	1.31	1.31	1.09	1.09	1.31																						
15	AF468018 Vietnam	1.09	2.20	1.09	1.30	1.09	0.00	1.31	1.09	1.09	1.09	0.87	0.87	1.09	0.21																					
16	DQ285578 Thailand	2.69	3.85	2.69	2.91	2.70	2.00	2.00	2.70	2.70	2.70	2.46	2.46	2.70	2.23	2.00																				
17	AF196273 Japan	2.44	3.60	2.44	2.67	2.45	2.22	2.69	2.45	2.45	2.45	2.22	2.22	2.45	2.45	2.22	2.45																			
18	AF196274 Australia	3.15	4.33	3.15	3.38	3.16	2.45	2.45	3.16	3.16	3.16	2.92	2.92	3.16	2.69	2.45	2.69	3.39																		
19	KC211251 China	2.91	4.08	2.91	3.14	2.92	3.16	2.92	2.92	2.92	2.92	2.69	2.69	2.92	3.40	3.16	3.40	4.12	4.12																	
20	KC211289 Japan	4.10	5.30	3.88	4.11	4.11	3.86	3.62	4.11	4.11	4.11	3.86	3.86	4.11	4.11	3.86	4.11	4.84	5.10	1.98																
21	**MH460421 Brazil FWBra**	1.98	3.12	1.98	2.20	1.99	1.76	1.53	1.99	1.99	1.99	1.76	1.76	1.99	1.99	1.76	1.99	3.15	2.91	1.31	1.98															
22	**FW 5**	3.15	4.33	3.15	3.38	3.16	2.92	2.69	3.16	3.16	3.16	2.92	2.92	3.16	3.16	2.92	3.16	3.88	4.12	1.09	0.86	1.09														
23	AF457991 Taiwan	3.39	4.58	3.39	3.62	3.40	3.16	2.92	3.40	3.40	3.40	3.16	3.16	3.40	3.40	3.16	3.40	4.12	4.37	1.31	1.08	1.31	0.21													
24	OM912053 Taiwan	3.39	4.58	3.39	3.62	3.40	3.16	2.92	3.40	3.40	3.40	3.16	3.16	3.40	3.40	3.16	3.40	4.12	4.37	1.31	1.08	1.31	0.21	0.00												
25	GQ401361 Hungary	3.39	4.58	3.39	3.62	3.40	3.16	2.92	3.40	3.40	3.40	3.16	3.16	3.40	3.40	3.16	3.40	4.12	4.37	1.31	1.08	1.31	0.21	0.43	0.43											
26	KT893369 China	3.39	4.58	3.39	3.62	3.40	3.16	2.92	3.40	3.40	3.40	3.16	3.16	3.40	3.40	3.16	3.40	4.12	4.37	1.31	1.08	1.31	0.21	0.43	0.43	0.43										
27	KY021080 Myanmar	3.15	4.33	3.15	3.38	3.16	2.92	2.69	3.16	3.16	3.16	2.92	2.92	3.16	3.16	2.92	2.69	3.88	4.12	1.09	1.30	1.09	0.43	0.65	0.65	0.65	0.65									
28	AF457993 Indonesia	3.39	4.58	3.39	3.62	3.40	3.16	2.92	3.40	3.40	3.40	3.16	3.16	3.40	3.40	3.16	3.40	4.62	4.12	0.87	1.98	1.31	1.09	1.31	1.31	1.31	1.31	1.09								
29	MN746822 Indonesia	3.14	4.32	3.14	3.37	3.15	2.91	2.68	3.15	3.15	3.15	2.91	2.91	3.15	3.15	2.91	3.15	4.36	3.86	0.65	1.75	1.09	0.86	1.09	1.09	1.09	1.09	0.86	0.65							
30	AF457992 Korea	1.99	3.13	1.99	2.21	2.00	1.77	1.77	2.00	2.00	2.00	1.77	1.77	2.00	2.00	1.77	2.00	2.69	2.92	2.22	2.44	1.31	1.53	1.76	1.76	1.76	1.76	1.09	2.22	1.98						
31	**FW 17**	1.99	3.13	1.99	2.21	2.00	1.77	1.31	2.00	2.00	2.00	1.77	1.77	2.00	2.00	1.77	2.00	2.69	2.45	2.45	3.14	1.09	2.22	2.45	2.45	2.45	2.45	2.22	2.45	2.21	1.77					
32	AY097295 Israel	1.09	2.20	1.09	1.30	1.09	1.31	0.87	1.09	1.09	1.09	0.87	0.87	1.09	1.54	1.31	2.46	3.16	2.92	2.92	3.62	1.53	2.69	2.92	2.92	2.92	2.92	2.69	2.92	2.68	1.77	1.31				
33	DQ285594 Indonesia	2.69	4.10	2.92	3.15	2.93	2.23	2.70	2.93	2.93	2.93	2.70	2.70	2.93	2.46	2.23	2.46	3.16	3.89	3.65	3.86	2.69	2.92	3.16	3.16	3.16	3.16	2.92	3.65	3.39	2.23	2.23	2.70			
34	DQ285581 Indonesia	3.16	4.34	3.16	3.39	3.17	2.93	2.93	3.17	3.17	3.17	2.93	2.93	3.17	3.17	2.93	1.77	2.92	4.14	3.40	3.62	2.45	2.69	2.92	2.92	2.92	2.92	2.22	3.40	3.15	2.00	2.46	2.93	1.54		
35	DQ285605 Indonesia	2.69	3.85	2.69	2.91	2.70	2.93	2.93	2.70	2.70	2.70	2.46	2.46	2.70	3.17	2.93	3.17	2.92	4.14	3.89	4.11	2.92	3.16	3.40	3.40	3.40	3.40	3.16	3.89	3.63	2.46	2.46	2.46	2.46	2.70	
36	AF196277 *Neocorbicula limosa*	24.01	24.44	23.68	23.32	23.27	23.65	24.04	23.27	23.27	24.04	23.65	23.65	23.65	24.04	23.65	26.06	25.20	25.69	23.68	24.47	24.47	24.47	24.87	24.87	24.87	24.87	24.47	24.47	24.04	24.83	25.24	23.65	25.65	25.24	25.24