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Geography and ecology of invasive *Pseudosuccinea columella* (Gastropoda: Lymnaeidae) and implications in the transmission of *Fasciola* species (Digenea: Fasciolidae) – a review

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Abstract

Pseudosuccinea columella is considered invasive and has become an important intermediate host of both *Fasciola* species in many regions of the world. This systematic review assessed the geographical distribution of *P. columella*, and its implications in the transmission of *Fasciola hepatica* and *Fasciola gigantica*, globally. A literature search was conducted on Google Scholar, JSTOR and PubMed databases using Boolean operators in combination with predetermined search terms for thematic analysis. Results show that *P. columella* has been documented in 22 countries from Europe (3), Africa (8), Oceania (2), North America (3) and South America (6). Furthermore, this snail species has shown to adapt to and inhabit a vast array of freshwater bodies including thermal lakes and ditches with acidic soils. Studies showed that *P. columella* transmits *F. hepatica*, with natural and experimental infections documented in sub-Saharan Africa, Europe, South America and North America. Experimental infection studies in Cuba showed the presence of *P. columella* populations resistant to *F. hepatica* infection. Furthermore, some populations of this invasive snail collected from *F. hepatica* endemic locations in Brazil, Venezuela, Australia, South Africa, Colombia and Argentina were found without *Fasciola* infection. As a result, the role played by this snail in the transmission of *Fasciola* spp. in these endemic areas is still uncertain. Therefore, further studies to detect natural infections are needed in regions/countries where the snail is deemed invasive to better understand the veterinary and public health importance of this snail species in *Fasciola*-endemic areas and determine the global dispersion of resistant populations of *P. columella*.

Background

Fasciolosis is a parasitic zoonotic disease caused by digenetic liver flukes *Fasciola hepatica* (Linnaeus, 1758) and *Fasciola gigantica* (Cobbold, 1856) (Valero *et al.*, 2001; Mas-Coma, 2004; Bargues *et al.*, 2007; Dung *et al.*, 2013; Sabourin *et al.*, 2018; Alemu, 2019). The disease affects a wide range of domesticated and wild ruminants (Correa *et al.*, 2010; Beesley *et al.*, 2018; Sabourin *et al.*, 2018; Alemu, 2019) and occasionally humans as accidental hosts (Magalhães *et al.*, 2004; Correa *et al.*, 2010; Beesley *et al.*, 2018; Alemu, 2019). This parasitic infection has been well recognized and documented for its veterinary importance throughout the world (Mas-Coma, 2004; Bargues *et al.*, 2007). The occurrences of human infections have been reported to be on the rise recently, documented in five continents except Antarctica (Mas-Coma, 2004; Alemu, 2019).

Previous research indicated that the epidemiology of fasciolosis is highly linked to the ecological characteristics of the snail vector involved in the transmission (Mas-Coma, 2004; Bargues *et al.*, 2011), and the susceptibility of these snail intermediate hosts (IHs) to these *Fasciola* species may differ (Alemu, 2009) depending on variations in the immunological responses of the IHs (Beesley *et al.*, 2018). Due to the wide range and distribution of IHs, *F. hepatica* has been documented as the most common and widely distributed liver fluke, particularly in temperate zones of Australia, Europe and the Americas (Dung *et al.*, 2013; Admassu *et al.*, 2015; Sabourin *et al.*, 2018; Alemu, 2019). The transmission of this *Fasciola* species is globally linked to Lymnaeidae species, including *Lymnaea tomentosa* (Pfeiffer, 1855), *Lymnaea bulimoides* (Pilsbry & Ferriss, 1906), *Lymnaea viator* (d'Orbigny, 1835), *Pseudosuccinea columella* (Say, 1817), *Lymnaea humilis* (Say, 1822), *Lymnaea diaphena* (Evans & Shumard, 1856) (Vorster & Mapham, 2008; Alemu, 2019; Leka, 2019), *Lymnaea cubensis* (Pfeiffer, 1839) (Bargues *et al.*, 2007; Pointier *et al.*, 2009) and *Lymnaea neotropica* (Bargues, Artigas, Mera y

Sierra, Pointier and Mas-Coma, 2007) (Bargues *et al*., 2007; Sanabria *et al*., 2012; Bargues *et al*., 2017). However, the main snail IH of *F. hepatica* in most regions of the world, particularly in Africa, South America, Europe and in some parts of Asia (Alemu, 2019), is *Galba truncatula* (Müller, 1774) (Caron *et al*., 2008; Alemu, 2019).

Fasciola gigantica is limited to the tropical and/or subtropical regions of Africa, Asia and the Far East (Correa *et al*., 2010; Mochankana & Robertson., 2018; Alemu, 2019). According to Mas-Coma (2005), limitations in the geographical distribution of this species is due to the slow spread of species from the genus *Radix* that have been implicated in the transmission of *F. gigantica*. These are species belonging to the *Radix auricularia* (Linnaeus, 1758) superspecies complex by Hubendick (1951), which comprises *Radix rubiginosa* (Minchelin, 1831) in Asia and *Radix natalensis* (Krauss, 1848) in Africa (Brown, 1994). Alemu (2019) named five *Lymnaea* (*Radix*) species involved in the transmission of *F. gigantica*, however, the author also reported *R. auricularia* and *R. natalensis* as the most important IHs of this *Fasciola* species.

The occurrence of overlapping distribution of both *Fasciola* spp. has been reported in some tropical regions of Asian and African countries (Mas-Coma *et al*., 2005; Dung *et al*., 2013; Malatji & Mukaratirwa, 2019) where co-infections in the definitive hosts have been documented (Chen *et al*., 2013; Sabourin *et al*., 2018). According to Mas-Coma *et al*. (2009), these overlaps occur in areas with climatic conditions that favour the existence of the intermediate hosts of both *F. hepatica* and *F. gigantica*. The overlap may also be caused by the presence of *P. columella*, the invasive snail originating from Central America, the Caribbean and the southern parts of North America (Mas-Coma *et al*., 2005). This species succeeded in being one of the most widely distributed freshwater snails in some countries (Prepelitchi *et al*., 2011), where it plays an important role in the transmission of fasciolosis (Zarco *et al*., 2011). According to Mas-Coma (2005), this invasive snail contributes to the secondary transmission of *F. hepatica* and has been shown to transmit *F. gigantica* in South Africa (Malatji & Mukaratirwa, 2019) and Egypt (Grabner *et al*., 2014). In countries such as South Africa, *P. columella* is presumed to transmit both *Fasciola* species, due to the observed increased prevalence in infection rate of both trematodes, which coincided with the introduction of *P. columella* in the country (Malatji & Mukaratirwa, 2019). Therefore, this article reviewed the geographical distribution of *P. columella* and its implications in the transmission of *F. hepatica* and *F. gigantica* worldwide. The knowledge on the global distribution and role played by *P. columella* in the epidemiology and transmission of *Fasciola* spp. is crucial in predicting the potential veterinary and public health risk and burden of fasciolosis.

Methodology

Searching strategy

A systematic search of literature was conducted on the electronic databases Google Scholar, JSTOR and PubMed. A literature search was limited to peer-reviewed articles, written in English, and conducted and published between 1990 and 2020 (30 years). The search was performed using the following search terms and Boolean operators (OR, AND): *Pseudosuccinea columella* AND *Fasciola* spp., *Fasciola hepatica* OR *Fasciola gigantica* AND *P. columella*, *P. columella* AND *Fasciola* infection. Additional articles were identified by screening through the reference lists of selected articles (snowballing). Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines were followed during the conduction and reporting of the systematic review.

Inclusion and exclusion criteria

Articles were included if they were published in peer-reviewed journals and explicitly reported on (1) the distribution and ecological preferences of *P. columella*, and (2) infections (natural and/or experimental) of *P. columella* with either *F. hepatica* or *F. gigantica* or both, globally.

The review excluded studies reporting on infections of *Fasciola* spp. in gastropods other than *P. columella*, those focusing on the distribution of *Fasciola* spp. with no link to *P. columella* and studies that did not identify *P. columella* up to species level.

Results

A literature search from the three databases yielded a total of 827 studies (fig. 1). An additional 26 articles were obtained through bibliographic searches from relevant articles. Thirty articles were removed because they were duplicated. A total of 719 were excluded after screening their titles and abstracts. The full texts of 89 articles were downloaded and screened for eligibility, and 33 studies were deemed ineligible since they did not explicitly report on the distribution of *P. columella* and the role it plays in the transmission of *F. hepatica* and *F. gigantica* globally, but reported on *Fasciola* species infections exclusively on definitive hosts and other Lymnaeidae snail species. A total of 56 studied were retained and used in this systematic review.

The distribution of studies which fulfilled the inclusion criteria on a geographical scale and scope varied across continents. Of the 56 articles reviewed, 19 were from the African continent (table 1), 17 from South America (table 2), 11 from North America and the Caribbeans (table 3), eight from Europe (table 4) and Oceania had one article documented in Australia by Molloy & Anderson (2006). Thirty-nine of these articles were field studies and 17 were experimental studies. Africa had the highest number of field-based studies, followed by South America, with 16 and 14 articles, respectively. Twenty-three studies assessed *Fasciola* infections in *P. columella*, while 33 articles reported solely on the distribution of *P. columella*.

Global distribution and abundance of P. columella

Pseudosuccinea columella was documented in 22 countries from Africa (table 1), South America (table 2), North America and the Caribbeans (table 3), Europe (table 4) and Oceania. However, the species was widely reported in African ($n = 18$) and South American ($n = 16$) countries. In the African continent, *P. columella* was documented in South Africa, Egypt, Madagascar, Cameroon, La Reunion, Zimbabwe, Namibia and Mayotte. However, the results also showed that this snail species was mostly reported and distributed in South Africa and Egypt. In South America, *P. columella* has been reported in Argentina, Uruguay, Brazil, Venezuela, Paraguay, Peru and Colombia. In this region, however, *P. columella* was shown to have a wide distribution in Argentina ($n = 8$), followed by Brazil ($n = 5$). In North America and the Caribbeans, *P. columella* has been documented in the USA, including Kansas and Hawaii states, Cuba and Guadeloupe. In Europe, *P. columella* has been recorded in

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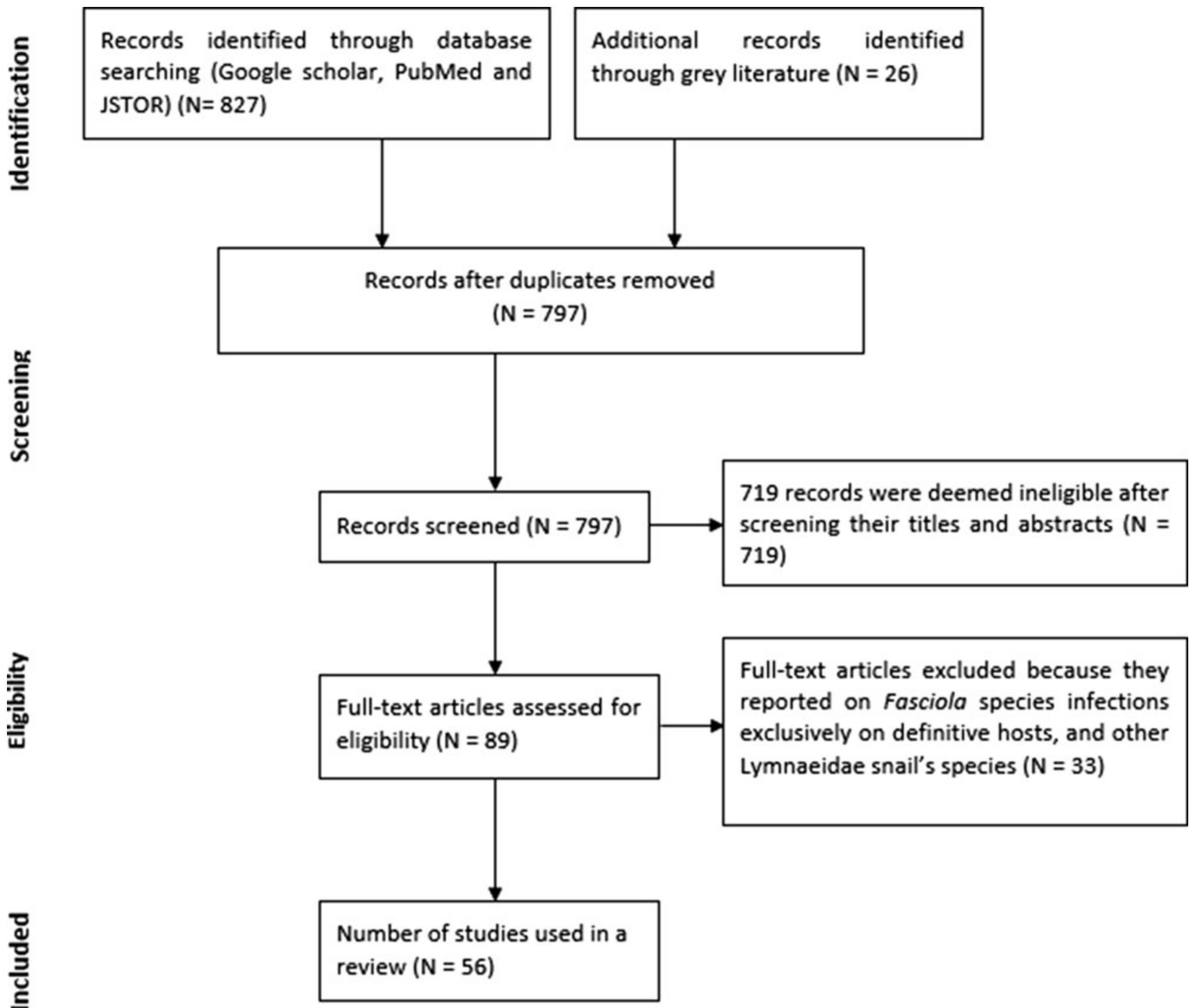

Fig. 1. PRISMA diagram.

France, Romania and Italy. Of all the continents, this freshwater snail is least distributed in Oceania, where it has only been reported in Australia and French Polynesia.

The results showed that *P. columella* inhabits a wide variety of natural and man-made freshwater systems (table 5). These freshwater systems included riverbanks, ponds (some in botanical gardens), canals, irrigation systems, ditches, ravines, lakes, dams, drain channels, streams, areas of estuarine lake that have low salinity, wetlands and a thermal lake. Although rivers/riverbanks were the most common habitat for *P. columella* throughout the world, this lymnaeid snail typically inhabits a wide variety of habitats.

Pseudosuccinea columella were collected during all seasons, both in winter (dry) and summer (rainy), or only in summer (table 5). There were no studies that were conducted during the winter season only. Reviewed studies showed that *P. columella* snails were collected in abundance during the summer (rainy) season (Cardoso *et al.*, 2006; Bargues *et al.*, 2011; Prepelitchi *et al.*, 2011; D'Almeida *et al.*, 2016) as compared to the winter season (Bargues *et al.*, 2011; Prepelitchi *et al.*, 2011; D'Almeida *et al.*, 2016). Results also showed that South American countries recorded the highest number of collected *P. columella* specimens globally involving field studies. The highest number of *P. columella* were collected in the wetlands of Argentina ($n = 7851$) over a period of two years and four months (tables 2 and 5) (Prepelitchi *et al.*, 2011). Lounnas *et al.* (2017) collected 1509 *P. columella* individuals over 16 years in 14 countries (tables 4 and 5). The lowest number of sampled *P. columella* ($n = 5$) was recorded in South Africa during the dry and rainy season of 2011 (table 5) (Kemp *et al.*, 2016).

Susceptibility of P. columella to Fasciola species infection

From the 56 reviewed studies, 28 assessed the epidemiological role played by *P. columella* in the transmission of *Fasciola* species, and these studies were reported in South America (tables 2 and 6), North America and the Caribbeans (tables 3 and 6), in Africa (tables 1 and 6) and Europe (tables 4 and 6). No studies reported on the infection of *P. columella* with *Fasciola* spp. in Oceania. Of these 28 studies, most studies ($n = 19$) assessed the susceptibility of *P. columella* to *Fasciola* spp. infection experimentally in all reviewed countries, with the exception of South Africa where natural infections were

Table 1. Summary of studies included in the distribution of *Pseudosuccinea columella* and its role in the transmission of *Fasciola* spp. in Africa for a period of 30 years (1990–2020).

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
Africa	South Africa	Malatji & Mukaratirwa (2019)	To confirm whether *P. columella* was transmitting *F. gigantica* and/or *F. hepatica* in selected locations of KwaZulu-Natal and Eastern Cape provinces of South Africa.	Field	100	Molecular	• *P. columella* from Eastern Cape and KwaZulu-Natal provinces were naturally infected with *F. gigantica*. • No *F. hepatica* natural infections were recorded.
		Malatji *et al.* (2019)	To identify populations of Lymnaeidae snails collected from selected areas of Botswana and South Africa.	Field	100	Molecular	– *P. columella* was reported in both Mpumalanga and KwaZulu-Natal provinces of South Africa.
		Wolmarans & de Kock (2006)	To determine the current status of the mollusc species diversity and to compare findings with a survey conducted in 2001 in Kruger National Park (KNP), South Africa.	Field	—	Morphology	– *P. columella* was found in three of the 42 sampled habitats.
		de Kock & Wolmarans (2008)	To evaluate the progress of four alien species colonizing water bodies in KNP, South Africa.	Field	—	—	– Ten new localities in the KNP were added to the distribution of *P. columella* in the KNP.
		de Kock & Wolmarans (1998)	To evaluate the effects of droughts which struck between 1966 and 1995 on the population of freshwater molluscs in the KNP.	Field	—	Morphology	– The droughts led to some molluscs species disappearance from the KNP. – *P. columella* screened for *Fasciola* spp. was negative for any infections.
		de Kock *et al.* (2002)	To establish the effects of high rainfall experienced between 1995 and 2000 on the population of freshwater molluscs in the KNP.	Field	—	Morphology	– Of the 43 sampled localities, *P. columella* was found in five of them.
		Perissinotto *et al.* (2014)	To provide a comprehensive list of the diversity of gastropod molluscs in the St Lucia estuarine lake.	Field	—	Morphology	– A total of 37 gastropod species have been reported from Lake St Lucia, iSimangaliso Wetland Park. – *P. columella* was reported to colonize areas that have low salinity.
		Kemp *et al.* (2016)	To compare mollusc diversity between the Marico and Crocodile rivers in South Africa.	Field	5	Morphology	– There was a high mollusc diversity in the Marico River, with juvenile specimens recorded throughout the study period when compared to the diversity from the Crocodile River. – *P. columella* was found in low abundance in both rivers.

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Cameroon	Tchakonté *et al.* (2014)	To investigate and study the diversity, ecology and dynamic of freshwater snails related to environmental factors in Cameroon.	Field	13	Morphology	– Ten species of freshwater snails were identified and recorded at nine of the ten urban stations. – *P. columella* was among the very rare species recorded with an occurrence frequency of less than 25%.
Zimbabwe	Carolus *et al.* (2019)	To illustrate how the construction of an artificial lake may lead to a cascade of biological invasions leading to parasite spillback.	Field	—	Molecular	– Lake Kariba only had *P. columella* and *Radix* sp. snails. – There was a high recorded prevalence of unidentified *Fasciola* sp. (that were neither *F. gigantica* nor *F. hepatica*) in *P. columella*.
Namibia	Curtis (1991)	To discuss the identification and conservation of Namibian freshwater invertebrate phyla.	Field	—	—	– In Namibia, *P. columella* occurs in scattered localities and in low numbers.
Egypt	Dar *et al.* (2015b)	To determine the capacity of three Egyptian *P. columella* populations to support larval development of *F. hepatica* collected from cattle and sheep.	Experimental	330	Molecular	– The prevalence of *F. hepatica* infection in the three populations when infected with five miracidia of cattle origin: Beni-Suef 60.4%, Behaira 79.2% and Qalyubiyah 58.9%. – Prevalence of infection of snails infected with two miracidia of sheep 30.4% and cattle 42.2% origin, and five miracidia of sheep 75.5% in Beni-Suef.
	Dar *et al.* (2014)	To determine the developmental pattern (normal or abnormal) of *F. hepatica* redial generations and specify the number of free rediae developing in snails according to their generation.	Experimental	400	—	– Most infected *P. columella* showed a normal development of redial generations. – The number of *F. hepatica* rediae present in *P. columella* was related to the number of fully grown sporocysts and the quantity of R1a rediae which developed into the snail body.
	Grabner *et al.* (2014)	Snails collected in irrigation canals were investigated for trematode occurrence with focus *P. columella* and the role it plays in the transmission of *F. gigantica*.	Field	296	Molecular	– *P. columella* was the most abundant snail in total numbers and the most dominant species in ten sites and the second most dominant species in one site (out of the 21 sampled sites). – 38 of the 296 *P. columella* specimens collected in total at all sampling sites were positive for trematode infection, and *F. gigantica* was detected in ten of those *P. columella*.

(*Continued*)

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Table 1. (*Continued.*)

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
		Dar *et al.* (2015a)	To determine the developmental pattern of redial generations and count free and live rediae according to their generation on juvenile *P. columella*, measuring 1 or 2 mm in height, subjected to one miracidium. *Galba truncantula* was used as the control.	Experimental	600	—	– Most infected snails showed a normal development of redial generations, whatever the lymnaeid species. – Total number of live rediae on day 49 was 24.6 in 1 mm and 34.6 in 2 mm group per infected *P. columella* snail.
		Dar *et al.* (2016)	To identify *P. columella* and *R. natalensis* in Egypt using shell measurements and molecular data.	Field	—	Morphology and molecular	– Morphometric parameters overlapped, indicating that they could not be used to differentiate between *P. columella* and *R. natalensis*. – There was an indication for the homogeneity of lymnaeid populations in Egypt since there were little intrasequence variations detected in the sequences of both gene loci.
		Lofty & Lofty (2015)	To present an update on the list of Egyptian freshwater fauna.	Field	—	—	– Report on 28 freshwater snails inhabiting various habitats in Egypt. – In Egypt, *P. columella* has been found to be naturally infected with *F. gigantica*.
		El-Kady *et al.* (2000)	To survey and study seasonal dynamics of freshwater snails occurring in two irrigation and three drainage systems in Egypt.	Field	24	Morphology	– 12 species of freshwater snails belonging to nine families and two subclasses of class Gastropoda were recorded. – Of all collected snails, *P. columella* and *G. truncatula* had the lowest abundance (0.1%).
		Abd El-Wakeil *et al.* (2013)	To survey benthic mollusc communities in the River Nile and their branches in Assiut governorate, Egypt.	Field	46	Morphology	– There were 26 recorded species belonging to 15 families. – *P. columella* constituted 29% of the sampled molluscs.

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Table 2. Summary of studies included in the distribution of *Pseudosuccinea columella* and its role in the transmission of *Fasciola* spp. in South America for a period of 30 years (1990–2020).

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
South America	Brazil	Coelho *et al.* (2008)	To determine the influence of shell size on the infection rate and on the outcome of rediae and cercariae in *P. columella* infected with *F. hepatica*.	Experimental	600	—	– *P. columella* with larger shell sizes showed lower infection rates. – The smallest size class had both the highest number of infected snails and the highest number of immature stages per snail.
		Mendes *et al.* (2008)	To investigate the influence of the definitive host on the development of *F. hepatica* in *P. columella* by infecting snails with miracidia derived from cattle or marmoset origin.	Experimental	600	—	– Survival rate of snails infected by cattle-derived miracidia was lower (41.0%) than that of snails infected by marmoset-derived miracidia (56.0%). – The percentage of positive snails from the marmoset group infections (28.0%) was higher than in those infected by the cattle group (25.3%).
		Cardoso *et al.* (2006)	To investigate genetic variability among and within nine Brazilian populations.	Field	205	Morphology and molecular	– There were low levels of genetic variability in the nine populations, and most of the genetic variation was interpopulational. – All screened *P. columella* were negative after shedding.
		D'Almeida *et al.* (2016)	To monitor *P. columella* population density in various aquatic habitats and in drinking water in Brazil.	Field	1558	Morphology	– Of the total 2038 molluscs collected, 1558 were identified as *P. columella*, which was the most abundant snail species in all sampling sites. – Seasonal changes had no significant impact on the relationship of specimens observed. – No *Fasciola* spp. and/or other digenean infections were detected.
		Pereira de Souza *et al.* (2002)	To experimentally infect *P. columella* with *F. hepatica* and maintain the life cycle in the laboratory.	Experimental	87	—	– An overall infection prevalence of 40.2% was noted.
	Argentina	Cucher *et al.* (2006)	To develop a sensitive polymerase chain reaction (PCR) assay for the specific detection of *F. hepatica* in naturally infected *Lymnaea* spp. snails by means of an optimized DNA extraction protocol.	Field	240	Molecular	– Successful development of PCR assay with a high specificity for *F. hepatica* in field-collected intermediate hosts. – *P. columella* showed an infection rate of 17.5 and 51.3% by direct examination and PCR, respectively.
		Martin *et al.* (2016)	To report the first record of the freshwater snail *P. columella* in southern Pampas, Argentina, and assess its future spread.	Field	—	Morphology	– *P. columella* was reported for the first time in southern Pampas, Argentina.
		Duffy *et al.* (2009)	To record the first report of a real-time PCR approach used to identify the main lymnaeid species from Argentina.	Field	—	Morphology and molecular	– Specific melting temperature peaks were obtained for the main lymnaeid species in Argentina, which are *P. columella*, *G. truncatula*, Lymnaea *diaphana* and Lymnaea *viatrix*.

(*Continued*)

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Table 2. (*Continued.*)

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
		Prepelitchi *et al.* (2011)	To examine the dynamics, abundance and population structure of *P. columella* in the Ibera Macrosystem, Argentina.	Field	7851	Morphology	– *P. columella* specimens were found throughout the study period except during the drought. – This was the first report of *P. columella* in wetland types.
		Prepelitchi *et al.* (2003)	To identify the species of snails collected in Berón de Astrada, Argentina, and to screen those snails for *F. hepatica* infections.	Field	601	Egg and adult fluke morphology (orally infected rats)	– All 601 collected snails were identified as *P. columella*. – 8.8% of *P. columella* were exclusively naturally infected with *F. hepatica*.
		Zarco *et al.* (2011)	To report the first record of *P. columella* in central Argentina (Córdoba province).	Field	44	Morphology	– *P. columella* was reported for the first time in Córdoba province, central Argentina.
		Davies *et al.* (2014)	To report the first record of *P. columella* from Salta province, north-west Argentina.	Field	98	Morphology	– *P. columella* was reported for the first time in Salta province, Argentina. – No trematode infections were recorded.
	Uruguay	Magalhães *et al.* (2004)	To design a pair of primers for the conserved and repetitive region of mitochondrial DNA from *F. hepatica* that could be used to detect infections by this trematode.	Experimental	24	Molecular	– Designed primers were able to detect the presence of *F. hepatica* in *P. columella* snails in the pre-patent period.
	Colombia	Pereira *et al.* (2020)	To identify the various lymnaeid snail species occupying different geographical regions of Santander and its bordering departments within Colombia.	Field	7	Molecular	– Four lymnaeid species are reported in the study area: *Galba cousin*, *G. truncatula*, *Galba schirazensis* and *P. columella*. – The freshwater snails *P. columella* and *G. schirazensis* were found free of infection.
		Salazar *et al.* (2006)	To examine the effects of exposure to *F. hepatica* on life history traits of *Lymnaea cousini* and P. *columella*.	Experimental	100	—	– Infection rates of P. *columella* and *L. cousini* at four weeks were 82.8 and 34.0%, respectively.
	Venezuela	Pointier *et al.* (2009)	To investigate the distribution of Lymnaeidae intermediate snail hosts of *Fasciola hepatica* in Venezuela.	Field	—	Morphology	– Four species were discovered in the duration of this study: *G. cousin*, *Galba cubensis*, *P. columella* and *G. truncatula*. – Susceptible *P. columella* was not found naturally infected by *F. hepatica*.
		Bargues *et al.* (2011)	To attain a new baseline for fasciolosis in Venezuela.	Field	6	Morphology and molecular	– *P. columella* specimens were confirmed using ribosomal and mitochondrial DNA markers. – There was no evidence to support *P. columella* as a source of the human fasciolosis cases reported in Venezuela.

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Table 3. Summary of studies included in the distribution of *Pseudosuccinea columella* and its role in the transmission of *Fasciola* spp. in North America and the Caribbeans for a period of 30 years (1990–2020).

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
North America and the Caribbeans	Cuba	Alba *et al.* (2018)	To explore the effect of different parasite doses, successive exposures and different parasite origins on the infection outcomes of susceptible and naturally resistant *P. columella* occurring in Cuba.	Experimental	120	—	– Resistant populations had zero parasite development – High *F. hepatica* miracidial doses and serial exposures resulted in an overall redial burden and an increase in prevalence in susceptible snails. – There were differences in compatibility of susceptible snails related to the geographical scale.
		Gutiérrez *et al.* (2002)	To analyse the influence of *F. hepatica* development on some of the life history traits of three Cuban isolates of *P. columella*.	Experimental	90	—	– Pargue Lenin and Punta Brava had 25/30 and 27/30 infected snails, respectively. – There were no infected snails in the La Palma population; thus, this constitutes the first report of *F. hepatica*-resistant *P. columella* in Cuba.
		Calienes *et al.* (2004)	To detect new *F. hepatica*-resistant populations of *P. columella* collected in the western and central regions of Cuba using previously identified random amplified polymorphic DNA markers.	Experimental	100 (12 populations)	Molecular	– Nine out of the 12 *P. columella* populations were susceptible to *F. hepatica* infections. – A new natural population of resistant *P. columella* was identified in the locality of El Azufre in Pinar del Rio Province in addition to the other two resistant populations previously reported.
		Gutiérrez *et al.* (2011)	To compare cellular reaction to miracidial development, shell morphometrics, mantle pigmentation pattern and egg-laying behaviour of isolates of Cuban *P. columella* susceptible and resistant to *F. hepatica*.	Field	100	Molecular	– Resistant snails encapsulated and phagocytized miracidium early, while in susceptible snails viable transforming miracidia was observed. – Susceptible snails laid eggs on container walls, while non-susceptible ones laid eggs on the bottom of container. – Susceptible snails have a significantly more rounded shell and aperture than the non-susceptible ones.
		Vázquez *et al.* (2014)	To compare the compatibility of *G. cubensis* and *P. columella* as intermediate hosts for *F. hepatica* in Cuba.	Experimental	150	—	– *G. cubensis* is a more compatible host for *F. hepatica* in Cuba when compared with *P. columella*.
		Gutiérrez *et al.* (2003)	To screen *P. columella* detected in a rice culture area at the El Pilon locality for *Fasciola* spp. natural infections.	Experimental	—	—	– First time reporting *P. columella* naturally infected with *F. hepatica* not only for Cuba but also for the Caribbean area.

(*Continued*)

Table 3. (*Continued.*)

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
		Alba *et al.* (2019b)	To present the ecology of resistant and susceptible *P. columella* in Cuba.	Field and experimental	329	Molecular	– No clear pattern of habitat types for non-susceptible *P. columella* populations were observed. – Low pH/TH affects *P. columella* negatively irrespective of whether it is resistant or susceptible to *Fasciola* spp. infections.
		Gutiérrez *et al.* (2001)	To investigate life history traits of *P. columella*.	Experimental	60	—	– Rates of increase (both finite and intrinsic) were lower in paired than in isolated snails. – Isolated snails showed the highest values of number of eggs per mass per individual.
		Gutiérrez *et al.* (2005)	To provide data on the variations of abundance of *F. hepatica* resistant and susceptible *P. columella* populations throughout the year under natural conditions.	Field	—	Morphology	– *P. columella* was the most abundant out of the gastropods sampled. – In El Azufre, resistant *P. columella* abundance was lower than the abundance attained by the susceptible strain.
	Kansas	McKown & Ridley (1995)	To ascertain the existence of possible snail intermediate hosts of *F. hepatica* within Kansas.	Experimental	—	—	– Of the five lymnaeid snails tested for susceptibility, only *P. columella* and *Fossaria bulimoides* proved susceptible to experimental infection by *F. hepatica*.
	USA (Hawaii)	Cowie (1998)	To examine patterns in the introductions of non-indigenous slugs and freshwater snails in the Hawaiian.	Field	—	—	– 22 species of freshwater snails and slugs have been reported in the wild in the Hawaiian Islands, and *P. columella* is one of them, introduced in 1950.

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Table 4. Summary of studies included in the distribution of *Pseudosuccinea columella* and its role in the transmission of *Fasciola* spp. in Europe for a period of 30 years (1990–2020).

Region	Country	Author	Objective	Type of study	Sample size (*N*)	Diagnostic method	Outcome
Europe	France	Pointier *et al.* (2007)	To test the capacity of *P. columella* populations recovered along the banks of the Lot River in France to act as intermediate hosts for *F. hepatica*.	Experimental	26	-	– First record of *P. columella* in the wild in France. – 26 experimentally infected *P. columella* had 100% prevalence of infection when exposed to *F. hepatica* miracidia.
		Dreyfuss *et al.* (2016)	To determine the ability of *P. columella* to ensure complete larval development of *F. hepatica*, *Calicophoron daubneyi* or both parasites (co-infection).	Experimental	200	-	– The highest prevalence of *F. hepatica* infections was recorded in in the 4 mm group. – Low frequencies were recorded in the co-infection groups and for *C. daubneyi* in the 3, 4 and 5 mm groups.
		Vázquez *et al.* (2020)	To study different intermediate and definitive host's susceptibility to *F. hepatica* using both field and experimental approaches.	Experimental	30	Molecular	– 60% of cattle were infected with *F. hepatica*, but nutria and wild boars had 19 and 4.5%, respectively. – All four snail species (*G. truncatula*, *P. columella*, *Lymnaea stagnalis* and *Radix balthica*) were susceptible *to F. hepatica* infection.
		Vignoles *et al.* (2018)	To investigate the consequences of *P. columella* invasion on the dynamics of native lymnaeids living on the acid soils of central France.	Field and semi-experimental	75	-	– *P. columella* colonization was more rapid in habitats with *G. truncatula* than those with *Omphiscola glabra*. – Colonization of *P. columella* in these habitats lead to a decrease in the abundance of native lymnaeids in these ditches.
		Lounnas *et al.* (2017)	To evaluate the distribution of genetic diversity in *P. columella* from 80 populations across 14 countries.	Field	1509	Molecular	– There was a lack of genetic polymorphism over thousands of kilometres. – There was a genetic distinction between liver fluke resistant and susceptible populations *of P. columella* in Cuba.
		Vignoles *et al.* (2015)	To determine the better intermediate host for metacercarial production between *G. truncatula* and *P. columella* infected with *F. hepatica*.	Experimental	200		– Overall, *P. columella* infections with *F. hepatica* resulted in higher metacercarial production than that noted with *G. truncatula*. – For *F. hepatica* infections, 38.2 and 33.3% prevalence were reported in the Egyptian and Italian *P. columella* populations, respectively.
	Romania	Glöer & Sîrbu (2005)	To present the new freshwater snail species found in Romania in the last years as well as build an updated systematic catalogue of these freshwater molluscs.	Field	-	-	– *P. columella* was newly identified in Romania in this thermal lake.
	Italy	Cianfanelli *et al.* (2007)	To map out the distribution of non-indigenous freshwater molluscs in Italy.	Field	-	-	– Report of *P. columella* in Italy.

Table 5. Global distribution of *Pseudosuccinea columella* between 1990 and 2020 (30 years).

Region	Country	Habitat	Sampling size (*N*)	Season of collection	Author (reference)
South America	Brazil	—	205	Summer and winter	Cardoso *et al.* (2006)
		Drinking reservoirs for domestic ruminants and wetland	1558	All seasons	D'Almeida *et al.* (2016)
	Venezuela	Irrigation canal	—	—	Pointier *et al.* (2009)
		Irrigation and water canals	6	Both dry and rainy	Bargues *et al.* (2011)
		Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	57	—	Lounnas *et al.* (2017)
	Colombia	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	497	—	Lounnas *et al.* (2017)
		—	7	—	Pereira *et al.* (2020)
	Peru	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	19	—	Lounnas *et al.* (2017)
	Argentina	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	84	—	Lounnas *et al.* (2017)
		—	—	Summer	Duffy *et al.* (2009)
		Wetlands	7851	All seasons	Prepelitchi *et al.* (2011)
		Riverbanks	44	Beginning of summer	Zarco *et al.* (2011)
		River	98	Summer and winter	Davies *et al.* (2014)
		Riverbanks	—	Summer	Martin *et al.* (2016)
	Paraguay	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	54	—	Lounnas *et al.* (2017)
Africa	South Africa	Rivers and dams	100	—	Malatji *et al.* (2019)
		Dams and rivers	—	—	Wolmarans & de Kock (2006)
		Rivers and dams	—	—	de Kock & Wolmarans (2008)
		River	—	—	de Kock & Wolmarans (1998)
		Rivers and dams	—	All seasons	de Kock *et al.* (2002)
		Estuarine lake (in areas with low salinity)	—	—	Perissinotto *et al.* (2014)
		Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	23	—	Lounnas *et al.* (2017)
		Rivers	5	Summer and winter	Kemp *et al.* (2016)
	Cameroon	Riverbanks	13	All seasons	Tchakonté *et al.* (2014)
	Mayotte	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	26	—	Lounnas *et al.* (2017)
	La Reunion	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	51	—	Lounnas *et al.* (2017)
	Namibia	River	—	—	Curtis (1991)
	Egypt	River	—	All seasons	Dar *et al.* (2016)
		Irrigation canals, streams, small dams and rivers	—	—	Lofty & Lofty (2015)

(*Continued*)

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Table 5. (*Continued*.)

Region	Country	Habitat	Sampling size (*N*)	Season of collection	Author (reference)
		Irrigation and drain channels	24	Summer	El-Kady *et al*. (2000)
		River	46	All seasons	Abd El-Wakeil *et al*. (2013)
	Zimbabwe	Lake banks	—	Dry and wet seasons	Carolus *et al*. (2019)
	Madagascar	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	14	—	Lounnas *et al*. (2017)
North America and the Caribbeans	Cuba	—	329	—	Alba *et al*. (2019b)
		Temporary pond	60	—	Gutiérrez *et al*. (2001)
		Small canal and a spring	—	All seasons	Gutiérrez *et al*. (2005)
		Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	244	—	Lounnas *et al*. (2017)
	Guadeloupe	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	60	—	Lounnas *et al*. (2017)
	USA	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	158	—	Lounnas *et al*. (2017)
	USA (Hawaii)	—	—	—	Cowie (1998)
Europe	Romania	Thermal lake	—	—	Glöer & Sîrbu (2005)
	Italy	Botanical garden pond	—	—	Cianfanelli *et al*. (2007)
	France	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	64	—	Lounnas *et al*. (2017)
		Riverbanks	75	—	Vignoles *et al*. (2018)
Oceania	Australia	Rivers	—	Dry season	Molloy & Anderson (2006)
	French Polynesia	Rivers, canals, irrigation systems, ravines, ditches, lakes and ponds	98	—	Lounnas *et al*. (2017)

reported. Only nine studies assessed natural infections of *Fasciola* species in *P. columella*, and these studies were from Africa (South Africa and Egypt), South America (Argentina, Brazil and Columbia) and North America and the Caribbeans (Cuba).

The results showed that *P. columella*/*F. hepatica* infections were more prevalent, reported in 22 studies, as compared to *P. columella*/*F. gigantica* infections, which were reported in two studies (table 6). *Pseudosuccinea columella* populations in Egypt were experimentally susceptible to both *F. hepatica* and *F. gigantica*. No *P. columella* populations have been found naturally infected with *F. hepatica* in the field in the African continent (table 6). Experimental studies from Cuba ($n = 2$) showed populations of *P. columella* resistant to *F. hepatica* infections. Furthermore, field studies from Brazil and Argentina also did not report natural *F. hepatica* infections in *P. columella* populations collected from *F. hepatica*-endemic areas.

Prevalence of *Fasciola* species infection intra-*P. columella* populations

Although most studies did not indicate the methods they used to check for infection, 13 studies checked snail infections using either cercarial shedding ($n = 4$), molecular techniques ($n = 8$) or checking for any of the developmental stages of *Fasciola* inside the IH tissue under the microscope ($n = 1$) (table 6).

The overall prevalence of *P. columella* infected with *Fasciola* spp. varied from 0 to 100%, the lowest (0%) recorded in Brazil (Cardoso *et al*., 2006; D'Almeida *et al*., 2016), Argentina (Davies *et al*., 2014) and Colombia (Pereira *et al*., 2020), and the highest (100%) recorded in South Africa (Malatji & Mukaratirwa, 2019), Uruguay (Magalhães *et al*., 2004) and France (Pointier *et al*., 2007). *Pseudosuccinea columella*/*Fasciola* spp. natural infections prevalence ranged from 0 to 100% (table 6). Experimental *P. columella*/*F. hepatica* infections showed prevalence ranging from 19.7% in Egypt (Dar *et al*., 2015a) to 100% in France (Pointier *et al*., 2007) and Uruguay (Magalhães *et al*., 2004) (table 6). No studies are reported on experimental *F. gigantica* intra-*P. columella* infections. *Pseudosuccinea columella* naturally infected with *F. hepatica* had a prevalence between 0 and 51.25%, with no infections documented in Brazil (Cardoso *et al*., 2006; D'Almeida *et al*., 2016), Argentina (Davies *et al*., 2014) and Colombia (Pereira *et al*., 2020), and a high infection rate of 51.25% was documented in Argentina (Cucher *et al*., 2006). The prevalence range for *F. gigantica* intra-*P. columella* natural infections was reported to be between 13.18 and 100% in Egypt (Grabner *et al*., 2014) and South Africa (Malatji &

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Mukaratirwa, 2019), respectively. The highest naturally occurring infections of *P. columella* with *F. hepatica* and *F. gigantica* were documented in Argentina (51.25%) (Cucher *et al.*, 2006) and South Africa (100%) (Malatji & Mukaratirwa, 2019).

Discussion

Pseudosuccinea columella is thought to have originated from Central America, the Caribbean and the southern part of North America (Mas-Coma *et al.*, 2005), and this review has shown that this species has been successfully introduced and established in other continents with varying environmental and ecological conditions. The results from this review showed that in addition to its native regions (Dar *et al.*, 2014; Martin *et al.*, 2016; Lounnas *et al.*, 2017; Alba *et al.*, 2018; Vignoles *et al.*, 2018; Carolus *et al.*, 2019), *P. columella* has been documented in Africa, Europe, South America (Martin *et al.*, 2016; Lounnas *et al.*, 2017; Alba *et al.*, 2018) and Oceania (Martin *et al.*, 2016; Lounnas *et al.*, 2017; Alba *et al.*, 2018; Vignoles *et al.*, 2018; Alba *et al.*, 2019b). The results further indicate that from these four newly invaded continents, this invasive freshwater snail has been reported in 19 countries, but is now well established and widely distributed in Africa and South America, and is least distributed in Oceania (Lounnas *et al.*, 2017). However, abundance varied with localities and various environmental factors, such as the availability of suitable habitats and seasonal changes, amongst other factors. Although the reviewed studies showed that *P. columella* specimens were collected in abundance in native Argentina (Prepelitchi *et al.*, 2011) and Brazil (D'Almeida *et al.*, 2016), this invasive snail is considered the most abundant lymnaeid species in Egypt (Grabner *et al.*, 2014), Brazil (D'Almeida *et al.*, 2016) and in Kansas, USA (McKown & Ridley, 1995), and the second most abundant species in Zimbabwe (Carolus *et al.*, 2019) in comparison to other freshwater lymnaeids.

According to de Kock *et al.* (2002), the availability of suitable water habitats largely influences the distribution of freshwater snails. Although an inspection of the frequency of habitats in reviewed studies showed that *P. columella* is commonly found on riverbanks, the results also showed that *P. columella* thrives in diverse freshwater habitats ranging from man-made, to natural, temporal and permanent habitats. In addition to freshwater habitats, this lymnaeid species has been found in ditches of acid soils that have water with low levels of calcium (Vignoles *et al.*, 2018) and areas with low salinity (Perissinotto *et al.*, 2014). Furthermore, it has been documented to occur in places with high altitudes and low temperatures (Bardales-Valdivia *et al.*, 2021). The ability of *P. columella* to adapt to and inhabit almost all types of freshwater bodies, including thermal lakes and acidic soils, and tolerate a wide range of climatic conditions are some of the factors that make this snail such a successful invader (Prepelitchi *et al.*, 2011; Vignoles *et al.*, 2018) and the most widely distributed invasive freshwater snail species globally (Pointier *et al.*, 2009; Lounnas *et al.*, 2017).

The abundance of freshwater snails varies throughout the year with seasonal changes such as temperature, rainfall and water levels (Kleiman *et al.*, 2007). According to D'Almeida *et al.* (2016), an increase in rainfall and temperature favours an increase in mollusc populations. This is consistent with the results from this review, as *P. columella* was noticeably more abundant during rainy seasons, and this was easily observed in studies that collected snails during all seasons of the year (de Kock *et al.*, 2002; Abd El-Wakeil *et al.*, 2013; Tchakonté *et al.*, 2014; D'Almeida *et al.*, 2016; Dar *et al.*, 2016). Studies in Egypt (El-Kady *et al.*, 2000) and Argentina (Kleiman *et al.*, 2007) showed that the best time to collect snails when they are in their highest numbers was in spring and summer due to favourable temperature conditions and the availability of plenty of vegetation cover in the aquatic habitats. However, Prepelitchi *et al.* (2011) noted that the highest number and largest size of specimens of *P. columella* populations in the north of Corrientes province (Argentina) were found during winter. This is, however, inconsistent with Charlier *et al.* (2014) and Beesley *et al.* (2018), who stated that adult snails are known to be abundant in summer and spring seasons, while juvenile snails are mainly found in autumn. These results show that although *P. columella* populations can be found throughout the year and in different seasons, the season in which *P. columella* may be found in abundance differs between and within countries due to varying habitats and climatic conditions.

The epidemiological importance of *P. columella* as an intermediate host for both *F. gigantica* and *F. hepatica* has been documented (de Kock *et al.*, 1989; Grabner *et al.*, 2014; Alba *et al.*, 2019a; Carolus *et al.*, 2019; Malatji *et al.*, 2019). From the review, infections were commonly detected through shedding of cercariae from snails collected from their natural environments, observation of different developmental stages of the parasites after crushing or dissecting snails (Magalhães *et al.*, 2004; Caron *et al.*, 2008; Beesley *et al.*, 2018) and through molecular techniques for better sensitivity (Magalhães *et al.*, 2004; Cucher *et al.*, 2006; Beesley *et al.*, 2018). Reviewed studies showed that *P. columella* infections with *F. gigantica* have only been reported in Egypt (Grabner *et al.*, 2014) and South Africa (Malatji & Mukaratirwa, 2019). Despite the high natural infections reported by Malatji & Mukaratirwa (2019) in South Africa, Grabner *et al.* (2014) still concluded that the maintenance of the natural life cycle of *F. gigantica* in *P. columella* remains uncertain. This conclusion may have been attributed to the low infection rate (13.18%) of *F. gigantica* observed in Egypt (Grabner *et al.*, 2014). The limited information on the role played by *P. columella* in the transmission of *F. gigantica* in the invaded countries highlights the need for more field and experimental infection studies in these areas. The high prevalence of *F. gigantica* intra-*P. columella* infection (100%) reported in South Africa by Malatji & Mukaratirwa (2019) could be due to livestock drinking from seasonal ponds/small dams with no other source of drinking water and thereby snails getting exposed to heavy infections from hatching miracidia. There are plenty of such scenarios in the rural areas of South Africa and elsewhere in southern Africa, where animals drink and graze around these areas which are heavily contaminated by *Fasciola* spp. cercariae (Malatji & Mukaratirwa, pers. comm.).

The results for this review show that *F. hepatica* infections in *P. columella* were the most documented in five continents. This is not surprising, as according to Mas-Coma *et al.* (2005), this invasive lymnaeid species is responsible for the secondary spread of *F. hepatica*. The results also show that most *F. hepatica* intra-*P. columella* infection studies were conducted in the laboratory (experimental infections), as compared to field reports, which is a great concern as this does not give a full representation of what happens in the field. Additionally, the recorded infection rate in the reviewed studies was generally low in natural/field infection studies (Prepelitchi *et al.*, 2003; Gutiérrez *et al.*, 2011) as compared to experimental studies, with exception to that reported by Cucher *et al.* (2006) in Argentina. Although the observed high experimental infection rates of *P. columella* with *F. hepatica* show the importance of this invasive snail as one of the vectors responsible for the transmission of fascioliasis (Dar *et al.*, 2015b), there is still a need for field-based studies to further

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Table 6. Natural and experimental *Fasciola* infections intra-*Pseudosuccinea columella* reported between 1990 and 2020 (30 years).

Region	Country	Study type	No. of snails collected/used	No. infected (prevalence)	Detection method	Species of infection	Author (Reference)
Africa	South Africa	Field	100	100 (100%)	Molecular	*F. gigantica*	Malatji & Mukaratirwa (2019)
	Egypt	Experimental	330	178 (54%)	Molecular	*F. hepatica*	Dar *et al.* (2015b)
		Experimental	400	145 (36.25%)	—	*F. hepatica*	Dar *et al.* (2014)
		Field	296	39 (13.18%)	Molecular	*F. gigantica*	Grabner *et al.* (2014)
		Experimental	100	38 (38%)	—	*F. hepatica*	Vignoles *et al.* (2015)
		Experimental	600	115 (19. 17%)	—	*F. hepatica*	Dar *et al.* (2015a)
Europe	France	Experimental	26	26 (100%)	—	*F. hepatica*	Pointier *et al.* (2007)
		Experimental	200	107 (53.5%)	—	*F. hepatica*	Dreyfuss *et al.* (2016)
		Experimental	30	17 (56.67%)	Molecular	*F. hepatica*	Vázquez *et al.* (2020)
		Experimental	100	33 (33%)	—	*F. hepatica*	Vignoles *et al.* (2015)
North America and the Caribbeans	Cuba	Experimental	120	—	—	*F. hepatica*	Alba *et al.* (2018)
		Experimental	90	52 (57.8%)	—	*F. hepatica*	Gutiérrez *et al.* (2002)
		Experimental	100 (12 populations)	Nine populations	Molecular	*F. hepatica*	Calienes *et al.* (2004)
		Experimental	—	Susceptible 92%; Resistant 0%	—	*F. hepatica*	Gutiérrez *et al.* (2003)
		Field	100	3 (3%)	Molecular	*F. hepatica*	Gutiérrez *et al.* (2011)
		Experimental	150	—	—	*F. hepatica*	Vázquez *et al.* (2014)
	Kansas	Experimental	—	—	—	*F. hepatica*	McKown & Ridley (1995)
South America	Brazil	Experimental	600	164 (27.33%)	—	*F. hepatica*	Mendes *et al.* (2008)
		Field	1558	0	Cercaria shedding	—	D'Almeida *et al.* (2016)
		Field	205	0	Cercaria shedding	—	Cardoso *et al.* (2006)
		Experimental	87	35 (40.2%)	—	*F. hepatica*	Pereira de Souza *et al.* (2002)
		Experimental	600	319 (53.17%)	—	*F. hepatica*	Coelho *et al.* (2008)
	Argentina	Field	240	123 (51.25%)	Molecular	*F. hepatica*	Cucher *et al.* (2006)
		Field	500	44 (8.8%)	Cercaria shedding	*F. hepatica*	Prepelitchi *et al.* (2003)
		Field	98	0	Cercaria shedding	-	Davies *et al.* (2014)
	Uruguay	Experimental	24	24 (100%)	Molecular	*F. hepatica*	Magalhães *et al.* (2004)
	Colombia	Experimental	100	82 (82%)	—	*F. hepatica*	Salazar *et al.* (2006)
		Field	7	0	Observation of the cercaria, metacercariae and rediae	-	Pereira *et al.* (2020)

determine not only the prevalence of *Fasciola* spp., but also the competence of different populations of *P. columella* in maintaining and transmitting both *Fasciola* species globally.

Literature has shown that geographical variations in *Lymnaea* species influence their susceptibility to infections by *F. hepatica* (Gasnier *et al.*, 2000; Coelho *et al.*, 2008). This has been observed by Gutiérrez *et al.* (2011) and Alba *et al.* (2018), who reported on variations within *P. columella* species that influenced their susceptibility to *F. hepatica* infections. In Cuba, two different phenotypes of *P. columella* populations have been identified and reported to show either resistance or susceptibility to *F. hepatica* infections (Alba *et al.*, 2018). These authors have shown that the resistant field-occurring *P. columella* phenotypes are characterized by their ability to encapsulate and phagocytize miracidia

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using their (host's) immune cells (Gutiérrez *et al.*, 2003, 2011; Alba *et al.*, 2018).

Although the presence of resistant *P. columella* phenotypes has not been extensively studied in most countries, the inability of some phenotypes of this invasive snail to be infected and transmit particularly *F. hepatica* in endemic areas may lead to the assumption that this phenotype is unknowingly widely distributed. Such cases have been reported in Australia (Molloy & Anderson, 2006), Venezuela (Pointier *et al.*, 2009; Bargues *et al.*, 2011), Colombia (Pereira *et al.*, 2020), north-west Argentina (Davies *et al.*, 2014) and Brazil (Cardoso *et al.*, 2006; D'Almeida *et al.*, 2016), where *P. columella* phenotypes collected in *Fasciola*-endemic areas were found with no infections. Additionally, *P. columella* phenotypes collected in locations in South Africa where both *F. hepatica* and *F. gigantica* overlap were only found infected with *F. gigantica* (Malatji & Mukaratirwa, 2019). This, therefore, raises concerns about the existence and geographical distribution of the different phenotypes of *P. columella*. As a result, there is still a need to conduct both an experimental and field assessment of the infection of *P. columella* phenotypes with both *Fasciola* species, especially in countries where this invasive snail has been reported with no clear epidemiological role in the transmission of *Fasciola* species, and in areas where both *F. hepatica* and *F. gigantica* overlap. This will help determine the geographical expansion of *P. columella* phenotypes resistant to *F. hepatica* infections, as well as the competence of the susceptible species in the transmission of both *Fasciola* species in fasciolosis-endemic areas.

In conclusion, it is evident that intensive research still needs to be conducted focusing on (1) assessing the global distribution and importance of this invasive snail in the transmission of both *Fasciola* species, especially in the field/natural environment, as there seem to be more countries where the snail is present and yet to be documented; (2) assessing the susceptibility of different *P. columella* phenotypes to *Fasciola* spp. populations to differentiate susceptible and resistant phenotypes, in countries where the species has been reported; (3) the experimental infection of *P. columella* populations not found with infections but collected in fasciolosis-endemic areas; and (4) studies to compare the competence of *P. columella* in the transmission of fasciolosis with other lymnaeid IHs native to those particular areas where fasciolosis is endemic. Additionally, this review has pointed out the importance of researchers to describe the ecological parameters of habitats where species have been collected from, as this could assist in explaining questionably high rates of documented *P. columella* naturally infected by either *Fasciola* species.

A limitation in this review might be that a number of studies published in languages other than English might not have been included and that the study only considered articles published in the last 30 years.

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