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First record of the freshwater snail *Pseudosuccinea columella* (Gastropoda: Lymnaeidae) in southern Pampas (Argentina) and assessment of future spread

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ABSTRACT
The freshwater snail *Pseudosuccinea columella* was recorded for the first time in Argentina more than 60 years ago. Since then its distribution in the wild has been restricted to the northeastern provinces. Here we record the presence of *P. columella* in southern Pampas for the first time, extending its distribution more than 500 km southwards. The climatic suitability of this and other areas of South America for its establishment and spread was analysed using habitat modelling software. Hitherto its spread within and between watercourses in southern Pampas has been very limited, probably through a combination of low climatic suitability, recent introduction and low connectivity of the drainage basins. The suitability of other areas where it has been recently recorded indicates a moderate risk of further spread in central and northwestern Argentina and in coastal areas of the Pacific rim of South America (southern Perú and northern Chile). The recent spread of *P. columella* in the wild in Argentina may be the result of an increase in the trade in aquarium plants or of the evolution of a new lineage with different ecological capabilities.

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Introduction

Five species of exotic freshwater gastropods are presently known to have established populations in the wild in Argentina (Rumi *et al*. 2008; Ovando and Cuezzo 2012). One of them, *Pseudosuccinea columella* (Say, 1817), has been considered native of North America (Van Eeden and Brown 1966; Cordeiro and Bogan 2012) but now has a near worldwide distribution, being found in Africa and the Middle East, Europe, Central America, South America, Australia, New Zealand and some Pacific islands (Paraense 1982; Pointier and Marquet 1990; Cowie 1998; Pointier *et al*. 2007). In Argentina, *P. columella* was recorded for the first time more than 60 years ago (Hylton Scott 1954) although its distribution in the wild did not increase further from the northeastern provinces of the country (Castellanos and Landoni 1981; Paraense 1982, 2005; Gutiérrez Gregoric *et al.* 2006). However, some new localities far from that original region have been recorded recently (Zarco *et al*. 2011; Davies *et al*. 2014). *Pseudosuccinea columella* has been reported as an important intermediate host of the trematode *Fasciola hepatica* (Linnaeus, 1758) in northeastern Argentina (Prepelitchi *et al*. 2003), which is the causal agent of fascioliasis, a parasitic disease of veterinary and medical importance (Mera y Sierra *et al.* 2011). In the present study we record for the first time the presence of *P. columella* in southern Pampas (Argentina), which extends its distribution more than 500 km southwards; we also investigate its spread within and between watercourses in the area and analyse the climatic suitability of this and other areas of South America for its establishment and spread.

Materials and methods

In November 2012 during a routine malacological survey a dense population of a previously unrecorded lymnaeids was discovered at Ventana stream (Site 1, Figure 1; Sauce Chico river basin, Buenos Aires province, Argentina). Site 1 was a shallow pool (15 m wide and 100 m long) formed upstream of a concrete low-water crossing. The surrounding area was mostly devoted to agriculture and cattle breeding. The bottom of the pool was composed mostly of small boulders and stones, covered at the time of sampling by filamentous green algae.

Specimens were manually collected *in vivo* along the banks of the stream and transferred alive to the laboratory for identification. They were relaxed in water at 70 °C and fixed with 70% ethanol. To confirm the identification of the species, the anatomy was studied under a stereomicroscope Leica MZ6 and the shell sculpture was examined using a JEOL 35 CF electron

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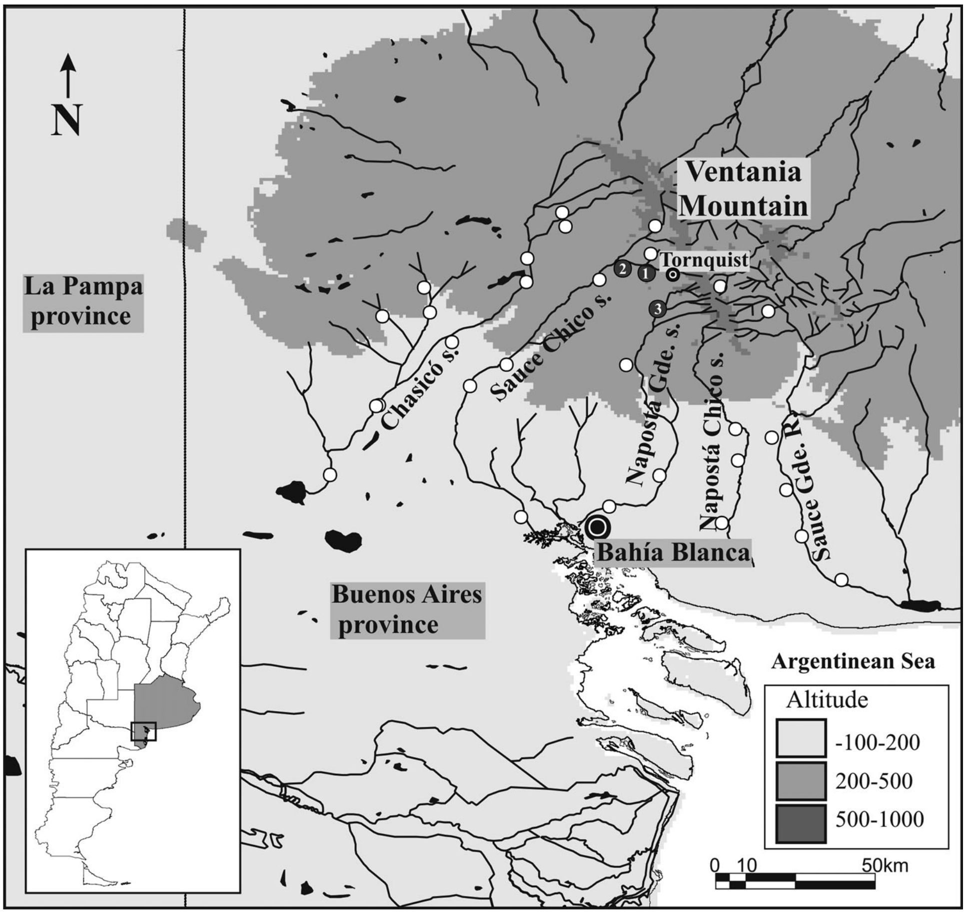

Figure 1. Map of the study area. Sampled sites are marked with numbered circles (*Pseudosuccinea columella* was detected) and empty circles (*P. columella* was absent), cities with concentric circles and lakes and ponds as black areas. Lower left margin: administrative map of Argentina, showing Buenos Aires province (grey) and study area (in frame).

microscope at Centro Integral de Microscopía Electrónica (Tucumán, Argentina). Voucher specimens were deposited at Instituto de Biodiversidad Neotropical, IBN Collection (BDAD 401, 403, 409).

The discovery of this population of *P. columella* prompted the search for other populations in the same river and in neighbouring streams and rivers (Figure 1). The survey was carried out from December 2012 to April 2013 and a total of 32 sites were visited in five independent basins. Snails were searched for visually among vegetation and other submerged substrata, picking up leaves, stems and stones (Martín *et al*. 2001); the material stranded on the banks was also examined for empty shells.

To estimate the probabilities of its further spread within the region, the potential distribution of *P. columella* was modelled using the MaxEnt software for species habitat modelling (https://www.cs.princeton.edu/~schapire/maxent/). MaxEnt models are based on presence records only and estimate geographic distributions of species from locality point data by finding the maximum entropy distribution (Phillips *et al*. 2006). Occurrence data for *P. columella* in Argentina, Uruguay and southern Brazil were obtained from published scientific literature (Hylton Scott 1954; Castellanos and Landoni 1981; Paraense 1982, 2005; Zelaya 2002; Prepelitchi *et al*. 2003; Gutiérrez Gregoric *et al*. 2006; Rumi *et al*. 2008; Zarco *et al*. 2011), malacological collections (Museo de La Plata [MLP], La Plata, Argentina and Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' [MACN], Buenos Aires, Argentina) and material collected during field work (Table 1). For those records obtained from the literature in which coordinates were not provided, the georeferenced location was obtained from the GEOLocate Web Application (http://www.museum.tulane.edu/geolocate/web/webgeoref.aspx). A total of 74 occurrence points was included in the model.

Table 1. Non-published records of *Pseudosuccinea columella* used as occurrence points for potential distribution modelling.

Locality	Latitude	Longitude	Sources
Ventana stream (Argentina)	−38,047	−62,141	This study
La Bolsa (Argentina)	−31,725	−64,43	Personal record, XMCO
Dique Campo Alegre (Argentina)	−24,55	−65,378	Personal record, XMCO
Laguna de Pocho (Argentina)	−31,4	−65,1	MACN 28666
Pozón Viejo (Argentina)	−25,689	−54,476	MLP 7366
Río Aguapey (Argentina)	−27,975	−56,207	MLP 7276
Carrasco (Uruguay)	−34,862	−56,374	Personal record, XMCO

Note: MACN—Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP—Museo de La Plata, La Plata, Argentina.

The environmental database was composed of 19 bioclimatic variables that include annual trends, seasonality and extreme conditions of temperature and rainfall (obtained from WorldClim: http://www.worldclim.org; Hijmans *et al*. 2005). These data layers were generated through interpolation of average monthly climate data on a 30 arcsecond resolution grid, representative of the period 1950–2000. The model was run with two different combinations of environmental variables: with all the 19 bioclimatic variables and with the 11 temperature variables only.

Data were randomly divided into training data (75% of the occurrence points) and model testing data (the remaining 25%). The output format chosen was the 'logistic' one that returns a continuous map with an estimate between 0 and 1 of probability of presence, scaled up in a non-linear way for easier distinction between the suitability of the different areas modelled. All other parameters of MaxEnt were used as established by default.

To analyse which variables contributed most to the development of the model, a jackknife test was run. The model was evaluated with the receiver operating characteristic curves analyses calculating the area under the curve (AUC; Fielding and Bell 1997), a threshold independent index commonly used to assess prediction maps. The higher the AUC the more sensitive and specific the model, ranging from 0.5 (random accuracy) to a maximum value of 1.0 (perfect prediction). MaxEnt calculates two values of AUC, one for model training and one for model testing.

Results

Species description

Type material

Lectotype and paralectotype ANSP 58791 (designated by Baker (1911); seen as photographs).

Type locality

Not specified in the original description. Baker (1911) and Paraense (1982) proposed that the type locality is probably located near Philadelphia because Thomas Say (1787–1834) was a member of the Academy of Sciences of Philadelphia and exhaustively explored all environments in this area.

Shell

Spire conical, acute. Three to four whorls separated by deep sutures (Figure 2A). Protoconch rounded, smooth, sometimes eroded (Figure 2B). Second whorl convex, sculpture with spiral striations crossed by radial lines (Figure 2C). Body whorl prominent, voluminous, longer than wide. Sculpture on penultimate and last whorl with well-marked spiral wrinkles, regular, closely spaced, crossed by distinct folds, with slight undulations in extended radial grooves (Figure 2D). Folds triangular in shape, arranged in longitudinal rows, between two spiral ridge rows (Figure 2E). Peristome fragile, edges smooth and sharp, columellar edge of peristome reflected just covering umbilicus. Shell aperture oval, with length greater than width (Figure 2A).

Anatomy

Dorsal mantle surface heavily pigmented, with numerous white spots varying in shape and size (Figure 3A) Tentacles triangular, broad and rounded ends, short, with flattened base. Foot oval with simple sole, rounded near end, light grey or sometimes without pigmentation.

Pallial system extends from right side from pericardium to mantle border; ureter running along mantle cavity between rectum and pericardium, with double flexure of ureter (Figure 3B). Female genital system with albumen gland voluminous; oviduct convoluted; nidamental gland with irregular edges, prominent. Male genital system with prostate from thread-like to ribbon-like; penis sheath cylindrical, short; preputium twice as long as penis sheath (Figure 3C).

Radula

Rachidian tooth small in relation to lateral teeth, with two minute pegs on each side of tooth base. Lateral teeth rectangular, tricuspid; mesocone triangular, blunt end; ectocone and endocone greater length; base plate trapezoidal (Figure 2F). From eighth lateral tooth to last marginal tooth, numbers of cusps increase toward outer side. Marginal teeth multicuspid (four to six cusps), cusps rounded ends similar in size and length (Figure 2G).

Present distribution

Pseudosuccinea columella was quite abundant at Site 1 at the Ventana stream; most stones examined had one to five adult snails (larger than 10 mm shell length) and many of them also had egg masses. This site was also inhabited by a native planorbid limpet, *Uncancylus concentricus* (d'Orbigny, 1835), although it was less abundant. Living freshwater snails were found at 26 of the 32 sites surveyed but *P. columella* was found at only two other sites (Figure 1). A single adult of *P. columella* was found among hundreds of specimens of *Physa acuta* (Draparnaud, 1805), *Uncancylus concentricus*, *Chilina parchappii* (d'Orbigny, 1835) and *Biomphalaria peregrina* (d'Orbigny, 1835) at Site 4 (Sauce Chico river basin), 7.25 km downstream of Site 1. Two juveniles of *P. columella* (less than 8 mm shell length) were found on boulders at Site 10 in the Napostá Grande stream basin among hundreds of specimens of *C. parchappii* and *U. concentricus*.

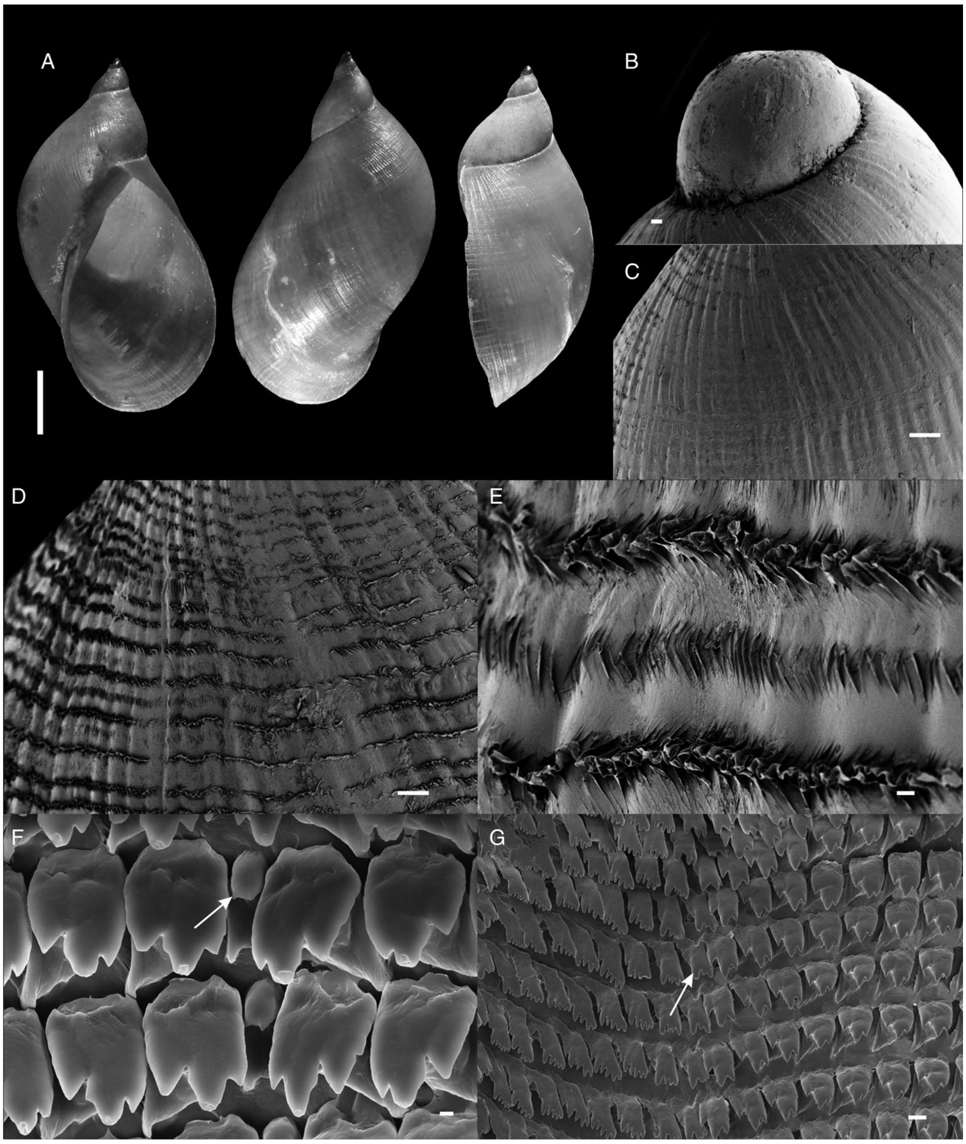

Figure 2. Shell morphology, sculpture and radula of *Pseudosuccinea columella* from Ventana stream (BDAD # 401) **A,** Shell morphology in ventral, dorsal and lateral views. Scale bar: 2 mm. **B,** Detail of protoconch showing absence of sculpture and erosion. Scale bar: 20 µm in scanning electron micrograph (SEM). **C,** Detail of sculpture of the second whorl. Scale bar: 100 µm in SEM. **D,** Shell sculpture of body whorl proximate to the shell aperture. Scale bar: 100 µm in SEM. **E,** Detail of sculpture of body whorl showing the two sculpture types. Scale bar: 10 µm in SEM. **F,** Detail of rachidian teeth and first lateral teeth. Note the size of rachidian (arrow) relative to lateral teeth. Scale bar: 10 µm in SEM. **G,** Detail of eighth and ninth lateral teeth (arrow) showing the transition from lateral to marginal teeth. Scale bar = 10 µm in SEM.

Potential distribution

The models generated by MaxEnt with the two different combinations of bioclimatic variables produced essentially the same outcome. The AUC values for the model including all 19 variables were 0.951 for training and 0.930 for testing data (standard deviation 0.018) whereas the model with only temperature variables showed AUC values of 0.940 for training and 0.933 for testing data (standard deviation 0.023), both suggesting a good predictive power. For this reason we present here only the results corresponding to the simplest model (Figures 4 and 5).

According to the selected model, the regions more susceptible to the spread of *P. columella* are localized in the coastal zones of southern Brazil, Uruguay and northern Buenos Aires province, Paraguay and the northeast of Argentina (Figure 4). Besides, the coast of Perú and northern Chile, the Yungas Ecoregion (northwestern Argentina, Bolivia and southern Perú) and the lowlands of Córdoba province (central Argentina) showed a moderate risk of spread. Interestingly, southern Pampas showed a very low risk of establishment and spread with both sets of bioclimatic variables.

The jackknife test showed that the variables with the highest gain when used in isolation were the minimum temperature of the coldest month, the mean annual temperature and the mean temperature of the coldest quarter, which have the most useful information

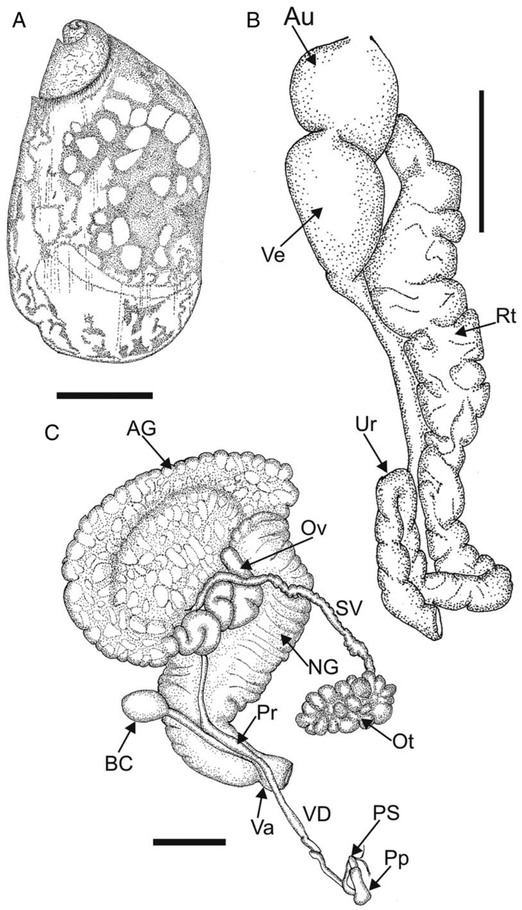

Figure 3. Anatomy of *Pseudosuccinea columella* from Ventana stream (BDAD # 401). **A,** Dorsal view of specimen without shell showing the mantle pigmentation. Scale bar = 1 mm. **B,** Detail of pallial system with pericardium and ureter morphology. Scale bar = 1 mm. **C,** Dorsal view of reproductive system showing male and female organs. Scale bar = 1 mm. Abbreviations: AG—album gland; Au— auricle; BC—bursa copulatrix; NG—nidamental gland; Ot—ovotestis; Ov—oviduct; Pp—preputium; Pr—prostate; PS—penis sheath; Rt—renal tube; SV—seminal vesicle; Ur—ureter; Va—vagina; VD—vas deferens; Ve— ventricule.

(Figure 5). On the other hand, the variable that decreased the gain the most when it was omitted was the mean temperature of the wettest quarter, having information necessary for the model that is not present in the other variables. The remaining variables contributed less to model development.

Discussion

Pseudosuccinea columella is one of the few lymnaeids that can be confidently identified by shell characters (Pointier *et al*. 2007). The shells of the specimens collected in southern Pampas show the same characteristics described by Hylton Scott (1954), Paraense (1982) and Pointier *et al*. (2007). However, electronic microscopy of the shell sculpture shows that the 'fine spiral ridges', described by Paraense (1983) and Pointier *et al*. (2007) are in fact a complex sculpture formed by high spiral wavy and triangular folds crossed by radial growth lines. Morphology of the reproductive, pallial system and radula also agree with the characters pointed out by Paraense (1983) and Pointier *et al*. (2007).

The nearest records of *P. columella* in the wild are located 670 km to the north-northwest in the Suquía river basin, Córdoba province (Zarco *et al*. 2011). These authors reviewed the distribution of *P. columella* in Argentina and concluded that those sites were the southernmost records in the Neotropical region, even though Paraense (1982) reported this species in Montevideo and Maldonado (Uruguay), both sites with more southerly locations than those from Córdoba. Until the present study, the southernmost wild records of *P. columella* were located more than 500 km to the northeast, where they were found in artificial ponds in botanical gardens at Buenos Aires and La Plata (Zelaya 2002; Zarco *et al*. 2011; pers. obs. PRM). The southernmost populations in the world are located in New Zealand at 43°S (Mitchel 1995).

The establishment of *P. columella* in southern Pampas is apparently quite recent, because it was not recorded during an extensive malacological survey covering 76 sites in 19 lakes and 35 independent lotic systems in southern and central Buenos Aires Province (Martín *et al*. 2001). Nor was it found in more recent malacological surveys in southern Buenos Aires Province (Tietze and De Francesco 2010; Seuffert and Martín 2013) or in the neighbouring La Pampa Province (Hassan *et al*. 2012). The Sauce Chico river and the Napostá Grande stream drain to the Argentine Sea from the southern slope of Tandilia and Ventania mountains, which constitute a hydrological barrier with the Río de la Plata basin (Figure 1), where there are most records of *P. columella*. To the west and southwest an arid zone of salty lakes constitutes an ecological barrier to the dispersal of freshwater molluscs (Martín *et al*. 2001) but notwithstanding its isolation, several freshwater molluscs have been recently introduced from outside the area, most probably by human action. There is intense sport fishing activity in Buenos Aires province and this may be a means of dispersion of molluscs at small and medium spatial scales (less than 250 km; Martín *et al*. 2001) but not for the introduction from the previously known localities in central and northeastern Argentina. The densest known population of *P. columella* is 5.3 km downstream of a small tourist village and the Ventana stream, which runs through the village, is a likely place for discarding material from aquaria and garden ponds. Interestingly, at the site of the first record of *P. columella* we have found an established population of the sponge plant *Limnobium laevigatum* (Humb. & Bonpl. *ex* Willd.) Heine, an invasive ornamental pond plant native from tropical South America that

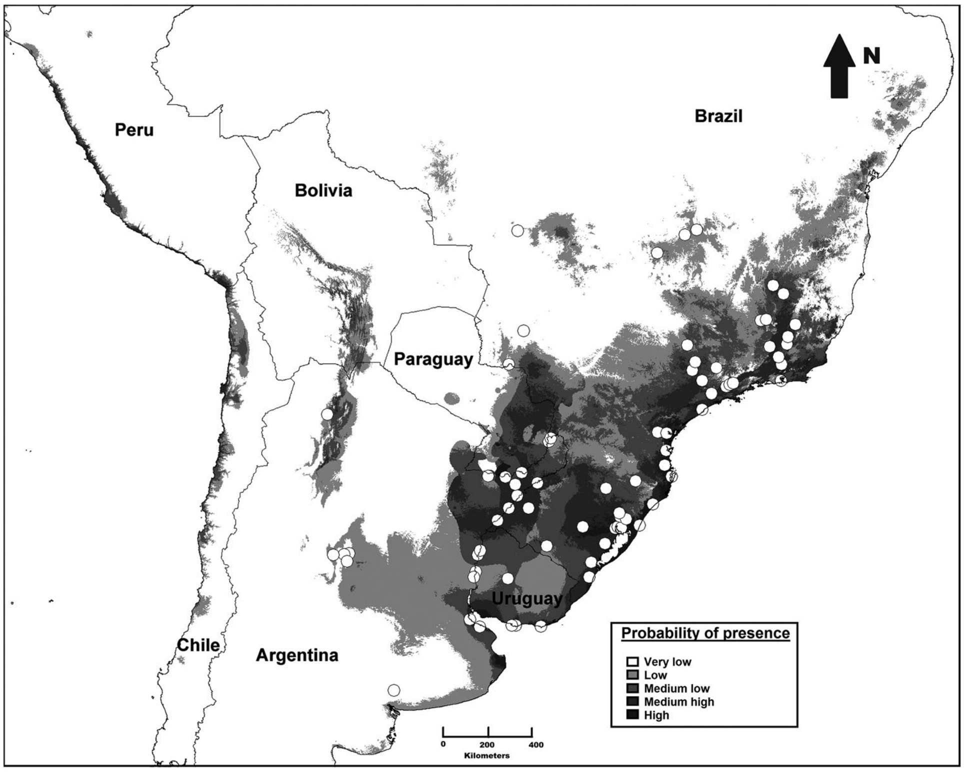

Figure 4. MaxEnt predictions of the potential distribution of *Pseudosuccinea columella* in South America on the basis of 11 temperature variables. Darker areas indicate higher probability of presence; points show the 74 occurrence points used for modelling. All the areas outside the portrayed area belong to the 'Very low' category.

has not been recorded previously in southern Pampas (pers. com. Carlos B. Villamil, BBB Herbarium). Zelaya (2002) pointed out that the trade in aquarium plants was the likely means of introduction of *P. columella* in the botanical gardens ponds in Buenos Aires and La Plata.

The site at Napostá Grande stream where two juveniles of *P. columella* were found in 2012 was intensively searched for aquatic snails in February 2011 but no specimens were found on that occasion. This is one of the nearest points of this stream to the Ventana stream (11.5 km) so a recent colonization from this

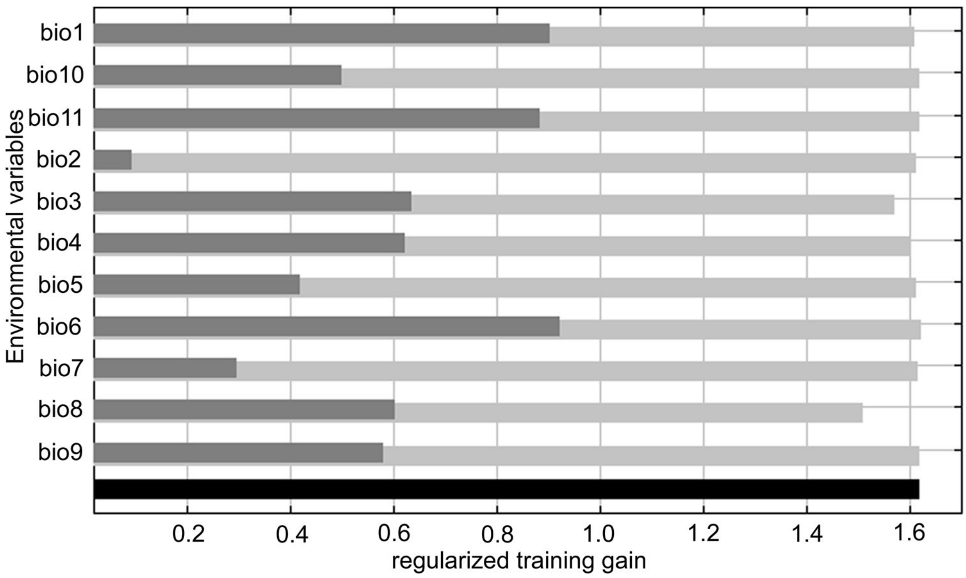

Figure 5. Jackknife test of variable importance of training gain for the MaxEnt model for *Pseudosuccinea columella*; the environmental variables are: bio1 (annual mean temperature), bio2 (mean diurnal range), bio3 (isothermality), bio4 (temperature seasonality), bio5 (maximum temperature of warmest month), bio6 (minimum temperature of coldest month), bio7 (temperature annual range), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio10 (mean temperature of warmest quarter) and bio11 (mean temperature of coldest quarter). Black bars show the training gain using all variables, dark grey bars the gain using only variable and light grey bars indicate the gain using all the remaining variables.

source is not unlikely but it may also be a recent independent introduction from the same original source. At first sight, the natural spread among basins in the region seems unlikely because of the very low connectivity of the drainage system of the southern slope of Tandilia and Ventania Mountains (Figure 1). However, the exotic freshwater snail *Physa acuta*, which was first reported in 1987 in the Napostá Grande stream at Bahía Blanca city—identified as *Physa venustula* Gould, 1847 in Martín (2001)—is today widely distributed in southern Pampas (Martín *et al*. 2001; Tietze and De Francesco 2010; Seuffert and Martín 2013); in fact, it was found at 13 of 32 sites and at all the basins surveyed in the present study. It seems clear that *P. columella* has not yet spread through the waterways of this area but this may be because of its very recent introduction or the low environmental suitability of the area.

The species diversity of native freshwater snails on the southern slopes of the Tandilia and Ventania Mountains is quite low: in addition to the four species found in the sampling, the native lymnaeid *Galba viator* (d'Orbigny, 1835) has been recorded in southern Pampas and northern Patagonia (Castellanos and Landoni 1981; Paraense 2005) although it is quite rare in these drainage systems (Martín *et al*. 2001; Tietze and De Francesco 2010; Seuffert and Martín 2013). The fast expansion of *Physa acuta* in the area in the last three decades indicates that the biotic resistance of these native snail assemblages is low. *Pseudosuccinea columella* is capable of reproducing by selfing (Gutiérrez *et al*. 2002) and if the area proves to be climatically suitable for its long-term establishment there is a chance that it will numerically dominate these snail assemblages, as has occurred in other invaded areas even when other highly invasive snails were present (Grabner *et al.* 2014).

The model generated for *P. columella* by MaxEnt with temperature variables only performed almost equally as well as those that included the rainfall variables, indicating that the former are strongly influential on its establishment or expansion. Man-made ponds, reservoirs and channels all make the distribution and spread of aquatic animals more independent of the natural patterns of rainfall and evapotranspiration. According to the MaxEnt model, *P. columella* has the potential to spread further in areas where it has been recorded recently, especially the lowlands of Córdoba province in central Argentina and the Yungas ecoregion in northwestern Argentina (Salta, Jujuy and Tucumán provinces), Bolivia and southern Perú. The southern coast of the Río de la Plata also seems especially suitable for establishment and the risk seems high as the species is already present (Castellanos and Landoni 1981; Zelaya 2002). The coastal areas of Chile and Perú between 10°S and 30°S also appear as suitable from a thermal regimen perspective; *P. columella* has not been recorded yet in Chile (Letelier *et al*. 2007) but it has been mentioned from the coast and eastern Andean slopes of Perú (Ramírez *et al*. 2003).

The MaxEnt model for *P. columella* predicted low suitability for its establishment and spread in southern Pampas. This could be related to the fact that most previous reports used for modelling are located at lower latitudes in southeastern Brazil, Uruguay and northeastern Argentina and so the model output may be biased to warmer climates. Other possibilities are that the southern Pampas populations represent an independent introduction from a different country or that the species has evolved some cold resistance since its introduction into Argentina. There has been almost no southwards spread of *P. columella* in Buenos Aires Province since its discovery in La Plata city (Castellanos and Landoni 1981). The populations in artificial ponds in Buenos Aires and La Plata are probably protected by the 'heat islands' of these big cities and perhaps served as invasion bridgeheads (*sensu* Lombaert *et al*. 2010) for the gradual adaptation to a colder climate.

Presence-only climatic matching models of distribution estimate the probability of occurrence in places where the climatic regimen is similar to that of sites already occupied. Although these models are only applicable nowadays to *P. columella*, they have some pitfalls. For instance, if an invasive species is still increasing its geographic range this method will probably underestimate the areas where the invader will potentially establish (Peterson 2003). The distribution of *P. columella* in the wild in Argentina remained stable for almost 30 years but new localities have been recorded in the last years at Córdoba, Salta and Buenos Aires provinces. This probably means that a new method of dispersal has appeared (e.g. an increase of aquarium plants trade) or that a new lineage with different ecological capabilities has evolved.

An important epidemiological role has been attributed to *P. columella* in the transmission of *Fasciola hepatica* in northeastern Argentina (Prepelitchi *et al*. 2003). The scarcity of human and veterinary cases of fascioliasis in Buenos Aires province (Mera y Sierra *et al*. 2011) is probably related to the scarcity of lymnaeid hosts, either native or exotic, in the area (Martín *et al*. 2001; Tietze and De Francesco 2010; Seuffert and Martín 2013). The discovery of a well-established population of an intermediate host together with a worldwide invasion history and the signs of its incipient spread within and among streams indicate an epidemiological scenario more favourable to the spread of the parasite.

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Disclosure statement

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