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Established but not spreading: the tropical invasive snail *Melanoides tuberculata* in a geothermally warmed channel in temperate Southern Pampas

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Abstract: *Melanoides tuberculata* is a freshwater snail native to Old World tropical areas but has invaded tropical and subtropical regions around the world. In Argentina, populations established in natural environments were reported from northeastern tropical provinces. Here we report for the first time the presence of *M. tuberculata* in a geothermally warmed channel in temperate Southern Pampas. We mapped its distribution in the channel, searched for its presence in five nearby basins, estimated the risk of establishment and expansion in Argentina with distribution models and analyzed shape variation through geometric morphometrics. *Melanoides tuberculata* was recorded exclusively in the channel in sites with temperatures between 20 and 40°C, with almost no overlap with other snails. No evidence of *M. tuberculata* was found in nearby basins. The distribution model predicted that only northernmost areas from Argentina are suitable for this species, where it could impact snail communities and food webs if introduction through the aquarium trade is not prevented. The absence of males indicates parthenogenetic reproduction and probably a recent invasion. Shell shape variation in this population, 15 % of which is attributable to allometry, encompasses the shapes of specimens from other South American populations, suggesting that all belong to the same lineage.

Key words: Thiaridae, distribution models, MaxEnt, geometric morphometrics, allometry.

INTRODUCTION

Biological invasions are among the greatest threats to biodiversity, being responsible for strong economic, health and social impacts (Simberloff et al. 2013, Pyšek et al. 2020). Freshwater mollusks are a group with a particularly great potential for ecosystem and socioeconomic impacts (Strayer 2010). In South America, the patterns of introduction and spread of non-native mollusks are still understudied even though the number of cases has increased exponentially during the last two centuries (Darrigran et al. 2020). In freshwater habitats from Argentina, five non-native species of snails and at least two of bivalves have been detected (Ovando & Cuezzo 2012, Martín & Tiecher 2009).

Melanoides tuberculata (Müller, 1774) is a freshwater snail belonging to the Thiaridae family (Caenogastropoda). Its original distribution range comprises the intertropical belt of the Old World, from Africa to southeastern Asia (Glaubrecht 2000), but this species has invaded tropical and subtropical regions all around the world, mainly as a result of the trade of aquarium plants (Facon et al. 2003). Its parthenogenetic reproduction, great fecundity, high tolerance to diverse physicochemical factors and to highly modified urban environments, has transformed *M. tuberculata* in a successful invader (Peso et al. 2010) that frequently dominates, both in terms of number and biomass, freshwater snails' communities (Almeida et al. 2018). This species also has the potential of acting as an intermediate host of both native and non-native parasites, which are responsible for several animal and human diseases (Gutiérrez Gregoric & Vogler 2010).

The first report of *M. tuberculata* in America was in 1964 in Texas, USA (Murray 1964) and ever since it has been successively reported in many South American countries: Venezuela, Perú, Ecuador, Colombia and Brazil (Fernandez et al. 2003, Velásquez et al. 2006, Peso et al. 2011, Coelho et al. 2018, Quirós-Rodríguez et al. 2018), reaching its southernmost limit in northern Argentina (Peso et al. 2011). In this country, established populations were reported to be present in natural environments from the Iguazú (Gutiérrez Gregoric et al. 2007) and the Paraná and Uruguay rivers (Peso et al. 2010), all of them in the tropical Misiones province (Peso et al. 2011). However, in 2010 *M. tuberculata* was found in aquarium shops from La Plata city in northern Buenos Aires province (located 850 km southwards from the known established populations; Gutiérrez Gregoric & Vogler 2010), indicating the risk of its imminent arrival in the Río de la Plata.

In this study we report for the first time the presence of a population of *M. tuberculata* in a semi-natural environment in Southern Pampas (Buenos Aires province, Argentina), located in a temperate region more than 1250 km southwards from the previous records in the wild. *Melanoides tuberculata* was first found in 2016 at an excavated channel that discharges slightly alkaline geothermal water into the Napostá Grande stream (Figure 1). Although newly introduced populations of *M. tuberculata* are usually constituted by one clonal morph without genetic or sexual variation (Samadi et al. 1999), we observed considerable morphological shell variation in this population. Such intrapopulation variation may be related to sexual dimorphism when males are present (Abdelhady et al. 2018), phenotypic plasticity or allometric growth (Elkarmi & Ismail 2007).

Based on these observations, our aims were to: 1) map the distribution of *M. tuberculata* in the above mentioned channel and in the nearby streams, 2) search for the possible establishment of *M. tuberculata* populations in other lotic environments in the region, 3) estimate the risk of establishment and expansion of *M. tuberculata* populations in Argentina using species distribution models, and, 4) perform a morphological study of the specimens found and compare them with other South American specimens.

MATERIALS AND METHODS

Sampling

An abundant population of *M. tuberculata* was discovered in a suburban area of Bahía Blanca city (La Carrindanga Road, 38.68° S, 62.24° W; Figure 1), in an excavated channel conducting water from a thermal well (upwelling temperature: 55° C) that runs for about 650 meters, gradually cooling down, and finally discharges into the Napostá Grande stream. Based on this finding, systematic samplings were performed in that channel and in the nearby reach of Napostá Grande stream during late winter in 2015 and late summer in 2016. Fourteen equidistant samples were taken in the channel by sweeping hand nets with a 1 mm mesh opening in a standardized way through the vegetation and fine sediments. Four (winter) and five (summer) equidistant

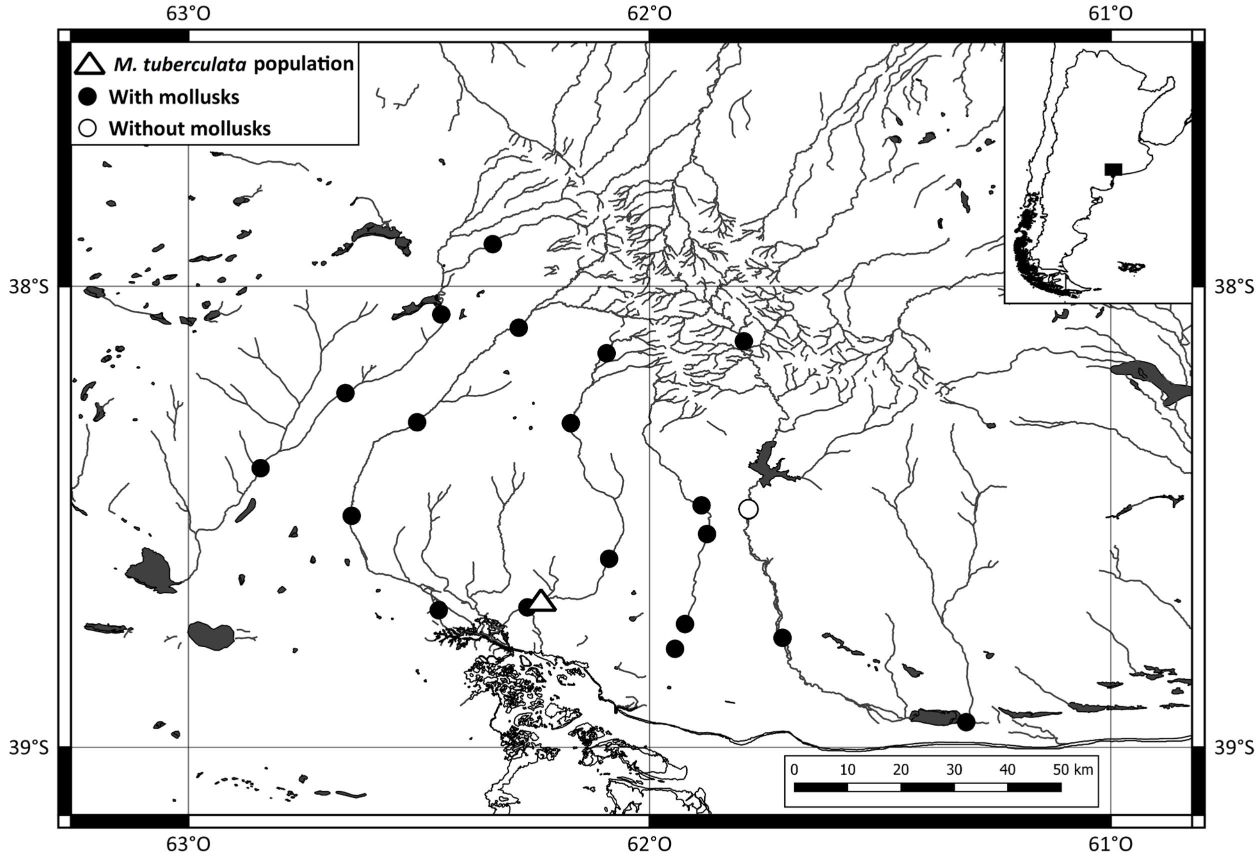

Figure 1. Sampling sites in five lotic waterbodies from Southern Pampas (from west to east: Chasicó stream, Sauce Chico river, Napostá Grande stream, Napostá Chico stream and Sauce Grande river). The white triangle indicates the location of the *M. tuberculata* population found at La Carrindanga Road (Bahía Blanca city).

samples were also taken in the stream reach, two upstream and the rest downstream, from the point where the water from the channel flows into the stream. In all sampling sites, water temperature, oxygen concentration and pH were recorded with a multimeter Horiba®; values recorded in the channel were compared with values recorded in the stream by means of t-tests, for both winter and summer seasons. In the laboratory, the material collected in the samples was cleaned from sediment, detritus and vegetation remains and then examined under a stereoscopic microscope in order to determine the snail species present at each site. (Permit from Buenos Aires Province: DI-2018-07062901-GDEBA-DAPYAMAGP).

A systematic sampling comprising the Napostá Grande stream and all the nearby lotic environments was later performed in order to determine whether *M. tuberculata* had expanded to other sites in Southern Pampas. The sampling scheme included Chasicó stream, Sauce Chico river, Napostá Grande stream, Napostá Chico stream and Sauce Grande river (Figure 1). During March 2018, four sites evenly distributed from the head to the mouth of each of the five watercourses were sampled, searching for living mollusks or their shells. In each site, macromollusks (larger than 1 cm) were carefully searched by wading and by direct observation in the vegetation, sediments and stones. For the micromollusks (smaller than 1 cm), standardized scoops were performed as detailed above for the channel. The samples were preserved in ethanol 70% and taken to the laboratory to search for individuals or empty shells of *M. tuberculata*.

Potential distribution

The potential distribution of *M. tuberculata* in Argentina was estimated with species distribution modeling performed with MaxEnt (Phillips et al. 2006). MaxEnt models are based on presence records only and estimate geographic distributions of species from locality point data and environmental variables by finding the maximum entropy distribution. Occurrence data for *M. tuberculata* in Argentina, Paraguay and Brazil were obtained from published scientific literature (Fernandez et al. 2003, Gutiérrez Gregoric et al. 2007, Peso et al. 2010, 2011, Coelho et al. 2018, Silva et al. 2019). A total of 939 occurrences were retrieved but after a spatial thinning of 20 km to avoid spatial autocorrelation, 357 localities were left. Records from Bahía Blanca and La Plata cities were not considered for modeling since at those sites individuals inhabit semi-natural and artificial environments not reflecting air temperature, the variable used to build several of the bioclimatic variables considered in the analysis (see below).

The environmental layers were composed of 19 bioclimatic variables at a spatial resolution of 30 arc seconds (around 1 km^2), including combinations of annual trends, seasonality and extreme temperature and rainfall conditions (obtained from WorldClim: http://www.worldclim.org; Hijmans et al. 2005). To avoid including highly correlated variables in the models, we performed Spearman's correlation and one variable was selected for the analysis among two or more if their correlation index was higher than 0.8 in absolute value (Jueterbock et al. 2016). Finally, seven among the 19 bioclimatic variables were selected: mean diurnal temperature range (BIO2), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the driest month (BIO14) and precipitation seasonality (BIO15). Models were first calibrated within an area defined with a buffer of 2.5° around the occurrence records and then projected to the boundaries of Argentina. Different combinations of variables were used for modeling and the set with the best performance was selected as detailed in Seuffert & Martín (2021).

Morphological study

The mean shape and the degree of variation of *M. tuberculata* snails found in La Carrindanga Road channel were analyzed using geometric morphometrics. A sample of 29 snails with a shell length between 11 and 27 mm, and so presumably mature snails (Heller & Farstay 1989), were randomly selected. Nine landmarks (Figure 2a; Bookstein 1997) were digitized using

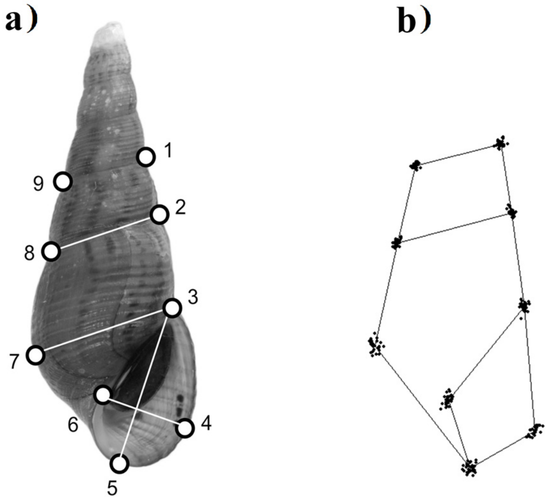

Figure 2. Geometric morphometric analysis of *Melanoides tuberculata* snails from La Carrindanga Road channel (Bahía Blanca city): **a)** landmarks defined on the shell (shell length of the specimen in the photograph is 21 mm) **b)** consensus shape of the set of 29 snails.

TPSdig2 software (Rohlf 2017). The landmarks were similar to those used previously by Brande et al. (1996), though we excluded the apex and the first whorls because they were eroded in many *M. tuberculata* snails from La Carrindanga Road channel. The sex of the snails was determined by the observation of shelled embryos within the snail body and by the red color of the distal part of the visceral mass (corresponding to the testicle in males; Heller & Farstay 1989). An additional set of 100 snails was examined to determine the presence of males in the population.

MorphoJ Software (Version 1.05a; c 2011) was used to perform the Procrustes superimposition of images to account for differences in position, orientation and scale and, later, to study in detail the aligned images (shape) and centroid size (size, Bookstein 1991). The consensus shape of the 29 snails was obtained as a descriptive generalization of the shape of this population of *M. tuberculata* (Figure 2b).

A regression analysis between shape and centroid size was performed in order to determine if the observed variation in shell shape can be explained by allometry. Three South American specimens reported in the literature were included in the same analysis using photographs presented in the following publications: an estuarine specimen from Brazil (12.97°S, 38.65°W, Salvador City; Silva & Barros 2015), another from Paraná river in Paraguay (27.29°S, 56.06°W, Ibicuí Island; Peso et al. 2011) and a third one from Paraná river in Argentina (27.56°S, 56.67°W, Ituzaingó City; Peso et al. 2011).

RESULTS

Sampling

The temperature range recorded in La Carrindanga Road channel was 25.6°C in late winter (44.4°C at the sampling site closest to the upwelling point and 18.8°C at the last sampling site of the channel) and 21.1°C in late summer (46.2°C and 25.1°C, respectively). The thermal range recorded in the samples from the Napostá Grande stream was almost null in both seasons; the mean water temperature in the stream was 13.8°C in winter and 22°C in summer (Figure 3). Mean temperature was significantly higher in the channel than in the Napostá Grande stream, both in winter (27.7-13.8°C, $p<0.001$) and in summer (34.5-22°C, $p<0.001$). Mean oxygen concentrations were also significantly lower in the channel than in Napostá Grande stream (10.42-18.72 mg.l^{-1}, $p<0.001$, in winter; 6.64-9.22 mg.l^{-1}, $p=0.020$, in summer). Water was slightly alkaline in both the channel and the stream, mean pH values not being significantly different between them in winter (7.86-7.97, p=0.286; data not recorded in summer).

Melanoides tuberculata was recorded in the channel at sampling sites with temperatures between 38.4 and 20.3°C in winter and between 40 and 25.5°C in summer but it was not found in the Napostá Grande stream nor in the channel sites located closest to it. Abundance of other native (*Heleobia parchappii* and *Chilina parchappii)* and exotic snails (*Physa acuta*) increased at sites with temperatures below 20°C in late winter and 25°C in late summer, temperatures at which *M. tuberculata* was absent. Furthermore, *M. tuberculata* was the most abundant snail in the channel whereas the native *H. parchappii* was dominant in the lower part of the channel and in the Napostá Grande stream (Figure 3). There was almost no overlap in the distribution of *M. tuberculata* and the other snails along the channel.

Living mollusks were found at 19 of the 20 sites sampled in the five independent basins in Southern Pampas (Napostá Grande stream and four nearby watercourses). No living *M. tuberculata* or shells were found at any of the

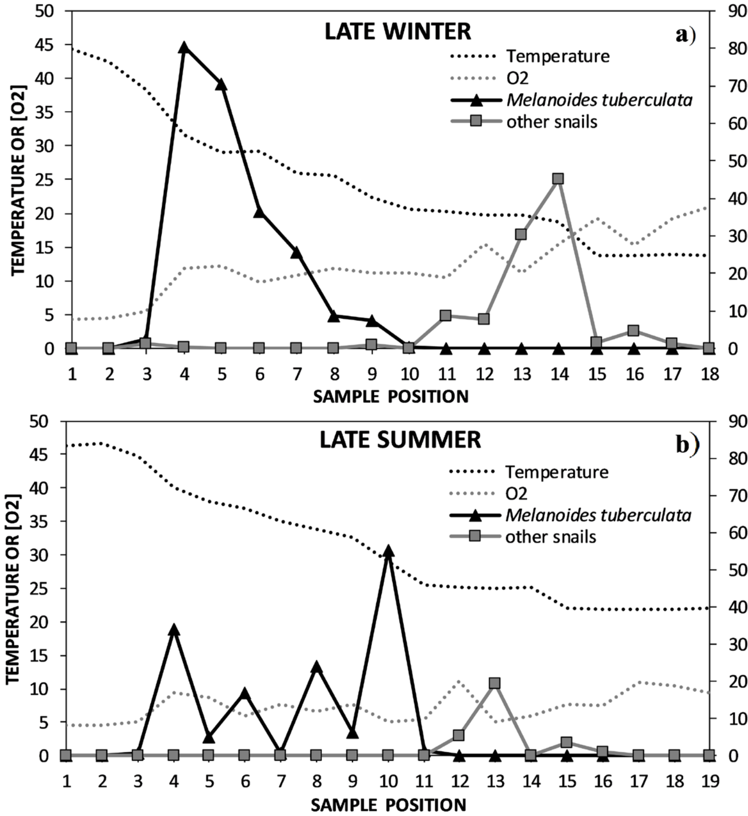

Figure 3. Abundance of *Melanoides tuberculata* and other snails, temperature (°C) and oxygen levels (mg.l^{-1}) recorded in two samplings performed in Bahía Blanca in an excavated channel (samples 1-14) that discharges in the Napostá Grande stream between sites 16 and 17: **a)** late winter 2015; **b)** late summer 2016.

20 sites sampled (Figure 1), including a site in the Napostá Grande stream located 3 km downstream from the discharge of the channel.

Potential distribution

The species distribution model generated with MaxEnt indicates that the areas around Bahía Blanca city where the new population of *M. tuberculata* was recorded are not suitable for its establishment (Figure 4). Moreover, most of Argentina appears to be unsuitable for this species; only some areas of the northernmost provinces would be suitable. The group of environmental variables with the best performance was the set that only includes temperature variables (BIO2, BIO4, BIO5 and BIO6). Temperature seasonality (BIO4), and mean diurnal temperature range (BIO2) were the variables with the greatest contribution for model development. The response curves show that the maximum values of suitability are in areas with intermediate values of temperature seasonality (Figure 5a) and the lowest values of mean diurnal temperature range (Figure 5b).

Morphological study

All the snails examined were females. The regression analysis performed to test for allometry in the set of *Melanoides tuberculata* snails was significant (Figure 6); variation in centroid size explains 15% of the shape variation in the size range studied (11-27 mm; permutation test, $p<0.01$). The allometry observed in the wireframe graphs was verified in the shells' photographs of the two snails with the most different regression scores. The overall shape of the body and the aperture shape become substantially more elongated as size increases, the change being more noticeable in the latter. The three snails from other populations fall well within the equal-frequency ellipse that contains *ca.* 90% of the snails.

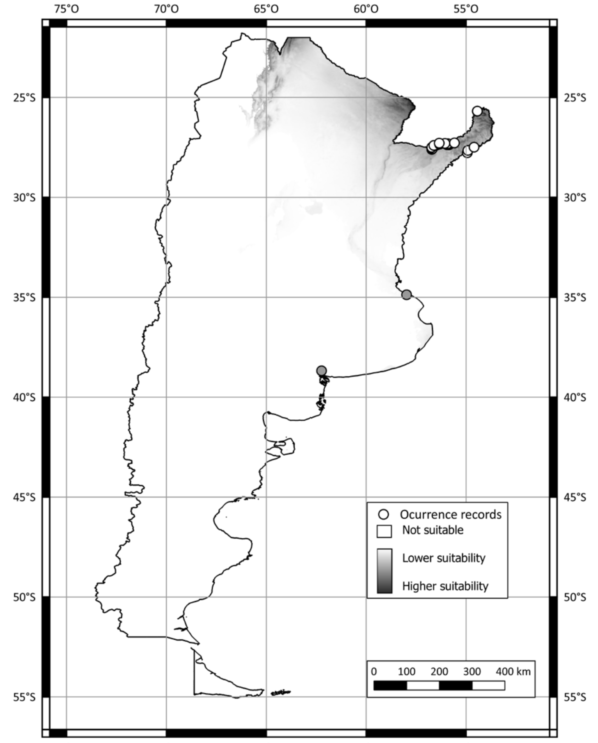

Figure 4. Occurrence records of *Melanoides tuberculata* in Argentina (white dots) and environmental suitability estimated with MaxEnt species distribution model. Grey dots indicate two records from aquarium shops in La Plata city and from the geothermally warmed channel in La Carrindanga Road (Bahía Blanca city).

DISCUSSION

Melanoides tuberculata was only found in a semi-natural channel receiving geothermal alkaline water, but not in the connected Napostá Grande stream nor in the nearby lotic environments of the region, which are characterized by a temperate climate. It is presumed it is the occurrence of low temperatures that precludes the persistence of populations of this species in the area. The establishment of the only population recorded in Bahía Blanca was most likely possible due to the existence of a geothermally warmed environment that exhibits much higher temperatures than those normally recorded in all nearby natural waterbodies. The presence of *M. tuberculata* populations has also been reported in thermally polluted, geothermally warmed or thermally stable spring environments from other temperate regions such as Poland, Southern United States, and New Zealand (Duggan 2002, Mitchell & Brandt 2005, Maciaszek et al. 2019).

The occurrence of *M. tuberculata* in Bahía Blanca might have been facilitated by anthropic actions associated with the aquarium trade, as has happened in other non-native places (Gutiérrez Gregoric & Vogler 2010, de Assis et al. 2014, Silva et al. 2019). Non-native species are likely to be found in aquaria containing aquatic plants and in those that are heated (Duggan 2010). This species is traded in Bahía Blanca city and is also easily available for sale and delivery on national websites (pers. obs., Peso et al. 2011). The presumption the latter has been the means of introduction is reinforced by the absence of hydrological connection between Bahía Blanca and the nearest place where *M. tuberculata* has been reported, at a distance of 630 km in La Plata city.

The result of the species distribution model performed with MaxEnt indicates that the climatic conditions in Bahía Blanca are not suitable for the establishment of *M. tuberculata*. In fact, most of Argentina would appear not to be suitable for this species, with only some areas of the northernmost provinces showing some level of suitability. These areas are comprised by part of the Yungas and the Mesopotamia regions, between the Uruguay and Paraná rivers, suggesting that this species could expand some distance beyond the already reported localities in Misiones province, Argentina. The presence of *M. tuberculata* in other invaded South American freshwater environments was pointed out as the fact responsible for a decrease in native mollusks diversity (Almeida et al. 2018). The lack of an overlap between the distribution of *M. tuberculata* and that of other snails in the channel in Bahía Blanca seems to

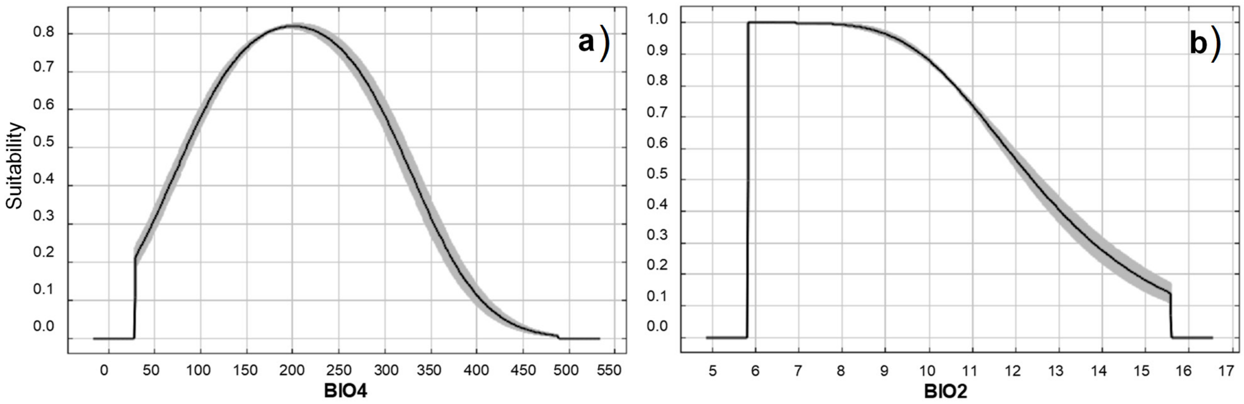

Figure 5. Response curves for the environmental variables with the highest contribution to the MaxEnt species distribution model for *Melanoides tuberculata* in Argentina: a) temperature seasonality (BIO4); b) mean diurnal range of temperature (BIO2). Values shown are averages (black line) and standard deviation (gray bands) calculated over 10 replicate runs. (BIO4 is temperature [°C] standard deviation × 100 and BIO2 is temperature [°C]).

indicate some antagonism, since a coincidence in their respective lower and upper thermal limits seems unlikely. Hence, it is important to discourage and prevent the release of this species in those climatically suitable regions from northern Argentina, where it could have an impact on the snail communities and food webs. The lack of records of *M. tuberculata* in the sampled waterbodies from Southern Pampas, and indeed in most of eastern Argentina (except for zones near the Capricorn tropic), supports the predictions of the distribution model, despite the likely presence of this species in aquaria from most cities of the region.

The main feature characterizing high suitability regions according to the species distribution model is a low variation in temperature, a climatic condition typical of subtropical areas from northern Argentina. High values of temperature seasonality usually implicate low temperatures during winter months, which are probably the reason precluding the establishment of *M. tuberculata* in regions with temperate climates such as Bahía Blanca and nearby basins. Mitchell & Brandt (2005) studied the temperature tolerance of *M. tuberculata* and concluded that snails will not survive in waters attaining temperatures below 18°C. In the basins from Southern Pampas, water temperature is below 18°C during six months, from April to September and also reaches values below 10°C during several days in winter (Seuffert et al. 2010), indicating that *M. tuberculata* will not be able to establish in this region. Weir & Salice (2012) also analyzed the thermal tolerance of *M. tuberculata* and concluded that cold temperatures are a likely limiting factor in its expansion as an invasive species in temperate climates.

The discharge of thermal water from the channel into the Napostá Grande stream does not change water temperatures in this watercourse, probably due to a previous cooling and its small volume discharge relative to that of the stream. The null thermal impact precluded the establishment of even temporal populations of *M. tuberculata* in the stream. However, the situation may be different in other watercourses in the region. For instance, the lower course of the Saladillo de García rivulet (38.68°S, 62.41°W) receives cooling water from Almirante Brown thermoelectric power plant, which may turn it into a suitable place for a localized establishment of *M. tuberculata*. Moreover, other geothermally

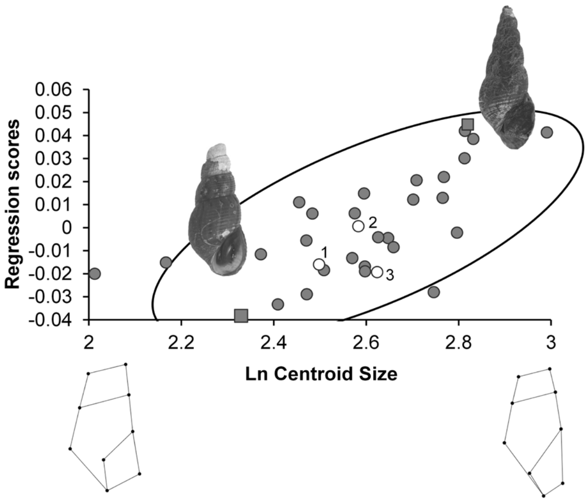

Figure 6. **Multivariate regression between shell size (Ln centroid size) and shape of *Melanoides tuberculata* performed to detect allometry. Gray dots correspond to snails from La Carrindanga Road (Bahía Blanca city) and white dots correspond to those from other localities (1: Paraguay; 2: Argentina; 3: Brazil). Wireframe snails were generated to indicate the shape variation along size axis (scale factor: ±1); photographs correspond to the snails with the smallest and largest regression scores (gray squares) that were re-scaled to the same shell length. Equal-frequency ellipse contains *ca.* 90% of the data.**

warmed or thermally polluted environments in Argentina located in regions *a piori* not climatically suitable for the establishment of this species, could serve as "thermal refuges" and therefore become colonized, especially in places near urbanizations.

The absence of male specimens in the samples from Bahía Blanca could be an indicator of a relatively recent invasion (Samadi et al. 2000). Approximately, 15% of the observed morphological variation is explained by allometry. This value could be higher if a larger range of sizes is considered, incorporating smaller, immature specimens. Similar to that reported by Elkarmi & Ismail (2007), an elongation of the shell and the aperture was observed with an increase in size. No important differences were observed when comparing the specimens from Bahía Blanca with three specimens corresponding to other localities from South America, suggesting that, although genetic studies are necessary, the specimens belong to the same, or at least a close, lineage.

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