Population structure of a native and an alien species of snail in an urban area of the Atlantic Rainforest

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Native \textit{Megalobulimus paranaguensis} was identified on Brazil’s Ilha Porchat promontory, an area that \textit{Achatina fulica} commonly populates. The population structures of these species were investigated for interactions. Spatial distribution, niche overlap and mark–recapture analysis were conducted. The outer lip of \textit{M. paranaguensis} and environmental variables were measured. One and two abundance peaks were observed for \textit{A. fulica} and \textit{M. paranaguensis}, respectively. Survivorship was higher in \textit{A. fulica}. Distribution was aggregate for \textit{M. paranaguensis}, whereas for \textit{A. fulica} it varied from random to aggregate. Both species aggregate as abundance increases. The lifespan of \textit{M. paranaguensis} in this location is shorter than its lifespan in a nearby location. \textit{Achatina fulica} was affected by soil temperature and humidity; \textit{M. paranaguensis} was influenced by humidity. Niche overlap was random. The results show that \textit{M. paranaguensis} can keep its natural activity and abundance in the presence of \textit{A. fulica}, but environmental degradation impacts \textit{M. paranaguensis} and should be evaluated.

\textbf{Keywords:} \textit{Achatina fulica; Megalobulimus paranaguensis; population structure; alien species}

\section*{Introduction}

\textit{Megalobulimus paranaguensis} (Pilsbry and Ihering in Pilsbry 1900) was originally described from the Brazilian state of Paraná from the southern coastal cities of Peruíbe and Iguape in the state of São Paulo (Morretes 1954; Simone 2006). This species was believed to be endemic to this region; however, since 2008, it has been found in Ilha Porchat, a promontory in the city of São Vicente, São Paulo, further north. This environment is already populated by the giant African snail, \textit{Achatina fulica} Bowdich, 1822, an invasive species.

The species of the genus \textit{Megalobulimus} tend to have low population densities (Eston et al. 2006) and, like other native species of terrestrial molluscs, have low reproductive potential (Simone 1999), spawning only two to five eggs per batch (Sobreira and Molina 2002). They are herbivorous and the most characteristic aspects of their behavioural ecology include burying themselves in the rainforest soil or leaf litter during the day and having a dormancy period (Bequaert 1948). The species also has a long lifespan, known to reach up to 35.5 years (Fontenelle and Miranda 2012), although the species population dynamics remain poorly understood, because it is not
commonly found. In addition, the species of the genus *Megalobulimus* possess large (approximately 10-cm shell length in *M. paranaguensis*) thick and round shells with vertical nepionic riblets, as well as a thickened outer lip as adults (Bequaert 1948) and a buccal fringe (Leme 1973).

In contrast, *A. fulica* is a pulmonate land snail with a shell 15–20 cm in length and 10–12 cm in width, listed as one of the top 100 most invasive species worldwide (Alowe et al. 2004). This snail, along with other molluscs, is the intermediate host of the nematode *Angiostrongylus cantonensis* (Chen, 1935), which causes eosinophilic meningoencephalitis (Teles et al. 1997; Caldeira et al. 2007). It is therefore a public health concern, because it is present in many Brazilian states (Thiengo et al. 2007). *Achatina fulica* is a generalist species (Albuquerque et al. 2008) which lays clutches of up to 400 eggs with an annual production of up to 1200 eggs (Rault and Baker 2002). It can be differentiated from *Megalobulimus* by its conical shell, lack of vertical nepionic riblets, lack of outer lip during adulthood and lack of buccal fringe.

Many species from the genus *Megalobulimus* are endangered as a consequence of popular management actions taken to control the spread of the giant African snail *A. fulica* (Colley and Fischer 2009). In addition, degradation of their natural habitat has considerably contributed to their decline. Previous research has reported on the extinction risk for some species of this genus (Leme 1989; Leme and Indrusiak 1990; Mansur and Leme 1996) as well as on their population decline (Fischer and Colley 2005). In fact, Bequaert (1948) had suggested a risk of population decline of species from this genus due to large-scale deforestation in some regions of Brazil. Despite the pressing issues affecting this species, data on population structure and dynamics and on interspecific interactions among cohabiting species of terrestrial molluscs are scarce. On some islands in the Pacific and Indian oceans, the efforts to biologically control the spread of *A. fulica* (through the introduction of predatory snails and flatworms) have led to the extinction or decline of locally endemic island species of land snails (Cowie 1992, 2001; Civeyrel and Simberloff 1996); however, to the best of our knowledge, no studies have provided evidence on the competition between *A. fulica* and the native fauna.

Understanding the population structure of both native and alien species and the interspecific interactions among them is important to assess the species’ conservation status and the development of appropriate policies for nature conservation and pest management. Here we aimed to: (1) assess the population structure and spatial distribution of *A. fulica* and *M. paranaguensis* in Ilha Porchat and their response to environmental variables, and (2) check for interspecific interactions between these species based on spatial niche overlap.

**Material and methods**

**Study site and data collection**

The study was conducted on a promontory known as Ilha Porchat (23°58246.37″ S, 46°22208.79″ W, Figure 1), located in the city of São Vicente, in the state of São Paulo. This promontory is a small island that is artificially connected to São Vicente Island with the urban area still containing small patches of original Atlantic Rainforest, one of the five most significant biodiversity hotspots worldwide (Myers et al. 2000).
Three areas were chosen for snail capture. Area 1 was 8309.02 m², Area 2 was 3819.08 m² and Area 3 was 2342.19 m². These areas were divided by existing streets and were approximately 15 m apart from each other. In each area, 5 × 5 m quadrats were marked by sticks. The number of quadrats per area was defined in relation to the area extension; hence, Area 1 contained six quadrats; Area 2 contained three
quadrats; and Area 3 contained two quadrats. The vegetation in Area 1 was denser, more arboreal, and had more leaf litter than that of Areas 2 and 3. Human influence was similar among areas, with residential garbage found in all areas. In addition, these areas were commonly used as sites for religious offerings, and were frequently occupied by homeless residents.

Both *M. paranaguensis* and *A. fulica* were collected bimonthly from all quadrats. To establish dispersal among areas, all the specimens found in the quadrats from 19 April 2011 to 9 April 2012 were marked using a different colour nail polish in each area. Each animal was marked individually with a number. All species from the genus *Megalobulimus* (Bequaert, 1948) and the species *A. fulica* (Tomiyama, 2000; Rault and Baker, 2002) are nocturnal species; therefore, collections were performed at dusk. Species abundances was determined in each quadrat. Humidity and soil temperature were also recorded in every quadrat from July 2011 to June 2012.

**Population structure**

Population parameters were estimated using the Schwarz–Arnason model (Schwarz and Arnason 1996). The fundamental model parameters were apparent survival rate ($\Phi$), detectability probability ($p$) and probability of entry of an individual into the population ($\beta$). These parameters were estimated using a Generalized Linear Model (GLM) using the multinomial logit link function for entry probability and the logit link function for apparent survival and detectability probability. The model also featured derived parameter recruitment ($B$) and the estimated abundance in each sample ($N_i$). All parameters were estimated with a 90% confidence interval, using multinomial distribution for entry probability, Poisson distribution for superpopulation and binomial distribution for all other parameters (Schwarz and Arnason 1996). The chi-square test ($\chi^2$) was used to test whether the assumption that all individuals were equally likely to be captured was violated. Mark–recapture analysis was performed on *M. paranaguensis* from 2 May 2012 to 24 October 2012 only because this species aestivates. Mark–recapture analysis was performed on *A. fulica* for a year-long period (from 19 April 2012 to 9 April 2013).

The basic parameters may remain constant or may vary over time and their combinations may lead to different models. The Akaike information criterion with corrections for small samples (AICc; Burnham and Anderson 2001) was used to determine which model best fitted the data. In addition, the $\Delta$AICc and Akaike weight were used to verify whether the model was the most parsimonious (Burnham and Anderson 2001; Johnson and Omland 2004). The data were considered to not fit the model when $\Delta$AICc was > 6. The over-dispersion index (c-hat) verified whether the data were over-dispersed.

**Spatial distribution, niche overlap and correlation with environmental variables**

Species’ spatial distribution was calculated using the standardized Morisita index (Krebs 1999), with a value > 0.5 indicating clumped distribution, values < −0.5 indicating uniform distribution and values between 0.5 and −0.5 indicating random distribution. Previous studies have shown that this index is best suited for analysing the spatial distribution, because it is not affected by sample size (Malhado and Petrere Jr 2004). The relationship between the dispersion index and the total number of
Specimens found in each collection was assessed using the Pearson linear correlation coefficient after the data had been log$_{10}$ transformed.

Spatial niche overlap was analysed with the Pianka index (1973) and randomness was tested using the Monte Carlo method, based on RA3 algorithm with 1000 permutations, recommended by Winemiller and Pianka (1990) as the ideal method to analyse non-random niche patterns. Dispersion index and inch overlap analysis were carried out using all data from May 2011 to June 2012.

A Spearman rank correlation was used to test for correlations between the environmental variables studied. We used a GLM with a log-link function and negative binomial errors using Achatina and Megalobulimus abundance determined for each quadrat as dependent variables. We used the environmental parameters as independent variables. The effect of each variable was tested using the $z$-test.

**Age and growth**

The outer lip (OL) of *M. paranaguensis* was measured, using a 0.01-mm precision digital calliper; age was subsequently determined using the formula: Age = 0.6633 × OL$^{1.8095}$ (Fontenelle and Miranda 2012). The data obtained were used to build a Von Bertalanffy curve.

Mark–recapture models were adjusted using Mark software (White and Burnham 1999). Niche overlap was analysed using the EcoSim 7.0 software (Gotelli and Entsminger 2001). The other analyses were performed in R 2.14.0 (R Development Core Team 2011), using the vegan package (Oksanen et al. 2011) to calculate the standardized Morisita index, the FSA package (Ogle 2011) to determine the Von Bertalanffy curve; the qpcR package (Spiess and Ritz 2012) to calculate the determination coefficient for the Von Bertalanffy curve and the MASS package (Venables and Ripley 2002) for GLM, used to test for correlations with environmental variables.

**Results**

**Population structure**

During the period studied, we found 121 *M. paranaguensis* specimens and recaptured 16. The number of specimens per quadrat ranged from 0 to 11 and average density was 0.04 individuals/m$^2$. Recaptures were generally low, as shown by the recaptured to marked ratio (0.11). There was not an equal catchability mark–recapture assumption violation ($\chi^2 = 3.36; \text{DF} = 5; p = 0.64$) and the data were not over-dispersed (c-hat = 0.67).

A total of 295 *A. fulica* specimens were found, and 89 were recaptured. The number of specimens per quadrat ranged from 0 to 22 while the average density was 0.07 individuals/m$^2$. The recaptured-to-marked ratio was relatively high (0.25). There was not an equal catchability mark–recapture assumption violation ($\chi^2 = 12.20; \text{DF} = 45; p = 1.00$) and the data were not over-dispersed (c-hat = 0.27).

The $\Phi(.p(t)\beta(t)$ model, which assumes constant survival rate and variable detectability and entry probability over time, was the best fit for the data (Table 1), for both species: *M. paranaguensis* (AICc = 222.76; AIC weight = 0.99) and *A. fulica*
Table 1. Results of the population model selection for mark–recapture analysis.

| Model          | Description                                                | Megalobulimus paranaguensis | Achatina fulica |
|----------------|------------------------------------------------------------|----------------------------|----------------|
|                | AICc  | ΔAIC | AIC weight | Parameters | AICc  | ΔAIC | AIC weight | Parameters |
| Φ(.)p(t)β(t)   | Constant survivorship; variable detectability and entry probabilities. | 222.76  | 0        | 0.99   | 19   | 859.82  | 0        | 0.99   | 44   |
| Φ(t)p(t)β(t)  | Saturated model                                            | 242.57  | 19.80    | 0       | 27   | 882.91  | 23.09    | 0.01   | 66   |
| Φ(.)p(.)β(t)  | Constant survivorship and detectability probability; variable entry probability. | 238.96  | 16.20    | 0.01   | 11   | 884.49  | 24.66    | 0       | 24   |
| Φ(t)p(t)β(.)  | Variable survivorship and detectability probability; entry probability constant. | 50,784.14 | 50,561.38 | 0       | 20   | 74,119.69 | 73,259.86 | 0       | 47   |
| Φ(t)p(.)β(.)  | Variable survivorship, constant detectability and entry probabilities. | 50,862.15 | 50,628.04 | 0       | 13   | 74,339.01 | 73,479.18 | 0       | 24   |
| Φ(t)p(.)β(t)  | Variable survivorship and entry probability; Constant detectability probability. | 241.26  | 7.16     | 0       | 22   | 74,390.02 | 73,530.19 | 0       | 45   |
| Φ(.)p(.)β(.)  | Reduced model.                                             | 50,939.90 | 50,705.8  | 0       | 4    | 75,230.37 | 74,370.54 | 0       | 4    |
| Φ(.)(t)pβ(.)  | Constant survivorship and entry probability; Variable detectability probability. | 50,937.46 | 50,714.74 | 0       | 12   | 75,238.86 | 74,379.03 | 0       | 24   |

Notes: The values of the most parsimonious model are in bold. Legends: AIC = Akaike information criterion; Φ = apparent survivorship; p = detectability probability; β = entry probability. The notation (.) indicates that the parameter was constant through time in the model and the notation (t) indicates that the parameter varied through time in the model.
For the alternative model, ΔAICc was > 6 for both species (M. paranaguensis: ΔAICc = 16.20; A. fulica: ΔAICc = 23.09).

The apparent survival rate per year for M. paranaguensis [Φ = 0.73; 90% confidence interval (90% CI) = 0.71–0.76] appeared to be high; however, detectability probability is low, because the value was often lower than 0.10. Detectability probability peaked during July and August, decreased in September and peaked again in October (Figure 2A). A single recruitment peak was observed at the end of July, when B = 151 specimens (Figure 2C). The abundance estimated by the model (Figure 2B) gave two peaks, one high peak in May (N_i = 402.24), and a smaller peak in early August (N_i = 238.45), because of the recruitment that occurred at the end of July.

Achatina fulica had a significantly higher apparent survival rate per year (Φ = 0.78; 90% CI = 0.77–0.80) than M. paranaguensis. At the beginning of the study period, detectability probability appeared to be low, but it increased during February and March (Figure 3A). Abundance peaked only once in the period with N_i = 592 specimens (90% CI = 324–860; Figure 3B) while recruitment peaked several times (Figure 3C), particularly from September to November and from January to March.

Spatial distribution, niche overlap and correlation with environmental variables

Spatial distribution data for both species and niche overlap are shown in Table 2. Megalobulimus paranaguensis was sighted a total of 239 times: 216 of the sightings were in Area 1, 12 in Area 2 and 11 in Area 3. The dispersion index was estimated for only 16 of the 29 collections, avoiding the aestivation period. Aggregation was observed in 10 of the 16 collections, indicating a predominantly aggregated spatial distribution pattern. No dispersion among areas was detected, as all individuals found always were marked with the colour assigned to the area. There was a positive correlation between abundance and the dispersion index (Pearson: r = 0.6; p < 0.0001; DF = 14).

A total of 598 A. fulica sightings occurred in the quadrats: 283 in Area 1, 165 in Area 2 and 150 in Area 3. Dispersion index was estimated for 26 of the 29 collections, and aggregation was observed in 13 of the 26 collections, indicating a mixed distribution pattern, with the species showing both aggregate and random distribution. A positive correlation was observed between abundance and the dispersion index (Pearson: r = 0.6; p <0.0001; DF = 22). Achatina fulica individuals were relatively well distributed over the three areas. As for M. paranaguensis, dispersion among areas was not detected.

Throughout the study, non-random niche overlap was estimated for four dates. For three of these dates, niche overlap was significantly higher than expected by chance; on one date (2 May 2011), the value was lower than expected.

Figure 4 shows humidity and soil temperature variation during the study period. Humidity fluctuated over time: it peaked in August, then decreased until the first half of November and increased again after that. Soil temperature increased from June to January and decreased after that, with the lowest (albeit abnormally low) value recorded on 27 September 2011.

Soil temperature and humidity were not correlated (r = −0.08; DF = 262; p = 0.21). Megalobulimus paranaguensis distribution and abundance were positively
Figure 2. Detectability probability (A), abundance (B) and recruitment (C) estimated for *Megalobulimus paranaguensis* during the study. The error bars show 90% confidence intervals.
affected by humidity ($b = 0.22; z = 7.99; p < 0.0001$), but not by soil temperature ($b = -0.07; z = -1.37; p = 0.16$). *Achatina fulica* distribution and abundance were positively influenced by both soil temperature ($b = 0.16; z = 4.65; p < 0.0001$) and humidity ($b = 0.04; z = 2.63; p = 0.008$).
Table 2. Results of the Standardized Morisita dispersion index (Stmo) for the spatial distribution of studied species and the Pianka index of niche overlap.

| Date       | *Megalobulimus paranaguensis* | *Achatina fulica* | Niche overlap |
|------------|-------------------------------|------------------|--------------|
|            | Stmo distr.                   | Stmo distr.      |              |
| 05/02/2011 | 0.52 aggregated               | 0.51 aggregated  |              |
| 06/06/2011 | −0.14 random                  | 0.26 Random      |              |
| 06/20/2011 | −0.07 random                  | 0.11 Random      |              |
| 07/11/2011 | 0.46 random                   | 0.56 aggregated  |              |
| 07/26/2011 | 0.53 aggregated               | 0.11 random      |              |
| 08/09/2011 | 0.53 aggregated               | −0.11 random     |              |
| 08/25/2011 | 0.53 aggregated               | −0.44 random     |              |
| 09/13/2011 | 0.01 random                   | 0.19 random      |              |
| 09/27/2011 | 0.55 aggregated               | −0.01 random     |              |
| 10/07/2011 | 0.53 aggregated               | 0.51 aggregated  |              |
| 10/24/2011 | −                               | 0.55 aggregated  |              |
| 11/23/2011 | −                               | 0.52 aggregated  |              |
| 12/06/2011 | −                               | −0.09 random     |              |
| 12/28/2012 | −                               | 0.73 aggregated  |              |
| 01/11/2012 | −                               | −0.29 random     |              |
| 01/23/2012 | −                               | 0.51 aggregated  |              |
| 02/06/2012 | −                               | 0.33 random      |              |
| 02/22/2012 | −                               | 0.51 aggregated  |              |
| 03/12/2012 | −                               | 0.62 aggregated  |              |
| 03/26/2012 | 0.57 aggregated               | 0.53 aggregated  |              |
| 04/09/2012 | 0.01 random                   | 0.56 aggregated  |              |
| 04/23/2012 | 0.52 aggregated               | 0.40 random      |              |
| 05/07/2012 | 0.55 aggregated               | 0.53 aggregated  |              |
| 05/21/2012 | 0.56 aggregated               | 0.13 random      |              |
| 06/04/2012 | 0.01 random                   | 0.59 aggregated  |              |
| 06/18/2012 | −                               | −0.09 random     |              |

| Observed index | Expected Index | $p_{\text{obs.} > \text{exp.}}$ | $p_{\text{obs.} < \text{exp.}}$ |
|----------------|----------------|-------------------------------|-------------------------------|
| 0.23           | 0.54           | 0.99                          | 0.01                          |
| 0.34           | 0.36           | 0.64                          | 0.36                          |
| 0.44           | 0.24           | 0.08                          | 0.92                          |
| 0.52           | 0.23           | 0.15                          | 0.85                          |
| 0.56           | 0.28           | 0.15                          | 0.85                          |
| 0.49           | 0.43           | 0.41                          | 0.59                          |
| 0.27           | 0.46           | 0.90                          | 0.10                          |
| 0.92           | 0.28           | 0                          | 1                              |
| 0.82           | 0.32           | 0.01                          | 0.99                          |
| 0.37           | 0.32           | 0.31                          | 0.69                          |
| −              | −              | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |
| −              | −0.29          | −                            | −                              |

Note: Values with superscript asterisk in the Pianka index indicate statistical differences between the observed and expected index.
Age and growth

The 75 outer lip measurements taken from *M. paranaguensis* specimens revealed a 1.86 mm average thickness, therefore, the Von Bertalanffy equation became \[ \text{OL} = 5.01(1 - e^{-0.15(t+0.85)}) \] \( r^2 = 0.94 \), with a maximum estimated age of 12.24 years.

Discussion

In this study, *M. paranaguensis* showed a low level of recruitment, which follows the low reproductive potential (two to five eggs per batch; Sobreira and Molina 2002) and low egg hatching rates (varying from 28.6% to 57.9%; Rios et al. 2004), previously reported for other species from the same genus. The two abundance peaks observed for *M. paranaguensis* can be also explained by the recruitment, because they happened at particular times. The probability of capture is associated with the level of activity of terrestrial snails (Cook 2001). The two peaks in detectability observed for *M. paranaguensis* could relate to reproductive activity and oviposition (first peak) and to an increase in pre-aestivation foraging (second peak).

The high number of recruitment peaks observed for *A. fulica* was expected because of the frequency with which the giant African snail mates (Ugwu et al. 2011). *Achatina fulica* lays clutches of up to 400 eggs with an annual production of up to 1200 eggs. This productivity also contributed to its ability to invade and survive in different environments (Rault and Baker 2002). In this species, recruitment also helped to keep the population steady during most of the sampling period (except for the beginning of the study, when the population peaked to subsequently decrease). The data showed that *A. fulica* detectability probability increased during the summer months (December to March), and the species did not show a significant dormancy period, probably because of the high temperatures. This result reinforces the hypothesis that *A. fulica* prefers warmer environments (Vogler et al. 2013).
Most populations, including terrestrial molluscs, present aggregated spatial distribution patterns (Krebs 1999) following the patchy distribution of environmental resources (Heller 2001). In this study, *M. paranaguensis* clearly displayed an aggregated spatial distribution pattern primarily in the most vegetated site (Area 1), while *A. fulica* showed a mixed pattern of both random and aggregated distribution. The heterogeneity of the area, with presence of patches with varying vegetation, and the presence of garbage, may also explain these distribution patterns.

In contrast, the *A. fulica* distribution, which was represented by proportional abundances throughout the study area, can be explained by the modified environment. Albuquerque et al. (2008) observed that *A. fulica* specimens are found more frequently in urban areas than in forested areas. Generally, they show a preference for gardens, abandoned land and walls, but they also occur at low densities in streets and on the outside walls of houses. These authors also found that this species is well established in modified environments, such as Ilha Porchat, facilitating colonization and further dispersion. Fischer et al. (2012) suggest that aggregation is not a common behaviour in *A. fulica*. This could be a strategy employed as protection against biotic and abiotic factors, overpopulation and used as a reproductive strategy.

The presence of conspecifics nearby affects the aggregation values. In this study, both species showed a positive correlation between the number of specimens found in the quadrat and the value of the dispersion index. Chase et al. (1980) verified that the level of aggregation found in *A. fulica* relates to three factors: (1) age – aggregation increased with an individual’s age; (2) genetic relatedness – genetically related individuals tend to aggregate; and (3) time – aggregation increases overnight. The authors also suggest olfactory stimulation as the basis for aggregation, a mechanism that is most probably present in both species, explaining the relationship found.

Dispersal among areas was not detected in this study. Very likely, flow of individuals among areas either did not occur or was very limited, since the areas are separated by streets and sidewalks. Terrestrial molluscs show limited dispersal ability (Baur and Baur 1993; Giokas and Mylonas 2004; Parmakelis and Mylonas 2004; Aubry et al. 2006), making the distance among individuals the main factor influencing genetic variability (Pfenninger et al. 1996). Hence, native species, with lower reproductive potentials and more rarefied populations, often occupying a more restricted variety of habitats, tend to be more susceptible to inbreeding and genetic drift, compared with invasive species (Jordaens et al. 1998). Fragmentation may even lead to species extinction in some cases. Stoll et al. (2009) showed that the level of degradation of vegetation has an influence over terrestrial gastropods, increasing extinction rates, with extinction frequency being directly proportional to time.

*Megalobulimus paranaguensis* lifespan was estimated to be 12.24 years, but it can reach up to 15.24 years with an average outer lip thickness of 1.86 mm while age of sexual maturity ranged from 1 to 3 years (Romero 2004). However, while studying the same species for more than 13 years (1998–2010), at the Orquidário Municipal de Santos, an urban park in a town near the study area, Fontenelle and Miranda (2012) reported a life span of 35.5 years, and found a predominant cohort of 3.5–4.5 mm in outer lip thickness that applied to 30% of the population. The authors also reported the presence of *A. fulica* in the parks; however, the spread of *A. fulica* is controlled through maintenance work carried out by the park staff. Calcium ions are the main
limiting factor for the survival of terrestrial molluscs, and can be absorbed through the sole of the animal’s foot or through their food sources (Fournier and Chétail 1984). The relatively short lifespan of *M. paranaguensis* compared with that reported for the Orquidario population may relate to calcium levels, with either the soil containing a low calcium concentration or the food sources being calcium-deficient due to competition with *A. fulica* in the study area. Although certain levels of synergism would not be impossible, the extent of the influence of these factors remains unclear.

Previous studies have reported on the effect of different environmental variables on these or related species. Albuquerque et al. (2009) reported on the effect of temperature range on the condition factor of *A. fulica*, which indicates the physiological status and welfare of the species. Furthermore, Romero (2004) reported that the growth rates of *Megalobulimus mogianensis* increases with increasing temperature. Choi et al. (2004) used ordinary differential equations to show that temperature affected the mortality rate of immature specimens while rain affected the adult mortality rate of the land slug *Deroceras reticulatum* (Muller 1774). The metabolism of *A. fulica* increased with the increase in soil temperature, a finding that reveals the species preference for warmer environments (Vogler et al. 2013). The effect of humidity on both species was also expected, because snail activity depends on high moisture levels (Baker 1958). In fact, snails are very sensitive to drought environments, which tend to restrict their movements (Getz 1974). Vegetation cover tends to enhance moisture (Burch 1957), explaining why *M. paranaguensis* showed a preference for densely vegetated sites. Nunes and Santos (2012) showed that these variables influence the distribution and abundance of terrestrial gastropods in Atlantic Rainforest. Environmental variables influence the activity of these two species, explaining why their population parameters varied considerably throughout the study and also why *M. paranaguensis* entered aestivation during the hottest months, when drying pressure increases.

Non-random niche patterns may indicate the impact of interspecific competition among species populating the same geographic area (Gotelli and Graves 1996). Colley and Fischer (2009) suggested that the impact of *A. fulica* in an area where it was introduced is related to the extent of the species’ consumption of native vegetation (seeds, shoots, leaves and fruits) as well as to competition for space. In this study, we did not find any evidence of competition for space among the study species, probably because the abundance cycles for these two species are controlled by different factors. While *A. fulica* is influenced by both soil temperature and humidity, *M. paranaguensis* abundances are mainly influenced by only humidity. The long aestivation period of *M. paranaguensis* also prevented competition for a long period during the year. Long-term studies would be necessary to further evaluate this fact. On the other hand, negative effects of competition among *A. fulica* and other native species should not be overlooked, particularly because of the short lifespan of the native species in this study compared with its lifespan elsewhere, and also due to the consumption of other terrestrial mollusc species by *A. fulica* (Meyer III et al. 2008).

Furthermore, *M. paranaguensis* populations may be affected by the effort to control *A. fulica* populations, such as soil contamination by salt (Fischer and Colley 2005) and accidental capture and over-killing of *M. paranaguensis* during *A. fulica* control campaigns (Colley and Fischer 2009), driven by the superficial resemblance between these two species (Thiengo et al. 2007). Cowie (1992, 2001)
and Civeyrel and Simberloff (1996) reported on the effect of flawed control policies and the decline of native land snail faunas. This finding shows that efforts to conserve *M. paranaguensis* should be intensified and should focus on education on the importance and current status of terrestrial molluscs, as suggested by Lydeard et al. (2004).

From our study, it can be concluded that competition is not a major factor influencing the distribution of the two species in this area. In addition, the differential influence of environmental factors over the two species may be leading to the separation of the ecological niches. Habitat modification and control policies for *A. fulica* are having a larger negative effect on *M. paranaguensis* than on *A. fulica*.

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