

Variation in the population density of the Giant African Snail (*Lissachatina fulica*) in the Neotropical region

Variación de la densidad poblacional del caracol gigante africano (*Lissachatina fulica*) en la región Neotropical

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ABSTRACT

The Giant African Snail (*Lissachatina fulica*) is one of the 100 world's worst invasive species and has been recorded in the Neotropical region since the 1980s. Temperature and precipitation variables affect snail population density; however, these relationships have not been investigated for *L. fulica* on a regional scale. Here, we made the first description of variation in population density of *L. fulica* in the Neotropical region using a literature search, descriptive statistics, and a Principal Component Analysis (PCA). We found 22 studies covering 36 localities in six countries. The mean snail density was 11.55 ± 28.32 ind/m², with the lowest value recorded in Cuba (0.0002 ind/m²) and the highest value recorded in Venezuela (150 ind/m²). These values were recorded between 21 % to 93 % of Human Footprint, 710 mm to 4438 mm of Annual Precipitation, 13 °C to 27 °C, Mean Temperature of the Coldest Quarter, and 3 °C to 40 °C of Temperature Seasonality. The PCA suggested that low densities can occur in various environmental conditions, whereas medium and high densities seem to appear in more specific climatic combinations. In conclusion, increased densities of *Lissachatina fulica* in the Neotropics seem to be influenced by climatic variations, especially the Mean Temperature of the Coldest Quarter and Annual Precipitation, supporting previous findings in the literature regarding the snail establishment. Future monitoring of this invasive species, performed at expanded spatial and temporal scales, may provide tools to establish a relationship between snail density values and impact.

Keywords: *Achatina fulica*, Invasive snail, Invasion Biology, Population ecology.

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RESUMEN

El caracol gigante africano (*Lissachatina fulica*) es una de las 100 peores especies exóticas invasoras del mundo, y se ha establecido en el Neotrópico desde los 80s. La temperatura y precipitación afectan la densidad poblacional en moluscos; sin embargo, esto no ha sido investigado en *L. fulica* a escala regional. Aquí, elaboramos la primera descripción de la variación de la densidad poblacional de *L. fulica* en la región Neotropical, mediante una búsqueda en la literatura, estadística descriptiva y un Análisis de Componentes Principales (ACP). Encontramos 22 estudios de 36 localidades en seis países. La densidad media fue de $11,55 \pm 28,32$ ind/m², con el valor más bajo en Cuba (0,0002 ind/m²) y el valor más alto en Venezuela (150 ind/m²). Estos valores se registraron entre 21 % y 93 % de Huella Humana, 710 mm a 4438 mm de Precipitación Anual, 13 °C a 27 °C Temperatura Media del Trimestre más Frío, y 3 °C a 40 °C Estacionalidad de la Temperatura. El ACP indicó que las densidades bajas pueden ocurrir en cualquier condición evaluada, pero las medias y las altas estarían en combinaciones más específicas. En conclusión, la densidad poblacional de *L. fulica* en el Neotrópico puede estar influenciada por variables climáticas, especialmente la Temperatura Media del Trimestre más Frío y la Precipitación Anual, corroborando lo encontrado en la literatura sobre el establecimiento del caracol. Monitoreos futuros de esta especie en diferentes escalas espaciales y temporales, pueden proveer herramientas para establecer la relación entre la densidad y el impacto de la especie.

Palabras clave: *Achatina fulica*, Caracol invasor, Ecología de poblaciones, Invasión biológica.

INTRODUCTION

The Giant African Snail, *Lissachatina fulica* (Bowdich, 1822), is one of the 100 world's worst invasive species (Lowe *et al.* 2004, Thiengo *et al.* 2007). In the invaded areas, *L. fulica* can cause impacts on health, agriculture, and the economy. In health, the snail can act as an intermediate host for nematode species of the genera *Angiostrongylus* and *Aelurostrongylus*, which cause eosinophilic meningitis and abdominal angiostrongyliasis in humans, besides other diseases in domestic animals (Fischer *et al.* 2010). *L. fulica* is recognized as a generalist herbivore that feeds on various cultivated plant species (Thiengo *et al.* 2007). Finally, the presence of *L. fulica* entails an expense of the public herald for the potential consequences and control that must be carried out (Roda *et al.* 2018). Therefore, ecological research on *L. fulica* is necessary to mitigate the negative impacts of its presence through the construction of comprehensive management plans.

In the Neotropics, *L. fulica* was first recorded in the 1980s in Martinique and Brazil (Mead and Palaci 1992, Santana-Teles *et al.* 1997). By the beginning of the 21st century, it has already been recorded in Cuba (Vázquez and Sanchez 2014), Venezuela (Martínez-Escarbassiere *et al.* 2008), Colombia (De la Ossa-Lacayo *et al.* 2012), Ecuador

(Goldyn *et al.* 2017) and Argentina (Gutierrez-Gregorin *et al.* 2011). After recording *L. fulica*, some countries have established regulations to control and manage the snail, besides inciting research to provide baseline knowledge (MAVDT 2011). However, this control has been based on the manual collection and subsequent culling with chemical or physical means (Thiengo *et al.* 2007), which requires ecological knowledge of local populations. As the species is widely distributed in the Neotropics (Darrigran *et al.* 2020), a better understanding of the mollusk population dynamics in this region could help for enhancing control and management plans.

Density is one of the population parameters considered to assess whether an exotic population is established and the possible impact it produces. In *L. fulica*, it is postulated that a population density higher than 10 ind/m² is already a cause for concern as an established population (De la Ossa *et al.* 2017). This argument is because population density influences parameters related to fitness such as growth, fecundity, egg viability, and dispersal (Dickens *et al.* 2018). Nevertheless, the relationship between population density and the impact of an invasive population is not linear (Jackson *et al.* 2015) and can be affected by other ecological factors such as the trophic level (Bradley *et al.* 2019). We would also expect that density is also affect-

ed by temperature and precipitation; however, as far as we know, these relationships have not been investigated for *L. fulica* on a regional scale. In heterogeneous environments, such as those found in the Neotropics, understanding the relationships between density and climate should contribute to modeling the link between density and impact.

Here, we estimated the amplitude of climatic and anthropic variables where the population density of *L. fulica* was recorded in the Neotropical region. Through the association of density values to climatic and anthropic variables, we aim to answer the following questions: How much does the population density of *L. fulica* varies in the Neotropical region? Which are the main climatic variables affecting the density of *L. fulica* in the Neotropical Region? How do these climatic variables, as well as the human footprint, affect snail density? This study is the first descriptive approach on the variation of the population density of *L. fulica* in the Neotropics, focusing on the intervals of climate and anthropic intervention where the species was recorded. We expect that this work will provide subsidies for decision-making for managing the giant African snail in the countries of the region.

MATERIALS AND METHODS

A directional search with the keyword “*Achatina fulica*” was performed in Google Scholar in English, Spanish and Portuguese. This keyword corresponds to the old name for the species, as the genus change from *Achatina* to *Lissachatina* was recently accepted (<https://www.marinespecies.org/aphia.php?p=taxdetails&id=881469>). We downloaded all documents presenting numerical values of population density in neotropical countries. Because some documents did not show the exact collection coordinates, the geographic coordinates of the localities recorded in each document were approximated in Google Earth, using the center of the locality recorded. To access the anthropic intervention in the Neotropics, we used the global human footprint index, which is expressed as a percentage representing the relative human influence in each terrestrial biome (WCS 2005). To access environmental parameters in the Neotropics, we used the nineteen current climate variables from WORLDCLIM 2.1 (<https://www.worldclim.org/data/worldclim21.html>, resolution 2.5 arcminutes). We extracted the Human Footprint and climate values for locations with density records with the vegan (Oksanen et

al. 2020) and raster (Hijmans 2021) packages in RStudio 4.1.0 (Supplementary material 1, Table S1).

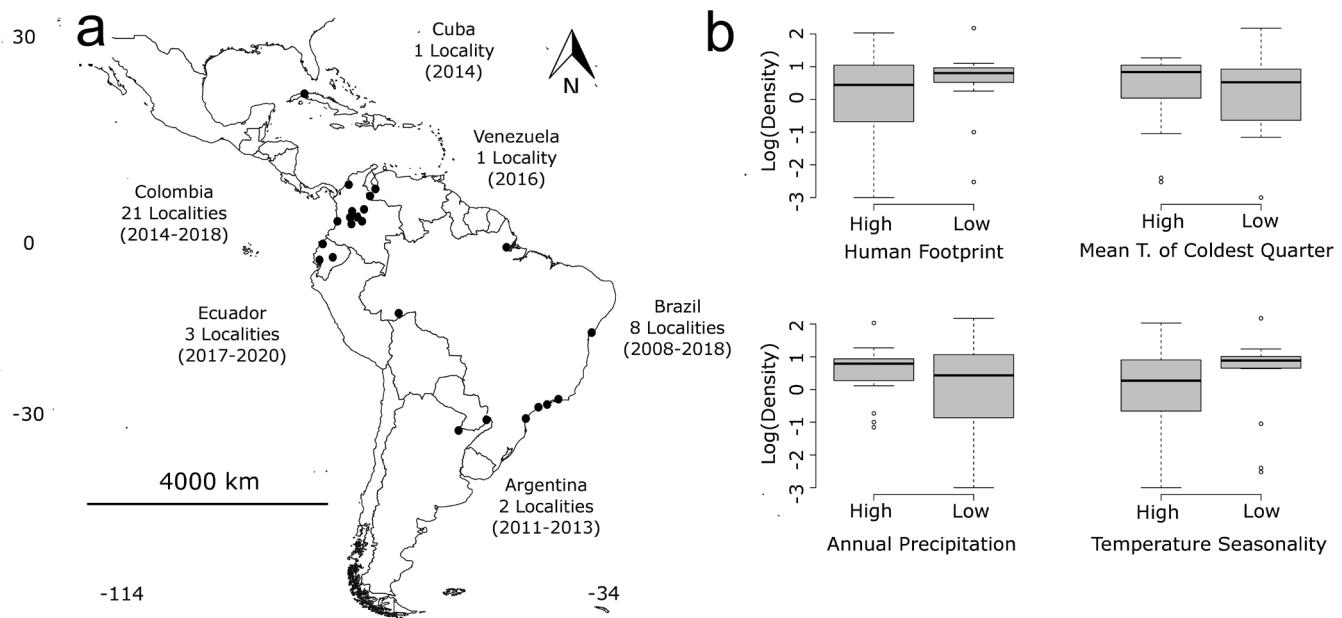
Based on Albuquerque et al. (2009) and Vogler et al. (2013), we identified Human Footprint, Annual Precipitation, Mean Temperature of the Coldest Quarter, and Temperature Seasonality as the most relevant predictors for *L. fulica* establishment. Then, we categorized each of these variables as “low” and “high”, taking as reference their median value in the collection sites, and constructed boxplots using density values of each point as the response variable.

To explore the population density variation of *L. fulica* in the Neotropical region, we performed a principal component analysis (PCA). Variation was represented in a Cartesian space defined by the human footprint and the 19 climatic variables. Density values were classified as low (<0.001 to 3.35 ind/m²), medium (4.03 to 9.2 ind/m²), and high (10.45 to 150 ind/m²), taking into account the median of the data and the suggestion of 10 ind/m² in the study of De la Ossa et al. (2017). The PCA and the graphical representation were elaborated with the packages FactoMineR (Lê et al. 2008) and factoextra (Kassambara and Mundt 2020) in RStudio 4.1.0.

RESULTS

In total, we found 22 papers estimating the population density of *L. fulica* in the Neotropics. These papers record snail density in 36 localities covering six countries: Argentina, Brazil, Colombia, Ecuador, Venezuela, and Cuba, from 2004 to 2020 (Fig. 1a). For these records, the mean density was 11.55 ± 28.32 ind/m² and the median was 4.03 ind/m². The lowest and highest densities were reported in Cuba (Havana, 0.0002 ind/m²) and Venezuela (Andres Bello, 150 ind/m²). In most sites (80%) density values scored below 10 ind/m² (Table 1).

Regarding the relevant predictors for *L. fulica* establishment suggested by the literature, we found density records in the following ranges: Human Footprint from 21% to 93%, Annual Precipitation between 710 mm to 4438 mm, Mean Temperature of the Coldest Quarter between 13 °C to 27 °C, and Seasonality of Temperature between 3 °C to 40 °C. In general, we found no density pattern between low or high values of these variables (Fig. 1b).



The first two components of the PCA explained 63.5% of the variance of the environmental data (Supplementary material 2, Table S2). Mean Temperature of the Coldest Quarter (bio11) and Mean Temperature of the Driest Quarter (bio9) had the largest contributions to the first component. In contrast, Annual Precipitation (bio12) and Precipitation of the Wettest Month (bio13) had the largest contributions to the second component. Human Footprint was the least contributing variable for both components (Supplementary material 2, Table S3). The Cartesian space defined by PC1 and PC2 shows that sites presenting low snail densities are distributed across the two components, indicating that different climatic combinations can maintain *L. fulica* populations. On the other hand, most sites presenting medium snail densities show positive values of the first component, whereas most sites presenting high densities show negative values of the second component. This pattern suggests that density increase can be influenced by specific temperature and precipitation ranges (Fig. 2).

DISCUSSION

In this study, we found a high variation in the population density of *L. fulica* in six Neotropical countries. Low

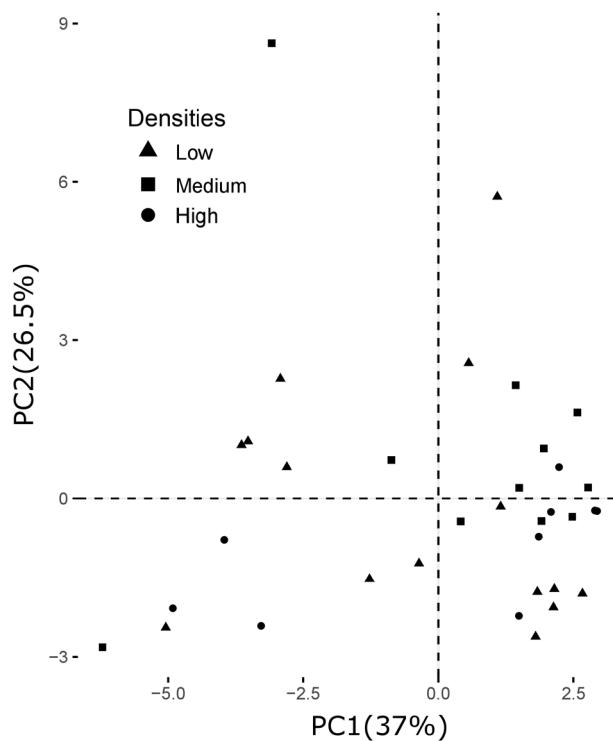


Table 1. Population density values at localities in the Neotropical region.

Reference	Country	Locality	Ind/m ²
Gutiérrez-Gregoric et al. 2011	Argentina	Puerto Iguazú	107.6
Gutiérrez-Gregoric et al. 2013		Corrientes	28
Santana and Batalla 2018		Caraguatatuba, SP	0.186
de Almeida 2018		Santo Antonio de Padua, RJ	0.23
Oliveira et al. 2013		Santana, Amapá	6.15
Albuquerque et al. 2008		Lauro Freitas, Bahia	4.03
Albuquerque et al. 2009	Brazil	Lauro Freitas, Bahia	2.2
Fischer et al. 2010		Paranagua	1.9
Lima and Guilherme 2018		Rio Branco, Acre	1.86
Simião and Fisher 2004		Pontal do Paraná	0.1
Miranda et al. 2015		São Vicente, SP	0.07
Cano 2018		Natagaima, Tolima	18.67
Cano 2018		Lerida, Tolima	17.33
Cano 2018		Alvarado, Tolima	12.67
Cano 2018		Chaparral, Tolima	11.83
Cano 2018		Honda, Tolima	11.2
Cano 2018		Venadillo, Tolima	9.2
Cano 2018		Mariquita, Tolima	8.86
Cano 2018		Carmen de Apicalá, Tolima	8
Cano 2018		Purificación, Tolima	7.33
Cano 2018		Armero-Guayabal, Tolima	6.4
Cano 2018		Ibagué, Tolima	4.89
Avendaño and Linares 2015	Colombia	Cundinamarca	4.6
Cano 2018		Melgar	4.34
Giraldo et al. 2017		Valle del Cauca	5.9
Avendaño and Linares 2015		Valle del Cauca	2
Avendaño and Linares 2015		Boyacá	1.8
Avendaño and Linares 2015		Meta	1.3
Avendaño and Linares 2015		Norte de Santander	1.1
De la Ossa-Lacayo et al. 2017		Tolú, Sucre	0.21
De la Ossa-Lacayo et al. 2017		Corozal, Sucre	0.09
De la Ossa-Lacayo et al. 2017		Sincelejo, Sucre	0.03
De la Ossa et al. 2017		Sincelejo, Sucre	0.004
De la Ossa-Lacayo and De la Ossa 2014		Sincelejo, Sucre	0.004
De la Ossa-Lacayo and De la Ossa 2014		Sampues, Sucre	0.003

(Continued)

Reference	Country	Locality	Ind/m ²
Villavicencio-Abril et al. 2020		Sto Domingo de los Tsáchilas	3.35
Cuasapaz-Sarabia and Salas 2019	Ecuador	Guayas	10.45
Goldyn et al. 2017		Puyo	8.4
Herrera et al. 2016	Venezuela	Andres Bello	150
Vazquez and Sanchez 2014	Cuba	Havana	<0.001

densities of the species can be maintained in an array of environmental conditions, but density increase seems to be influenced by the Mean Temperature of the Coldest Quarter (bio11) and Annual Precipitation (bio12). The possible influence of bio11 on *L. fulica* density seems to be associated with establishment (Vogler et al. 2013) and survival (Sharma and Dickens 2018). Annual Precipitation, in turn, may be related to physiological processes, like estivation (Rahman and Raut 2010), that influence population dynamics. However, the low number of localities with density records does not capture all the environmental conditions that could explain the variation in density of the invasive mollusk.

Our data did not show the clear effects of human intervention on snail population density. The human footprint did not contribute significantly to the principal components, and the highest population density (150 ind/m²) was recorded in a site presenting the lowest value of human footprint (21%) ([Supplementary material 1](#)). In general, disturbed areas provide unique habitat opportunities and potential refugia for invasive alien species (Cadotte et al. 2017) and may even promote adaptation (Borden and Flory 2021). What is interesting in the case of *L. fulica* is its ability to maintain populations in low percentages of the human footprint, which would turn conservation units and rural areas of countries into refuges for the species (Fischer et al. 2010). Since *L. fulica* can occur from low to high human intervention, we call attention to direct management strategies in rural human populations.

According to the latest distribution model of the species in South America (Vogler et al. 2013), localities with low temperatures and high seasonal variation are less suitable for *L. fulica*. However, in our study the highest density values (150 - 107.6 ind/m²) were found in localities with 4 °C and 34 °C temperature seasonality ([Supplementary material 1](#)). It is, therefore, possible to postulate that after es-

tablishment, *L. fulica* can maintain high densities in high seasonality. In Andrés Bello, a tropical locality presenting a very weak seasonal climate, the high snail density could be explained by resource availability (Martínez-Escarbasiere et al. 2008, Herrera et al. 2016). In the subtropical locality Puerto Iguazú, the high density could be explained by the sampling period: the collections were conducted in March, when temperatures around 31 °C and humidity around 70% (Gutiérrez-Gregoric et al. 2011) represent optimal conditions for *L. fulica*. This difference demonstrates that temporal monitoring is necessary to identify the influence of climate and resource availability on the viability of populations.

In conclusion, the population density of *Lissachatina fulica* in the Neotropical region would be more influenced by climatic variables than by the degree of anthropogenic intervention. In this study, we postulate the Mean Temperature of the Coldest Quarter (bio11) and Annual Precipitation (bio12) as key climate variables influencing snail density, supporting the results found by Albuquerque et al. (2009) and Vogler et al. (2013) regarding *L. fulica* establishment. We call attention to the ability of the species to maintain low population densities over wide ranges of environmental variables. Since at high population densities, there is a greater perception of damage (Jackson et al. 2015), low-density localities are ignored when establishing control actions. In the future, a spatial and temporal expansion of local monitoring of this invasive species may provide sufficient tools to develop a relationship between density values and the impact produced by the species in the region.

■ PARTICIPATION OF AUTHORS

APM Conceived ideas, data analysis and writing; AG data analysis and writing; RT data analysis and writing.

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CONFLICT OF INTEREST

The authors have no relevant financial or nonfinancial interest to disclose.

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