



Universidade do Estado do Rio de Janeiro

Rafael Alves Esteves

**Fatores ambientais e aspectos ecológicos que afetam a diversidade
e a distribuição dos gastrópodes terrestres em uma área de Mata
Atlântica em Sooretama, norte do Espírito Santo, Brasil**

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Tese apresentada, como requisito parcial para obtenção do título de Doutor em Ciências, ao Programa de Pós-Graduação em Meio Ambiente, da Universidade do Estado do Rio de Janeiro.

Orientador Prof. Dr. Carlos Frederico Duarte da Rocha
Coorientador Prof^a Dr^a Sonia Barbosa dos Santos

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Rafael Alves Esteves

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Rio de Janeiro
2022

DEDICATION

Promete que não vai crescer distante
Promete que vai ser pra sempre assim
Promete esse sorriso radiante
Todas as vezes que você pensar em mim.
Promete cuidar bem dos seus cachinhos
E sempre me abraçar quando eu chegar
Promete sorrir sempre com os olhinhos
E cantar cantigas na sala de estar.
Que eu prometo ser pra sempre o seu porto seguro
Prometo dar-te eternamente o meu amor.
Promete aproveitar cada segundo
Desse tempo que já passa tão veloz
Me lembro quando você chegou nesse mundo
Sorrindo aos poucos quando ouviu minha voz.
E hoje corre pela sala, brinca de existir
Giz de cera, pega-pega
E eu só sei sorrir
Ao imaginar você crescer.
Para um pouco com a bagunça, deixa eu te olhar
Que o tempo voa e olha só
Você sabe falar
E diz tudo que eu preciso escutar, la, la.
Promete ser pra sempre o meu menino
Me deixar cantar pra te fazer dormir
Que eu prometo que vou te cuidar pra sempre
Eu te amo infinito, meu guri.

Promete (Ana Vilela, 2017)

Ao Ítalo, meu guri, com todo meu amor.

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A chave de todas as ciências é inegavelmente o ponto de interrogação.

Honoré de Balzac

ABSTRACT

ESTEVEES, Rafael Alves. *Environmental factors and ecological aspects affecting the diversity and distribution of land gastropods in an Atlantic Forest area in Sooretama, northern Espírito Santo, Brazil*. 2022. 165 f. Tese (Doutorado em Meio Ambiente) - Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

Different species of land molluscs are recognized as reliable indicators of environmental quality due to their limited dispersal ability, dependence on stable microclimatic conditions, relatively strict habitat preferences, and high sensitivity to environmental changes. Ecologically, these organisms perform key ecosystem services essential to environmental health, particularly in nutrient cycling through litter decomposition, thus providing vital resources for wildlife. They constitute an important source of calcium for birds, amphibians, reptiles, small mammals, and several other invertebrates, in addition to acting as intermediate hosts for numerous parasites. The rapid loss and fragmentation of natural habitats caused by anthropogenic activities have led to immeasurable losses to land snail communities. This thesis evaluated how environmental factors and ecological attributes affect the diversity, distribution, and functional and behavioral ecology of land snails in an area of the Atlantic Forest, one of the world's biodiversity hotspots, located in Sooretama, Espírito Santo State, Brazil. Taking the Sooretama Biological Reserve as the study area, the research addressed the following questions: (a) what is the current knowledge base on litter-dwelling mollusks in Brazil? (b) which environmental factors most influence the structure and composition of terrestrial gastropod communities? (c) what are the effects of seasonality on land snail assemblages? (d) what is the edge effect caused by the BR-101 highway crossing the Sooretama Biological Reserve? (e) how does microhabitat use relate to shell morphology? (f) what are the daily activity patterns of land snails? and (g) what is the ecological profile, including occurrence and activity, of gastropods found as agricultural pests in papaya plantations? The information generated in this thesis contributes to advancing knowledge on the ecology of tropical land snails, discussing how species respond to the environmental factors and ecological attributes evaluated, and providing data on this faunal group to support management actions and public policies for biodiversity conservation.

Keywords: Conservation of biodiversity; Community ecology; Gastropoda; Terrestrial molluscs; Sooretama Biological Reserve.

RESUMO

ESTEVEES, Rafael Alves. *Fatores ambientais e aspectos ecológicos que afetam a diversidade e a distribuição dos gastrópodes terrestres em uma área de Mata Atlântica em Sooretama, norte do Espírito Santo, Brasil*. 2022. 165 f. Tese (Doutorado em Meio Ambiente) - Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

Diferentes espécies de moluscos terrestres possuem status de bons indicadores da qualidade ambiental devido à sua capacidade reduzida de dispersão, associada à dependência de microclima estável, preferências relativamente estritas de habitat e elevada sensibilidade às condições ambientais. Em termos ecológicos, realizam importantes serviços ecossistêmicos para a saúde ambiental, especialmente na reciclagem de nutrientes via decomposição do folhiço, fornecendo nutrientes essenciais para a vida selvagem, sendo fonte de cálcio para aves, anfíbios, répteis, pequenos mamíferos e diversos outros invertebrados, além de participarem diretamente como hospedeiros intermediários de diversos parasitos. A perda e fragmentação de habitats naturais em ritmo acelerado devido às intervenções antrópicas tem causado perdas incalculáveis às comunidades de moluscos terrestres. A presente tese avaliou como os fatores ambientais e os atributos ecológicos afetam a diversidade, a distribuição e a ecologia funcional e comportamental dos gastrópodes terrestres em uma área de Mata Atlântica, um dos hotspots de biodiversidade do planeta, localizada em Sooretama, estado do Espírito Santo, Brasil. Tendo a Reserva Biológica de Sooretama como área de estudo, esta pesquisa buscou responder as seguintes questões: a) como está alicerçada a base de conhecimento em moluscos de folhiço no Brasil atualmente; b) quais fatores ambientais mais afetam a estrutura e composição da comunidade dos gastrópodes terrestres; c) qual o efeito da sazonalidade sobre a comunidade de moluscos terrestres; d) qual o efeito de borda causado pela Rodovia BR-101 que atravessa a Reserva Biológica de Sooretama; e) qual a relação entre o uso de microhabitats e a morfologia da concha; f) qual o padrão de atividade dos moluscos terrestres em diferentes períodos do dia; e g) qual o perfil ecológico, incluindo ocorrência e atividade, dos gastrópodes encontrados como pragas agrícolas em plantações de mamão. Esperamos que as informações aqui geradas possam contribuir para elevar o grau de conhecimento sobre a ecologia dos gastrópodes terrestres tropicais, discutindo como as espécies respondem aos fatores ambientais e aos atributos ecológicos avaliados, bem como fornecer dados deste grupo faunístico para subsidiar ações de manejo e elaboração de políticas públicas voltadas para a conservação da biodiversidade.

Palavras-chave: Conservação da biodiversidade; Ecologia de comunidade; Gastropoda; Moluscos terrestres; Reserva Biológica de Sooretama.

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GENERAL INTRODUCTION

Tropical regions are characterized by high environmental heterogeneity (Myers, 1997), which is considered the main driver of biological diversity (Ricklefs, 2003). This heterogeneity has great potential to generate different niches, with varied microenvironments within the same location that favor the establishment, survival, persistence, and multiple interactions among numerous species, providing favorable conditions for many life forms. These factors account for the great relevance of tropical forests in terms of global diversity. They are considered the most diverse terrestrial environment on the planet, comprising 7% of the world's land surface and harboring about 50% of described species (Myers, 1997). In terms of biological diversity, tropical regions are rivaled only by coral reefs (Myers *et al.*, 2000; Ricklefs, 2003).

Tropical ecosystems are the most species-rich on the planet and, at the same time, the most endangered (Myers, 1988). Anthropogenic influence on the environment has become increasingly intense, resulting in what has been called the biodiversity "crisis", a reference to extinctions caused by various factors related to human activities (Di Minin *et al.*, 2016). Current extinction rates resulting from anthropogenic activities are unprecedented and highly unusual in the history of planet Earth (Ceballos *et al.*, 2015). Habitat fragmentation, overexploitation of natural resources, and the introduction of invasive species are interrelated impacts associated with human occupation of natural landscapes, and constitute the main threats to biodiversity worldwide (Hoffmann *et al.*, 2011). The need for new areas for agriculture, livestock farming, and logging is the main reason for the elimination or alteration of native vegetation cover, which results in the loss of other life forms, including animals, fungi, and microorganisms (Whitmore, 1997; Foley *et al.*, 2005).

Brazil is the country with the largest area of humid tropical forest in the world (Tanzikaki-Fonseca & Mouton, 2000), and is considered a megadiverse country due to its continental extension and its great variety of climatic conditions, biomes, and ecosystems (Coimbra-Filho, 1998). The main ecosystems include the Cerrado, Caatinga, Amazon, Pantanal, and Atlantic Forest (Lima, 2002; Ramos, 2002; Brandon *et al.*, 2005).

The great variety of microhabitats found in the Atlantic Forest, besides favoring biodiversity, favors a high degree of endemism. It represents the second largest block

of tropical forest in the country in terms of extent, behind only the Amazon Forest (Tabarelli *et al.*, 2005). These factors place the Atlantic Forest among the five main biodiversity hotspots in the world (Myers *et al.*, 2000; Kageyama & Lepsch-Cunha, 2001) and one of the most threatened, due to its high deforestation rate.

Biodiversity hotspots are designated priority conservation regions that simultaneously exhibit high rates of species diversity, endemism, and degree of threat (Myers *et al.*, 2000). There are 35 recognized hotspots on the planet, which together cover only 2.3% of the Earth's surface but hold 50% of all vascular plant species and 42% of all known vertebrate species as endemics (Mittermeier *et al.*, 2004; Mittermeier *et al.*, 2011). The Atlantic Forest is considered one of the five most diverse hotspots (Mittermeier *et al.*, 2004; Mittermeier *et al.*, 2011), being a complex set of ecosystems that harbors a significant portion of Brazilian biological diversity. With an original area of approximately 1,300,000 km² in Brazil, corresponding to 15% of the national territory, the Atlantic Forest biome spans 15 states, extending from Rio Grande do Sul to Piauí, and is home to about 61% of the Brazilian population (SOS Mata Atlântica, 2014). Currently, the Atlantic Forest is restricted to less than 26% of its original forest cover (SOS Mata Atlântica, 2014; Rezende *et al.*, 2018), and about 80% of its remnants are represented by fragments smaller than 50 hectares (Ribeiro *et al.*, 2009).

Faunal studies conducted in the Atlantic Forest generally address large-bodied species, or species with strong sentimental appeal; as a result, knowledge remains restricted to a few zoological groups (Nunes, 2007), generally associated with popular charisma. There is a large gap in the knowledge of tropical invertebrates, which, besides representing a large share of animal diversity (Otero *et al.*, 2000; Lydeard *et al.*, 2004), are disappearing rapidly without even being known (Coimbra-Filho, 1998), mainly due to the great destructive impact their habitats have been suffering (Barbosa, 2001). Of the few ecological studies conducted with invertebrates in tropical environments, the vast majority address Arthropoda, and even within this group, only a few orders of medical or economic importance are more extensively studied, especially ants and butterflies (Myers *et al.*, 2000; Otero *et al.*, 2000; Leandro & D'Almeida, 2005; Lewinsohn *et al.*, 2005; Santos *et al.*, 2006).

There are currently around 700 native species of land snails described from Brazil (Salvador, 2019). Simone (1999), however, estimated that only a third of the land mollusk species in Brazil were known and described at the time, which would

increase this number to about 2,000. Since the publication of Simone's catalog in 2006, 52 new species of land mollusks have been described from Brazil.

Land mollusks perform important ecosystem services for the health of forest systems, especially in nutrient recycling through leaf-litter decomposition, and are the main source of calcium for birds, amphibians, reptiles, small mammals, and various other invertebrates (Curry *et al.*, 2008). Different species of land snails have status as good indicators of environmental quality due to their relatively low dispersal capacity, associated with dependence on a stable microclimate, relatively strict habitat preferences, and high sensitivity to environmental conditions (Ström, 2004; Kappes, 2006). Since they cannot quickly escape disturbed areas (Strayer *et al.*, 1986), the effects of environmental impacts can be measured through richness, abundance, and diversity in their habitats (Hawkins, 1997). These characteristics make them good study models, which can be used as tools in environmental change management and assessment processes.

Considering the high significance of the Atlantic Forest biome, one of the richest and most threatened in the world (Myers *et al.*, 2000), the need for studies on land mollusk biodiversity becomes evident, since these organisms have the highest extinction rate recorded in modern times, and many of these species are threatened or may be lost even before being known, as detailed in the study by Lydeard *et al.* (2004). According to Schilthuizen & Rutjes (2001), it is surprising that land mollusks have received little attention in tropical forest regions, despite their diversity and ecosystem role in nature.

Thus, the present study is grounded in the need to obtain environmental and ecological data that can support an understanding of the factors structuring the populations of different land mollusk species in an Atlantic Forest area, based on consistent field sampling, aiming not only to understand how the diversity of these organisms varies in space, but also how they respond locally to environmental factors and ecological interactions.

Our objective was therefore to evaluate how environmental factors and ecological attributes affect the diversity, distribution, and functional and behavioral ecology of land snails in an Atlantic Forest area in Sooretama, Espírito Santo, Brazil. Beyond patterns of richness, composition, and spatial distribution, we also investigated how shell morphology relates to microhabitat use, how activity patterns vary throughout the day, and how these organisms interact with human land use, including their role as

agricultural pests. We expect that the information generated here can contribute to raising the level of knowledge on the ecology of tropical land snails, discussing how species respond to the environmental factors and ecological attributes evaluated, as well as providing data on this faunal group to support management actions and the development of public policies aimed at biodiversity conservation.

This thesis is divided into seven chapters, strategically organized to foster understanding of the environmental and ecological parameters evaluated. As permitted by the resolution of the Graduate Program in Environment (Programa de Pós-Graduação em Meio Ambiente, PPGMA/UERJ), the chapters were conceived in the format of standalone papers, which facilitates the submission of the studies for publication in scientific journals.

In the first chapter, we present a literature review of what is known to date about leaf-litter mollusks in Brazil. The specific focus on leaf-litter mollusks stems from the ecological importance of this animal group, which is traditionally overlooked in malacology. There is a clear distinction between terrestrial, freshwater, and marine mollusks. Within the terrestrial environment, mollusks use a variety of microhabitats, with leaf litter being a particularly complex microhabitat that, in theory, has the potential to harbor the greatest diversity of land mollusks. Drawing on references spanning more than 100 years, the literature review in Chapter 1 consolidates the knowledge accumulated to date, allowing for the formulation of a definition for leaf-litter mollusks.

In Chapter 2, we evaluated a set of nine environmental parameters (atmospheric temperature, soil temperature, soil moisture, atmospheric humidity, leaf-litter depth, light intensity, canopy cover, soil pH, and leaf-litter moisture) on the land snail community of the Sooretama Biological Reserve, retaining for analysis those variables that were not collinear with one another.

In Chapter 3, besides evaluating the response of the land snail community to environmental parameters, we assessed seasonal variation in land mollusks along the moisture gradient in the study area, including changes in community composition between seasons. This third chapter presented important autecological responses regarding the tolerance of certain land mollusk species, a group well known for its dependence on environmental moisture.

As detailed further below, the Sooretama Biological Reserve is crossed by the BR-101 highway along a stretch of approximately 5 km. Accordingly, in Chapter 4 we evaluated the effect of the edge-interior gradient associated with the highway on the

land mollusk community. With well-defined results showing species markedly established along the edge-effect gradient, the data presented in this fourth chapter help to understand the dynamics and consequences of linear infrastructure development on land mollusk diversity.

In Chapter 5, we studied the relationship between the shell shape of land snail species and the microhabitats they use. We selected five microhabitats and tested three predictions: that more abundant species occupy a broader range of microhabitats, that species show non-random associations with particular microhabitats, and that species sharing the same microhabitat exhibit convergent shell morphologies. Discussing these patterns in light of microhabitat niche breadth and morphological convergence, this chapter examines whether and how shell morphology affects microhabitat use and occupation.

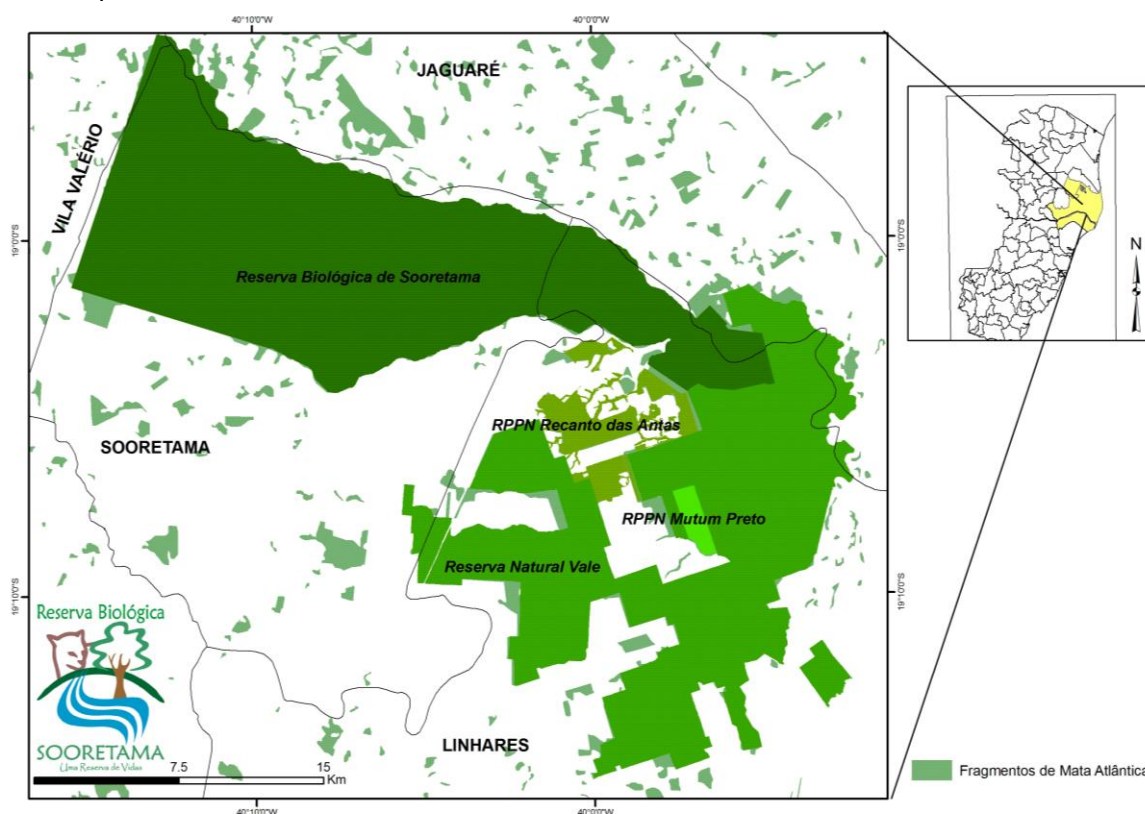
In Chapter 6, we studied the activity pattern of land mollusk species from the Sooretama Biological Reserve across different periods of the day. Starting from the general hypothesis that mollusks are more active at night, when temperatures are milder and humidity is higher, we assessed the circadian rhythm of land mollusks in the field and tested whether this assumption holds. The results revealed a more complex picture than expected, with substantial activity recorded during the daytime, contributing not only to the bioecological knowledge of these species but also raising important implications for the design of sampling effort in field surveys.

Finally, in Chapter 7 we present an ecological assessment of land mollusk species found acting as agricultural pests of papaya trees in plantations bordering the Sooretama Biological Reserve, addressing aspects such as their occurrence, activity, and impact on the crop. This seventh chapter is of great interest to agribusiness, given that the state of Espírito Santo is one of the main producers of papaya in Brazil, exporting the fruit to major destinations such as Europe and the United States of America.

The Sooretama Biological Reserve (REBIO SOORETAMA – RBS)

The study was conducted in the Sooretama Biological Reserve (RBS), located in the municipalities of Sooretama, Linhares, Jaguaré, and Vila Valério, in the northern region of Espírito Santo state ($19^{\circ}0'50.87''\text{S}$ and $40^{\circ}5'48.96''\text{W}$). The area covers 27,858.68 hectares and, together with the Vale Natural Reserve (RNV) (22,711 ha), the Recanto das Antas Private Natural Heritage Reserve (RPPN) (2,212 ha), and the Mutum Preto RPPN (379 ha), forms the largest continuous forest remnant in Espírito Santo, corresponding to 10% of the state's forested area (SOS Mata Atlântica & INPE, 2017) (Figure 1).

Figure 1 - Map of the geographic location of the forest complex, including the Sooretama Biological Reserve, Vale Natural Reserve, Recanto das Antas RPPN, and Mutum Preto RPPN, in the municipalities of Linhares and Sooretama.



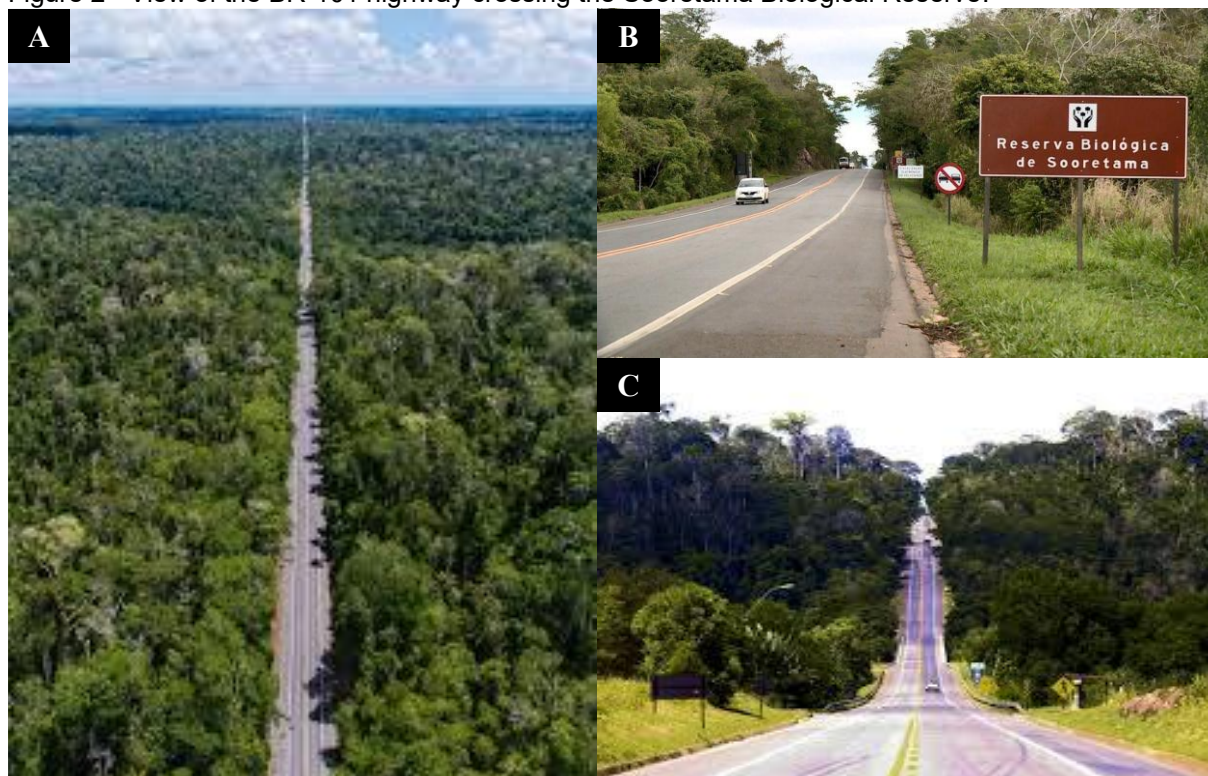
Source: Sooretama Biological Reserve, 2016.

A natural shelter for wildlife threatened with extinction, the Sooretama Biological Reserve was officially known as the "Sooretama Wildlife Reserve, Refuge, and Breeding Park" until the 1960s. This park comprised an area donated to the Federal

Government by the state of Espírito Santo, through Decree-Law No. 14,977 of 09/21/1943 (IBDF, 1981). Its current designation, "Sooretama Biological Reserve", was given through IBDF Ordinance No. 939 of June 6, 1969, and its area was later expanded with the addition of the Barra Seca Forest Reserve (IBDF Ordinance No. 2,015 of 03/04/1971).

The forest complex area is designated for biodiversity conservation and was created with the objective of full protection of its biota (SNUC, Federal Law No. 9,985/2000). In the 1960s and 1970s, construction of the BR-101 highway began in the state of Espírito Santo. Although the area was designated a Zone of Conflicting Use, incompatible with the objectives of creating and managing the conservation unit (IBDF, 1981), a 5.1 km stretch of the highway came to cross the reserve (Figure 2). However, not limited to the Sooretama Biological Reserve alone, the entire forest complex in the municipalities of Linhares and Sooretama is crossed by 25 km of the BR-101 highway.

Figure 2 - View of the BR-101 highway crossing the Sooretama Biological Reserve.

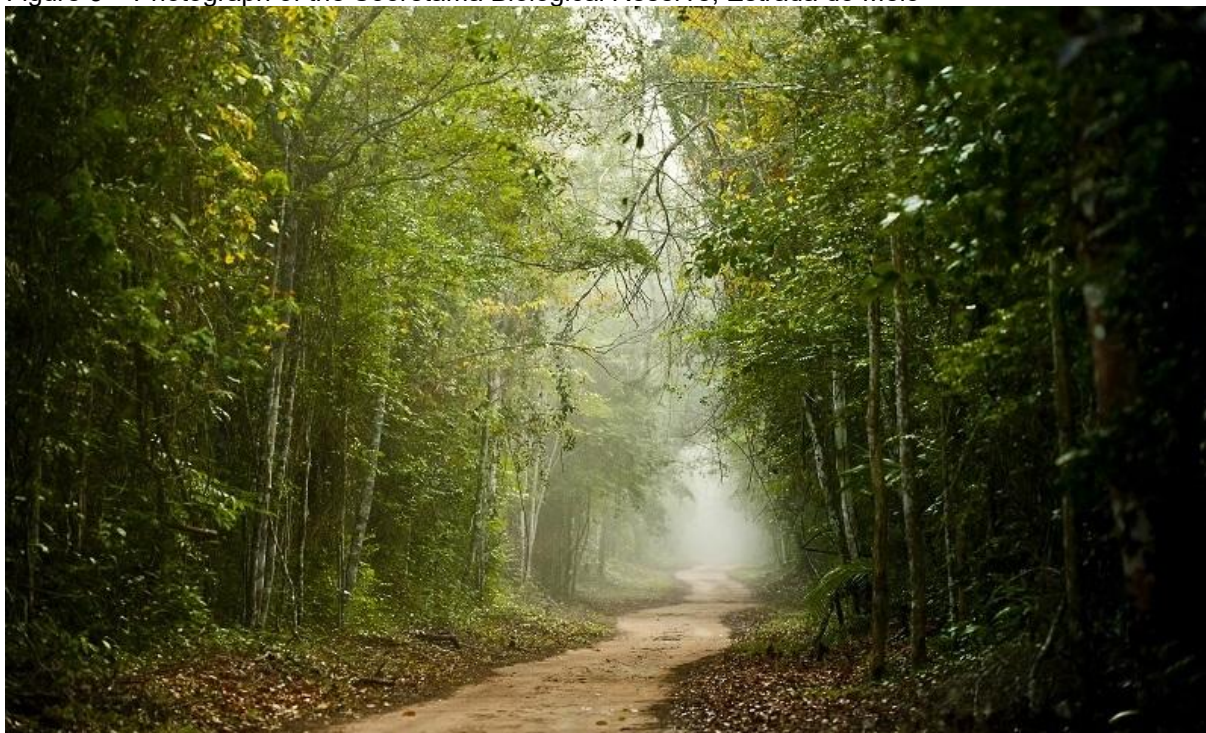


Legend: A) Aerial view of the highway along the entire extent of the Biological Reserve; B) Beginning of the highway stretch crossing REBIO Sooretama, heading north; C) Stretch of the highway crossing REBIO Sooretama, heading south.

Source: A: Sooretama Biological Reserve, 2016. B and C: Author, 2017.

The vegetation of the Sooretama Biological Reserve is classified as Lowland Dense Ombrophilous Forest, commonly known as "Tabuleiro Forest" (Figure 3), situated within the Atlantic Province, Southeastern Subprovince (Rizzini, 1997). Although the IBGE (1987) classification considers the Tabuleiro Forests of northern Espírito Santo as ombrophilous, other authors have highlighted the deciduous character of this forest, naming it the "Tabuleiro Mesophilous Tree Community" (Azevedo, 1962), "Semideciduous Tropical Seasonal Forest" (Strang, 1970), and "Semideciduous Seasonal Forest" (Jesus, 1988), with a generally very short period of deciduousness.

Figure 3 – Photograph of the Sooretama Biological Reserve, Estrada do Meio



Source: Conexão Planeta, 2020 (<https://conexaoplaneta.com.br/blog/sooretama-a-reserva-capixaba-onde-inumeras-evidencias-indicam-que-mata-atlantica-e-amazonia-ja-estiveram-ligadas/>).

The region's climate is classified as Aw under the Köppen system, characterized by a hot, humid rainy season in summer and a dry season in winter. The mean annual temperature is above 23°C (IBDF, 1981). The reserve's area belongs to the Eastern Basins group, with the Barra Seca River being the main watercourse in Sooretama.

1. RESEARCH TRENDS ON LEAF-LITTER MOLLUSKS FROM BRAZILIAN PROTECTED AREAS: A CENTURY OF STUDY

Esteves, R. A., Santos, S. B., & Rocha, C. F. D.

In preparation.

In forests floor, leaf-litter mollusks act as primary consumers of vegetal, animal and fungal matter, aiding in the process of organic matter decomposition and contributing to nutrient cycling and soil formation and productivity (Oliveira *et al.*, 2010; Meyer *et al.*, 2013; Astor *et al.*, 2015). The decomposition of the foliage by the mollusks also contributes to the dispersion of some fungi (Burke, 1999), and by physic-chemically altering the dispersed plant material in the leaf-litter, it favors the growth of fungi and bacteria (Jenning and Barkham, 1979).

Leaf-litter mollusks have an important role in the ecology of the forest ground by providing food for different species, including invertebrates (Frest and Johannes, 1995; Martin, 2000; Nyffeler and Symondson, 2001), amphibians (Drewes and Roth, 1981), birds (South, 1980), snakes (Maia-Carneiro *et al.*, 2012) and small mammals (Rudge, 1968; Whitaker and Mumford, 1972; Churchfield, 1984). They also participate as intermediate hosts in the reproductive cycle for several parasitic helminths that affect wild animals and humans (Raskevitz *et al.*, 1999; Ball *et al.*, 2001; Lu *et al.*, 2018). Once shells of mollusks are rich in calcium, gastropods have an important role in the storage, release and cycling of calcium in the ecosystems they inhabit (Caldwell, 1993). Shells from terrestrial mollusks are the primary source of calcium for eggs of some bird species, and the decline in gastropods abundance in some forest ecosystems have been related to defects in eggshells, which tend to reduce the reproductive success and fall of some birds' species populations (Graveland *et al.*, 1994, Graveland and van der Wal, 1996).

Although pollination by leaf-litter mollusks is a poorly studied phenomenon, at least one study demonstrates the role of the species *Lamellaxis gracilis* (Hutton, 1834) in the pollination of *Volvulopsis nummularium* (L.) Roberty, 1952 (Sarma *et al.*, 2007). Since some fruit may compose the diet of some leaf-litter mollusks which release the seeds in the feces, they also play a significant role in some seed dispersal process (Gervais *et al.*, 1998; Thomé *et al.*, 2006).

Despite the importance of terrestrial mollusks as indicators of environmental conditions (Santos and Monteiro, 2001; Douglas *et al.*, 2013; Nunes and Santos, 2012),

there are no systematized studies on biology and ecology of these organisms in Brazil, contrary to some other countries (Santos *et al.*, 2009). As they are sensitive to changes in the structural and climatic parameters of the habitat and therefore, good study models, the increase in knowledge about terrestrial mollusk communities, especially those inhabiting the leaf-litter, may better subsidize conservation strategies and actions of forests and other environments in which they occur. So far, the knowledge on the leaf-litter mollusks fauna in preserved areas in Brazil is relatively low, with the available knowledge being, in general, restricted to a few records of species that were found in different locations.

In this review, we summarize what is known for leaf-litter mollusks from Brazilian preserved areas, assessing the possible trends that can be drawn from the available information and we propose a concept for leaf-litter mollusks. We believe that this review will fill gaps in the understanding of leaf-litter mollusks of preserved areas in Brazil and then contribute to insert these animals as a relevant group in the conservation of biodiversity.

1.1. Measuring the current knowledge from the available literature on the WEB

To evaluate the state of general knowledge about leaf-litter mollusks from Brazilian preserved areas, we reviewed the information available in the literature found through the bibliographic search carried out from the titles accessible in the databases of SciELO (Scientific Electronic Library Online), Scopus (Elsevier), Web of Science (ISI – Thomson Scientific), JSTOR and the repository Google Scholar.

The search was carried out separately in the databases with keywords containing the following expressions: "*leaf-litter", "*forest floor", "*foliage" and "*forest leaf". Each of these expressions were used separately and also using "AND" or "OR" combining with the expressions "land snails", "terrestrial mollusks / molluscs)" and "Brazil", searching for those expressions throughout the document, depending on the consulted page search engine. In addition, we performed searches combined with the equivalent expressions in Portuguese ("Serapilheira", "Folhiço", "Solo de Floresta" + "Moluscos Terrestres" + "Brasil") and in Spanish ("Hojarasca", "Suelo de Bosque" + "Moluscos Terrestres" + "Brasil"). In our search, we did not consider grey literature as undergraduate thesis, dissertations or thesis.

We used Mendeley software to aid in the management of papers and optimize the removal of duplicate files. After sorting the obtained material, through reading the papers,

we discarded those that did not approach the central question of this study, which are the mollusks that inhabit the leaf-litter in Brazilian preserved areas. We did not consider studies carried out in urban areas or altered by anthropic actions.

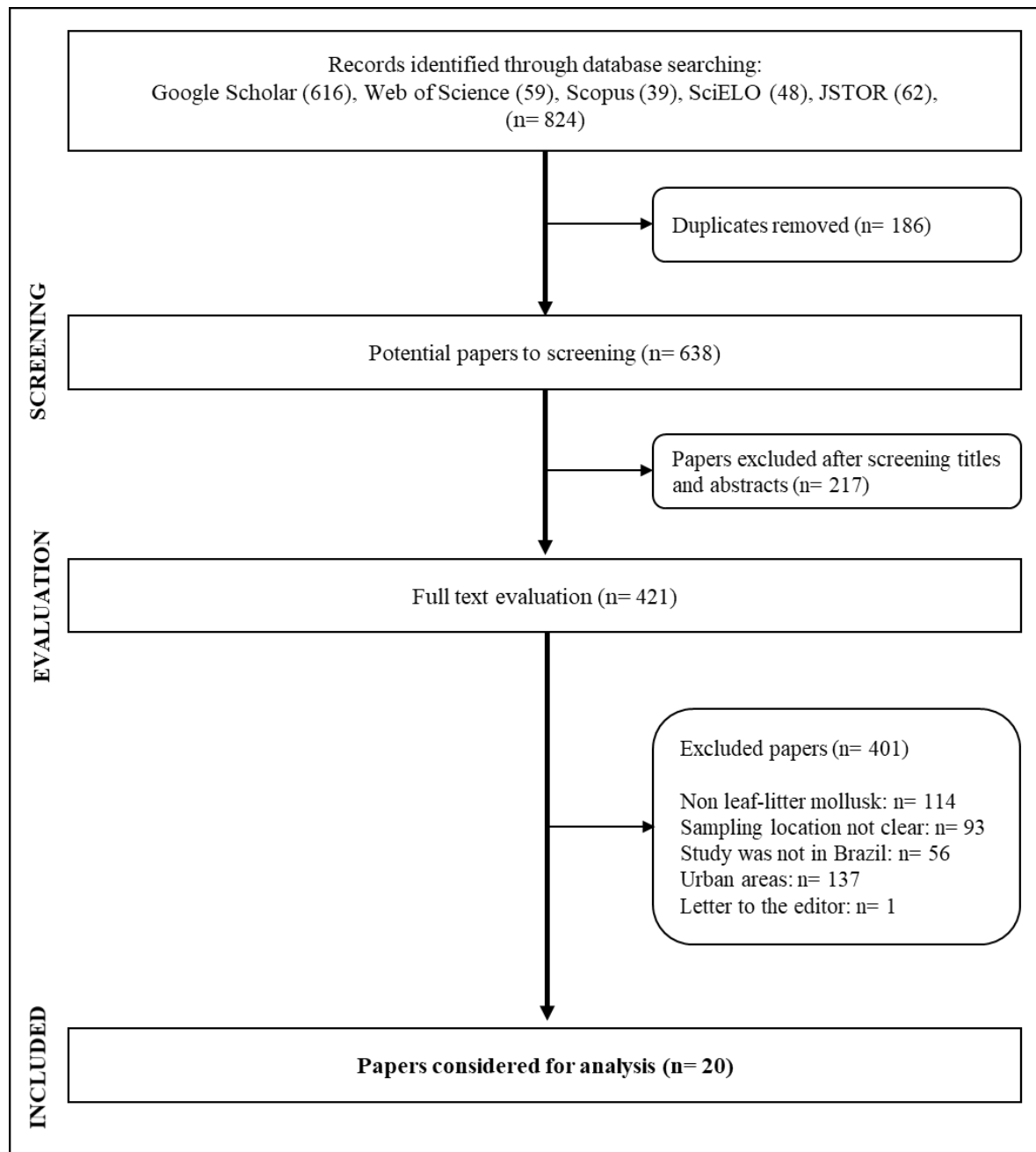
After reading papers and processing the data obtained from them, those considered as satisfying to the subject of this review were grouped according to the main trends (Conservation, Distribution, Ecology, Morphology, Literature Review, Public Health and Taxonomy). The papers were then analyzed regarding their main trend, year, place of research, the presence of theoretical reference and work methodology, ecological aspects and correlations between the species diversity with environmental conservation.

1.2. Leaf-litter mollusks from Brazilian preserved areas: how much do we know?

A total of 824 papers were identified. We excluded 186 papers due to the duplicity through Mendeley. After initial screening of the papers by titles and abstracts, 421 of them remained as under full consideration, especially in terms of their methodological procedures adopted. After carefully reading and analyzing them, only 20 papers were considered as having adherence to the question of this review. The selection process of the papers and the reasons for the exclusions are presented in Figure 4 and the main features of the selected papers are shown in Table 1.

The 20 studies identified in this review showed that the accumulated knowledge on leaf-litter mollusks from Brazilian preserved areas is distributed over a period of 105 years (1913-2018) (Figure 5). The first paper on leaf-litter mollusks was published in 1913 and reported to the Stanford Expedition of Frederick Baker and other researchers in Brazil to study Neotropical fauna. The paper brought a detailed description of the taxonomy of the species collected and, for some, brought some biological aspects of the specimens and described the habitat characteristics where the specimens were collected. The higher concentration of papers about leaf-litter mollusks from Brazilian preserved areas was published in the last 17 years (2001-2018), corresponding to 60% (n= 12) of published studies. No scientific papers about leaf-litter mollusks that had been published between 1920 and 1949 were found, indicating a gap of 29 years without publishing studies about leaf-litter mollusks from Brazilian preserved areas in the databases surveyed.

Figure 4 - Summary of the selection process of scientific articles analyzed in this review.



Source: Author, 2022.

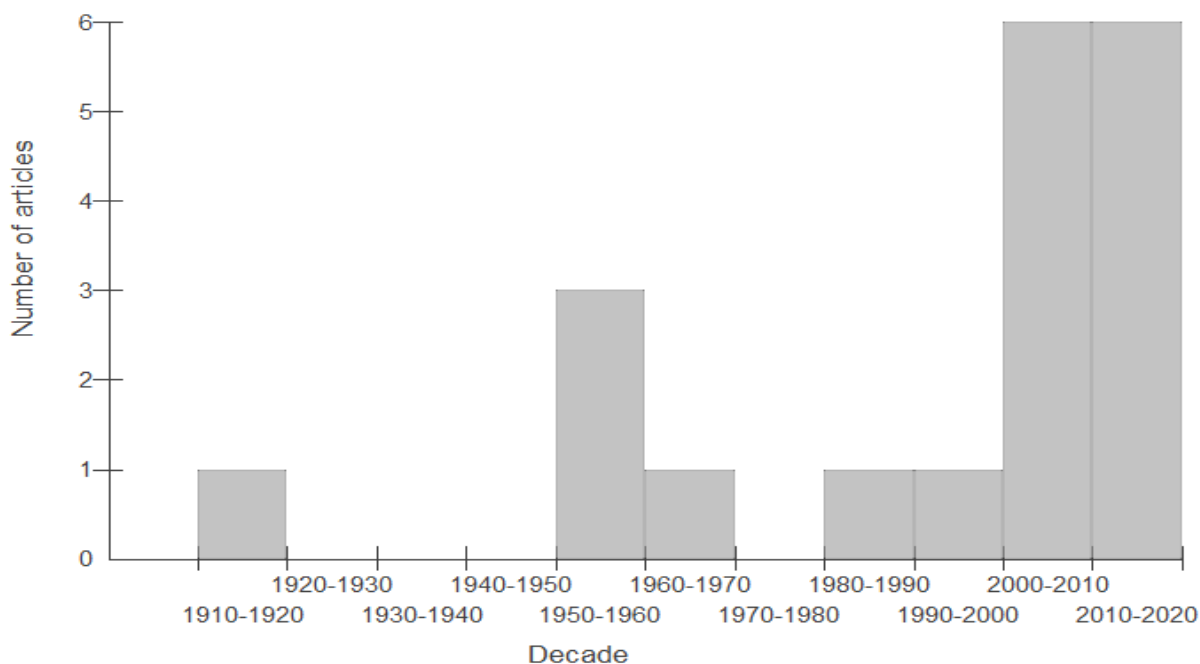
Table 1 - Overview of the studies on leaf-litter mollusks from Brazilian preserved areas in the period of 1913 to 2018 included in this review.

Reference	Data base	Family	Species	Trend	Summary
Baker (1913)	J	4	5	Tax	The article is a report of Frederick Baker & Cia's Stanford Expedition to Brazil to research neotropical malacofauna. It gives a detailed description of the taxonomy of the collected species and, for some, describes the collected habitat
Haas (1950)	J	2	2	Dist	Description of the distribution of species found in Pará State
Jaeckel (1952)	GS	4	11	Rev	The author revised the studies on terrestrial and freshwater mollusks of the Northeast region of Brazil
Morretes (1952)	GS	2	11	Tax	Catalog with description and characterization of species of the Family Strophochelidae
Sawaya & Petersen (1962)	GS	1	1	Tax	Characterization of a species from the Megalobulimidae Family (previously included in Strophochelidae) for the city of Porto Alegre (RS)
Rezende (1975)	GS, SC	1	1	Morph	The author studied in detail the anatomy and histology of the genital system of <i>Drymaeus papyraceus</i> . It also describes the morphology of the concha, radula, mandible and pallial chamber
Coelho & Salgado (1989)	GS, SC	1	1	Morph	Description of the morphoanatomy of specimens deposited in the RJ National Museum Collection
Araujo & Bessa (1993)	GS, SC	1	1	Morph	Analysis of the anatomical structures of <i>Subulina octona</i> populations from several locations under the Atlantic Rainforest domain
Castro & Silva (2001)	GS, SC	4	10	Eco	Composition of terrestrial mollusks in a Natural Park in the Minas Gerais State with richness and abundance in different habitats
Santos & Monteiro (2001)	GS, SC	12	17	Eco	Study conducted in two areas of Ilha Grande to analyze diversity and similarity in terrestrial mollusk communities
Santos <i>et al.</i> (2002)	GS	1	1	PubH	Report of the occurrence of <i>Achatina fulica</i> in the Ilha Grande (RJ). The article addresses the ecological and public health implications that the occurrence of this invasive species represents for the region
Miquel <i>et al.</i> (2004)	SC	3	4	Tax	Characterization of micro mollusk species, describing two new species for southern Brazil
Gomes <i>et al.</i> (2004)	GS, SC	1	1	Morph	Description of the morpho-anatomic structures of <i>Simpulopsis ovata</i> , with little data on the biological aspects presented
Arruda <i>et al.</i> (2006)	GS, SC	1	1	Morph	The article analyzed the morphology of two <i>Omalonyx</i> species, a terrestrial mollusk, but with a strong dependence on flooded environments (amphibian habit)

Nunes & Santos (2012)	GS, SC	9	24	Eco	The article aimed to understand the relationship between environmental factors and terrestrial gastropod communities in two trails in the Ilha Grande (RJ) in different gradients of environmental conservation
Salvador <i>et al.</i> (2014)	GS, SP	1	1	Dist	Geographic expansion of <i>Helicina inaequistriata</i> , previously only found in Ilha Grande (RJ). The article expanded the occurrence of the species to Cabo Frio (RJ) and Mariporã and Piracicaba (SP)
Barbosa & Santos (2014)	GS, SC, WS, SP	1	1	Morph	The authors analyzed the morphological and morphometric variations of <i>Happiella cf. insularis</i> in three trails, at different levels of environmental degradation, in Ilha Grande (RJ)
Salvador <i>et al.</i> (2014)	GS, WS, SP	1	2	Dist	First record of <i>Happia</i> sp. and <i>Succinea lopesi</i> in Trindade Island (ES)
Oliveira & Santos (2018)	GS, SC, WS, SP	1	1	PubH	The authors analyzed cyst distribution of <i>Strongyluris</i> sp. (Nematoda) in the pallial cavity of <i>Achatina fulica</i> from Dois Rios Village and Abrão Village, in Ilha Grande (RJ)

Legend: J: JSTOR; GS: Google Scholar; SC: SciELO; WS: Web of Science; SP: Scopus; Tax: Taxonomy; Dist: Distribution.
Source: Author, 2022.

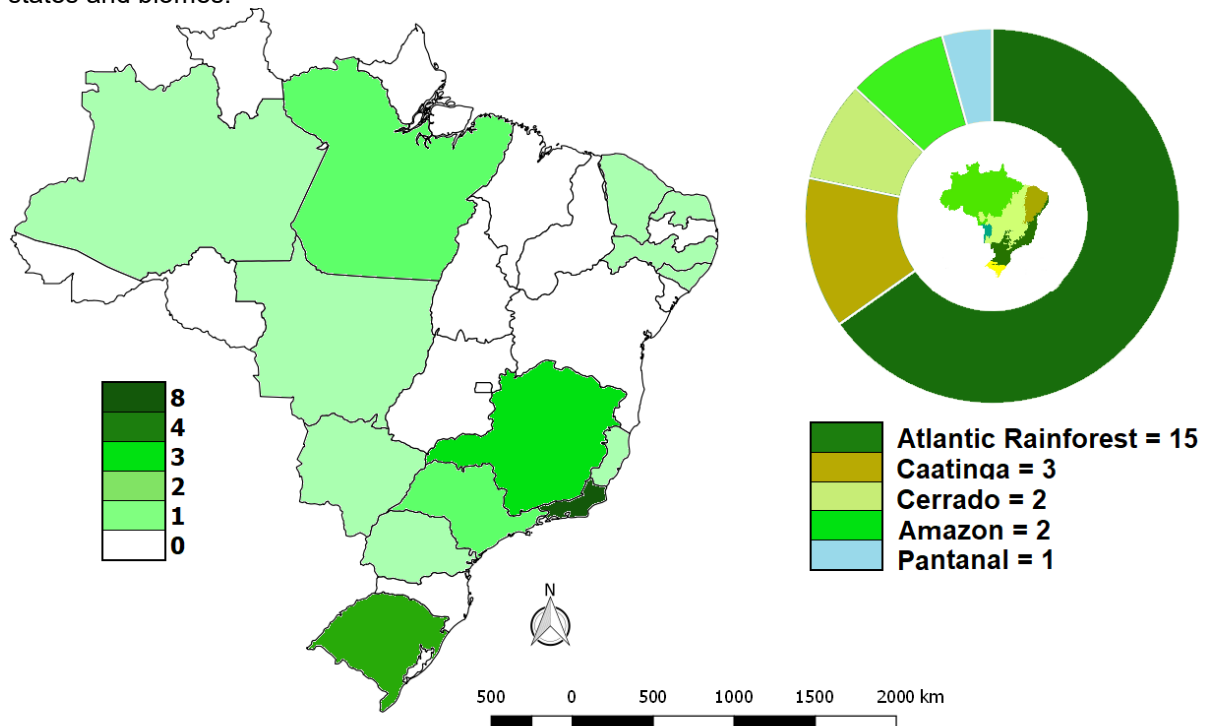
Figure 5 - Distribution of published articles on leaf-litter mollusks from Brazilian preserved areas in the period of 1913 to 2018.



Source: Author, 2022.

The studies considered in this review showed results from 14 Brazilian states (Alagoas, Amazonas, Ceará, Espírito Santo, Mato Grosso do Sul, Mato Grosso, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Norte, Rio Grande do Sul and São Paulo). We found the highest number of studies in the states of Rio de Janeiro (n= 8; 38%) and Rio Grande do Sul (n = 4; 19%). In terms of biomes, the available literature showed that the highest number was found in the Atlantic Rainforest (n= 16), followed by Caatinga (n= 3), Amazon (n= 2), Cerrado (n= 2) and Pantanal (n= 1) (Figure 6). We did not find published papers on the Pampas biome.

Figure 6 - Distribution of published studies on leaf-litter mollusks from Brazilian preserved areas by states and biomes.

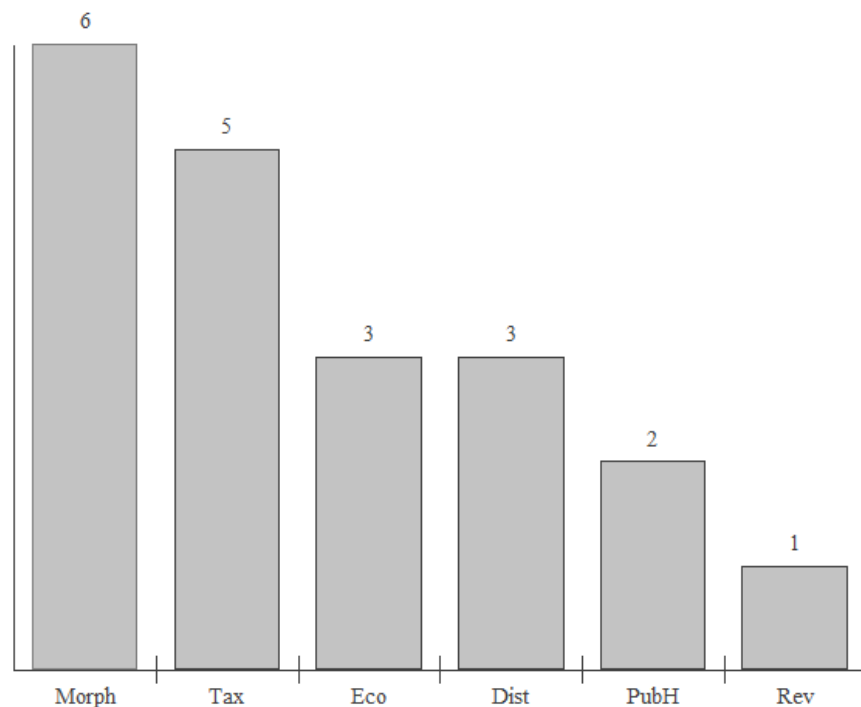


Source: Author, 2022.

A total of six research trends were identified in the 20 studies considered (Figure 7): 1) Morphology (n= 6; 30%), carrying out the analysis of the soft parts and shells (Rezende, 1975; Coelho and Salgado, 1989; Araújo and Bessa, 1993; Gomes *et al.*, 2004; Arruda *et al.*, 2006; Barbosa and Santos, 2014); 2) Ecology (n= 3; 15%), approaching aspects of community or population structure, biotic and abiotic factors affecting the composition, the methodologies used, richness and abundance of species and distribution patterns, habits, reproduction, among other ecological aspects (Castro and Silva, 2001; Santos and Monteiro, 2001; Nunes and Santos, 2014); 3) Taxonomy (n= 5; 25%),

describing and characterizing species collected in leaf-litter habitats and deposited in collections from different parts of Brazil (Baker, 1913; Morretes, 1952; Sawaya and Petersen, 1962; Miquel *et al.*, 2004; Salvador *et al.*, 2018); 4) Distribution (n= 3; 15%), listing the distribution of leaf-litter mollusk species from Brazilian preserved areas (Haas, 1950; Salvador *et al.*, 2014a; 2014b); 5) Public Health (n= 2; 10%), analyzing the distribution of species vectors of diseases caused by parasites that have the leaf-litter mollusk as an intermediate host and evaluating the risks and impacts for public health and for the ecosystem dynamics (Santos *et al.*, 2002; Oliveira and Santos, 2018); 6) Literature Review (n= 1; 5%), presenting a synthesis of the terrestrial and freshwater mollusks of the Northeast region, including the leaf-litter mollusks in Brazil (Jaeckel, 1952).

Figure 7 - Distribution of published studies on leaf-litter mollusks from Brazilian protected areas in the period of 1913 to 2018 by the research trends.



Legend: Morph: Morphology; Tax: Taxonomy; Eco: Ecology; Dist: Distribution; PubH: Public Health; Rev: Literature review.
Source: Author, 2022.

Although Rezende (1975) and Gomes *et al.* (2004) studied populations of typically arboreal species, *Drymaeus papyraceus* (Mawe, 1823) and *Simpulopsis ovata* (Sowerby, 1822) respectively, we considered those studies in this review because the authors collected significantly number of alive specimens in the leaf-litter and on fallen trunks in the ground. Hass (1953) studied the mollusks of Ilha Grande (marine and non-marine);

however, we did not consider this survey because it does not address the habitats where the mollusks were collected.

1.3. What does the available information reveal about leaf-litter mollusks from Brazilian preserved areas?

Our results showed that five studies (25%) did not present a sampling protocol, being one on Literature Review (Jaeckel, 1952), in which the analyzed studies in that review also did not presented any consideration on sampling protocol, two on Morphology (Araújo and Bessa, 1993, Barbosa and Santos, 2014) and one on Distribution (Salvador *et al.*, 2014b). Twelve studies (60%) obtained their samples through visual searches, not presenting a standard methodological procedure established previously that would allow quantitative analysis. Of these, six were on Taxonomy, with analysis of specimens deposited in Scientific Collections in Brazil and in other countries (Baker, 1913; Morretes, 1952; Sawaya and Petersen, 1962; Miquel, 2004; Salvador *et al.*, 2014; Salvador *et al.*, 2018), one on Distribution, providing the dispersion of several species from the Amazon region (Haas, 1950), three studies on Morphology (Rezende, 1975; Coelho and Salgado, 1989; Arruda *et al.*, 2006), and two studies analyzed the issue of Public Health involving one invasive terrestrial mollusk species in Ilha Grande, Rio de Janeiro (Santos *et al.*, 2002; Oliveira and Santos, 2018).

The methodologies used in the studies that presented a sampling protocol included visual searches in previously demarcated area (Castro and Silva, 2001; Gomes *et al.* 2004; Salvador *et al.*, 2018), quadrats 5x10m (Santos and Monteiro, 2001) and quadrats 25x75cm (Nunes and Santos, 2012). In terms of abundance, the species of leaf-litter mollusks most commonly collected in the presented studies were some representatives of the families Euconulidae, Simpulopsidae, Scolodontidae, Subulinidae and Charopidae (Table 2).

Table 2 - Most abundant species of leaf-litter mollusks collected in the presented studies, with the indication of the locality and the sampling method used by author.

Family	Species	Abundance	Sampling method	Local	Reference
Euconulidae	<i>Pseudoguppya semenline</i> (Moricand, 1846)	194	Visual search	Pedra Talhada - AL	Salvador <i>et al.</i> 2018**
Simpulopsidae	<i>Simpulopsis ovata</i> * (Sowerby, 1822)	162	Visual search	São Francisco de Paula - RS	Gomes <i>et al.</i> 2004
Scolodontidae	<i>Happiella</i> sp.	155	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Subulinidae	<i>Bekianum bekianum</i> (Pfeiffer, 1846)	101	Quadrats 5x10m	Ilha Grande - RJ	Santos & Monteiro 2001
Charopidae	<i>Stephanoda</i> sp.	82	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Scolodontidae	<i>Miradiscops</i> sp.	80	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Scolodontidae	<i>Tamayoa banghaasi</i> (Thiele, 1927)	78	Quadrats 5x10m	Ilha Grande - RJ	Santos & Monteiro 2001
Streptaxidae	<i>Streptaxis iheringi</i> (Pilsbry, 1930)	69	Visual search	Pedra Talhada - AL	Salvador <i>et al.</i> 2018**
Euconulidae	<i>Habroconus semenlini</i> (Moricand, 1845)	66	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Diplomatinidae	<i>Adelopoma</i> sp.	63	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Subulinidae	<i>Opeas beckianum</i> (Pilsbry, 1906)	46	Quadrats 25x75cm	Ilha Grande - RJ	Nunes & Santos 2012
Scolodontidae	<i>Happia</i> sp.	40	Quadrats 5x10m	Ilha Grande - RJ	Santos & Monteiro 2001

* Although *Simpulopsis ovata* is typically an arboreal species, Gomes *et al.* (2004) found many alive specimens active on the leaf-litter.

** Salvador *et al.* (2018) did not provide specific abundance, only relative abundance for the family.

So, we consider only families represented by only one species.

Source: Author, 2022.

The high values of the abundance recorded suggest that different variables such as the sampling method, the season of the year in which the study was carried out, the type of environment and the adaptation of the species to the leaf-litter seemed to influence abundances. Regarding to the sampling method, the results suggested relevant interference of the sampling methods used. In a similar study, Rocha *et al.* (2001), compared two sampling methods to evaluate the density of the leaf-litter frog community

in an Atlantic Rainforest area and concluded that the size of the plots used affects the final result in terms of individuals found, demonstrating that reduced plots had advantages and were more efficient compared to larger plots, since they provide more accurate estimates of abundance and biomass per unit of forest ground. This explains the difference between the values of richness and relative abundance for the studies of Nunes and Santos (2012) and Santos and Monteiro (2001), both carried out in the Ilha Grande, Rio de Janeiro. The study of Santos and Monteiro (2001) used larger plots (5x10m) and the searches were performed on a set of smaller transects in a determined period, looking for the organisms on the foliage. On the other hand, in the study carried out by Nunes and Santos (2012), because of the use of the smaller plots (25x75cm), all material contained in the quadrat was turned and taken to the laboratory, where it was carefully searched for mollusks in a detailed screening of this material, allowing the finding of most of gastropods present in the collected foliage.

The data from the studies indicated that some environmental factors affected the richness and abundance of the leaf-litter mollusks from Brazilian preserved areas. Some habitat parameters such as relative humidity of the air (Baker, 1913; Jaeckel, 1952; Santos and Monteiro, 2001; Gomes *et al.*, 2004; Nunes and Santos, 2012), leaf-litter humidity (Santos and Monteiro, 2001; Araújo and Bessa, 2012), relative air temperature (Santos and Monteiro, 2001; Gomes *et al.*, 2004; Nunes and Santos, 2012; Barbosa and Santos, 2014), soil temperature (Santos and Monteiro, 2001; Nunes and Santos, 2012), depth of the leaf-litter layer (Santos and Monteiro, 2001; Nunes and Santos, 2012; Barbosa and Santos, 2014) and environmental degradation level (Santos and Monteiro, 2001; Nunes and Santos, 2012; Barbosa and Santos, 2014), were shown as environmental factors that most affected the abundance and distribution of leaf-litter mollusks.

1.4. Leaf-litter mollusk aspects and conservation perspectives

Based on the available knowledge, we consider that leaf-litter mollusk is all species of terrestrial mollusk which inhabits the leaf-litter (layer of vegetable waste formed by fallen leaves, branches and trunks, which is deposited on forest ground) and participates in food webs related to this microenvironment. The available studies presented species distributed in the leaf-litter and related them to ecosystem factors, predicting that these mollusks depend directly or indirectly on this habitat to perform their biological functions (foraging, reproduction and ecological interaction).

Our results showed that only four studies (20%) approached aspects of conservation (Castro and Silva, 2001; Santos and Monteiro, 2001; Nunes and Santos, 2012; Salvador *et al.*, 2018). These four studies presented categories inherent to the field of conservation that can contribute to insert the leaf-litter mollusks on the agenda of conservationist policies in Brazil: 1) Biodiversity Conservation, which relate the ecological aspects, mainly richness and abundance of mollusk communities with different impacts (Castro and Silva, 2001; Nunes and Santos, 2012; Salvador *et al.*, 2018); 2) Biodiversity Management, in which the authors discuss the structural dynamics of populations and communities of leaf-litter mollusks in terms of management and decision-making processes (Santos and Monteiro, 2001) and 3) Bioindicators, when the authors use or mention leaf-litter mollusks as models to study the effects of environmental stressors on the richness, abundance or changes in distribution patterns of populations and communities (Santos and Monteiro, 2001; Nunes and Santos, 2012).

Salvador *et al.* (2018) found a live specimen of *Megalobulimus cardosoi* (Morretes, 1952) in a biological reserve of Atlantic Rainforest in the Alagoas state, northeastern Brazil. *Megalobulimus cardosoi* was declared extinct in the IUCN Red List (MANSUR, 1996) and is currently considered critically extinct by the Brazilian official list of threatened fauna (ICMBio, 2018). The result of the Salvador *et al.* (2018) highlights the need for efforts focused on expanding knowledge about terrestrial mollusk fauna in Brazil, especially the leaf-litter mollusks, a poorly studied group. This gap in the knowledge is an impediment to conservation action. According to Baillie *et al.* (2004), the global conservation status of almost 90% of mammal species and of all bird and amphibian species has been evaluated, whereas only 3% of mollusk species and 0.08% of insect species have been assessed. Indeed, invertebrates receive much less attention than vertebrates, and our knowledge of them is sparse (Gaston and May, 1992; McKinney, 1999). The value of the molluscan fauna should be highlighted and taken into account in future conservation efforts, as leaf-litter mollusks are the most threatened animal group and good indicators of well-preserved areas (Lydeard *et al.*, 2004; Régnier *et al.*, 2009).

1.5. Conclusion

The scientific knowledge base on leaf-litter mollusks from Brazilian preserved areas is still incipient and insufficient to understand trends or patterns on the relationships between populations and communities of leaf-litter mollusks with biological aspects and

the ecological dynamics of the species. Although there are sampling methodologies for leaf-litter mollusks well accepted by the scientific community, the studies assessed in this review did not follow standardization in terms of methodological procedures for the sampling of leaf-litter mollusks, limiting the comparative approach of ecological studies, which is the discipline that most integrates with conservation actions. Environmental factors such as air humidity, leaf-litter humidity, air temperature, soil temperature and leaf-litter depth interfere in the richness, abundance and distribution of leaf-litter mollusks, indicating that these variables can serve as parameters of future environmental assessment of this group of animals. Considering the current high rate of habitat loss and fragmentation in all biomes, it is important to expand the knowledge on leaf-litter mollusks in Brazil. Leaf-litter mollusks constitute good indicators of the environmental quality. They are susceptible to the effects of environmental stressors, which results in losses of their diversity and affects the size of their populations and thus, potentially altering communities' number and structure. As the leaf-litter mollusks are good models of study and environment quality, it is urgent that they are integrated into biodiversity conservation plans.

2. LOCAL ENVIRONMENTAL PARAMETERS AFFECTING THE STRUCTURE OF A LAND SNAIL COMMUNITY IN AN ATLANTIC RAINFOREST AREA IN SOUTHEASTERN BRAZIL¹

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In preparation.

¹Note: Taxonomic identifications of several land snail species recorded in this chapter have been revised in studies published from 2024 onward, based on the same sampling dataset, but these revisions had not yet been incorporated at the time of the thesis defense and are therefore not reflected here. Unlike the published chapters derived from this dataset, which consider only live individuals, this chapter considered all species recorded, including those represented solely by empty shells. A taxonomic inventory of the land snail species of the Sooretama Biological Reserve, incorporating these revisions, is currently in preparation and was beyond the scope of this thesis.

A community is most frequently defined as a set of interacting populations inhabiting the same space at the same time and under similar environmental effects (Pianka, 1973) and community ecology aims to understand the patterns of distribution, abundance, interactions among organisms and community structure (Leibold *et al.*, 2004; Keller *et al.*, 2009). Community structure encompasses the intricate relationships among the local component populations of interacting species (Pianka, 2000), which might involve trophic structure, energy flow, alpha and beta diversity, and the distribution of individuals in space and time (Magurran, 2011), for both aquatic and terrestrial communities. For most communities, there is an increasing knowledge regarding the role of factors affecting them in the last decades. However, for some other communities, as example, those involving organisms living in the leaf-litter of forests, the scientific knowledge on which factors most importantly affect parameters determining community structure, and whether species assemblies follow any general ecological trend, is comparatively more restricted (Siqueira *et al.*, 2014).

Studies of the relationship between the distribution and abundance of terrestrial gastropods and environmental predictors are scarce for Brazil, with only one published study on land snail fauna of Atlantic Forest (Nunes & Santos, 2012). Although the Atlantic forest is one of the world's biodiversity hotspots (Myers *et al.*, 2000) and land snail species account for a significant component of faunistic biodiversity and

endemism in this biome, these organisms have been poorly studied (Santos & Monteiro, 2001; Thomé, Gomes & Picanço, 2006).

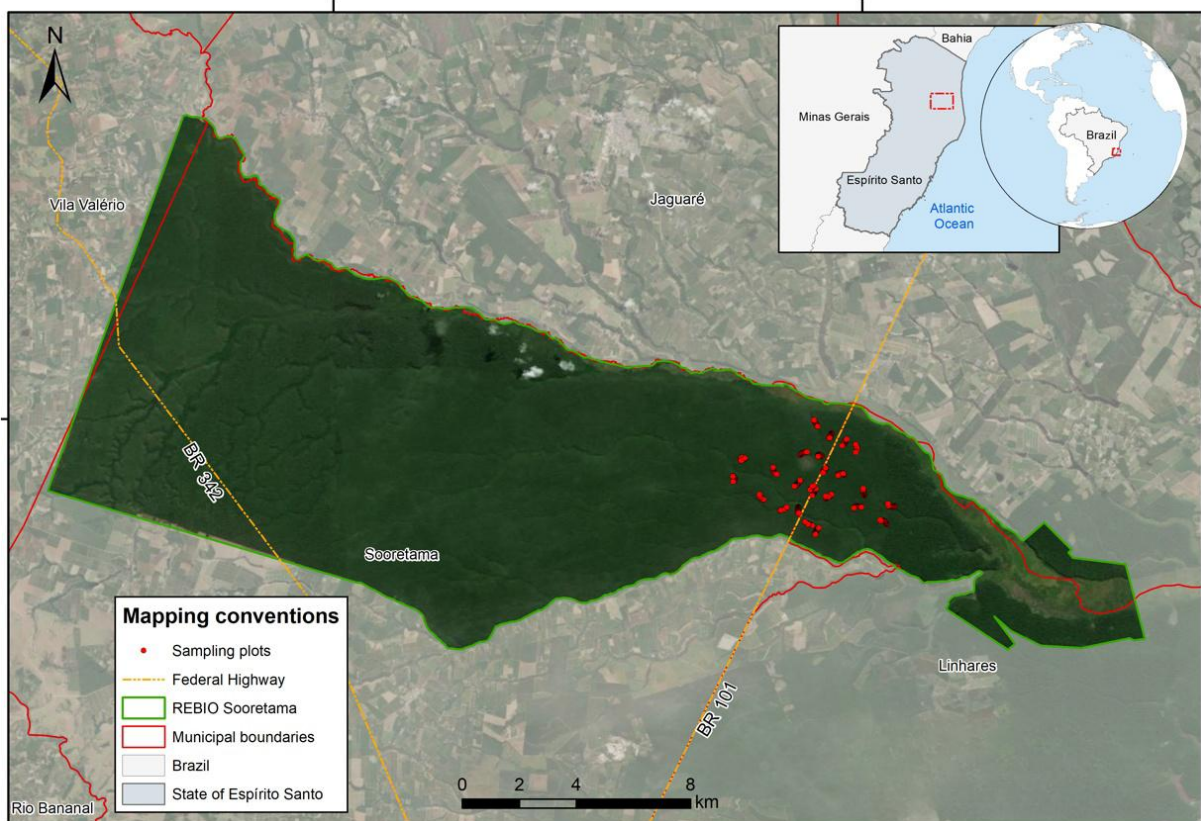
In this study, along two years using a standardized method of permanent plots (RAPELD method, see below), we investigated the influence of selected environmental factors on snail species richness, total abundance and community composition in the one of the largest Brazilian Atlantic forest remnants. We address the questions (1) which environmental predictors better explains the snail distribution and diversity, (2) does the species richness and total abundance affected by the selected environmental predictors, and (3) how the pattern of species composition changes along the gradients of the selected environmental predictors (even for short gradients).

2.1. **Material and methods**

2.1.1. Study area

We conducted the study in the Sooretama Biological Reserve (19°0'50.87" S, 40°5'48.96" W, mean altitude: 46 m), the largest remnant of Atlantic Rainforest in Espírito Santo State, south-eastern Brazil (Fig. 8). The reserve has approximately 28,000 ha and is one of the remnants with higher importance for conservation of biological diversity of the Brazilian Atlantic forest, and is located in the Central Corridor of the Atlantic Forest Biome (MMA, 2000). The climate in the region is tropical hot and humid, with mean annual rainfall of 1,202 mm and mean annual temperature of 23.3 °C. The vegetation physiognomy of the reserve comprises the Coastal Plain Forest (locally called "Floresta de Tabuleiro") whose canopy trees may reach up to 40 m high (Peixoto & Gentry 1990).

Figure 8 - Map of the studied area with the 24 sampling plots following the RAPELD method in the Sooretama Biological Reserve, south-eastern Brazil.



Source: Author, 2022.

The region is classified as Aw (tropical savanna climate), characterized by a rainy summer and a dry winter (Alvares *et al.* 2014). The climate in the region is tropical hot and humid, presenting a mean annual precipitation of approximately 1,257.6 mm and mean annual temperature of 24.2 °C (INCAPER, 2024).

According to the Management Plan of the Sooretama Biological Reserve, there are no significant records of established invasive alien species within the reserve's boundaries (ICMBio, 2019), indicating a well-preserved ecosystem. However, the reserve is subject to anthropogenic pressures, particularly along its borders. Human activities in surrounding areas, such as agriculture and informal settlements, pose risks, including forest fires, which have affected the reserve in recent decades (e.g., a major fire in 1998 and another in the Lagoa do Macuco region in 2016).

2.1.2. Data sampling

Field sampling was carried out in 2017 (January, June, August and November) and 2018 (January, June, September and December), including both the months of the dry (April to September) and of the rainy season (October to March) in the area. We conducted sampling during the diurnal period (05:00 h to 10:00 h), using 24 plots distributed along the Coastal Plain Forest physiognomy, following the RAPELD method (Magnusson *et al.*, 2005). The RAPELD method consists of permanent and standardized 250 meters long plots, following the terrain contours and 1 km distant from each other. The name for the method RAPELD mixes the acronym RAP (Rapid Assessment Program) with that of PELD (the Brazilian acronym for Long-term Ecological Research - LTER). In the 250 m long plots, the land snails were sampled at a walking pace and using the active search method, with visual sampling for macro-gastropods (> 5 mm in diameter or height) by two observers (the same people during all period of study). The plots were carefully inspected, looking for land snails in the leaf-litter, on trees, on branches, in the bushes, on fallen logs and in other microhabitats, when present. For the micro-gastropods (< 5 mm in diameter or height), we used three subplots (25 x 75 cm) distributed in a standard way along the plots (50, 100 and 200 meters) to collect leaf-litter (approximately 4 litters each subplot). All specimens recorded were analyzed under a stereomicroscope, quantified and deposited at the Malacological Collection of the Rio de Janeiro State University.

2.1.3. Environmental variables

A set of nine environmental variables that might be important predictors of land snail species richness, total abundance and species composition was measured for each plot prior removing the leaf-litter: (1) Air temperature (°C), using the Incoterm Digital Hygrometer (0 - 50 ± 0.1 °C), with the device placed next to the subplot; (2) Soil temperature (°C), using the Instrutemp Digital Thermometer (-50 - 300 ± 0.1 °C), with the bulb inserted in the ground inside the subplot; (3) Relative air humidity (%), using the Incoterm Digital Hygrometer (15 - 99 ± 1%), with the device placed next to the subplot; (4) Soil humidity (%), using the PH-1000 soil pH and humidity meter (10 - 80 ± 1%), with the sensor inserted in the ground; (5) Leaf-litter depth (cm), using a common rule of 30 cm in length sunk in the leaf-litter inside the subplot until it found resistance from the soil. Five measures were taken to calculate the mean (four squares and one at the centre); (6) Light intensity (lux), using the LDR-208 Luxmeter (200 -

200,000 lux $\pm$ 3%), measured with the sensor facing up inside the subplot above the leaf-litter; (7) Canopy closure (%), using the Spherical Concave Densiometer. With the observer positioned on the subplot, four measurements were taken towards the cardinal points (north, south, east and west). Subsequently, the values were added, divided by four (mean) and the result multiplied by the correction factor 1.04 to obtain the percentage of canopy closure for each subplot; (8) Soil pH (upH), using PH-1000 soil pH meter ($3 - 8 \pm 0.1$) with the device inserted in the ground into the center of the subplot; and (9) Leaf-litter humidity (%), using thermogravimetric method. The leaf-litter was packed in paper bags of known weight, and we measured the mass of this leaf-litter to obtain the wet weight. Then, the bags with the leaf-litter were placed in an oven at 60 °C until the material was completely dried (constant weight). The leaf-litter was weighed again to obtain the dry weight. The difference between wet and dry weight provided the humidity percentage of the leaf-litter.

2.1.4. Statistical analysis

Based on the number of land snails of each species found in the plots and subplots, we estimated the abundance for each species for the macro and micro gastropods found and the species richness. We considered in the species inventory all live specimens and empty shells with entire periostracum. For multivariate analyses we used numbers of live individuals only.

The evaluation of sampling effectiveness was undertaken by a species accumulation curve (collector curve) and by estimators: Chao 1 Estimator (Colwell & Coddington, 1994) and Bootstrap (Efron, 1979). Species abundances were transformed as $y = \ln(x + 1)$ to decrease the importance of dominant species and to give a stronger weight to species compositional variance. Species-by-sample matrix of forest sites was subjected to Multidimensional Scaling (MDS; also known as Principal Coordinates Analysis, PCoA) using Bray-Curtis dissimilarity (Faith, Minchin & Belbin, 1987) to explore the main gradients of species compositional variance. A Spearman's rank correlation coefficient was calculated for the environmental variables to check if there was a high intercorrelation among them. To avoid multi-collinearity, we excluded from further analyses those variables showing a Spearman's correlation value were > 0.75 (in module) among them in order to minimize overestimating their effect. To associate the main gradient of changes in species composition with measured

environmental predictors, we used “*envfit*” function from the “vegan” package with 1000 permutations. Relationship between species richness and total abundance in response to measured variables was explored the Spearman’s rank correlation coefficient. Snail species response curves were modelled to explain the distribution of species along the environmental gradients by using the “*generico*” function (Landeiro, 2011), which produces a graph that orders species in relation to an environmental gradient. Non-transformed species abundance (density) was used to explain the distribution of species along the environmental gradients. We used R program (version 3.6.0, R Core Team, 2019), using the “vegan” (Oksanen *et al.*, 2012) package for all statistical analyses.

2.2. Results

We recorded a total of 1,507 individuals (440 alive specimens and 1,067 empty shells) belonging to 47 species from 13 families (Table 3). The species accumulation curve analysis produced a clear asymptotic shape, and the predicted estimates of land snail richness (Chao1 = 51 ± 4.0 species; Bootstrap = 51 ± 2.4 species) were close to the richness value we obtained using plot and subplot sampling (47 species). The number of specimens per plot varied between 23 and 158. Species richness per plot ranged from 4 to 22 (Table 3). Achatinidae was the most speciose family, with nine registered species (all species belonging the subfamily Subulininae). However, *Leiostracus perlucidus* (Simpulopsidae) was the most abundant species in all plots in the entire sampling period.

We excluded the variables air temperature, relative air humidity and light intensity as they were highly correlated with the variables soil temperature and canopy closure by the Spearman’s rank correlation coefficient (Table 4). The highest rates of variation among the plots were found for the variables soil humidity (40.4%), leaf-litter humidity (33.4%) and leaf-litter depth (31.2%), contrasting with those that least varied among the plots, soil temperature (2.5%) and soil pH (4.0%) (Table 5). The main gradients of species composition were explored by indirect ordination (MDS) that explained 40.4% of the variation in species composition by the first two ordination axes (Fig. 9). We found five main changes in the snail composition at the sampled plots related to soil temperature ($R^2 = 0.3181$, $P = 0.015$) and soil pH ($R^2 = 0.3337$, $P = 0.011$) on the first MDS axis (Table 6; Fig. 9), and soil humidity ($R^2 = 0.3911$, $P =$

0.004), canopy closure ($R^2 = 0.6217$, $P = 0.001$) and leaf-litter humidity ($R^2 = 0.2494$, $P = 0.047$) on the second MDS axis (Table 6; Fig. 10). The first two axes explained 38.5%, and 1.9% of the total variation in species composition, respectively. Numbers of species as well as numbers of individuals were strongly correlated with soil temperature, soil humidity, canopy closure and soil pH (Table 7).

Table 3 - List of all analyzed species, frequency of live and all individuals, number of all live individuals, and number of all empty shells of the Atlantic forest of Sooretama Biological Reserve.

Species	Freq. of live individuals	Freq. of all individuals	N° of live individuals	N° of empty shells
ACHATINIDAE				
<i>Allopeas gracilis</i> (Hutton, 1834)	3	7	3	17
<i>Allopeas micrum</i> (d'Orbigny, 1835)	3	4	5	27
<i>Leptinaria bequaerti</i> Pilsbry, 1926	4	8	14	43
<i>Leptinaria concentrica</i> (Reeve, 1849)	2	7	12	38
<i>Leptinaria unilamellata</i> (d'Orbigny, 1835)	6	8	16	44
<i>Leptinaria anomala</i> (Pfeiffer, 1846)	0	2	0	5
<i>Leptinaria orysa</i> (Bruguière, 1789)	0	1	0	3
<i>Dysopeas muibum</i> Marcus & Marcus, 1968	0	1	0	3
<i>Subulina parana</i> Pilsbry, 1906	0	2	0	11
BULIMULIDAE				
<i>Cochlorina aurisleporis</i> (Bruguière, 1792)	2	2	2	0
<i>Cochlorina intensior</i> (Pilsbry, 1898)	4	6	7	31
<i>Pseudoxychona pileiformis</i> (Moricand, 1836)	8	12	10	36
<i>Drymaeus flexilabris</i> (Pfeiffer, 1853)	3	8	9	42
<i>Auris bilabiata</i> (Broderip & Sowerby, 1830)	0	2	0	12
CHAROPIDAE				
<i>Radiodiscus goeldii</i> (Thiele, 1927)	1	2	3	4
<i>Lilloiconcha superba</i> (Thiele, 1927)	1	1	1	0
<i>Radiodiscus costeliffer</i> Hylton Scott, 1957	0	2	0	3
<i>Rotadiscus amancaezensis</i> (Hidalgo, 1869)	0	1	0	2
EUCONULIDAE				
<i>Euconulus martinezi</i> (Hidalgo, 1869)	1	1	1	0
<i>Pseudoguppya semenlini</i> (Moricand, 1846)	4	4	13	4
<i>Pseudoguppya aenea</i> (Scott, 1948)	6	7	61	15
HELICINIDAE				
<i>Helicina angulata</i> Sowerby, 1873	1	8	3	13
<i>Helicina angulifera</i> Wagner, 1910	3	9	6	25
<i>Helicina inaequistriata</i> Pilsbry, 1900	2	2	2	0
<i>Alcadia</i> sp.	0	1	0	2
ODONTOSTOMIDAE				
<i>Bahiensis albofilosus</i> (Dorhn, 1853)	3	4	9	13
<i>Bahiensis bahiensis</i> (Moricand, 1833)	2	4	2	36
<i>Burringtonia pantagruelina</i> (Moricand, 1833)	2	4	3	7

<i>Burringtonia labrosa</i> (Menke, 1828)	0	1	0	3
<i>Moricandia dubiosa</i> (Jay, 1839)	0	1	0	1
ORTHALICIDAE				
<i>Orthalicus prototypus</i> Pilsbry, 1899	1	1	7	0
PLEURODONTIDAE				
<i>Solaropsis amazonicus</i> (Pfeiffer, 1854)	4		4	12
<i>Solaropsis rosarium</i> (Pfeiffer, 1849)	2	6	2	8
SCOLODONTIDAE				
<i>Happia pilsbryi</i> Gube, 1902	6	7	12	18
<i>Scolodonta spirorbis</i> (Deshayes, 1950)	10	11	31	39
<i>Scolodonta bounobaena</i> (Orbigny, 1835)	2	5	14	29
<i>Systrophia circumplexa</i> Ferussac, 1839	3	4	6	25
<i>Happiella</i> sp. Baker, 1925	2	2	3	0
<i>Tamayoa banghaasi</i> (Thiele, 1927)	5	6	32	25
<i>Tamayoa decolorata</i> (Dronët, 1859)	3	3	7	9
SIMPULOPSIDAE				
<i>Leiostracus perlucidus</i> Spix, 1827	17		99	211
<i>Rhinus ciliatus</i> (Gould, 1846)	2	9	4	19
<i>Simpulopsis atrovirens</i> (Moricand, 1836)	2	2	5	0
STREPTAXIDAE				
<i>Rectartemon iguapensis</i> (Pilsbry, 1930)	9	17	24	155
<i>Rectartemon iheringi</i> (Thiele, 1927)	3	7	8	73
PUNCTIDAE				
<i>Paralaoma pilsbryi</i> (Hylton Scott, 1957)	0	1	0	2
STROPHOCHEILIDAE				
<i>Megalobulimus intercedens</i> (Martens, 1876)	0	2	0	2

Source: Author, 2022.

Table 4 - Values of Spearman's rank correlation coefficient between environmental variables and their significance

Variables	Air Temp	Soil Temp	Air Hum	Soil Hum	Leaf Depth	Lux	Canopy	Soil pH	Leaf Hum
Air Temp		0.0000	0.0385	0.0989	0.0012	0.0144	0.1318	0.0031	0.1944
Soil Temp	0.7817		0.0057	0.0053	0.0208	0.0044	0.0244	0.0011	0.7023
Air Hum	-0.4249	-0.5468		0.0000	0.9236	0.0000	0.0000	0.0007	0.4451
Soil Hum	-0.3448	-0.5505	0.7529		0.8820	0.0000	0.0000	0.0685	0.3053
Leaf Depth	-0.6224	-0.4690	-0.0207	0.0320		0.5434	0.9726	0.2419	0.1293
Lux	0.4930	0.5606	-0.8015	-0.8111	-0.1305		0.0000	0.0052	0.1246
Canopy	-0.3166	-0.4580	0.8034	0.7464	0.0074	-0.9285		0.0025	0.2647
Soil pH	-0.5772	-0.6242	0.6417	0.3781	0.2484	-0.5515	0.5891		0.3306
Leaf Hum	-0.2744	-0.0823	0.1636	0.2184	0.3185	-0.3222	0.2371	0.2075	

Legend: Spearman's statistic under the diagonal / P-value above the diagonal. High intercorrelation among the variables are in bold (> 0.75 in module).

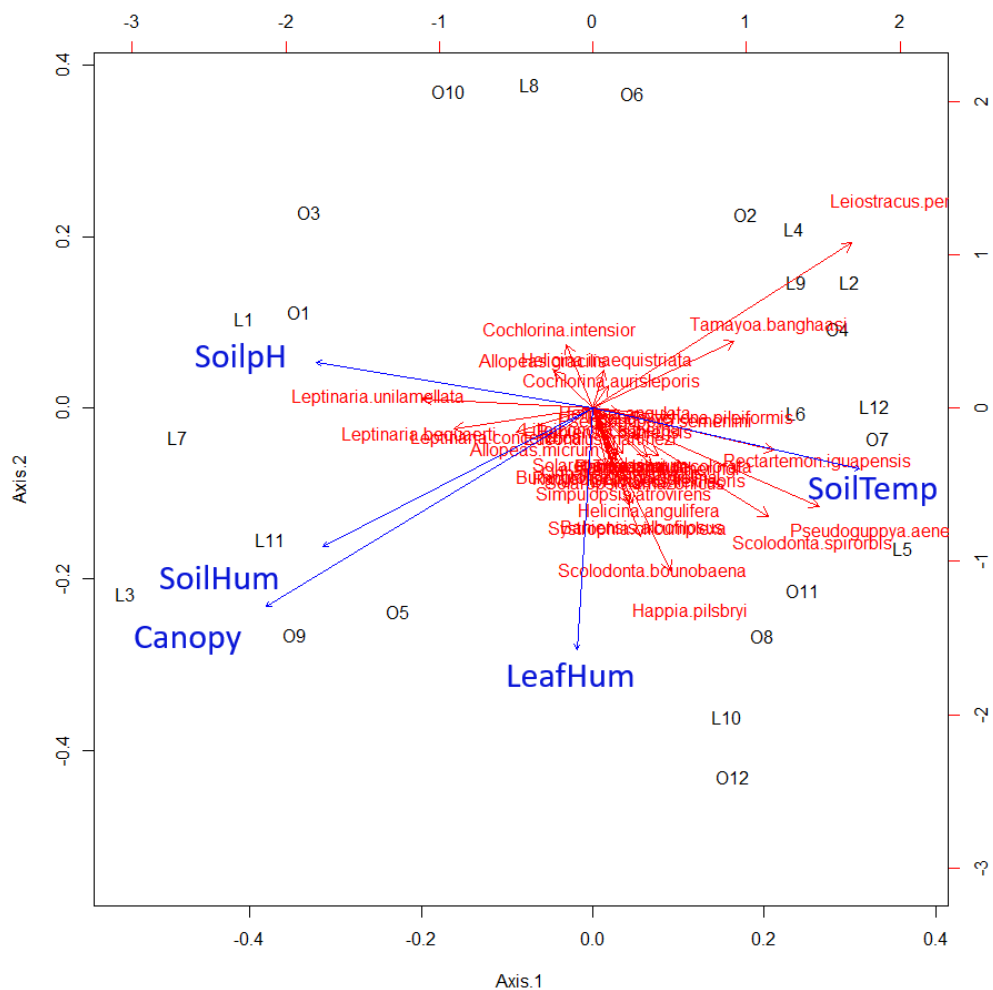
Source: Author, 2022.

Table 5 - Descriptive statistics of response variables (numbers of species and individuals) and environmental variables used in the analyses.

Variables	Unit	Min	Max	Mean	SD	Median	% Var.
Soil temperature	°C	19.3	22.3	20.8	0.5	21.0	2.5
Soil humidity	%	17.0	100	52.2	21.1	48.0	40.4
Leaf-litter depth	cm	2.0	10.8	5.8	1.8	5.8	31.2
Canopy closure	%	50.0	100	82.3	12.4	81.0	15.0
Soil pH	upH	5.7	7.0	6.7	0.3	6.8	4.5
Leaf-litter humidity	%	16.0	98.0	58.0	19.4	60.0	33.4
N° of live species		1	17	5.5	4.0	5.0	74.3
N° of live individuals		1	56	18.3	16.4	13	89.9
N° of all individuals		23	158	62.7	33.0	55.5	52.6
Species richness		4	22	9.7	4.6	9.0	47.8

Legend: Min: Minimum; Max: Maximum; SD: Standard deviation; % Var.: Percentage of variation.
Source: Author, 2022.

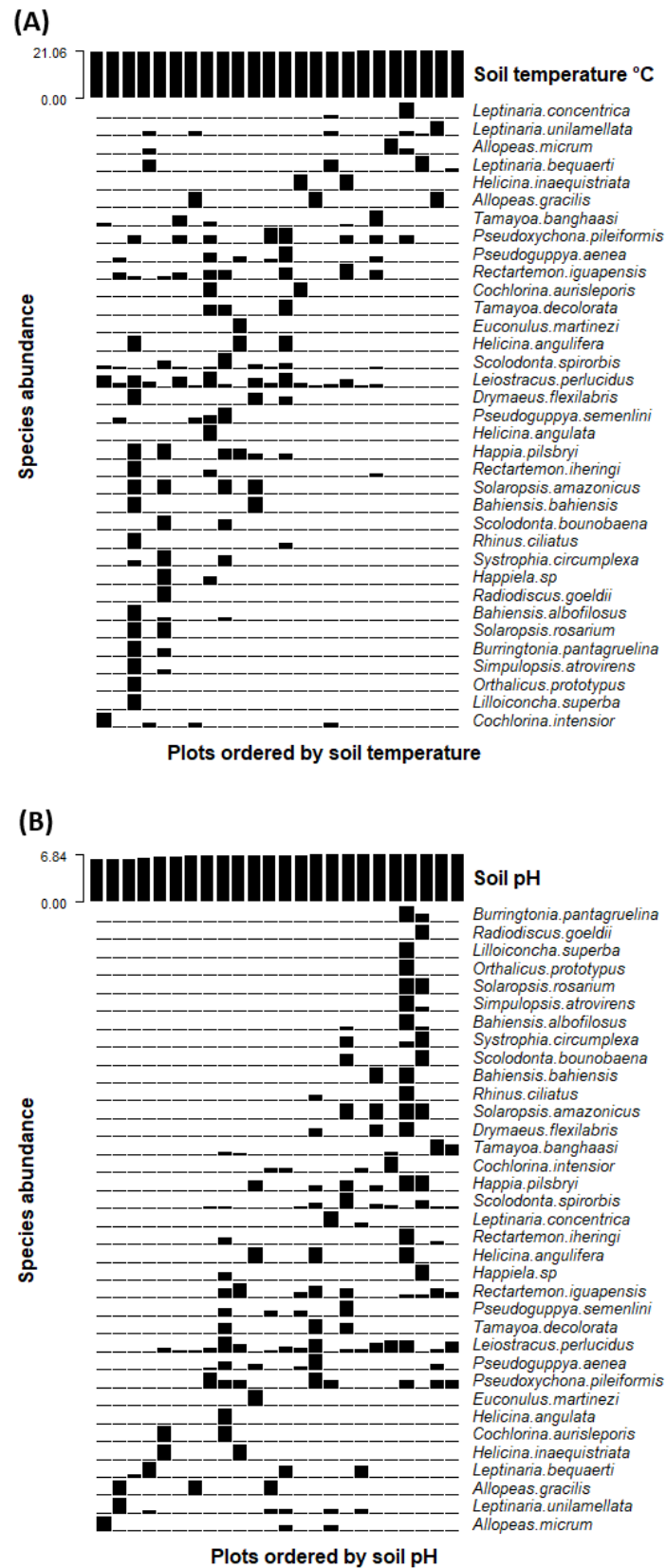
Figure 9 - Multidimensional Scaling (MDS) using Bray-Curtis dissimilarity of snail community: ordination plots on the first two MDS axes.



Legend: The first two axes explained 40.4% of total variation in snail data (first axis 38.5%). Only variables significantly related to species composition ($P < 0.05$) are shown. SoilTemp: soil temperature; SoilHum: soil humidity; Canopy: canopy closure; SoilpH: soil pH; LeafHum: leaf-litter humidity.

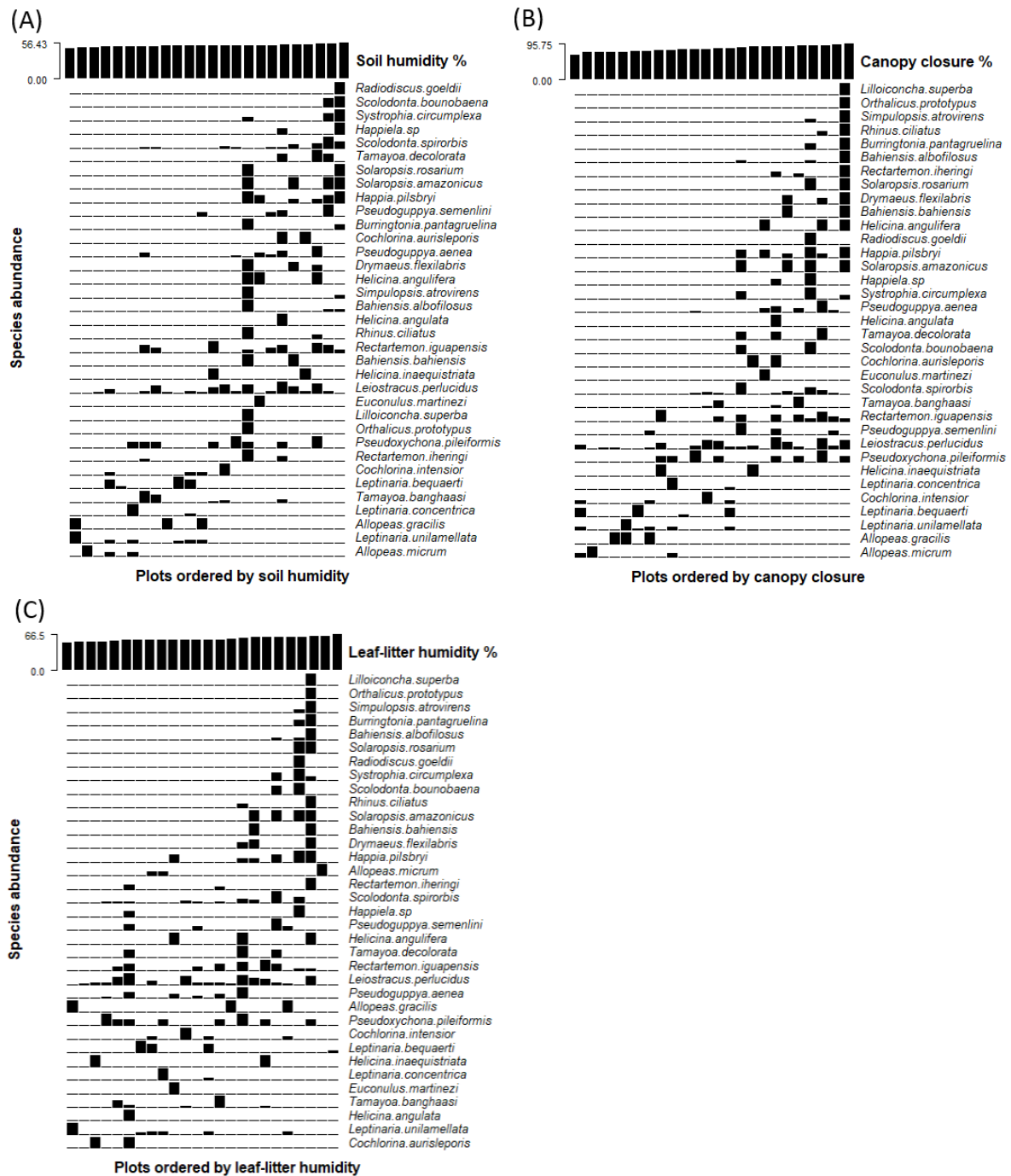
Source: Author, 20122.

Figure 10 - (A-B) Species responses along the gradients on the first MDS axis.



Legend: (A) species pattern in a soil temperature gradient; (B) species pattern in a soil pH gradient.
Source: Author, 2022.

Figure 11 - (A-C) Species responses along the gradients on the second MDS axis.



Legend: (A) species pattern in a soil humidity gradient; (B) species pattern in a canopy closure gradient; (C) species responses pattern in a leaf-litter humidity gradient.

Source: Author, 2022.

Table 6 - Fit of environmental variables on the MDS in two dimensions based on Bray-Curtis dissimilarity among land snail community.

Variable	1MDS	2MDS	R2	P
Soil temperature	0.9746	-0.2236	0.3181	0.015
Soil humidity	-0.8893	-0.4572	0.3911	0.004
Leaf-litter depth	0.3866	0.9224	0.003	0.973
Canopy closure	-0.8542	-0.5199	0.6217	0.001
Soil pH	-0.9867	0.162	0.3337	0.011
Leaf-litter humidity	-0.0669	-0.9977	0.2494	0.047

Legend: The dataset consists of species abundance data for 24 plots (250m m along) and subplots (25 x 75 cm) in the Sooretama Biological Reserve. Bold numbers indicate $P < 0.05$ (*Envfit* with 999 permutations).

Source: Author, 2022.

Table 7 - Values of Spearman's rank correlation coefficient between species data and environmental variables.

Variables	N° of live individuals	N° of live species	N° of all individuals	N° of all species
Soil temperature	-0.520**	-0.595**	-0.686**	-0.699**
Soil humidity	0.537**	0.632**	0.493*	0.819**
Leaf-litter depth	n.s.	n.s.	0.428*	n.s.
Canopy closure	0.707**	0.724*	0.453*	0.747**
Soil pH	0.766**	0.743**	0.605**	0.527**
Leaf-litter humidity	n.s.	n.s.	n.s.	n.s.

Legend: Significance is given as: n.s. = not significant; * = $p < 0.05$; ** = $p < 0.01$.

Source: Author, 2022.

2.3. Discussion

Our results showed that soil temperature, soil humidity, soil pH, canopy closure and leaf-litter humidity were the environmental factors that most explained the snail species composition, whereas only leaf-litter depth had no significant correlation with the snail species composition. On the other hand, only soil temperature, soil humidity, soil pH and canopy closure affected the snail species richness and total abundance. Surprisingly, leaf-litter depth and leaf-litter humidity had no significant correlation with the snail species richness and total abundance in the studied community. Although the leaf-litter depth had shown a significant correlation with the distribution and diversity of land snails in the only one study that investigated the influence of environmental factors on snail fauna in the Brazilian Atlantic forest (Nunes & Santos, 2012) as well as in other

studies from different parts of the world (e.g. Cameron, 1986; Getz & Uetz, 1994; Emberton *et al.*, 1997; Wronski *et al.* 2014), this variable had no effect on species richness, total abundance or species composition in the studied community. Our results suggest that the climatic condition, such as soil temperature and soil humidity, is more important than the amount of leaf-litter in the environment. Which is intriguing, since a strong correlation between leaf-litter depth and canopy closure and soil temperature were to be expected. A forest with lower light intensity and higher percentage of canopy closure (consequently lower soil temperature), tends to have a higher amount of aerial material, such as leaves, branches and vines, which when falling, form a thick layer of leaf-litter on the forest ground. However, we did not find a significant correlation between these variables.

Based on our data, we found high positive correlations between variables reflecting similar conditions (soil humidity, canopy closure and soil pH) and snail species richness and total abundance. In contrast, we found a high negative correlation between soil temperature and snail species richness and total abundance. This result was not surprising, since the land snails are known to be quite susceptible to dehydration and that humidity play an important role in their ecological physiology. The parameters related to humidity and canopy closure (as a proxy for insolation and, as a consequence, temperature and desiccation on the forest floor), may be of special relevance for the terrestrial gastropods, because, by they having permeable skin and moving by laying down moist mucus trails, they need continuously to maintain comparatively high body humidity to live and is easily subject to suffer high rates of dehydration (Prior, 1985; Luchtel & Deyrup-Olsen, 2001). Moist conditions are also necessary for land snail respiration, for reproduction (Coney *et al.*, 1982) and for the production of mucus, which is vital for their locomotion (Cameron, 1970). Our results agree with Boycott's (1934), pioneering study on land snails, as well as with studies carried out over the last decades in several countries (e.g., Millar & Waite, 2002; Martin & Sommer, 2004; Tattersfield *et al.*, 2006; Horsák *et al.*, 2007; Nunes & Santos, 2012) which showed that the humidity acts as a limiting factor for land snail communities. Investigating *Happiella cf. insularis* (Boettger, 1889) in Ilha Grande (Rio de Janeiro, Brazil), Barbosa & Santos (2014) found changes in the shell morphology in populations of three areas in environments with different degrees of humidity. According to Emberton, Pearce & Randalana (1999), snail diversity can be explained by the increased humidity of the environment. In fact, more species and individuals of

terrestrial gastropods are found in moister zones compared to less humid areas (Tattersfield, 1990; Ports, 1996; Moreno-Rueda *et al.*, 2009). Nevertheless, some snails dwell in arid zones thanks to a set of adaptations against dehydration (Shmidt-Nielsen, Taylor & Skolnik, 1971). One of such adaptation is the use of appropriated microhabitats where the risk of dehydration is lower (Cook, 2001).

Although the humidity factor had a significant effect on snail species composition, leaf-litter humidity did not have a significant correlation with snail species richness and total abundance in the studied community. The leaf-litter humidity provides a higher supply of organic matter (nutrients), as it allows the survival of numerous microorganisms, fungi and small insects, which are food source for some snail species (Barker, 2001), and offering propitious microhabitats for a high number of snail species (Getz & Uetz, 1994; Nakamura *et al.*, 2003; Tattersfield *et al.* 2006; Heydrich, 2007). However, our results suggest that the conditions of the soil and the environment, such as temperature, humidity and canopy closure are more important than the conditions of the leaf-litter. The leaf-litter acts as an environmental filter, providing shelter against the incidence of heat in areas with high light intensity. Therefore, in areas where the soil has high temperatures it is very likely that the leaf-litter is completely dry.

Our data also indicated that the soil pH had a significant effect on the snail species richness, total abundance and species composition. It is well known that soil pH, as an approximate measure of calcium content, is of particular importance, because it is essential for snail shell formation (Martin & Sommer, 2004). Usually, this relationship between soil pH and calcium content in the soil or in the leaf-litter could help to explain the ranking of species shown in the MDS ordination. Accordingly, although calcium has not been measured in this study, it would be possible to suggest that the plots with higher soil pH values, also could be those having higher sources of available calcium for the land snail community. Several studies have confirmed strong positive correlations between calcium content in the soil or in the leaf-litter and soil pH with species richness (e.g., Burch, 1955; Wärerborn, 1970; Martin & Sommer, 2004; Juříčková *et al.*, 2008). However, other studies found no correspondence between soil pH and land snail abundance (Bishop, 1977, 1980, 1981). It is possible that these exceptions are closely similar to situations where soil humidity is the main factor analyzed (Juříčková *et al.*, 2008).

Our results showed, for the first time in the Brazilian Atlantic forest, therefore there are no studies to compare the species turnover, interesting autecological conclusions for the species found in the studied area. Although in the studied area there were no gradients with a high rate of variation, we found a clear species compositional change along the gradients, suggesting differences in species preferences even at a fine-scale. In general, the pattern of species turnover along the gradients showed forest-specialist species (e.g., *Radiodiscus goeldii*, *Scolodonta bounobaena*, *Systrophia circumplexa*, *Scolodonta spirorbis*, *Lilloiconcha superba*, *Simpulopsis atrovirens*, *Orthalicus prototypus* and *Burringtonia pantagruelina*) more susceptible to the environmental variables than the synanthropic species (*Allopeas micrum*, *Allopeas gracilis*, *Leptinaria bequaerti*, *Leptinaria unilamellata*, *Leptinaria concentrica*), mostly introduced or presumably introduced species, typically known by their generalist habits (Cowie, 1998). The most abundant species (*Leiostracus perlucidus*, *Rectartemon iguapensis*, *Rectartemon iheringi*, *Pseudoxychona pileiformis*, *Tamayoa banghaasi*, *Pseudoguppya aenea*) showed an intermediate pattern of environmental demand, occupying areas with high rates of variation among the environmental variables.

The results of the present study indicated that soil temperature, soil pH, soil humidity, canopy closure and leaf-litter humidity were the environmental predictors that most affected the snail species composition and, except by leaf-litter humidity, these predictors also significantly affected the snail species richness and total abundance in the Sooretama Biological Reserve. Diverging from other studies, we did not find any effect of the leaf-litter depth on snail species richness, total abundance or species composition. Although a wide range of environmental variables certainly interact with each other and in some way affect the distribution of organisms in nature, for land snails, the variables related with soil humidity, temperature and pH were fundamental for the distribution and diversity in the studied community. In this sense, the Brazilian Atlantic forest is a favorable environment for land snails, which certainly provided the high species richness and density we found in the studied remnant. Contrary to Solem's prediction (1984), which land snails generally are neither diverse nor abundant in tropical forests, the Brazilian Atlantic forest has the fundamental environmental and climatic conditions to shelter the diversity of land snail species, which has been poorly studied.

Considering the high rate of deforestation and loss of natural habitat in the Atlantic forest, it is necessary to carry out the inventory of snail species throughout the national territory, as soon as possible, in order to increase the scientific knowledge of this important component of the terrestrial invertebrate biodiversity before they disappear. Thus, stimulating the taxonomical, biological and also autecological study of the species, aiming to use these data on faunal biodiversity conservation and management strategies.

3. SEASONAL VARIATION AND PATTERNS IN THE LAND SNAIL COMMUNITY ALONG A FINE-SCALE HUMIDITY GRADIENT IN AN ATLANTIC RAINFOREST REMNANT, SOUTHEASTERN BRAZIL

Esteves, R. A., Santos, S. B., & Rocha, C. F. D. (2025). Seasonal variation and patterns in the land snail community along a fine-scale humidity gradient in an Atlantic Rainforest remnant, Southeastern Brazil. *Brazilian Journal of Biology*, 85, e287884. <https://doi.org/10.1590/1519-6984.287884>.

Community structure encompasses the intricate relationships among the component populations (Pianka 2000), which might involve trophic structure, energy flow, alpha and beta diversity, and the distribution of individuals in space and time (Magurran 2011). To identify characteristics of populations and communities along environmental gradients has been of interest to many ecologists (Rosenzweig 1995, Kessler 2009), once that the distribution of organisms in nature does not occur randomly (Simaiakis and Martínez-Morales 2010). Bearing in mind that the basic problem of ecology is to determine the causes of distribution and abundance of organisms (Krebs 2001), considerable effort has been done to document the differences between these two aspects and understand why they occur (Pianka 1999).

The composition and richness of land snail communities is linked mainly with available calcium content (Wäreborn 1969; Dallinger *et al.* 2001; Goodfriend 1986; Juříčková *et al.* 2008) and humidity (Pollard 1975, Čejka *et al.* 2008). Humidity has been identified as the second main driver of snail distribution with positive effect on species richness and abundance, especially in dry habitats where it acts as a limiting factor for the majority of species (Martin and Sommer 2004). But the relationship between land snails and humidity is not studied at the same way as calcium is. The humidity has rarely been directly measured (Hettenbergerová *et al.* 2013). Humidity was mostly only estimated (Getz and Uetz 1994; Chiba 2007), or the studied sites were classified into several moisture categories (Martin and Sommer 2004). Some snail ecology studies in Europe used Ellenberg indicator values (Ellenberg *et al.* 1992) as a proxy for soil humidity obtained from vegetation samples (Horsák *et al.* 2007; Čejka *et al.* 2008; Čejka and Hamerlík 2009).

Terrestrial gastropods represent a diverse group of soil-dwelling invertebrates occurring in various forest ecosystems (e.g., Barker and Mayhill 1999; Barker 2001; Cameron *et al.* 2010; Schilthuizen 2011). Land snail communities have been studied in detail particularly in the boreal and temperate zones of Europe (e.g., Wäreborn 1969; Hylander *et al.* 2005; Juříčková *et al.* 2008; Horsák *et al.*, 2010, Horsák *et al.* 2018). On the other hand, the biota of the tropical regions is the least studied (Lewinsohn and Prado 2005), contrasting with the data from the few studies for the region (e.g., Emberton *et al.* 1996; Schilthuizen *et al.* 2003; Nunes and Santos 2012; Wenderbourg and Hausdorf 2019), which shows terrestrial gastropod communities with high values of richness and abundance.

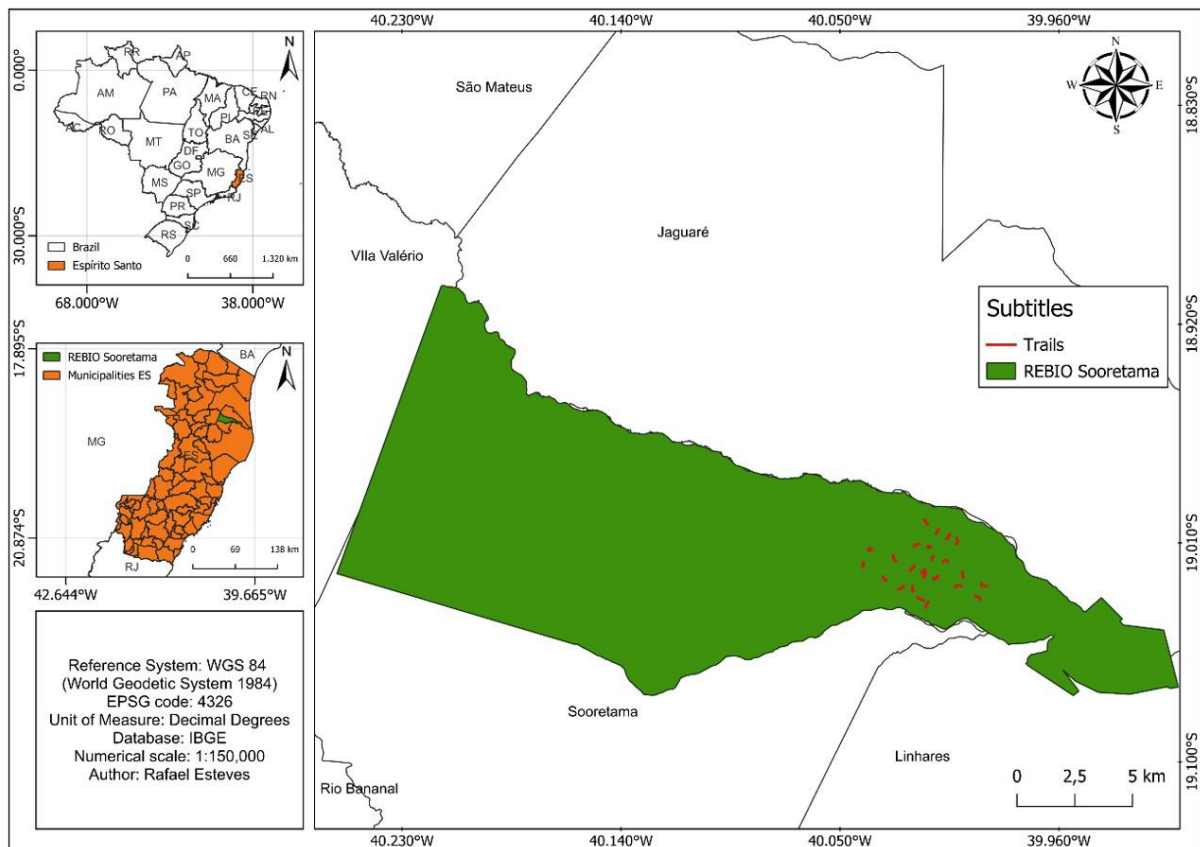
Despite the Brazilian Atlantic Rainforest is a global biodiversity hotspot, with a high endemism rate, sheltering approximately 7% of the world's plant and animal species (Meyers *et al.* 2000) and the land snails account for a significant component of faunistic endemism in this region, there is no study on the seasonality effects on land snail communities. Therefore, in this paper, we studied the influence of seasonality and species patterns along a fine-scale of humidity gradient on the community parameters, such as richness and abundance, of land snails in the Sooretama Biological Reserve, southeastern Brazil.

3.1. **Material and methods**

3.1.1 Study area

The study was conducted in the Sooretama Biological Reserve (19°0'50.87" S, 40°5'48.96" W, mean altitude: 46 m), the greatest remnant of Atlantic Rainforest in Espírito Santo State, southeastern Brazil (Figure 12). The reserve has approximately 28,000 ha and is one of the areas with a higher importance for conservation of biological diversity of the Atlantic Rainforest, and it is located in the Central Corridor of the Atlantic Forest Biome (MMA 2000). The climate in the region is tropical hot and humid, with annual rainfall of 1,202 mm and mean annual temperature of 23.3 °C. The vegetation cover of the reserve comprises the Coastal Plain Forest (locally called "Floresta de Tabuleiro") whose canopy trees may reach up to 40 m high (Peixoto and Gentry 1990).

Figure 12 - Sampling plots following the RAPELD methodology at the Sooretama Biological Reserve, Espírito Santo, Brazil.



Source: Author, 2022.

According to the Management Plan of the Sooretama Biological Reserve, there are no significant records of established invasive alien species within the reserve's boundaries (ICMBIO, 2019). The absence of introduced species is a positive indicator of the ecological integrity of the reserve.

The reserve faces anthropogenic pressures, particularly along its borders. Human activities in the surrounding areas, such as agriculture and irregular settlements, can lead to forest fires, which pose a significant threat to local ecosystems. A severe fire occurred in the western area of the reserve in 1998, and another more recent fire affected the Lagoa do Macuco in 2016, causing considerable damage.

The Sooretama Biological Reserve exhibits notable environmental heterogeneity. In addition to the Dense Ombrophilous Forest, the reserve also contains unique vegetation formations, such as “muçunungas” – low and open forests – as well as wetlands, including lakes and marshes. The altitudinal variation within the reserve

is modest, ranging from 5 to 197 meters above sea level, contributing to the diversity of habitats and species found in the area.

3.1.2. Data sampling

Field sampling was carried out in 2017 (January, June, August and November) and 2018 (January, June, September and December), including both the months of the dry (April to September) and of the rainy season (October to March) in the area, covering the four seasons (winter, spring, summer and autumn). We conducted the sampling during the diurnal period (05:00 h to 10:00 h), using 24 plots distributed in the Coastal Plain Forest, following the RAPELD methodology (Magnusson *et al.* 2005). The RAPELD methodology consists of permanent and standardized 250 meters long plots, following the terrain contours and 1 km distant from each other. The land snails were sampled by performing transects along the plots using the active search method, with visual sampling for macro gastropods (> 5 mm) by one observer. We carefully inspected the plot during each transect, looking for land snails in the leaf-litter, on trees, on branches, in the bushes, on fallen logs and in other microhabitats, when present. For the micro gastropods (< 5 mm), we used three quadrats (subplots of 25 x 75 cm) in each plot to collect leaf-litter (approximately 4 litters each quadrat) and carried out time searching for shells and live animals (Getz and Uetz 1994; Emberton *et al.* 1996). The leaf-litter collected down to the soil surface was stored in labelled plastic bags, and later, transported to the Laboratory of Malacology - UERJ, where it was searched for snails. All specimens recorded were observed under a stereomicroscope and morphotypes separated, quantified and deposited at the Malacological Collection of UERJ (Col. Mol. UERJ).

3.1.3. Environmental variables

A set of nine environmental variables that might be important predictors of land snail species richness, total abundance and species composition was measured for each plot prior removing the leaf-litter: (1) Air temperature ($^{\circ}\text{C}$), using the Incoterm Digital Hygrometer ($0 - 50 \pm 0.1$ $^{\circ}\text{C}$), with the device placed next to the subplot; (2) Soil temperature ($^{\circ}\text{C}$), using the Instrutemp Digital Thermometer ($-50 - 300 \pm 0.1$ $^{\circ}\text{C}$), with the bulb inserted in the ground inside the subplot; (3) Relative air humidity (%), using

the Incoterm Digital Hygrometer ($15 - 99 \pm 1\%$), with the device placed next to the subplot; (4) Soil humidity (%), using the PH-1000 soil pH and humidity meter ($10 - 80 \pm 1\%$), with the sensor inserted in the ground; (5) Leaf-litter depth (cm), using a common rule of 30 cm in length sunk in the leaf-litter inside the subplot until it found resistance from the soil. Five measures were taken to calculate the mean (four squares and one at the centre); (6) Light intensity (lux), using the LDR-208 Luxmeter ($200 - 200,000 \text{ lux} \pm 3\%$), measured with the sensor facing up inside the subplot above the leaf-litter; (7) Canopy closure (%), using the Spherical Concave Densiometer. With the observer positioned on the subplot, four measurements were taken towards the cardinal points (north, south, east and west). Subsequently, the values were added, divided by four (mean) and the result multiplied by the correction factor 1.04 to obtain the percentage of canopy closure for each subplot; (8) Soil pH (upH), using PH-1000 soil pH meter ($3 - 8 \pm 0.1$) with the device inserted in the ground into the center of the subplot; and (9) Leaf-litter humidity (%), using thermogravimetric method. The leaf-litter was packed in paper bags of known weight, and we measured the mass of this leaf-litter to obtain the wet weight. Then, the bags with the leaf-litter were placed in an oven at 60°C until the material was completely dried (constant weight). The leaf-litter was weighed again to obtain the dry weight. The difference between wet and dry weight provided the humidity percentage of the leaf-litter.

3.1.4. Statistical analysis

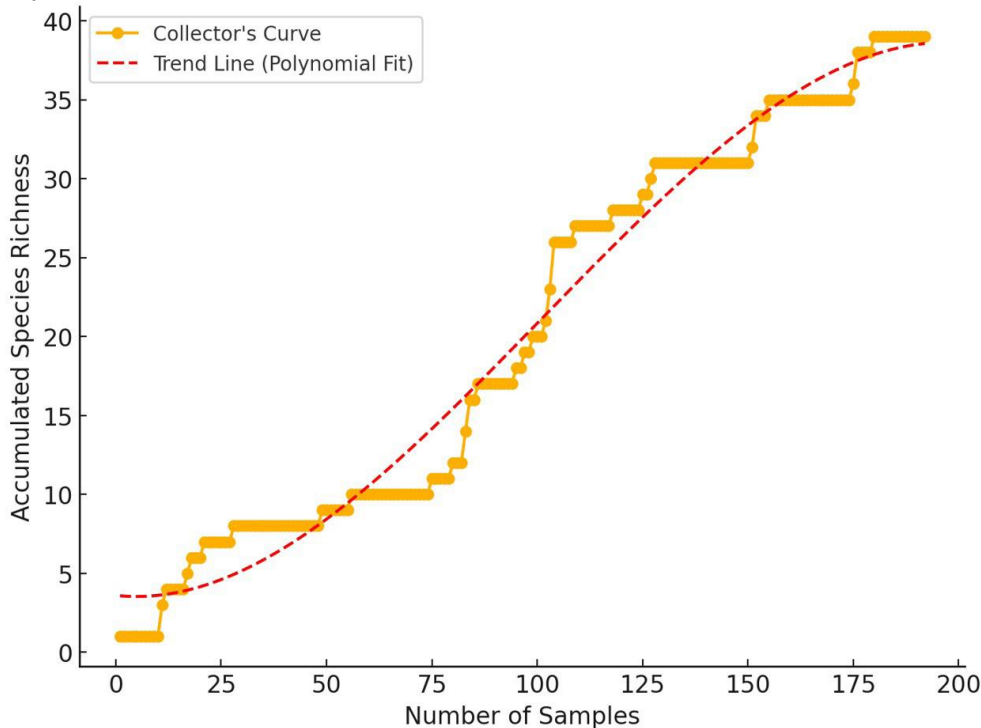
The evaluation of collection effectiveness was undertaken by a species accumulation curve (collector curve) and by estimators (Chao 1, Jack 1 and Bootstrap). The ordination was based on a Bray-Curtis dissimilarity matrix of ecological distance (Faith *et al.* 1987). The composition of community of land snail among seasons was analyzed using non-metric multidimensional scaling (NMDS) (Clarke 1993). We performed the Envfit Test (a test that fits environmental vectors onto an ordination) to analyze the relative importance of the variables (temperature and moisture) on the land snail abundances in the local community ($p < 0.05$). Statistical significance between the seasons was tested using analysis of variance (ANOVA) and Tukey test. Snail species response curves were modelled to explain the distribution of species along the moisture gradient by using the “*generico*” function (Landeiro 2011), which produces a graph that orders species in relation to an environmental gradient. We used R Studio

(RStudio Team 2018), Package Vegan (Oksanen *et al.* 2009) for all statistical analyses.

3.2. Results

The species accumulation curve analysis produced a clear asymptotic shape, and the predicted estimates of land snail richness (Chao 1 = 36 ± 2.3 species; Jack 1 = 37 ± 2.0 species; Bootstrap = 39 ± 2.2 species) were close to the richness value obtained by us with plot sampling (35 species) (Figure 13). We collected 440 alive specimens belonging to 35 species representing 11 families (Table 8). Scolodontidae (7 spp., 20%) was the most speciose family followed by Achatinidae (5 spp., 14.2%), Bulimulidae (4 spp., 11.4%), Euconulidae (3 spp., 8.5%), Helicinidae (3 spp., 8.5%), Odontostomidae (3 spp., 8.5%), Simpulopsidae (3 spp., 8.5%), Pleurodontidae (2 spp., 5.7%), Charopidae (2 spp., 5.7%), Streptaxidae (2 spp., 5.7%) and Orthalicidae (1 spp., 2.8%). The most abundant family was Simpulopsidae (25.2%) and the most abundant species was *Leiostracus perlucidus* Spix, 1827 (22.5%).

Figure 13 - Cumulative curve of richness of land snails recorded at the Sooretama Biological Reserve, Espírito Santo, Brazil.



Legend: Richness = 35; Chao 1 = 36 ± 2.3 ; Jack 2 = 37 ± 2.0 ; Bootstrap = 39 ± 2.2 .
Source: Author, 2022.

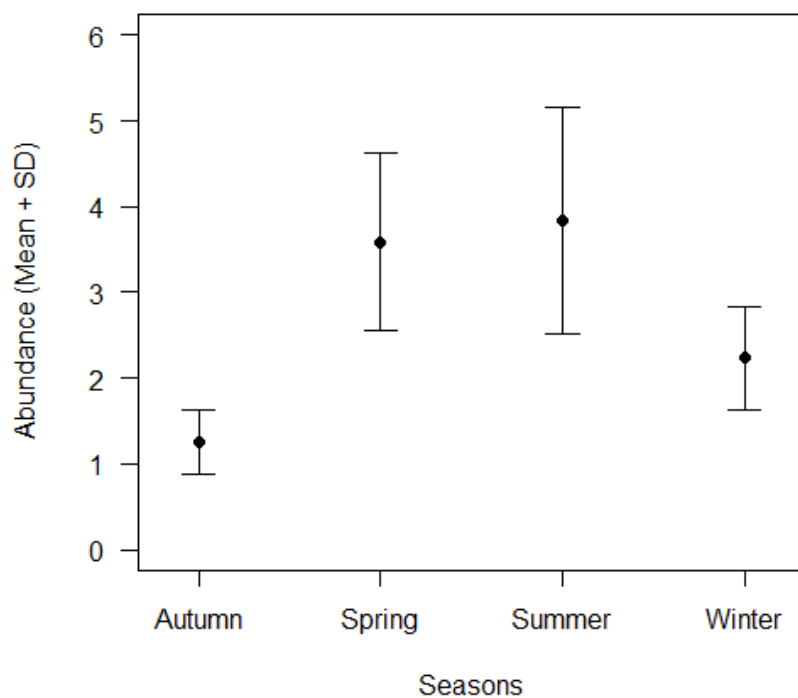
The composition of the land snail in the community varied among seasons (ANOVA; $DF = 3$; $F = 3.565$, $p = 0.016$), with the highest mean values in summer and spring seasons (Table 8, Figure 14). The highest variation occurred between summer and autumn seasons (Tukey's Test; $Q = 4.035$, $p = 0.026$) and the smallest variation occurred between spring and summer ($Q = 0.399$, $p = 0.992$). Comparatively, the rainy season was hotter and wetter than the dry season. There was a sharp moisture gradient along each plot, with the measured relative air humidity varying from 17% to 53% and soil humidity varying from 43% to 91% in the dry season and relative air humidity varying from 28% to 100% and the soil humidity varying from 50% to 100% in the rainy season. The environmental parameters that showed the highest rates of variation among the plots were leaf-litter humidity in the dry season (37.2%) and soil humidity in the rainy season (34.7%), contrasting with those that least varied among the plots, soil temperature at both seasons (2.8% and 1.6%, dry and rainy season respectively) (Table 9).

Table 8 - Abundance of the land snail species found in each season at Sooretama Biological Reserve, Espírito Santo.

Species	Summer	Autumn	Winter	Spring	Overall
Achatinidae					
<i>Allopeas gracilis</i> (Hutton, 1834)	1	1	0	1	3
<i>Allopeas micrum</i> (Orbigny, 1835)	0	1	1	3	5
<i>Leptinaria bequaerti</i> Pilsbry, 1926	2	5	4	3	14
<i>Leptinaria concentrica</i> (Reve, 1849)	2	0	0	10	12
<i>Leptinaria unilamellata</i> (Orbigny, 1835)	11	0	5	0	16
Bulimulidae					
<i>Cochlorina aurisleporis</i> (Bruguière, 1792)	0	0	0	2	2
<i>Cochlorina intensor</i> (Pilsbry, 1898)	0	0	1	6	7
<i>Pseudoxychona pileiformis</i> (Moricand, 1836)	1	0	7	2	10
<i>Drymaeus flexilabris</i> (Pfeiffer, 1853)	2	3	1	3	9
Charopidae					
<i>Radiodiscus goeldii</i> (Thiele, 1927)	0	0	0	3	3
<i>Lilloiconcha superba</i> (Thiele, 1927)	0	0	1	0	1
Euconulidae					
<i>Euconulus martinezi</i> (Hidalgo, 1869)	1	0	0	0	1
<i>Pseudoguppya semenlini</i> (Moricand, 1846)	8	3	0	2	13
<i>Pseudoguppya aenea</i> (Scott, 1948)	37	4	13	7	61
Helicinidae					
<i>Helicina angulata</i> Sowerby, 1873	0	3	0	0	3
<i>Helicina angulifera</i> Wagner, 1910	4	2	0	0	6
<i>Helicina inaequistriata</i> Pilsbry, 1900	1	0	1	0	2
Odontostomidae					

<i>Bahiensis albofilosus</i> (Dorhn, 1853)	1	4	0	4	9
<i>Bahiensis bahiensis</i> (Moricand, 1833)	0	0	1	1	2
<i>Burringtonia pantagruelina</i> (Moricand, 1833)	0	0	0	3	3
Orthalicidae					
<i>Orthalicus prototypus</i> Pilsbry, 1899	3	0	2	2	7
Pleurodontidae					
<i>Solaropsis amazonicus</i> (Pfeiffer, 1854)	0	1	2	1	4
<i>Solaropsis rosarium</i> (Pfeiffer, 1849)	0	0	0	2	2
Scolodontidae					
<i>Happia pilsbryi</i> Gube, 1902	3	0	3	6	12
<i>Scolodonta spirorbis</i> (Deshayes, 1950)	5	10	9	7	31
<i>Scolodonta bounobaena</i> (Orbigny, 1835)	0	0	6	8	14
<i>Systrophia circumplexa</i> Ferussac, 1839	1	0	2	3	6
<i>Happiella</i> sp.	1	2	0	0	3
<i>Tamayoa banghaasi</i> (Thiele, 1927)	19	0	0	13	32
<i>Tamayoa decolorata</i> (Dronët, 1859)	0	0	5	2	7
Simpulopsidae					
<i>Leiostracus perlucidus</i> Spix, 1827	32	9	19	39	99
<i>Rhinus ciliatus</i> (Gould, 1846)	1	0	1	2	4
<i>Simpulopsis atrovirens</i> (Moricand, 1836)	0	0	1	4	5
Streptaxidae					
<i>Rectartemon iguapensis</i> (Pilsbry, 1930)	18	2	2	2	24
<i>Rectartemon iheringi</i> (Thiele, 1927)	2	0	3	3	8
Overall	156	50	90	144	440

Figure 14 - Boxplot with the variance between seasons of the land snail community at Sooretama Biological Reserve, Espírito Santo, Brazil. ($F = 3.565$, $p = 0.016$).



Source: Author, 2022.

Table 9 - Descriptive statistical of all environmental parameters analyzed at the plots in the Sooretama Biological Reserve, Southeastern Brazil.

Environmental parameters	Unit	Dry season					Rainy season				
		Min	Mean	Max	SD	% Var	Min	Mean	Max	SD	% Var
Atmospheric temperature	°C	22.0	24.3	27.0	1.6	6.9	23.0	25.2	28.0	1.1	4.6
Soil temperature	°C	19.3	20.5	21.5	0.6	2.8	20.0	21.0	22.3	0.3	1.6
Relative air humidity	%	43.0	70.3	91.0	14.0	19.9	50.0	86.1	100	12.9	15.0
Soil humidity	%	17.0	39.9	53.0	10.2	25.9	28.0	63.8	100	22.1	34.7
Leaf-litter humidity	%	16.0	50.7	85.0	18.8	37.2	33.0	64.8	98.0	17.3	26.7

Legend: Min: minimum; Max: maximum; SD: standard deviation; % Var: variation rate among each plot.

Source: Author, 2022.

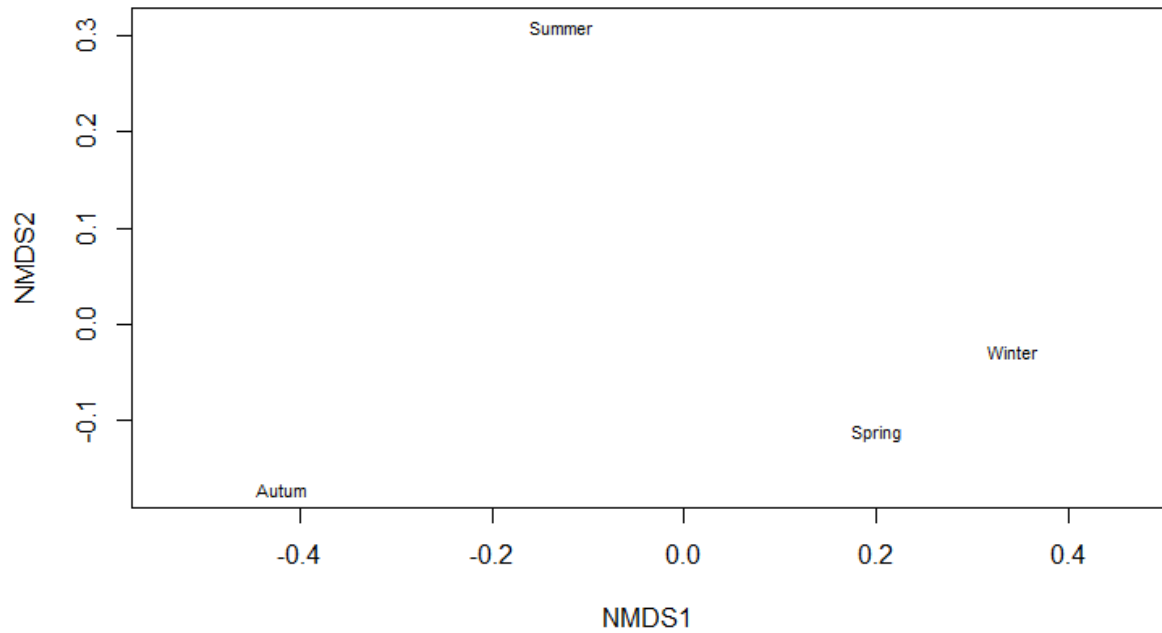
The NMDS obtained a stress value of 0.1032 and the Envfit Test indicated that the environmental parameters soil temperature ($r^2 = 0.4113$, $p = 0.008$), relative air humidity ($r^2 = 0.7406$, $p = 0.001$) and soil humidity ($r^2 = 0.5111$, $p = 0.001$) affected significantly the overall land snail abundance in the local community. Atmospheric temperature ($r^2 = 0.0953$, $p = 0.355$) and leaf-litter humidity ($r^2 = 0.0316$, $p = 0.692$), in contrast, did not affected overall the land snail abundance (Table 10). The NMDS showed a similarity between spring and winter, although there was no grouping between summer and autumn (Figure 15).

Table 10 - Summary of the NMDS performed for seasonal variables used to characterize plots and overall land snail species distribution among them at the Sooretama Biological Reserve, Espírito Santo, Brazil. Bold numbers indicate $p < 0.05$.

	NMDS1	NMDS2	r^2	Pr(>r)
AirTemp	-0.99716	-0.07529	0.0953	0.355
SoilTemp	-0.86829	0.49605	0.4113	0.008
AirHumidity	0.98166	-0.19064	0.7406	0.001
SoilHumidity	0.97473	0.22338	0.5111	0.001
LeafHumidity	-0.44584	-0.89511	0.0316	0.692

Source: Author, 2022.

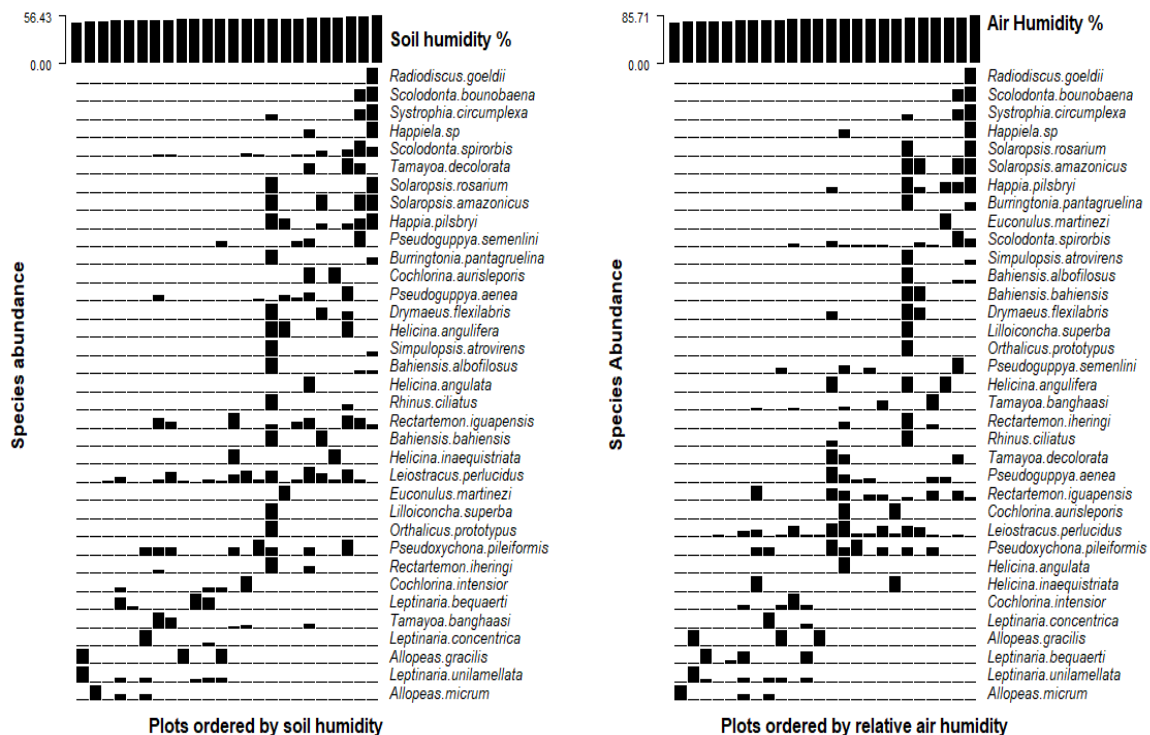
Figure 15 - Non-metric multidimensional scaling (NMDS) ordination using a Bray–Curtis similarity matrix indicating the community composition of overall land snail during the four seasons sampled in the Sooretama Biological Reserve, Espírito Santo, Brazil.



Source: Author, 2022.

Considering the relative air and soil humidity, *Radiodiscus goeldii*, *Systrophia circumplexa*, *Scolodonta bounobaena*, *Solaropsis amazonicus*. and *Happia pilsbryi* were the species most associated with moisture environments. In contrast, *Allopeas micrum*, *Leptinaria unilamellata*, *Leptinaria bequaerti* and *Allopeas gracilis* were the species less demanding of moisture (Figure 16).

Figure 16 - Species occurrences along a fine-scale moisture gradient at the Sooretama Biological Reserve, Espírito Santo, Brazil: pattern in a soil humidity gradient (left side); pattern in a relative air humidity gradient (right side).



3.3. Discussion

The present study assessed how seasonality influenced land snail composition in an Atlantic Rainforest area. This is the first study evaluating the effect of the seasonality on land snail community in Brazil. Scolodontidae was the most speciose family, with ten registered species. *Tamayoa banghaasi* (Thiele, 1927) was the most abundant species among the Scolodontidae family (Table 8). However, *Leiostracus perlucidus* Spix, 1827 (Simpulopsidae) was the most abundant species in the entire sampling period. Representatives of the family Scolodontidae, which currently covers the species of the old family Systrophiidae, can be found frequently and often abundantly across Central and South America from Mexico to Argentina and Chile (Hausdorf 2006). Our results corroborate previous results regarding the community composition (Brazil: Ilha Grande (Santos and Monteiro 2001; Nunes and Santos 2012); Peru: San Martin (Ramirez and Cordová 1997), Cashiriani (Ramirez and Caro 1998), Lower Urubamba Forest (Ramírez *et al.* 2001), Los Amigos (Ituarte *et al.* 2008), Panguana (Wenderbourg and Hausdorf 2019); Venezuela: La Fría (Baker 1925)).

Our data showed that the composition of land snail community of Sooretama Biological Reserve varied among seasons. The highest values were recorded in summer and spring on land snail community parameters, as species richness and abundances (Table 8). Curiously, as evidenced by the NMDS ordination, there was clustering between spring and winter, which indicates that the parameters of land snail community in these seasons are similar, indicating an influence of seasonality in the land snail community of the studied area. However, at the studied period included a relatively atypical rainfall season as it was a period under El Niño's climatic effect (AGERH 2017) and, therefore, a comparatively drier period in the region, which may have affected the species composition. Unfortunately, there are no previous studies on the seasonal variation of terrestrial gastropod community in Brazil to compare at the same climatic conditions the distribution of species found in the present study.

Our data showed that the community of land snails in Sooretama Biological Reserve was strongly affected by relative air humidity and soil humidity ($p = 0.001$), but not affected by the leaf-litter humidity ($p = 0.692$). Our results agree with Boycott's (1934), pioneering study on land snails, as well as with studies carried out over the last decades in several countries regarding the species patterns on different seasons (e.g., Emberton *et al.* 1999; Millar and Waite 2002; Martin and Sommer 2004; Tattersfield *et al.* 2006; Horsák *et al.* 2007; Nunes and Santos 2012). Terrestrial gastropods, having permeable skin and moving by laying down moist mucus trails, suffer high rates of dehydration (Prior 1985; Luchtel and Deyrup-Olsen 2001). Moist conditions are necessary for land snail respiration and reproduction (Coney *et al.* 1982) and for the production of mucus, which is vital for locomotion (Cameron 1970).

However, all mentioned studies assessed the influence of soil humidity on land snail distribution have analyzed assemblages of isolated and distant sites, mostly at relatively large, regional sampling scale. This sampling protocol may introduce bias, caused by other site characteristics independent of soil moisture, which can influence land snail distribution as well (Hettenbergerová *et al.* 2013). Considering a fine-scale moisture gradient, our data indicate a remarkable change of species composition over the gradient. For both relative air humidity and soil humidity, species differed in their optima along the gradient, with five species preferring wetter plots (*R. goeldii*, *S. circumplexa*., *S. bounobaena*, *S. amazonicus* and *H. pilsbryi*), other four species being more abundant in drier plots (*A. micrum*, *L. unilamellata*, *L. bequaerti* and *A. gracilis*) and the other 30 species in an intermediary environment. In different environmental

and climatic conditions, Hettenbergerová *et al.* (2013) found a pattern of species displacement in the gradient similar to our results, suggesting a species turnover from drier to wetter plots rather than species accumulation towards wetter plots.

Our study is the first providing data regarding seasonal variation and patterns along a moisture gradient in a land snail community in Brazil, with results from natural environment. Although the region has undergone climatic influence that led to a prolonged drought in the studied period due to the El Niño, our results showed that the community of land snail varies among seasons, especially between summer and autumn. Despite the studied period was drier compared to the historical average, the highest richness and abundances were found in the summer and spring, which are the rainy seasons, indicating a positive relationship between land snails and humidity. Our results showed different autecological conclusions. Although in our system there were no extremely dry plots, our results showed a clear compositional change along the moisture gradient, suggesting differences in species preference to moisture conditions even at a fine-scale.

4. EFFECT OF THE EDGE-INTERIOR GRADIENT ASSOCIATED TO ROAD ON THE LAND SNAIL ASSEMBLAGE IN A BRAZILIAN ATLANTIC FOREST REMNANT

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In preparation.

Roads are among the most pervasive forms of linear infrastructure affecting forest ecosystems worldwide, generating physical barriers and environmental gradients that extend well beyond the pavement edge into the forest interior (Trombulak and Frissell, 2000; Forman *et al.*, 2003). At forest edges created by roads, abrupt reductions in canopy cover combined with increases in solar radiation, air temperature, and wind exposure produce microclimatic conditions that differ markedly from those of the forest interior, with documented effects penetrating hundreds of meters into otherwise intact forest (Murcia, 1995; Laurance *et al.*, 2009). In protected areas, where conservation objectives require the maintenance of structurally and functionally intact biological communities, roads represent a particularly critical management challenge because their edge effects may reorganize biodiversity even in the absence of direct habitat loss, undermining the conservation value of areas formally shielded from extraction and land-use change (Ibisch *et al.*, 2016).

Roads affect terrestrial gastropods through multiple pathways: in addition to generating microclimatic gradients that alter habitat suitability, paved roads with high traffic density act as effective barriers to dispersal, as the energetic costs of crossing a dry, hard substrate and mortality from vehicles substantially reduce crossing rates in land snail populations (Baur & Baur, 1990). Despite growing recognition of road ecology as a discipline, the mechanisms by which road-induced microclimatic gradients filter and restructure forest-floor invertebrate communities remain poorly understood, limiting the ability of managers to define effective buffer zones around road-bisected reserves.

Beta diversity, defined as the variation in species composition among sites, provides a powerful framework for quantifying how road-induced disturbance reorganizes biological communities along edge-interior gradients (Baselga, 2010). Decomposing beta diversity into its two additive components, turnover and nestedness, allows a mechanistic distinction between alternative assembly processes.

Turnover reflects the replacement of species by environmentally filtered alternatives, while nestedness reflects the progressive loss of species from a shared pool (Baselga, 2010; Baselga and Orme, 2012). When turnover dominates, communities at each point along a disturbance gradient are compositionally distinct, implying that no single protected zone can capture the full diversity of the gradient (Socolar *et al.*, 2016; Bergamin *et al.*, 2017). When nestedness dominates, interior communities subsume the diversity of edge communities, suggesting that protecting the interior suffices to conserve regional biodiversity (Baselga, 2010; Socolar *et al.*, 2016). This distinction has direct implications for buffer zone design in road-bisected protected areas (Socolar *et al.*, 2016), yet it has rarely been examined in forest-floor invertebrate assemblages in tropical forests, where road edge effects may extend far beyond distances currently assumed by management guidelines derived from vertebrate and plant data (Ibisch *et al.*, 2016; Banbury Morgan and Jucker, 2025).

Taxonomic composition captures the identity of species that change along a gradient but not the functional traits that determine why particular species are filtered in or out. Functional ecology posits that environmental filters act on organismal traits rather than on species identities per se, such that taxonomic turnover along disturbance gradients should be accompanied by predictable shifts in the functional composition of communities (McGill *et al.*, 2006; Violle *et al.*, 2007). In terrestrial gastropods, the shell spire index, defined as the ratio of shell height to maximum diameter (H/D), is a well-established functional proxy for desiccation resistance. High-spined morphotypes present proportionally smaller apertures that reduce evaporative water loss under thermally stressful and low-humidity conditions, while low-spined morphotypes are associated with the stable humidity conditions of intact forest interiors (Machin, 1967; Giokas *et al.*, 2014; Schweizer *et al.*, 2019).

Road edges generate precisely the microclimatic gradients, including reduced air and soil humidity, increased solar radiation and temperature, and reduced canopy closure, that are expected to impose desiccation-related filters on gastropod communities (Chen *et al.*, 1995; Zellweger *et al.*, 2019), favoring high-spined morphotypes near the road and allowing low-spined forest specialists to recover with increasing distance into the interior (De Smedt *et al.*, 2019). If this microclimatic filtering hypothesis holds, functional diversity should increase with distance from the road edge, and the spatial pattern of functional composition should be predictable from

measured environmental variables rather than from spatial distance alone (McGill *et al.*, 2006; De Frenne *et al.*, 2019).

Land snails are among the most abundant and functionally diverse components of Atlantic Forest floor communities, playing key roles in nutrient cycling, fungal regulation, and energy transfer within the detritivore food web (Barker, 2001; Schilthuizen, 2011). Their acute sensitivity to microhabitat conditions, particularly air and soil humidity, canopy cover, leaf-litter depth, and calcium availability, renders them precise biological indicators of forest floor integrity and microclimatic change (Čejka and Hamerlík, 2009; Horsák *et al.*, 2018). Despite this conservation relevance, land snails are systematically absent from road ecology studies and from biodiversity monitoring programs in Atlantic Forest protected areas. Studies on land snail communities in the Atlantic Forest have focused primarily on taxonomic composition and species richness in undisturbed forest remnants or urban fragments (Nunes and Santos, 2012; Rangel *et al.*, 2021; Fernandes *et al.*, 2025; Salvador *et al.*, 2026) and no study has yet examined how road edges reorganize land snail communities along a continuous disturbance gradient, nor integrated the taxonomic and functional dimensions of community response with measured microclimatic variables. This gap is consequential because buffer zone standards for road-bisected protected areas in Brazil are currently derived from vertebrate and plant data, groups that may systematically underestimate the spatial extent of road influence on sensitive forest-floor invertebrates with narrow environmental tolerances.

Here, we investigate how road edges associated with the BR-101 federal highway, which bisects the Sooretama Biological Reserve in the Atlantic Forest of southeastern Brazil, restructure land snail communities along an edge-interior gradient spanning 2500 m. Using standardized permanent plots distributed across six distance classes from the road edge, combined with measurements of microclimatic and edaphic variables at each plot, we test four hypotheses. First, taxonomic beta diversity along the gradient is dominated by species turnover rather than nestedness, indicating that road edges impose differential environmental filters that generate compositionally distinct communities at each distance (H1). Second, functional diversity increases with distance from the road edge, reflecting functional homogenization of shell morphotypes near the road driven by desiccation-related filtering (H2). Third, the functional gradient is mediated by microclimatic variables associated with the road edge, particularly air humidity and canopy cover, rather than by spatial distance per se (H3). Fourth,

taxonomic turnover and functional dissimilarity are spatially congruent across plot pairs, indicating that species replacement along the gradient reflects the replacement of morphofunctional strategies (H4). Together, our results provide the first integrated assessment of taxonomic and microclimate-mediated functional responses of land snail communities to road edge effects in Atlantic Forest, with direct implications for buffer zone design in road-bisected protected areas.

4.1. **Material and methods**

4.1.1. Study area

The Sooretama Biological Reserve (REBIO Sooretama; 19°0'50.87" S, 40°5'48.96" W; mean altitude: 46 m) is a federally protected area covering approximately 27,858 ha of continuous Atlantic Forest in northern Espírito Santo state, southeastern Brazil, spanning the municipalities of Sooretama, Jaguaré, and Vila Valério (Fig. 8). Together with the adjacent Vale Nature Reserve (23,500 ha) and two Private Natural Heritage Reserves, the area forms a forest complex of approximately 53,000 ha, representing the largest remaining fragment of Tabuleiro Coastal Forest under formal protection in Espírito Santo (Rolim *et al.*, 2016). This complex is included in the Discovery Coast Atlantic Forest Reserves, designated as a UNESCO World Heritage Site (UNESCO, 2025), and constitutes part of the Hileia Baiana, a subdivision of the Tabuleiro Forest regarded as one of the most threatened and biodiverse phytophysognomies within the Atlantic Forest domain, with strong floristic affinities to Amazonian forests and high levels of regional endemism (Rolim *et al.*, 2016; Faria *et al.*, 2021).

The Tabuleiro formation is characterized by dense ombrophilous lowland forest over flat tertiary sedimentary plateaus, with a closed canopy, well-developed leaf-litter layer, and high structural complexity at the forest floor, conditions that support a diverse and abundant land snail fauna (Esteves *et al.*, 2025). The region is classified as Aw (tropical savanna climate), characterized by a rainy summer and a dry winter. The climate in the region is tropical hot and humid, presenting a mean annual precipitation of approximately 1,257.6 mm and mean annual temperature of 24.2 °C. REBIO Sooretama is protected under the strictest category of Brazilian environmental law (Lei

nº 9.985/2000), prohibiting human occupation and resource extraction within its boundaries.

The BR-101 federal highway bisects the reserve along a north-south axis, creating a continuous linear disturbance approximately 20 m wide (carriageway plus shoulders) that imposes a sharp transition between the road matrix and the forest interior on both sides. This configuration, a high-traffic road embedded within a large, strictly protected and continuous forest block, provides a controlled setting for isolating road edge effects from confounding anthropogenic disturbances such as logging, agriculture, or habitat fragmentation.

4.1.2. Sampling design and data collection

Field sampling was conducted in 2017 (January, June, August, and November) and 2018 (January, June, September, and December), covering both the dry season (April–September) and the rainy season (October–March), ensuring seasonal representation across the entire study period. All sampling sessions were conducted between 05:00 and 10:00 h to standardize activity periods.

The RAPELD method (Magnusson *et al.*, 2005) was employed using 24 permanent plots of 250 m length, distributed across six distance classes from the road edge: 50, 250, 500, 750, 1500, and 2500 m, with four replicate plots per distance class. Plots were established on both sides of the BR-101, following topographic contour lines to minimize confounding effects of elevation on microhabitat conditions. This framework integrates the Rapid Assessment Program (RAP) and the Brazilian Long-Term Ecological Research Program (PELD), providing a standardized platform for biodiversity surveys.

Along each plot, macro-gastropods (shell diameter or height > 5 mm) were sampled by active search conducted at a slow walking pace by a single observer throughout the entire study period, ensuring consistency in sampling effort. Micro-gastropods (shell diameter or height ≤ 5 mm) were sampled using three quadrats of 25 × 75 cm established along each plot at standardized distances of 50, 100, and 200 m. Leaf-litter within each quadrat was collected and examined under a stereomicroscope to detect small-bodied specimens. All collected individuals were counted and deposited in the Malacological Collection of the Universidade do Estado do Rio de Janeiro.

At each plot, microclimatic and edaphic variables were measured concurrently with biological sampling: air temperature (°C), soil temperature (°C), air humidity (%), soil humidity (%), leaf-litter depth (cm), light intensity (lux), canopy closure (%), soil pH, and leaf-litter moisture (%). Each variable was recorded repeatedly across sampling campaigns and plot-level means were used in subsequent analyses to represent the average environmental conditions experienced by the snail community at each site.

4.1.3. Species identification

Terrestrial gastropods were identified using a stereomicroscope, based on conchological characteristics to the lowest possible taxonomic level. Family-level classification followed Bouchet *et al.* (2017), except where superseded by the treatment adopted in Salvador *et al.* (2024), which was used as the primary reference for species-level nomenclature and checklist verification of the Brazilian fauna. Specimen identification was carried out by comparing observed morphological characteristics with descriptions and illustrations available in specialised references (Salgado and Coelho, 2003; Simone, 2006; Míquel *et al.*, 2007; Salvador and Simone, 2015). Species-level identifications were subsequently verified against Salvador *et al.* (2024). Specimens that could not be identified to species level are treated as morphospecies and listed under their respective genus (*Helicina* sp., *Simpulopsis* sp., *Scolodonta* sp. 1, and *Scolodonta* sp. 2).

One nomenclatural issue requires explicit acknowledgment. "*Happia*" *pilsbryi* Gude, 1912, recorded here as a significant indicator species of the leaf-litter microhabitat, may not belong to *Happia* Bourguignat, 1890 in its strict sense. Roosen and Breure (2024) revised the genera of Scolodontidae and transferred several Brazilian species to *Systrophiella*, *Austroselenites*, and *Prohappia*; however, a significant portion of Brazilian species previously placed in *Happia*, including *H. pilsbryi*, were not addressed by that revision and remain without a confirmed generic assignment. Following Salvador *et al.* (2024), we provisionally retain the name "*Happia*" *pilsbryi*, with the generic name in quotation marks to signal its uncertain status, pending a comprehensive systematic revision of these orphaned taxa. None of these nomenclatural uncertainties affect the ecological analyses presented here, as all results are based on morphological and abundance data independent of generic assignment.

4.1.4. Functional trait

High-spired morphotypes are consistently associated with drier, more thermally stressful conditions, while low-spired morphotypes predominate in moist and thermally stable microhabitats such as intact forest-floor litter, a pattern attributed to differential water-loss rates among morphotypes and to the greater capacity of high-spired forms to reduce exposure of soft tissues during aestivation (Machin, 1967; Giokas *et al.*, 2014; Schweizer *et al.*, 2019).

The H/D index was measured for all 30 species recorded in the community matrix using adult specimens with fully formed peristome to ensure morphological stability. Measurements were taken with a digital caliper (precision 0.01 mm) on a minimum of five individuals per species when available, and species mean values were used in subsequent analyses. H/D values ranged from 0.38 to 3.11 across the species pool, reflecting the broad functional diversity of the assembled community.

4.1.5. Statistical analysis

Pairwise taxonomic beta diversity among plots was quantified using the Sørensen dissimilarity index and partitioned into turnover (Simpson dissimilarity, β_{sim}) and nestedness-resultant dissimilarity (β_{nes}) following Baselga (2010), using the betapart package (Baselga and Orme, 2012) in R (R Core Team, 2024). Mean values of total beta diversity, turnover, and nestedness were calculated across all pairwise plot combinations, and the relative contribution of each component was assessed through the turnover-to-nestedness ratio (T/N ratio). To test whether taxonomic dissimilarity increased with distance from the road edge, a Mantel test was performed between the pairwise Sørensen dissimilarity matrix and a matrix of pairwise differences in distance-to-edge values, using Spearman correlation and 9999 permutations (H1).

Two complementary metrics were used to characterize the functional dimension of community response along the gradient. Rao's quadratic entropy (RaoQ) was calculated for each plot as a measure of functional diversity weighted by species abundances (Rao, 1982), using pairwise H/D differences between species as the distance matrix. RaoQ values were regressed against distance from the road edge

using ordinary least squares regression to assess the functional diversity gradient. The community-weighted mean (CWM) of the H/D index was calculated for each plot as the abundance-weighted mean trait value across species (Garnier *et al.*, 2004). CWM was modeled as a function of distance from the road edge using both linear and quadratic regression, and model selection was based on the Akaike Information Criterion (AIC). The inflection point of the best-fit quadratic model, representing the distance at which the rate of CWM change is maximized, was calculated analytically as $x = -b/2c$, where b and c are the linear and quadratic coefficients of the fitted model, respectively. A Mantel test between the pairwise functional dissimilarity matrix, derived from Euclidean distances between plot-level CWM values, and the matrix of pairwise differences in distance-to-edge was also performed to assess the spatial structure of functional dissimilarity (H2).

To test whether the functional gradient was mediated by microclimatic variables rather than by spatial distance per se (H3), two complementary analyses were performed. First, Spearman correlations were calculated between each environmental variable and both CWM and RaoQ values across plots, to identify which microclimatic and edaphic variables were most strongly associated with the functional gradient. Second, variation partitioning (Borcard *et al.*, 1992) was used to separate the independent contributions of the environmental matrix and spatial distance to variation in plot-level CWM, using the varpart function of the vegan package (Oksanen *et al.*, 2022). The environmental matrix included all measured microclimatic and edaphic variables, and the spatial matrix consisted of the distance-to-edge value for each plot. The analysis estimated the fraction of CWM variation explained uniquely by environment, uniquely by distance, and jointly by both, allowing a direct test of whether functional patterns were environmentally mediated or spatially structured.

To evaluate whether taxonomic turnover and functional dissimilarity were spatially congruent across plot pairs (H4), a Mantel test was performed between the pairwise Sørensen taxonomic dissimilarity matrix and the pairwise functional dissimilarity matrix derived from Euclidean distances between plot-level CWM values, using Spearman correlation and 9999 permutations. A significant positive correlation would indicate that pairs of plots with high taxonomic dissimilarity also exhibit high functional dissimilarity, supporting the hypothesis that species replacement along the gradient reflects replacement of morphofunctional strategies.

4.2. Results

A total of 440 live individuals belonging to 30 species were recorded across the 24 RAPELD plots distributed along the edge-interior gradient. Species richness and abundance per distance class, along with H/D values for each species, are provided in Table 11.

Table 11 - Species list of terrestrial gastropods recorded along the road edge-interior gradient at REBIO Sooretama, with abundance per distance and shell spire index (H/D).

Family	Species	H/D	Shell shape	50 m	250 m	500 m	750 m	1500 m	2500 m
Helicinidae	<i>Helicina variabilis</i>	0.70	Low-spired	—	—	—	—	5	4
	<i>Helicina</i> sp.	0.65	Low-spired	—	—	2	—	—	—
Achatinidae	<i>Leptinaria unilamellata</i>	1.47	High-spired	8	20	—	—	—	—
	<i>Leptopeas bequaerti</i>	1.80	High-spired	6	8	—	—	—	—
	<i>Allopeas micra</i>	2.03	High-spired	3	2	—	—	—	—
	<i>Allopeas gracile</i>	2.80	High-spired	1	1	1	—	—	—
Bulimulidae	<i>Pseudoxychona pileiformis</i>	1.36	High-spired	—	1	1	2	5	1
	<i>Sanniostracus</i> cf. <i>obliquus</i>	2.00	High-spired	—	—	—	—	2	7
	<i>Cochlorina</i> cf. <i>lateralis</i>	1.33	High-spired	—	3	—	4	—	—
	<i>Cochlorina aurisleporis</i>	1.47	High-spired	—	—	1	—	1	—
Cyclodontinidae	<i>Bahiensis albofilosus</i>	2.68	High-spired	—	—	—	—	1	8
	<i>Bahiensis bahiensis</i>	3.11	High-spired	—	—	—	—	—	2
	<i>Burringtonia pantagruelina</i>	2.67	High-spired	—	—	—	—	—	3
Orthalicidae	<i>Orthalicus prototypus</i>	1.54	High-spired	—	—	—	—	—	7
Simpulopsidae	<i>Leiostracus perlucidus</i>	1.63	High-spired	—	8	12	26	33	20
	<i>Simpulopsis</i> sp.	1.18	High-spired	—	—	—	—	—	5
	<i>Rhinus velutinohipsidus</i>	1.11	High-spired	—	—	—	—	1	3
Charopidae	<i>Radiodiscus</i> sp.	0.86	Low-spired	—	—	—	—	—	3
	<i>Lilloiconcha superba</i>	1.06	High-spired	—	—	—	—	—	1
Solaropsidae	<i>Solaropsis planior</i>	0.45	Low-spired	—	—	—	—	1	3
	<i>Solaropsis</i> cf. <i>rosarium</i>	0.49	Low-spired	—	—	—	—	—	2
Scolodontidae	<i>Tamayoa banghaasi</i>	0.49	Low-spired	—	—	1	28	10	—
	<i>Scolodonta</i> sp. 1	0.38	Low-spired	—	—	—	5	17	9
	<i>Scolodonta</i> sp. 2	0.45	Low-spired	—	—	—	—	6	8
	" <i>Happia</i> " <i>pilsbryi</i>	0.46	Low-spired	—	—	—	—	3	9
	<i>Systrophiella circumplexa</i>	0.55	Low-spired	—	—	—	—	3	6
Streptaxidae	<i>Rectartemon regius</i>	0.62	Low-spired	—	—	5	7	10	2
	<i>Rectartemon piquetensis</i>	0.64	Low-spired	—	—	—	1	2	5
Euconulidae	<i>Habroconus semenlini</i>	0.94	Low-spired	—	2	—	15	49	8
	<i>Euconulus martinezi</i>	0.59	Low-spired	—	—	—	—	—	1
Total				18	45	23	88	149	117

Legend: High-spired: H/D > 1.0; Low-spired: H/D ≤ 1.0. Dashes indicate absence.

Source: Author, 2022.

Taxonomic beta diversity among plots was high (mean Sørensen dissimilarity = 0.763). Partitioning revealed that turnover was the dominant component ($\beta_{sim} = 0.628$), accounting for 82.3% of total dissimilarity, while nestedness contributed 17.7% ($\beta_{sne} = 0.135$). The turnover-to-nestedness ratio was 4.665. Taxonomic

dissimilarity increased significantly with distance from the road edge (Mantel $r = 0.445$, $p < 0.001$; Fig. 17).

Rao's quadratic entropy (RaoQ) increased significantly with distance from the road edge ($R^2 = 0.717$, $p = 0.033$; Fig. 18), ranging from 0.096 at 50 m to 0.536 at 2500 m. Functional dissimilarity among plots also increased significantly with distance from the road edge (Mantel $r = 0.250$, $p = 0.006$).

The community-weighted mean of the H/D index (CWM) showed a non-linear pattern along the gradient. Model selection based on the Akaike Information Criterion favored the quadratic model ($AIC = -0.242$) over the linear model ($AIC = 4.758$). The quadratic model explained 85.6% of CWM variation ($R^2 = 0.856$, $p = 0.055$), compared to 53.8% for the linear model ($R^2 = 0.538$, $p = 0.097$; Fig. 19). The inflection point of the fitted quadratic curve was calculated at 1719 m from the road edge ($x = -b/2c$, where $b = -1.102 \times 10^{-3}$ and $c = 3.205 \times 10^{-7}$).

Six of the nine measured environmental variables showed significant correlations with distance from the road edge (Table 2). Air humidity ($r = 0.857$, $p < 0.001$), canopy closure ($r = 0.758$, $p < 0.001$), and soil humidity ($r = 0.757$, $p < 0.001$) increased with distance from the road edge, while light intensity ($r = -0.751$, $p < 0.001$), soil temperature ($r = -0.633$, $p < 0.001$), and soil pH ($r = 0.594$, $p = 0.002$) also varied significantly along the gradient. Air temperature, leaf-litter depth, and leaf-litter moisture did not show significant correlations with distance from the road edge.

Among the environmental variables significantly associated with distance, five were also significantly correlated with CWM. Air humidity showed the strongest negative correlation with CWM ($r = -0.795$, $p < 0.001$), followed by canopy closure ($r = -0.731$, $p < 0.001$), soil humidity ($r = -0.663$, $p < 0.001$), soil pH ($r = -0.607$, $p = 0.002$), and light intensity ($r = 0.659$, $p < 0.001$). Soil temperature was positively correlated with CWM ($r = 0.493$, $p = 0.014$). The same variables were significantly correlated with RaoQ, with soil humidity ($r = 0.509$, $p = 0.011$), soil temperature ($r = -0.595$, $p = 0.002$), light intensity ($r = -0.470$, $p = 0.021$), air humidity ($r = 0.459$, $p = 0.024$), soil pH ($r = 0.449$, $p = 0.028$), and canopy closure ($r = 0.406$, $p = 0.049$) all reaching statistical significance. Leaf-litter depth and leaf-litter moisture were not significantly correlated with either CWM or RaoQ.

Table 12 - Mean values of microclimatic and edaphic variables per distance class, and Spearman rank correlations with distance from road edge, community-weighted mean H/D (CWM H/D), and Rao's quadratic entropy (RaoQ).

Environmental variable	Mean value per distance class						Distance from road edge		CWM H/D		RaoQ	
	50 m	250 m	500 m	750 m	1500 m	2500 m	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Air temperature (°C)	25.25	24.57	25.08	24.42	24.86	24.77	-0.285	0.176	0.305	0.147	-0.301	0.153
Soil temperature (°C)	21.03	20.81	20.88	20.70	20.77	20.70	-0.633	< 0.001	0.493	0.014	-0.595	0.002
Air humidity (%)	73.84	77.72	77.50	79.78	80.06	82.52	0.857	< 0.001	-0.795	< 0.001	0.459	0.024
Soil humidity (%)	49.94	51.28	51.84	51.84	54.03	53.82	0.757	< 0.001	0.663	0.001	0.509	0.011
Leaf-litter depth (cm)	5.68	6.01	5.65	6.08	5.73	5.78	-0.009	0.967	0.062	0.773	0.086	0.689
Light intensity (lux)	976.85	904.19	870.19	645.77	594.95	514.41	-0.751	< 0.001	0.659	< 0.001	-0.470	0.021
Canopy closure (%)	75.13	76.47	77.94	87.01	86.78	91.14	0.758	< 0.001	-0.731	0.001	0.406	0.049
Soil pH	6.23	6.79	6.57	6.82	6.74	6.80	0.594	0.002	-0.607	0.002	0.449	0.028
Leaf-litter moisture (%)	59.47	57.94	56.00	56.51	57.69	60.59	0.120	0.577	-0.018	0.934	0.195	0.360

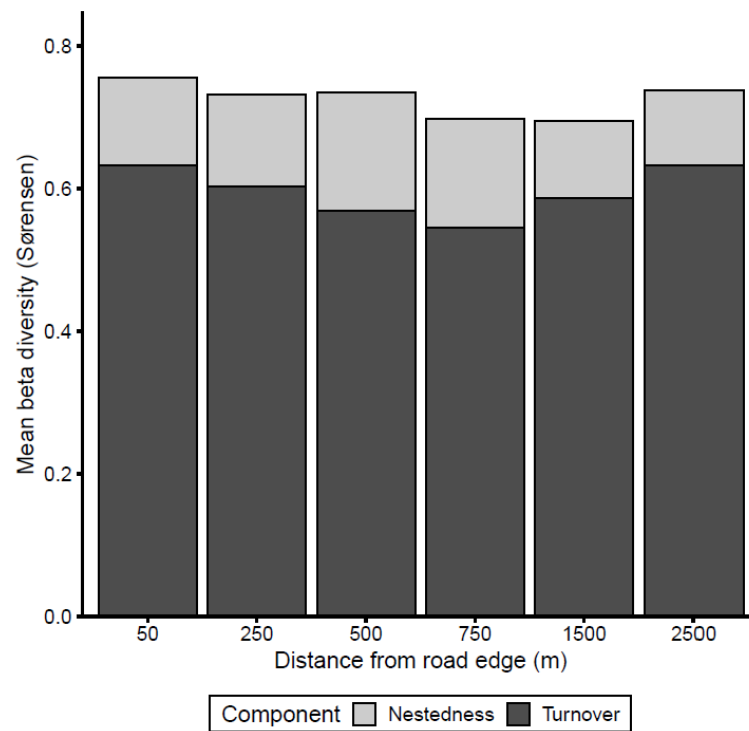
Legend: Bold *p*-values indicate statistical significance ($\alpha = 0.05$). *n* = 24 plots (4 per distance class).

Source: Author, 2022.

Variation partitioning indicated that the environmental matrix explained 49.2% of CWM variation (adjusted R^2 , fraction a+c), while distance from the road edge explained 29.4% (fraction b+c). The fraction of CWM variation explained uniquely by environment, independent of distance, was 16.3% (fraction a), while the fraction explained uniquely by distance, independent of environment, was negative (-3.6%, fraction b), indicating that distance from the road edge had no independent effect on CWM beyond what was already captured by the measured environmental variables. The joint fraction explained by both environment and distance was 32.9% (fraction c; Fig. 20).

Taxonomic and functional dissimilarity matrices were significantly correlated across all plot pairs (Mantel $r = 0.419$, $p < 0.001$; Fig. 21), indicating that plots with greater differences in species composition also showed greater differences in shell morphology.

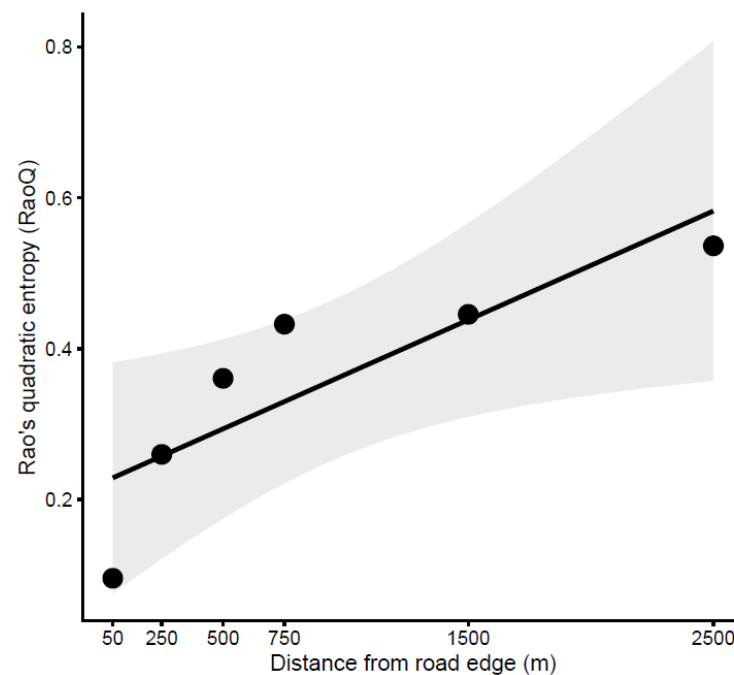
Figure 17 - . Mean beta diversity (Sørensen dissimilarity) partitioned into turnover (dark grey) and nestedness (light grey) components for land snail communities at each distance class from the road edge.



Legend: Values represent mean pairwise dissimilarity between each distance class and all other distance classes.

Source: Author, 2022.

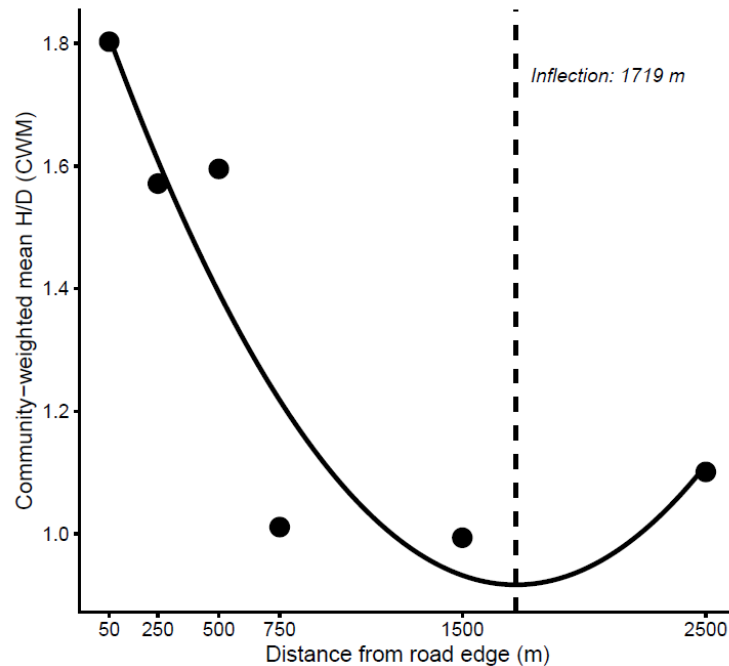
Figure 18 - Rao's quadratic entropy (RaoQ) of land snail communities as a function of distance from the road edge. Points represent mean RaoQ per distance class (n = 4 plots per class).



Legend: The fitted line and shaded area show the ordinary least squares linear regression and 95% confidence interval ($R^2 = 0.717$, $p = 0.033$).

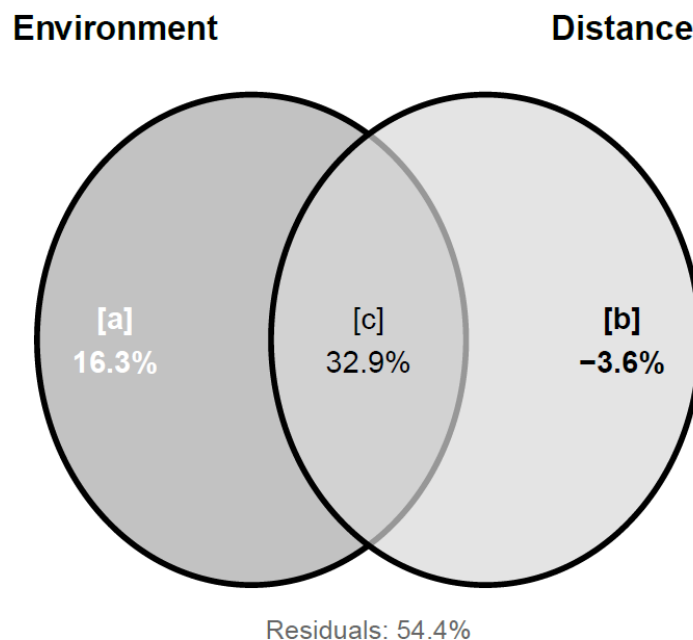
Source: Author, 2022.

Figure 19 - Community-weighted mean of the shell spire index (CWM H/D) as a function of distance from the road edge. Points represent mean CWM per distance class (n = 4 plots per class).



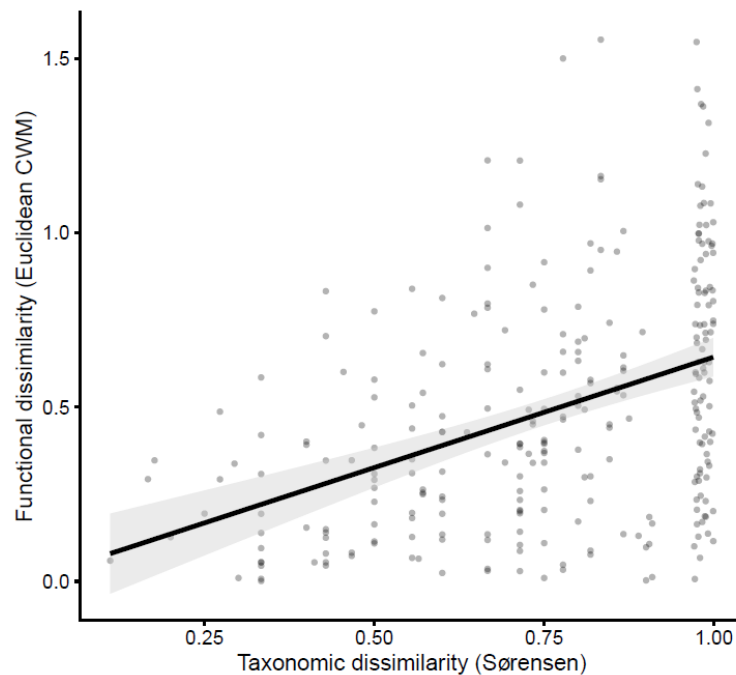
Legend: The fitted curve shows the best-fit quadratic regression ($R^2 = 0.856$, $AIC = -0.242$). The dashed vertical line indicates the inflection point of the quadratic curve at 1719 m from the road edge. Source: Author, 2022.

Figure 20 - Variation partitioning of community-weighted mean H/D (CWM) between the environmental matrix and distance from the road edge.



Legend: Values represent adjusted R^2 fractions: [a] unique contribution of environment (16.3%); [b] unique contribution of distance (-3.6%); [c] shared contribution (32.9%); residuals (54.4%). The negative value of fraction [b] indicates that distance from the road edge has no independent effect on CWM beyond what is already explained by the measured environmental variables. Source: Author, 2022.

Figure 21 - Relationship between pairwise taxonomic dissimilarity (Sørensen index) and pairwise functional dissimilarity (Euclidean distance between plot-level CWM H/D values) across all plot pairs (n = 276 pairs).



Legend: The fitted line and shaded area show the ordinary least squares linear regression and 95% confidence interval (Mantel $r = 0.419$, $p < 0.001$).

Source: Author, 2022.

4.3. Discussion

Our results demonstrate that the BR-101 federal highway imposes a pervasive and spatially structured reorganization of land snail communities across the interior of the Sooretama Biological Reserve, affecting simultaneously the taxonomic composition, the functional diversity, and the morphofunctional strategies of communities distributed along a gradient spanning 2500 m. The coherence among the four dimensions tested, turnover dominance, functional homogenization, microclimatic mediation, and taxonomic-functional congruence, provides an integrated picture of how road edges restructure forest-floor invertebrate communities at scales well beyond the immediate boundary of the disturbance.

4.3.1. Turnover dominates community reorganization along the road edge gradient

Our results show that land snail communities at different distances from the road are compositionally distinct assemblages rather than impoverished or enriched versions of one another, with turnover accounting for more than 80% of total beta

diversity and a T/N ratio approaching 5. The dominance of turnover indicates that the road edge imposes differential environmental filters at each distance, generating communities that are compositionally distinct rather than progressively impoverished.

The dominance of turnover over nestedness is consistent with findings for other invertebrate taxa along road edge gradients in forested landscapes, where directional environmental filtering has been repeatedly identified as the primary driver of community differentiation. Knapp *et al.* (2013) documented significant compositional turnover in ground-dwelling beetles and spiders along highway gradients in Central European forests, with forest specialist species responding negatively to road proximity while open-habitat generalists benefited, a pattern attributed to microclimatic differences between road edges and forest interiors. Dambros *et al.* (2013) showed that road-associated changes in soil moisture drove termite species turnover in an Amazonian forest fragment in Brazil, with community composition shifting significantly along a gradient of road proximity mediated by reductions in soil moisture and canopy closure. The barrier effect of the road itself may further reinforce compositional divergence: paved roads with high traffic density substantially reduce crossing rates in land snails, effectively isolating populations on either side (Baur and Baur, 1990). In the context of the BR-101, which carries heavy traffic through the reserve, this isolation may amplify the compositional divergence between plots, contributing to the high turnover values observed.

4.3.2. Road edges drive functional homogenization through environmental filtering

Our results reveal that communities nearest to the road are functionally homogeneous, dominated by morphologically similar high-spired species, while interior communities support a substantially broader range of shell morphotypes, as evidenced by the nearly sixfold increase in RaoQ from 50 m to 2500 m. The non-linear pattern of CWM along the gradient, with the rate of functional change maximized at approximately 1700 m from the road edge, indicates that the transition between the functionally impoverished edge community and the functionally diverse interior community is progressive and extends deep into the reserve.

This pattern is consistent with the predictions of environmental filtering theory, whereby stressful or novel abiotic conditions reduce the realized functional space of a community by excluding species that lack the traits necessary to tolerate those

conditions (McGill *et al.*, 2006; Violle *et al.*, 2007). In land snails, the shell spire index is a functional axis of desiccation tolerance with well-documented ecological relevance: high-spired morphotypes are consistently associated with reduced evaporative water loss and greater tolerance of thermally stressful and low-humidity conditions, a pattern well documented across latitudinal and altitudinal gradients in land snail assemblages (Machin, 1967; Giokas *et al.*, 2014; Schweizer *et al.*, 2019). The dominance of high-spired species near the road is therefore interpretable as the outcome of a desiccation filter acting on community assembly, analogous to patterns documented in other systems where open or disturbed habitats consistently favor functionally convergent, stress-tolerant communities.

Schmera *et al.* (2023), working with land snail assemblages at forest-pasture transitions in the Swiss Jura, showed that functional diversity was significantly higher in forest interiors than in open or disturbed habitats, with desiccation-tolerant species disproportionately associated with edge and open conditions. De Smedt *et al.* (2019), in a large-scale study across 224 forest fragments in Western Europe, found that slug abundance was reduced near forest edges while snail abundance showed no overall response, and attributed this difference to the higher desiccation tolerance of snails, which can withdraw into their shells during unfavorable conditions while slugs must actively seek shelter. This finding highlights that analyses based solely on abundance may fail to detect the functional reorganization that occurs within snail communities near edges, as the maintenance of abundance does not preclude a shift in the morphofunctional composition of the assemblage. Nekola (2012) similarly documented approximately two thirds turnover in gastropod species composition along a powerline corridor in North America, with forest-specialist species replaced by open-habitat species, a pattern mechanistically analogous to the functional homogenization we document along the road edge gradient in Sooretama. Our results extend these patterns to a continuous tropical forest gradient spanning more than 1700 m, and add a mechanistic layer by linking the functional reorganization directly to measured microclimatic variables, demonstrating that the desiccation filter is not restricted to an abrupt forest boundary but operates progressively and measurably across the forest interior.

4.3.3. Microclimatic gradients mediate the functional response to road edges

Our results show that the functional gradient documented along the edge-interior transect is explained by the environmental gradient generated by the road rather than by spatial distance per se, as evidenced by the variation partitioning analysis in which the unique fraction of CWM variation explained by distance, independent of measured environmental variables, was negligible and negative. Air humidity, canopy closure, and soil humidity were the variables most strongly associated with both the distance gradient and the functional composition of communities, with high-humidity, high-canopy plots consistently harboring low-spined communities and low-humidity, high-radiation plots harboring high-spined communities.

This result is mechanistically coherent with the well-documented microclimatic signature of road edges in tropical forests, where reduced canopy cover near the edge drives cascading increases in solar radiation, air temperature, and vapor pressure deficit that propagate hundreds of meters into the forest interior (Murcia, 1995; Laurance *et al.*, 2009; Banbury Morgan and Jucker, 2025). The buffering role of canopy cover in modulating forest floor microclimate is well established: dense canopies reduce incoming radiation and maintain high air humidity through transpiration, creating the stable thermal and hydrological environment that supports humidity-dependent forest-floor invertebrates (Zellweger *et al.*, 2019). The progressive recovery of canopy closure and air humidity with increasing distance from the road thus provides a direct mechanistic link between road infrastructure and the functional composition of the land snail community. The absence of significant associations between leaf-litter depth or leaf-litter moisture and either distance or functional metrics suggests that the functional filter operates primarily through microclimatic pathways rather than through substrate availability, which appeared relatively homogeneous across the gradient. This finding narrows the set of plausible mechanisms and focuses management attention on the canopy and microclimate axis as the primary driver of community reorganization.

4.3.4. Species replacement reflects replacement of morphofunctional strategies

Our results demonstrate that the taxonomic turnover documented along the gradient is not ecologically neutral: pairs of plots that differ most in species composition also differ most in shell morphology, indicating that the road edge imposes filters that

act simultaneously and coherently on taxonomic identity and functional strategy. Species replacement along the gradient therefore reflects a directional shift in the functional spectrum of the community rather than the random substitution of ecologically equivalent species.

This taxonomic-functional congruence has been documented in other taxa along disturbance gradients in tropical forests. Razafindratsima *et al.* (2018), working in a tropical rainforest in Madagascar, showed that edge effects erode functional and phylogenetic diversity of tree communities in a spatially structured manner, with taxonomic and functional gradients operating in concert. Gheoca *et al.* (2023) similarly demonstrated that the functional trait composition of land snail communities in riparian forests was tightly coupled to taxonomic composition responses to habitat complexity, with desiccation-related traits shifting predictably alongside species identity. Our results add terrestrial gastropods in a tropical road edge context to this growing body of evidence, and demonstrate that the taxonomic-functional congruence holds across a continuous gradient rather than a simple edge-interior comparison. This strengthens the interpretation that the organizing process is environmental filtering rather than stochastic assembly, and suggests that functional monitoring using shell morphology could serve as a cost-effective indicator of road edge influence in land snail communities.

4.3.5. Management relevance for buffer zone design in road-bisected protected areas

Our results establish that the functional zone of road influence on land snail communities extends to approximately 1700 m from the road edge, substantially exceeding the buffer distances commonly prescribed in current management frameworks, which are typically derived from studies of vertebrates and vascular plants and range from 50 to 500 m for most documented edge effects (Murcia, 1995; Ibisch *et al.*, 2016). Dambros *et al.* (2013) proposed a buffer zone of 81 m along roads based on termite community data from an Amazonian forest fragment, while Knapp *et al.* (2013) documented highway edge effects on arthropod assemblages extending up to 100 m into Central European forests. Our results extend this picture substantially, suggesting that the spatial reach of road influence on forest-floor invertebrates in continuous tropical forest may be an order of magnitude greater than previously estimated from fragmented or temperate systems.

For the Sooretama Biological Reserve specifically, where the total width of continuous forest substantially exceeds the estimated zone of influence, the documented edge effects do not necessarily imply irreversible biodiversity loss, but they do mean that ecological communities within the identified zone of influence should not be treated as equivalent in conservation planning to those in the undisturbed interior. For smaller Atlantic Forest fragments, where the total area may fall entirely within the zone of road influence, the implications are more severe and potentially affect the conservation value of the entire fragment. These findings align with the broader recognition that road ecology must be integrated into protected area planning not merely as a threat to connectivity but as a source of persistent internal disturbance that reorganizes community structure far from the pavement edge (Trombulak & Frissell, 2000; Ibisch *et al.*, 2016; Banbury Morgan & Jucker, 2025).

4.4. Conclusion

Road edges associated with the BR-101 highway impose an extensive restructuring of land snail communities across the interior of the Sooretama Biological Reserve, extending well beyond the immediate forest boundary. Species turnover dominates beta diversity along the gradient, indicating that each distance class harbors a compositionally distinct and irreplaceable assemblage. Functional diversity increases progressively with distance from the road, with an inflection point at approximately 1700 m, and this functional gradient is explained by microclimatic variables, particularly air humidity and canopy closure, rather than by spatial distance alone. The congruence between taxonomic turnover and functional dissimilarity demonstrates that species replacement reflects the replacement of morphofunctional strategies rather than the stochastic replacement of functionally equivalent species. These results provide the first biologically grounded estimate of the functional zone of road influence for a forest-floor invertebrate group in Atlantic Forest, and highlight the need to incorporate taxon-specific functional thresholds into buffer zone design for road-bisected protected areas, where standards based on vertebrate and plant data may systematically underestimate the spatial reach of road-induced disturbance.

5. DOES THE SHAPE MATTER? MICROHABITAT USE BY SPECIES IN A LAND SNAIL COMMUNITY IN A BRAZILIAN ATLANTIC REMNANT

Esteves, R. A., Santos, S. B., & Rocha, C. F. D. (2026). Shell shape predicts microhabitat use in a land snail assemblage from the Atlantic Forest. *Journal of Conchology*, 45(6), 117 - 1132. <https://doi.org/10.61733/jconch/4586>.

In terrestrial ecosystems, species differ in their use of available microhabitats, and these differences often correlate with morphological traits that influence locomotion, substrate adhesion, and exposure to environmental conditions (Schowalter 2012). In land snails, shell morphology represents one such trait: the spire index, expressed as the ratio between shell height (H) and maximum diameter (D), follows a characteristic bimodal distribution in assemblages worldwide, with species clustering into two distinct morphological groups, high spired ($H > D$) and low spired ($H < D$), that differ systematically in their microhabitat affinities (Cain 1977, 1978a, b, 1980, 1981; Goodfriend 1986; Emberton 1995). High-spired species tend to occur on vertical surfaces such as tree trunks and herbaceous vegetation, whereas low-spired species are predominantly associated with ground-level substrates and leaf litter (Cain & Cowie 1978; Cameron 1978; Heller 1987).

These associations have been attributed to biomechanical constraints imposed by shell geometry on locomotion and substrate adhesion: a narrower profile and elevated centre of mass favour adhesion to inclined and vertical surfaces, while a flattened shell provides greater stability on horizontal substrates (Cook & Jaffar 1984; Cowie 1995). Okajima & Chiba (2009) formally quantified these constraints using a moment-of-force model, demonstrating that low-spired shells minimise gravitational torque on horizontal surfaces, whereas both low- and high-spired shells are well balanced on vertical surfaces, with shells of intermediate spire index ($H/D \approx 1.4$) being the least stable on vertical substrates. This biomechanical model predicts a valley in the frequency distribution of spire indices near $H/D = 1.4$, a prediction supported by empirical data across multiple regions and faunas, and provides a formal physical basis for the bimodal distribution of shell shape observed in land-snail assemblages worldwide.

The relationship between species abundance and microhabitat breadth has been documented across diverse taxa. More abundant species tend to exploit a

broader range of habitat conditions, a pattern associated with ecological generalism and greater niche flexibility (Brown 1984; Schamp *et al.* 2010). Whether this relationship holds in land-snail assemblages structured by shell morphological constraints remains largely untested.

An additional methodological consideration in assemblage-level analyses of shell morphology and microhabitat use is the potential for phylogenetic non-independence. Species sharing a common ancestor tend to resemble each other in morphology and ecology due to shared ancestry rather than independent ecological responses to current conditions (Harvey & Pagel 1991). In assemblages composed of multiple families spanning several superfamilies, as is the case in diverse tropical faunas, this non-independence can inflate apparent ecological signals. Controlling for phylogenetic structure is therefore an important step in evaluating whether the observed associations between shell shape and microhabitat use persist across independently derived lineages.

Despite the Brazilian Atlantic Forest being one of the world's most important biodiversity hotspots, with exceptional levels of species richness and endemism (Ribeiro *et al.* 2009), the ecology of its land-snail assemblages remains poorly studied. In particular, no study has examined fine-scale patterns of microhabitat use in Atlantic Forest gastropod communities in relation to shell morphology, species abundance, and phylogenetic affinity.

In this study, we investigated microhabitat use in a land-snail assemblage from the Sooretama Biological Reserve, a large remnant of Atlantic Forest in southeastern Brazil, and tested three predictions: (1) more abundant species will show broader microhabitat use, reflecting greater ecological generalism; (2) species will show significant, non-random associations with particular microhabitats; and (3) species co-occurring in the same microhabitat will exhibit convergent shell morphologies. All predictions were evaluated with phylogenetic correction at the superfamily level to account for non-independence among species.

5.1. **Material and methods**

5.1.1. Study area

The study was conducted in the Sooretama Biological Reserve (19°00'50.87"S, 040°05'48.96"W; mean altitude: 46 m), the largest remnant of Atlantic Forest in Espírito Santo state, southeastern Brazil (Fig. 8). The reserve comprises approximately 28,000 ha and represents one of the most important areas for biodiversity conservation within the Atlantic Forest biome, forming part of the Central Corridor of the Atlantic Forest (MMA 2000).

The regional climate is classified as tropical hot and humid, with mean annual precipitation of approximately 1,202 mm and a mean annual temperature of 23.3 °C. The dominant vegetation physiognomy corresponds to Coastal Plain Forest (locally known as "Floresta de Tabuleiro"), characterised by tall canopy trees that may reach heights of up to 40 m (Peixoto & Gentry 1990).

According to the management plan of the reserve, there are no significant records of established invasive alien species within its boundaries (ICMBio 2019), suggesting that the ecosystem remains relatively well preserved. Nevertheless, anthropogenic pressures occur mainly along the reserve's borders, particularly due to surrounding agricultural activities and informal settlements, which have occasionally resulted in forest fires, such as those recorded in 1998 and in the Lagoa do Macuco region in 2016.

The reserve presents considerable environmental heterogeneity, including dense ombrophilous forest, muçununga formations (low and open forests), wetlands, lakes, and marshes. Despite relatively modest altitudinal variation (5–197 m above sea level), this environmental diversity contributes to the high biological richness recorded in the region

5.1.2. Data sampling

Field sampling was conducted in 2017 (January, June, August, and November) and 2018 (January, June, September, and December), covering both the dry season (April–September) and the rainy season (October–March), ensuring seasonal representation across the entire study period. All sampling sessions were conducted between 05:00 and 10:00 h to standardise activity periods.

The RAPELD method (Magnusson *et al.* 2005) was employed using 24 permanent trails of 250 m length distributed within the Coastal Plain Forest. Trails followed terrain contours and were spaced approximately 1 km apart, ensuring spatial

independence among sampling units. This framework integrates the Rapid Assessment Program (RAP) and the Brazilian Long-Term Ecological Research Program (PELD), providing a standardised platform for biodiversity surveys.

Along each trail, macro-gastropods (shell diameter or height >5 mm) were sampled by active search conducted at a slow walking pace by a single observer throughout the entire study period, ensuring consistency in sampling effort (Oliveira *et al.* 2021). At each encounter, the individual was assigned to one of five microhabitat categories (see below) and counted. Micro-gastropods (shell diameter or height ≤5 mm) were sampled using three quadrats of 25 × 75 cm established along each trail at standardised distances of 50, 100, and 200 m. Leaf litter within each quadrat was collected and examined under a stereomicroscope to detect small-bodied specimens. All collected individuals were counted and deposited in the Malacological Collection of the Universidade do Estado do Rio de Janeiro (Col. Mol. UERJ).

We note that the leaf-litter quadrat method was applied exclusively to that microhabitat, providing a more intensive sampling effort for micro-gastropods in the litter stratum. Microhabitats in the arboreal stratum (tree trunk and tree leaves) were surveyed exclusively by visual active search during macro-gastropod sampling, without a dedicated intensive method for small-bodied arboreal species. As a consequence, micro-gastropods restricted to arboreal substrates may be underrepresented in our dataset, which should be taken into account when interpreting patterns in those microhabitats.

5.1.3. Species identification

Terrestrial gastropods were identified using a stereomicroscope, based on conchological characteristics to the lowest possible taxonomic level. Family-level classification followed Bouchet *et al.* (2017), except where superseded by the treatment adopted in Salvador *et al.* (2024), which was used as the primary reference for species-level nomenclature and checklist verification of the Brazilian fauna. Specimen identification was carried out by comparing observed morphological characteristics with descriptions and illustrations available in specialised references (Salgado & Coelho 2003; Simone 2006; Míquel *et al.* 2007; Salvador *et al.* 2015; Salvador & Simone 2015). Species-level identifications were subsequently verified against Salvador *et al.* (2024) and cross-checked against Salvador *et al.* (2026), which

surveyed the land-snail fauna of Sooretama specifically. Specimens that could not be identified to species level are treated as morphospecies and listed under their respective genus (*Helicina* sp., *Simpulopsis* sp., *Scolodonta* sp. 1, and *Scolodonta* sp. 2).

One nomenclatural issue requires explicit acknowledgment. "*Happia*" *pilsbryi* Gude, 1912, recorded here as a significant indicator species of the leaf-litter microhabitat, may not belong to *Happia* Bourguignat, 1890 in its strict sense. Roosen & Breure (2024) revised the genera of Scolodontidae and transferred several Brazilian species to *Systrophiella*, *Austroselenites*, and *Prohappia*; however, a significant portion of Brazilian species previously placed in *Happia*, including *H. pilsbryi*, were not addressed by that revision and remain without a confirmed generic assignment. Following Salvador *et al.* (2024), we provisionally retain the name "*Happia*" *pilsbryi*, with the generic name in quotation marks to signal its uncertain status, pending a comprehensive systematic revision of these orphaned taxa. None of these nomenclatural uncertainties affect the ecological analyses presented here, as all results are based on morphological and abundance data independent of generic assignment.

5.1.4. Microhabitat classification

For each recorded individual, the microhabitat at the moment of encounter was registered. Five mutually exclusive microhabitat categories were considered: ground, leaf litter, vegetation, tree trunk, and tree leaves (Fig. 22).

Ground included individuals located directly on the exposed soil surface, with no accumulated organic matter beneath them. Leaf litter comprised individuals found within or beneath the accumulated layer of decomposing organic matter on the forest floor. This distinction between ground and leaf litter was made at the time of collection: individuals resting on bare soil were assigned to ground, while individuals found among or beneath leaf litter were assigned to the leaf-litter category. Vegetation corresponded to individuals found on herbaceous plants or shrubs up to approximately 1.5 m in height. Tree trunk referred to individuals attached to the vertical surfaces of tree trunks above that height. Tree leaves included individuals found on leaves within the arboreal canopy or sub-canopy. All five microhabitat categories were potentially available along each trail, as the Coastal Plain Forest presents a continuous vertical stratification

throughout the sampled area; however, the frequency of records per microhabitat varied among plots depending on local structural conditions.

Figure 22 - Representative examples of microhabitats used by land snails in the Sooretama Biological Reserve, southeastern Brazil (not to scale).



Legenda: (A) Three live individuals of *Simpulopsis* sp. on a tree leaf (tree leaves microhabitat). (B) Two live individuals of *Allopeas gracile* on the ground (ground microhabitat). (C) A live individual of *Rectartemon regius* within the leaf litter (leaf-litter microhabitat). (D) A live individual of *Cochlorina* cf. *lateralis* on a tree trunk (tree trunk microhabitat). (E) A live individual of *Leiostracus perlucidus* on vegetation (vegetation microhabitat).

Source: Author, 2022.

The abundance of each species in each microhabitat category was compiled into a species-by-microhabitat matrix in which rows represented species and columns represented the five microhabitat types.

5.1.5. Statistical analysis

Shell height (H) and maximum diameter (D) were measured only in adult individuals to avoid potential ontogenetic variation in shell proportions. All measurements were taken using a digital micrometer (precision: ± 0.01 mm). Following Cain (1977), the spire index (H/D ratio) was calculated for each species as the mean ratio across all measured individuals, and species were classified as high-spired ($H > D$, i.e. $H/D > 1$) or low-spired ($H < D$, i.e. $H/D < 1$).

To assess sampling completeness, we constructed species accumulation curves using the *specaccum* function in the *vegan* package (Oksanen *et al.* 2024), with 999 random permutations, at two levels: by plot ($n = 24$) and by plot $\times$ microhabitat sample ($n = 64$ non-empty combinations).

To evaluate overall differences in microhabitat use across the assemblage, we performed a likelihood-ratio test (G-test) on a contingency table of species abundance by microhabitat (Sokal & Rohlf 1981).

To quantify microhabitat breadth for each species, we calculated the standardised Levins' niche breadth index (B'), based on the proportional distribution of individuals across the five microhabitat categories. B' ranges from 0 (maximum specialisation, all individuals in one microhabitat) to 1 (maximum generalisation, individuals distributed equally across all microhabitats). Species recorded as a single individual were excluded from this analysis, as a single record always yields $B' = 0$ regardless of ecological affinity, which would introduce a systematic artefact in the correlation. To test whether more abundant species occupied a broader range of microhabitats, we performed a Spearman rank correlation between log₁₀-transformed total abundance and B' .

To classify species according to their patterns of microhabitat use, we performed a hierarchical cluster analysis on log-transformed abundance data [$\log(x + 1)$] using the Bray–Curtis dissimilarity index (Faith *et al.* 1987) and the beta-flexible linkage method ($\beta = -0.25$), as implemented in the *agnes* function of the *cluster* package (Maechler *et al.* 2023). The resulting dendrogram was inspected with $k = 3$ and $k = 4$ groups; the solution with $k = 4$ was retained on the basis of ecological coherence with the five microhabitat categories. Each species label in the dendrogram was colour-coded according to shell shape (high spired: blue; low spired: red) to allow visual assessment of morphological convergence within clusters.

To identify species with statistically significant associations with particular microhabitats, we performed an Indicator Species Analysis (IndVal; Dufrêne &

Legendre 1997) using the *indval* function in the *labdsv* package (Roberts 2019). The *IndVal* combines a measure of specificity (proportion of a species' abundance concentrated in a given microhabitat) and fidelity (proportion of samples of that microhabitat in which the species occurs). Statistical significance was assessed by permutation test (999 permutations); only species with $p < 0.05$ were considered significant indicators.

To test for differences in shell shape (H/D ratio) among microhabitat categories, we used the Kruskal–Wallis test (Kruskal & Wallis 1952), treating individual records as observations. Shell-shape values were assigned to individual records based on species-level mean H/D ratios, such that multiple individuals of the same species carry the same value within each microhabitat category. This approach evaluates shell-shape differences at the level of observed microhabitat use, weighted by species abundance; the resulting non-independence of individual records within species should be taken into account when interpreting the magnitude of the test statistic, although it does not affect the direction or biological interpretation of the pattern. When significant differences were detected, pairwise comparisons were performed using Dunn's post-hoc test with Bonferroni correction for multiple comparisons (*dunn.test* package; Dinno 2017).

To account for phylogenetic non-independence among species, we performed a phylogenetically stratified permutation multivariate analysis of variance (PERMANOVA; Anderson 2001) using the *adonis2* function in *vegan*, with superfamily membership as strata. This approach constrains permutations within phylogenetic groups, preventing the inflation of statistical significance that would arise from treating species of the same superfamily as independent observations. Superfamily assignment followed the classification of Salvador *et al.* (2024). The analysis was performed on the log-transformed species-by-microhabitat matrix using Bray-Curtis dissimilarities, with primary microhabitat (the microhabitat category with the highest recorded abundance for each species) as the explanatory grouping factor and permutations constrained within superfamilies (999 permutations).

All analyses were performed in R v. 4.4.2 (R Core Team 2024) using the packages *vegan* (Oksanen *et al.* 2024), *labdsv* (Roberts 2019), *cluster* (Maechler *et al.* 2023), *dendextend* (Galili 2015), and *dunn.test* (Dinno 2017).

5.2. Results

We recorded 440 individuals belonging to 30 species from 12 families across 24 plots and 64 non-empty plot $\times$ microhabitat combinations (Table 13). Species-accumulation curves approached an asymptote before the full complement of sampling units was exhausted, at both the plot and sample levels, indicating adequate sampling completeness (Fig. 23).

Species differed significantly in their distribution across microhabitat categories (G-test: $G = 943.51$, $df = 116$, $p < 0.0001$). Leaf litter was the most species-rich microhabitat (17 species), followed by tree trunk (8), ground (6), vegetation (3), and tree leaves (3). The full distribution of individuals per species and microhabitat is presented in Table 13.

Eighteen species (60% of the assemblage) showed statistically significant associations with particular microhabitats (IndVal permutation test, $p < 0.05$; Table 14). Leaf litter had the highest number of indicator species ($n = 8$), followed by ground ($n = 4$), vegetation ($n = 2$), tree trunk ($n = 2$), and tree leaves ($n = 2$). Twelve species showed no statistically significant microhabitat association ($p \geq 0.05$; Table 14).

The Spearman correlation between log₁₀-transformed total abundance and standardised Levins' niche breadth (B') was not statistically significant ($\rho = 0.251$, $S = 2735.7$, $p = 0.197$). The majority of species (29 of 30) showed B' values at or near zero. Individual species abundances and B' values are presented in Table 13.

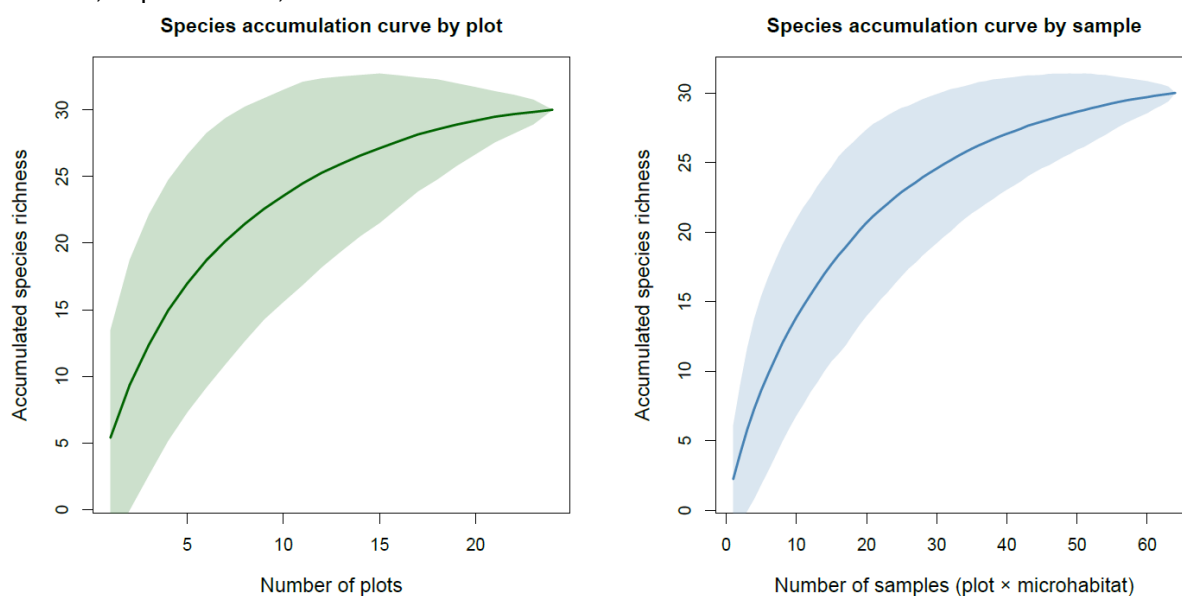
Hierarchical cluster analysis (Bray–Curtis dissimilarity, β -flexible linkage, $k = 4$) resolved the 30 species into four groups corresponding to distinct microhabitat use patterns (Fig. 24): a ground-dwelling cluster (4 species, 100% high spired), a semi-arboreal cluster (5 species, 80% high spired), an arboreal cluster concentrated on tree trunks (6 species, 83% high spired), and a litter-dwelling cluster (15 species, 80% low spired). Species composition of each cluster is detailed in Table 13.

Shell shape (H/D ratio) differed significantly among microhabitat categories (Kruskal–Wallis: $H = 274.43$, $df = 4$, $p < 0.0001$) (Fig. 25). Post-hoc Dunn comparisons with Bonferroni correction revealed significant differences between leaf litter and all other microhabitats: leaf litter vs ground ($Z = 10.09$, $p < 0.001$), leaf litter vs vegetation ($Z = -14.31$, $p < 0.001$), leaf litter vs tree trunk ($Z = -8.09$, $p < 0.001$), and leaf litter vs tree leaves ($Z = -3.55$, $p = 0.002$). No significant differences were detected among ground, tree trunk, and vegetation ($p = 1.000$ in all three pairwise comparisons), nor

between ground and tree leaves ($Z = 2.54$, $p = 0.056$) or tree trunk and tree leaves ($Z = -2.22$, $p = 0.131$). Tree leaves differed significantly from vegetation ($Z = -3.47$, $p = 0.003$).

Microhabitat explained a significant proportion of variation in species composition after controlling for superfamily-level phylogenetic non-independence (PERMANOVA stratified by superfamily: $F = 32.345$, $R^2 = 0.838$, $df = 4$, $p = 0.001$). At the superfamily level, differences were observed in the relative distribution of individuals across microhabitats (Fig. 26). Achatinoidea was exclusively associated with ground habitats. Scolodontoidea, Streptaxoidea, Trochomorpoidea, Punctoidea, and Sagdoidea were recorded exclusively in leaf litter. Helicinoidea and Orthalicoidea were distributed across arboreal and semi-arboreal microhabitats, with Orthalicoidea also presenting a small proportion of individuals in leaf litter.

Figure 23 - Species-accumulation curves for the land-snail assemblage of the Sooretama Biological Reserve, Espírito Santo, Brazil.



Source: Author, 2022.

Table 13 - Shell shape measurements and microhabitat use of land snail species recorded in the Sooretama Biological Reserve, southeastern Brazil.

					Microhabitat						
Superfamily / family / species	H (mm)	D (mm)	H/D	Shell shape	Ground	Leaf-litter	Vegetation	Tree trunk	Tree leaves	n / plots	Habitat category*
Helicinoidea Férussac, 1822											
Helicinidae Férussac, 1822											
<i>Helicina variabilis</i> Wagner, 1827	9.81	14.03	0.70	Low-spired	0	0	0	1	8	9/4	Semi-arboreal
<i>Helicina</i> sp.	7.06	10.94	0.65	Low-spired	0	0	0	2	0	2/2	Arboreal
Achatinoidea Swainson, 1840											
Achatinidae Swainson, 1840											
<i>Leptinaria unilamellata</i> (d'Orbigny, 1838)	8.04	5.49	1.47	High-spired	28	0	0	0	0	28/6	Ground-dweller
<i>Leptopeas bequaerti</i> (Pilsbry, 1926)	7.39	4.12	1.80	High-spired	14	0	0	0	0	14/4	Ground-dweller
<i>Allopeas micra</i> (d'Orbigny, 1835)	3.90	1.92	2.03	High-spired	5	0	0	0	0	5/3	Ground-dweller
<i>Allopeas gracile</i> (Hutton, 1834)	7.96	2.85	2.80	High-spired	3	0	0	0	0	3/3	Ground-dweller
Orthalicoidea Martens, 1860											
Bulimulidae Tryon, 1867											
<i>Pseudoxychona pileiformis</i> (Moricand, 1836)	17.64	13.01	1.36	High-spired	0	1	9	0	0	10/8	Semi-arboreal
<i>Sanniostracus</i> cf. <i>obliquus</i> (Reeve, 1849)	20.83	10.43	2.00	High-spired	0	0	0	9	0	9/3	Arboreal
<i>Cochlorina</i> cf. <i>lateralis</i> (Menke, 1828)	32.00	24.03	1.33	High-spired	0	0	0	7	0	7/4	Arboreal
<i>Cochlorina aurisleporis</i> (Bruguère, 1792)	31.48	21.45	1.47	High-spired	0	0	0	2	0	2/2	Arboreal
Cyclodontinidae Salvador & Breure, 2023											
<i>Bahiensis albofilosus</i> (Dohrn, 1883)	19.61	7.31	2.68	High-spired	0	0	9	0	0	9/3	Semi-arboreal
<i>Bahiensis bahiensis</i> (Moricand, 1834)	15.13	4.87	3.11	High-spired	0	0	0	2	0	2/2	Arboreal
<i>Burringtonia pantagruelina</i> (Moricand, 1833)	54.39	20.40	2.67	High-spired	0	3	0	0	0	3/2	Litter-dweller
Orthalicidae Martens, 1860											
<i>Orthalicus prototypus</i> Pilsbry, 1899	36.52	23.71	1.54	High-spired	0	0	0	7	0	7/1	Arboreal

Simpulopsidae Schileyko, 1999											
<i>Leiostracus perlucidus</i> (Spix, 1827)	15.12	9.31	1.63	High-spired	0	8	81	4	6	99/17	Semi-arboreal
<i>Simpulopsis</i> sp.	7.10	6.01	1.18	High-spired	0	0	0	0	5	5/2	Semi-arboreal
<i>Rhinus velutinohipsidus</i> (Moricand, 1836)	20.56	18.45	1.11	High-spired	1	3	0	0	0	4/2	Litter-dweller
Punctoidea Morse, 1864											
Charopidae Hutton, 1884											
<i>Radiodiscus</i> sp.	2.06	2.41	0.86	Low-spired	0	3	0	0	0	3/1	Litter-dweller
<i>Lilloiconcha superba</i> (Thiele, 1927)	2.64	2.49	1.06	High-spired	0	1	0	0	0	1/1	Litter-dweller
Sagdoidea Pilsbry, 1895											
Solaropsidae Nordsieck, 1986											
<i>Solaropsis planior</i> (Pilsbry, 1890)	17.12	37.82	0.45	Low-spired	0	4	0	0	0	4/4	Litter-dweller
<i>Solaropsis</i> cf. <i>rosarium</i> (Pfeiffer, 1850)	16.10	32.54	0.49	Low-spired	0	2	0	0	0	2/2	Litter-dweller
Scolodontoidea Baker, 1925											
Scolodontidae Baker, 1925											
<i>Tamayoa banghaasi</i> (Thiele, 1927)	1.87	3.80	0.49	Low-spired	0	39	0	0	0	39/7	Litter-dweller
<i>Scolodonta</i> sp. 1	1.36	3.59	0.38	Low-spired	0	31	0	0	0	37/10	Litter-dweller
<i>Scolodonta</i> sp. 2	2.11	4.72	0.45	Low-spired	0	14	0	0	0	14/2	Litter-dweller
" <i>Happia</i> " <i>pilsbryi</i> Gude, 1902	1.74	3.77	0.46	Low-spired	0	12	0	0	0	12/6	Litter-dweller
<i>Systrophiella circumplexa</i> (Deshayes, 1839)	2.43	4.40	0.55	Low-spired	0	9	0	0	0	9/4	Litter-dweller
Streptaxoidea Gray, 1860											
Streptaxidae Gray, 1860											
<i>Rectartemon regius</i> (Löbbecke, 1881)	14.39	23.15	0.62	Low-spired	3	21	0	0	0	24/9	Litter-dweller
<i>Rectartemon piquetensis</i> (Pilsbry, 1930)	5.04	7.82	0.64	Low-spired	0	8	0	0	0	8/3	Litter-dweller
Trochomorpoidea Mörch, 1864											
Euconulidae Backer, 1928											
<i>Habroconus semenlini</i> (Moricand, 1846)	2.76	2.94	0.94	Low-spired	0	74	0	0	0	74/8	Litter-dweller
<i>Euconulus martinezi</i> (Hidalgo, 1869)	1.01	1.70	0.59	Low-spired	0	1	0	0	0	1/1	Litter-dweller

Total					54	234	99	34	24	440	
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Legend: H: shell height (mm); D: shell diameter (mm); H/D: spire index. Microhabitat columns show number of individuals recorded per microhabitat. *n* / plots: total individuals / number of plots in which the species was recorded.

Source: Author, 2022.

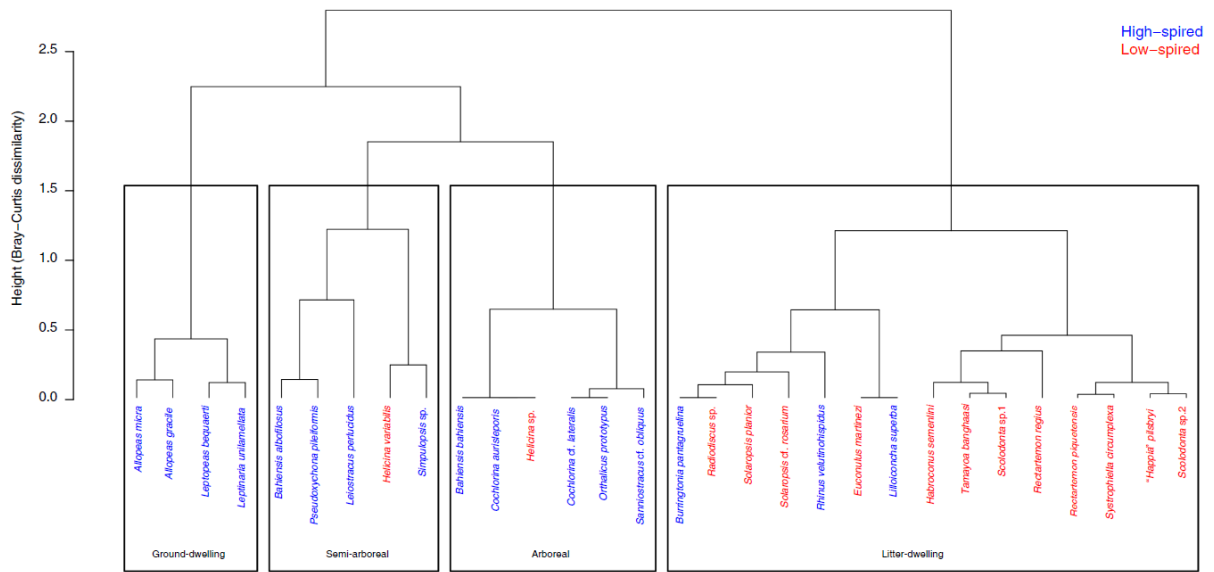
Table 14 - Indicator species analysis results for land snail species showing statistically significant associations with particular microhabitats ($p < 0.05$, 999 permutations) in the Sooretama Biological Reserve, southeastern Brazil.

Species	Microhabitat	IndVal	p	Shell shape
Ground				
<i>Leptinaria unilamellata</i>	Ground	0.462	< 0.001	High-spired
<i>Leptopeas bequaerti</i>	Ground	0.308	0.004	High-spired
<i>Allopeas micra</i>	Ground	0.231	0.025	High-spired
<i>Allopeas gracile</i>	Ground	0.231	0.028	High-spired
Leaf litter				
<i>Scolodonta</i> sp. 1	Leaf-litter	0.714	< 0.001	Low-spired
<i>Habroconus semenlini</i>	Leaf-litter	0.571	< 0.001	Low-spired
<i>Tamayoa banghaasi</i>	Leaf-litter	0.500	< 0.001	Low-spired
<i>Rectartemon regius</i>	Leaf-litter	0.495	0.002	Low-spired
" <i>Happia</i> " <i>pilsbryi</i>	Leaf-litter	0.429	0.003	Low-spired
<i>Solaropsis planior</i>	Leaf-litter	0.286	0.010	Low-spired
<i>Systrophieilla circumplexa</i>	Leaf-litter	0.286	0.016	Low-spired
<i>Rectartemon piquetensis</i>	Leaf-litter	0.214	0.039	Low-spired
Vegetation				
<i>Leiostracus perlucidus</i>	Vegetation	0.627	< 0.001	High-spired
<i>Pseudoxychona pileiformis</i>	Vegetation	0.389	0.004	High-spired
Tree trunk				
<i>Cochlorina</i> cf. <i>lateralis</i>	Tree-trunk	0.308	0.006	High-spired
<i>Sanniostracus</i> cf. <i>obliquus</i>	Tree-trunk	0.231	0.037	High-spired
Tree leaves				
<i>Helicina variabilis</i>	Tree-leaves	0.630	< 0.001	Low-spired
<i>Simpulopsis</i> sp.	Tree-leaves	0.333	0.013	High-spired

Legend: Species are grouped by microhabitat.

Source: Author, 2022.

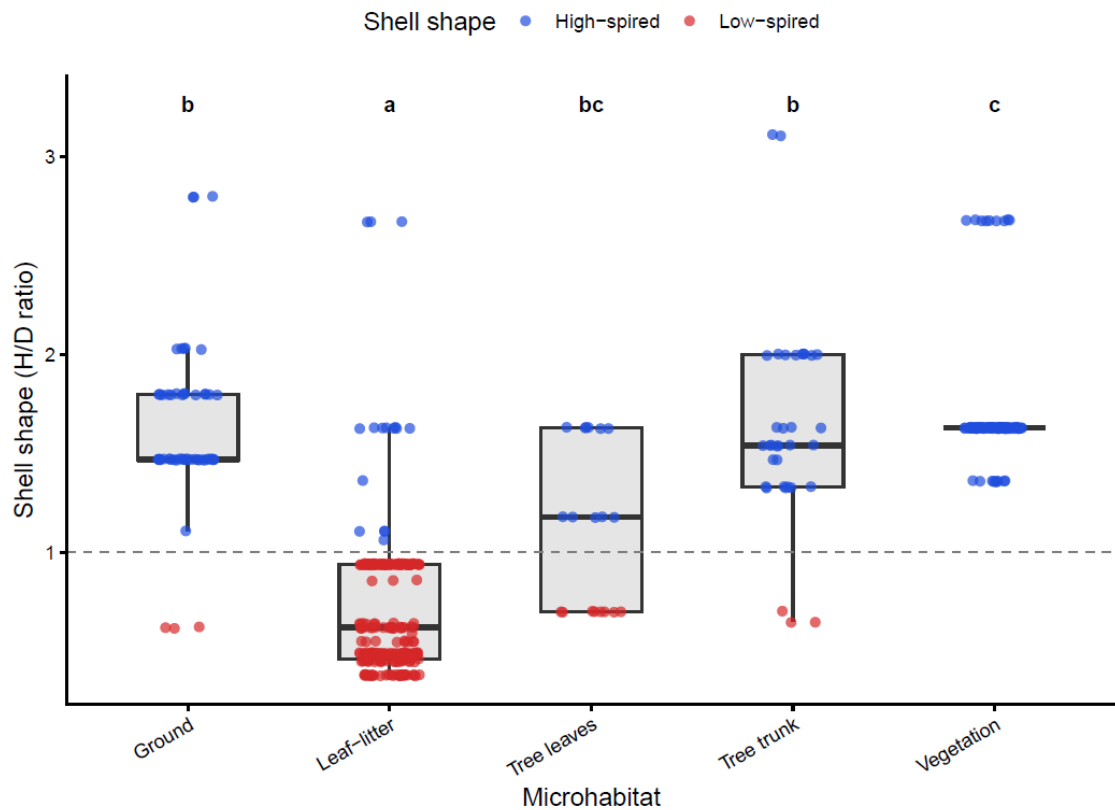
Figure 24 - Hierarchical cluster analysis of land snail species from the Sooretama Biological Reserve based on microhabitat use.



Legend: The dendrogram was constructed from log-transformed abundance data [$\log(x + 1)$] using Bray-Curtis dissimilarity and the β -flexible linkage method.

Source: Author, 2022.

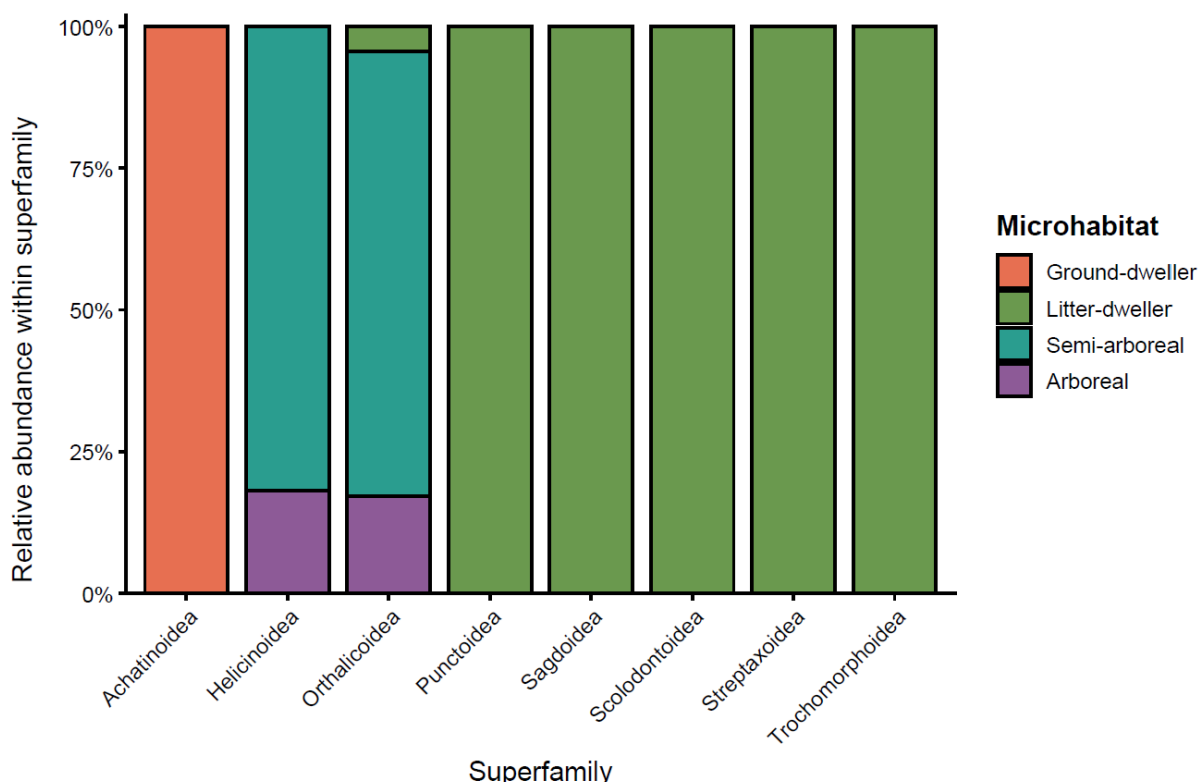
Figure 25 - Shell shape (H/D ratio) across microhabitat categories in the land snail assemblage of the Sooretama Biological Reserve.



Legend: Each point represents one recorded individual, with H/D ratio assigned from the species mean. The dashed horizontal line marks $H/D = 1.0$. Different letters above boxplots indicate significant differences between microhabitat categories (Kruskal-Wallis test followed by Dunn post-hoc test with Bonferroni correction, $p < 0.05$).

Source: Author, 2022.

Figure 26 - Relative abundance of individuals across microhabitats within each superfamily of land snails recorded in the Sooretama Biological Reserve.



Source: Author, 2022.

5.3. Discussion

Our results indicate that shell shape is a major correlate of microhabitat use in this Atlantic Forest land-snail assemblage, extending to Brazil the bimodal pattern documented worldwide (Cain 1977, 1978a, b, 1980, 1981; Goodfriend 1986; Emberton 1995). Hierarchical cluster analysis (Bray–Curtis, β -flexible, $k = 4$) resolved the assemblage into four groups corresponding to distinct microhabitat use patterns: a ground-dwelling group, a litter-dwelling group, a semi-arboreal group, and an arboreal group. Shell shape showed strong correspondence with group membership: groups associated with ground and arboreal microhabitats were composed predominantly of high-spined species (100% and 80–83%, respectively), while the litter-dwelling group was composed predominantly of low-spined species (80%). These associations are consistent with biomechanical arguments in the literature: high-spined shells confer a narrower profile and a higher centre of mass facilitating adhesion to vertical and inclined surfaces, while low-spined shells provide greater stability on horizontal substrates (Cain & Cowie 1978; Cameron 1978; Cook & Jaffar 1984; Heller 1987). The

formal physical basis for this pattern was provided by Okajima & Chiba (2009), whose moment-of-force model demonstrated that low-spired shells minimise gravitational torque on horizontal surfaces, and that shells with intermediate spire indices ($H/D \approx 1.4$) are the least stable on vertical substrates, generating a functional valley that separates the two morphological groups and predicts the bimodal distribution observed empirically across diverse faunas and regions. The strong correspondence between shell shape and microhabitat cluster membership documented here is consistent with these biomechanical predictions, and extends their empirical support to a diverse Neotropical assemblage. Beyond the biomechanical framework, these associations may be understood as the product of environmental filtering acting on shell morphology as a functional trait: communities assembled under similar substrate and microclimatic conditions tend to converge on predictable subsets of shell shapes from the available regional pool (Schamp *et al.* 2010; Wehner *et al.* 2021). This interpretation is consistent with the observation that land-snail assemblages in structurally complex habitats support broader morphological diversity than simplified or disturbed ones, as environmental heterogeneity expands the range of available niches (Gheoca *et al.* 2023; Čiliak *et al.* 2024).

An important caveat must be acknowledged regarding the interpretation of shell shape as a predictor of microhabitat use. In this assemblage, shell shape and body size are partially confounded: high-spired species tend to have larger shells overall, while low-spired species are predominantly small-bodied, a pattern consistent with observations in other geographically and ecologically distinct assemblages (Goodfriend 1986; Emberton 1995). Body size is itself an ecologically meaningful trait in land snails, independently associated with desiccation tolerance, locomotion efficiency, and calcium requirements, all of which vary across microhabitats (Calder 1984; Heller 1987). Smaller species tend to be more dependent on the buffered microclimatic conditions of the litter stratum, where high humidity and reduced thermal fluctuation compensate for their lower water-retention capacity, while larger species are better able to tolerate the exposure associated with vertical and open substrates (Heller 1987; Cook 1997). This means that the microhabitat associations documented here may reflect the combined and partially inseparable influence of shell geometry and body size on substrate use, rather than shell shape acting as an independent functional predictor. Our analyses did not statistically separate these two sources of variation, which limits the causal interpretation of the shell shape-microhabitat

relationship. Future work should treat shell size and shell shape as independent covariates in multivariate models of microhabitat use, an approach that has been applied productively in studies of morphological trait-environment associations in land snail communities (Astor *et al.* 2017).

Three categories of exception to the expected shell shape–microhabitat correspondence deserve attention, as they illuminate the limits of the bimodal framework. *Helicina variabilis* and *Helicina* sp. (Helicinidae) are both low-spired yet were recorded predominantly or exclusively in arboreal microhabitats. Helicinidae are operculate snails phylogenetically distant from the stylommatophoran families that dominate the assemblage, and arboreal habits are a well-documented ancestral characteristic of the family throughout the Neotropics, where species are typically found on tree trunks, branches, and leaves at various strata of humid forests (Richling 2004; Simone 2006; Vasconcelos 2015; Simone 2018). Their arboreal habits in this assemblage therefore likely reflect family-level ancestral traits rather than convergent ecological adaptation to vertical surfaces driven by shell geometry, consistent with the broader principle that phylogenetic constraints can generate systematic deviations from expected morphological–ecological associations (Hirano *et al.* 2015). This is precisely the type of non-independence that the phylogenetically stratified PERMANOVA was designed to address: by controlling for superfamily-level structure, the analysis ensures that the shell-shape–microhabitat signal is not driven by a single family's idiosyncratic ecology. Among litter-dwellers, *Lilloiconcha superba* and *Rhinus velutinohipidus* are classified as high spired but both have H/D ratios close to 1.0, placing them near the morphological boundary between the two groups. Their occurrence in leaf litter likely reflects the ecological flexibility associated with intermediate shell shape, and is consistent with Emberton's (1995) observation that species near the morphological boundary between high- and low-spired groups do not reliably predict substrate affiliation in the same way as strongly polarised forms.

Sixty percent of the species in this assemblage showed statistically significant associations with particular microhabitats (IndVal, $p < 0.05$; Table 2), indicating that non-random microhabitat use is a widespread pattern in this assemblage rather than a property restricted to a few dominant species. Leaf litter harboured the greatest number of indicator species ($n = 8$), all low spired, consistent with the well-documented affinity of small-bodied, flat-shelled gastropods for the litter stratum across diverse geographic contexts (Heller 1987; Emberton 1995). In the Atlantic Forest specifically,

the litter layer functions as the primary refuge for the bulk of the land-snail diversity, providing stable moisture regimes, organic food resources, and calcium inputs from decomposing plant material, which are critical for shell maintenance and reproduction in small-bodied species (Nunes & Santos 2012). The dominance of Scolodontidae, Streptaxidae, Euconulidae, and Trochomorpha in this stratum reflects the close ecological association between these predominantly micro-gastropod families and the structural and chemical properties of tropical forest leaf litter, a pattern documented across diverse Neotropical assemblages (Salvador *et al.* 2026). Ground was the second-richest microhabitat in indicator species ($n = 4$), all high-spined Achatinidae, reflecting the locomotory advantages of elongate shells on open horizontal surfaces. The two indicator species of the arboreal stratum were *Leiostracus perlucidus* and *Pseudoxychona pileiformis* in vegetation, and *Cochlorina cf. lateralis* and *Sanniostracus cf. obliquus* on tree trunks, all high spired. Similar patterns of strong species–habitat association structured by shell morphology and driven by environmental filtering have been reported in studies examining land-snail responses to habitat gradients in both tropical and temperate systems (Nandy *et al.* 2022; Pokou *et al.* 2026).

No significant correlation was detected between species abundance and standardised Levins' niche breadth (Spearman: $\rho = 0.251$, $p = 0.197$), and Prediction 1 was not supported by the data. This result differs from the positive abundance–breadth relationship documented across diverse taxa (Brown 1984; Schamp *et al.* 2010), but its interpretation requires care. The most immediate explanation is distributional: 29 of the 30 species recorded B' values at or near zero, producing a strongly right-skewed distribution that severely constrains the statistical power of any correlation test. Under these conditions, the absence of a significant result reflects the structure of the assemblage rather than a genuine biological absence of the abundance–breadth relationship. The near-universal microhabitat specialization observed here is consistent with theoretical predictions for communities organised by strong environmental filtering in structurally stable habitats: when a particular substrate is sufficiently abundant, predictable, and resource-rich, high local abundance and narrow microhabitat use are not mutually exclusive outcomes, as specialists can achieve high densities by optimising exploitation of a single stratum (Wilson 1975; Emberton 1995; Büchi & Vuilleumier 2014). *Leiostracus perlucidus* was the single clear exception, combining the highest abundance in the assemblage with broad use across

four of the five microhabitat categories. This combination of high abundance and broad microhabitat use is characteristic of ecologically plastic species in heterogeneous environments and has been reported in other land-snail assemblages where a dominant generalist coexists with a diverse guild of specialists (Schamp *et al.* 2010; Nandy *et al.* 2022). By contrast, several of the most abundant specialist species, including *Habroconus semenlini* ($n = 74$, exclusively in leaf litter) and *Tamayoa banghaasi* ($n = 39$, exclusively in leaf litter), demonstrate that dominance in abundance is fully compatible with strict microhabitat fidelity when the preferred stratum is structurally stable and spatially extensive, as is the leaf-litter layer in a well-preserved coastal plain forest (Nunes & Santos 2012).

The phylogenetically stratified PERMANOVA demonstrated that microhabitat accounted for 83.8% of the variation in species composition even after controlling for superfamily-level non-independence ($F = 32.345$, $R^2 = 0.838$, $p = 0.001$). This result indicates that the associations between shell morphology and microhabitat are not attributable to shared ancestry alone, but persist across independently derived lineages within the assemblage. Similar patterns of non-random habitat use and environmentally structured community assembly have been reported in other land-snail assemblages across contrasting geographic and ecological contexts, including urban areas of India (Nandy *et al.* 2022), tropical land-use gradients in West Africa (Pokou *et al.* 2026), and riparian forests in Europe (Gheoca *et al.* 2023), suggesting that environmental filtering may represent a broadly recurring structuring force in terrestrial gastropod communities regardless of regional species pool composition.

Two methodological limitations deserve explicit acknowledgment. First, the active search method applied along linear transects does not guarantee equal sampling effort across microhabitat types, as encounter frequency depends on observer efficiency in each substrate and on snail activity patterns. Arboreal microhabitats may be undersampled relative to ground-level habitats, potentially biasing richness and abundance estimates for tree trunk and tree leaves categories. Second, while the leaf-litter quadrat method was effective for micro-gastropods in the litter stratum, no equivalent intensive method was applied to arboreal substrates, meaning that small-bodied arboreal species are likely underrepresented in the dataset.

Taken together, our results demonstrate that shell shape is a significant correlate of microhabitat use in the land snail assemblage of the Sooretama Biological Reserve, with the associations between shell morphology and microhabitat persisting

across phylogenetically independent lineages. While no support was found for the predicted positive relationship between abundance and microhabitat breadth, the non-random associations between species and microhabitat categories, confirmed by indicator species analysis, cluster classification, and phylogenetically corrected multivariate analysis, reinforce the correspondence between shell shape and microhabitat across multiple independently derived lineages. These findings extend the bimodal shell-shape framework to the Brazilian Atlantic Forest and provide a quantitative baseline for comparative studies of land-snail assemblages across this threatened and understudied biome.

6. IS THE NIGHT A KID? ASSESSING THE SNAIL'S ACTIVITY PATTERN AMONG DIFFERENT PERIODS OF THE DAY IN AN ATLANTIC FOREST REMNANT

Esteves, R. A., Santos, S. B., & Rocha, C. F. D. (2025). Temporal activity patterns of land snails in the Atlantic Forest reveal substantial daytime activity and potential sampling bias. *Invertebrate Biology*, 144(4), 00031. <https://doi.org/10.71161/ivb.144.4.2025.00031>

The study of terrestrial snail communities relies on various sampling methods, typically involving replicate small units, such as plots or quadrats, arranged randomly or systematically within a given area (e.g., Emberton *et al.* 1999, Schilthuizen *et al.* 2002, Cameron & Pokryszko 2005, Fontaine *et al.* 2007). These standardized methods allow researchers to estimate species richness and abundance, with manual searches in microhabitats being a common approach. In tropical forests, a combination of quadrat sampling and standardized leaf-litter collection has proven to be effective in short-term surveys, particularly for micro-gastropods (<5 mm) (e.g., De Winter & Gittenberger, 1998; Clements *et al.*, 2008; Nunes & Santos, 2012).

Despite advances in optimizing spatial sampling protocols, comparatively little attention has been given to the temporal dimension of sampling, particularly the time of day when surveys are conducted. Terrestrial gastropods are generally assumed to be active when environmental humidity is high, engaging in behaviours such as locomotion, foraging, reproduction, or vertical movement (Duncan *et al.*, 2003). Consequently, many field surveys implicitly or explicitly assume that nocturnal sampling is sufficient to capture most active individuals. However, empirical studies evaluating daily activity patterns of land snails under natural field conditions remain scarce, especially in tropical regions. Understanding when land snails are active is therefore essential not only for improving survey efficiency but also for avoiding temporal biases in biodiversity assessments, particularly in poorly studied ecosystems such as the Brazilian Atlantic Forest. Activity patterns in terrestrial gastropods are influenced by a complex interaction of environmental factors, including temperature, light intensity, and moisture availability. Temperature can directly influence metabolic rates and locomotor performance, thereby constraining periods of surface activity (e.g., Cook, 2001; Barker, 2001). Light intensity has been associated with circadian

regulation and shelter-seeking behaviour in land snails, often reinforcing assumptions of nocturnal activity (e.g., Bailey, 1981; Prior, 1985). Moisture availability, in turn, plays a critical role in reducing desiccation risk and facilitating movement, particularly in humid forest environments (e.g., Nicolai *et al.*, 2010; Cameron, 2016). Traditionally, land snails have been characterized as predominantly nocturnal, a pattern commonly interpreted as an adaptive response to minimize desiccation risk (Sokolove *et al.*, 1977; Rayah *et al.*, 1984; Attia, 2004; Ademolu *et al.*, 2011; Schweizer *et al.*, 2019). Nevertheless, recent syntheses indicate that this view represents an oversimplification. While nocturnality is widespread, activity in terrestrial gastropods is often plastic, frequently extending into crepuscular and diurnal periods when environmental conditions are favorable, particularly in humid and shaded habitats (Salvador & Tomotani, 2024). In such contexts, activity observed outside the night period may reflect environmental masking rather than the absence of endogenous biological rhythms. Importantly, a distinction must be made between daily activity patterns observed in the field and circadian rhythms, which refer to endogenously generated cycles demonstrated under controlled conditions. Most field-based studies, including community-level assessments, document daily rhythms shaped by both endogenous processes and immediate environmental constraints. Thus, patterns of diurnal or crepuscular activity do not contradict the existence of circadian clocks but instead highlight the ecological flexibility of gastropod behaviour in response to local conditions (Salvador & Tomotani, 2024).

Given the high humidity, dense canopy cover, and pronounced microhabitat heterogeneity of the Atlantic Forest, it remains unclear whether land snail assemblages in this biome conform to the traditional assumption of strict nocturnality or exhibit broader temporal flexibility. Such uncertainty is particularly relevant for biodiversity inventories, as surveys restricted to a single period of the day may systematically underestimate species richness and abundance.

In this study, we investigated the daily activity patterns of terrestrial land snails in a remnant of the Brazilian Atlantic Forest, assessing activity during morning, afternoon, and nighttime periods. We tested the hypothesis that, despite the generally accepted nocturnal tendency of terrestrial gastropods, local assemblages in humid tropical forests may exhibit significant activity outside the nocturnal window. Specifically, we addressed the following questions: (1) What are the predominant

activity periods of each snail species? and (2) How are diurnal and nocturnal activity proportions distributed within the community as a whole?

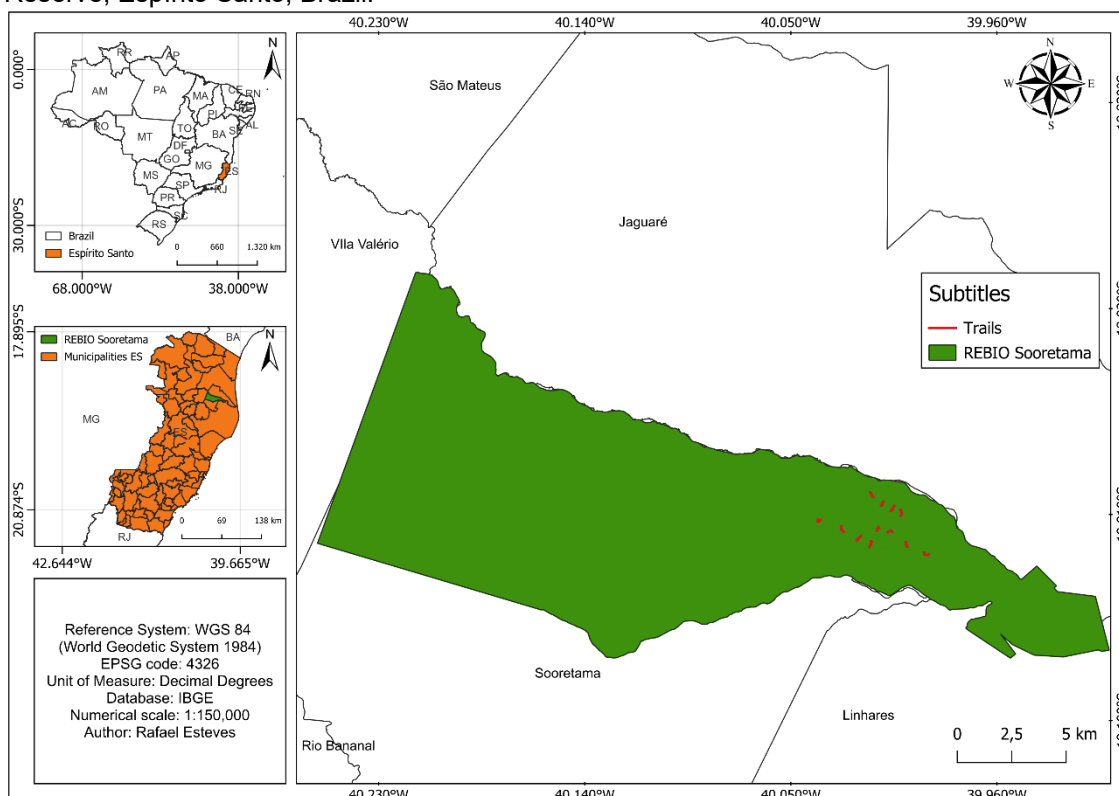
By clarifying these activity patterns, our study contributes to improving survey methodologies for land snails and provides insights into the ecological factors shaping their behavioral adaptations in neotropical forests.

6.1. Material and methods

6.1.1. Study area

We conducted the study in the Sooretama Biological Reserve (REBIO Sooretama, 19°0'50.87" S, 40°5'48.96" W, mean altitude: 46 m), the largest remnant of Atlantic Forest in the Espírito Santo State, south-eastern Brazil (Fig. 27). The reserve has approximately 28,000 ha and it is one of the remnants with higher importance for conservation of biological diversity of the Brazilian Atlantic Forest, and it is located in the Central Corridor of the Atlantic Forest Biome (MMA, 2000).

Figure 27 - Sampling plots (trails) following the RAPELD methodology at the Sooretama Biological Reserve, Espírito Santo, Brazil.



Source: Author, 2022.

The climate in the region is tropical hot and humid, with mean annual rainfall of 1,202 mm and mean annual temperature of 23.3 °C. The vegetation physiognomy of the reserve comprises the Coastal Plain Forest (locally called “Floresta de Tabuleiro”) whose canopy trees may reach up to 40 m high (Peixoto and Gentry, 1990).

According to the Management Plan of the Sooretama Biological Reserve, there are no significant records of established invasive alien species within the reserve’s boundaries (ICMBio, 2019), indicating a well-preserved ecosystem. However, the reserve is subject to anthropogenic pressures, particularly along its borders. Human activities in surrounding areas, such as agriculture and informal settlements, pose risks, including forest fires, which have affected the reserve in recent decades (e.g., a major fire in 1998 and another in the Lagoa do Macuco region in 2016).

The reserve exhibits considerable environmental heterogeneity, including dense ombrophilous forest, muçununga formations (low and open forests), wetlands, lakes, and marshes. Despite modest altitudinal variation (ranging from 5 to 197 m above sea level), this diversity of habitats contributes to the region’s high species richness.

6.1.2. Data sampling

Fieldwork was conducted in 2018, with surveys performed in January, June, September, and December, ensuring data collection during both dry (April–September) and rainy (October–March) seasons. To assess the daily activity patterns of land snails, we conducted surveys during three distinct periods: morning (05:00 – 10:00 a.m.); afternoon (12:00 p.m. – 05:00 p.m.); and night (06:00 p.m. – 11:00 p.m.).

Sampling was carried out in 12 plots (trails), distributed across the Coastal Plain Forest physiognomy, following the RAPELD methodology (Magnusson *et al.*, 2005). The RAPELD combines the Rapid Assessment Program (RAP) with Brazil’s Long-Term Ecological Research (PELD) framework, allowing standardized and replicable biodiversity surveys. Along the 250 m long trails, land snails were sampled using the active search method, with observers walking at a slow pace and visually inspecting macro-gastropods (>5 mm in diameter or height). Sampling was conducted by one observer (the same person throughout the entire study) (Oliveira *et al.*, 2021). In each plot, we performed time-constrained visual search surveys (40 minutes per plot) using two observers (the same individuals throughout the study period) to ensure

consistency. Observers carefully examined microhabitats, including leaf-litter, tree trunks, branches, bushes and fallen logs. We recorded only active individuals, defined as snails outside their shells and engaged in movement, foraging, mating, or climbing. This criterion was used to accurately assess activity patterns rather than mere presence. A total of 144 survey episodes were conducted, resulting in 96 hours of sampling across all plots.

6.1.3. Statistical analysis

For analytical purposes, sampling periods refer to the time of day when field surveys were conducted (morning, afternoon, and night), whereas activity trends describe inferred behavioral patterns based on the relative frequency of active individuals recorded during each sampling period.

Species were classified as matutinal, vespertine, or nocturnal when 40% or more of individuals were recorded during the morning, afternoon, or night sampling periods, respectively. Species with 40% or more of individuals recorded during both the morning and afternoon periods were classified as diurnal. For completeness, species recorded across non-adjacent sampling periods (e.g., morning and night) without reaching the classification threshold in a single period were defined as exhibiting mixed activity patterns. Species with fewer than four individuals were classified as insufficient data (IDI) to infer species activity.

To analyze the differences in species richness and abundance across sampling periods, we applied the Kruskal-Wallis test (Kruskal & Wallis, 1952) followed by Dunn's post-hoc test to identify significant pairwise differences. This analysis was performed using PAST v. 4.03 (Hammer *et al.*, 2001), with a significance threshold of $p < 0.05$.

We applied circular statistics to analyse the relationship between the frequency of gastropod species and the time of the day in which they were recorded in each plot. The mean vector length (r) was used as a measure of dispersion around the mean angle (μ), representing the degree of clustering of activity times. The values of r range from 0 to 1, where $r = 1$ indicates a perfectly concentrated distribution around a preferred time, while $r = 0$ suggests a uniform, random distribution. To assess whether species activity patterns were non-randomly oriented, we applied Rayleigh's uniformity test (Z). This test evaluates whether gastropod activity is significantly concentrated

around a particular time period or if it is uniformly distributed throughout the 24-hour cycle (Zar, 1999). We performed this analysis using Oriana v. 4.02 (Kovach, 2013).

6.2. Results

A total of 360 individual snails belonging to 23 species across nine families were recorded (Table 15). Species richness varied significantly among sampling periods, with the highest richness observed during the morning (median = 5; range = 2–9 species), followed by the night period (median = 2; range = 0–6 species). The lowest species richness was recorded during the afternoon (median = 2.5; range = 1–4 species).

The Kruskal-Wallis test revealed significant differences in species richness among sampling periods ($H = 7.732$; $p = 0.020$). Pairwise comparisons indicated significant differences between the morning and vespertine periods ($p = 0.016$), as well as between the morning and nocturnal periods ($p = 0.015$). However, no significant difference was found between the vespertine and nocturnal periods ($p = 0.976$) (Fig. 28).

When analysing species-specific activity patterns, most species exhibited a predominance of activity during the morning sampling period. Specifically, eight species (32.0%) were recorded exclusively during morning surveys, whereas no species were recorded exclusively during the afternoon sampling period, and two species (8.0%) were recorded exclusively during night surveys.

Based on the predefined activity trend criteria, fourteen species (55.8%) were classified as matutinal, four species (16.0%) as nocturnal, and two species (8.0%) as vespertine, despite not being recorded exclusively during the afternoon. Two species (8.0%) were classified as diurnal, as more than 40% of individuals were recorded during both the morning and afternoon sampling periods. Although some species were recorded across more than one sampling period, all taxa met the classification threshold for at least one activity pattern, and no species exhibited mixed activity patterns. A summary of activity pattern classifications for all species is provided in Table 15. The distribution of species among inferred activity patterns is summarized in Fig. 29, which provides a visual synthesis of the classification results presented also in Table 15.

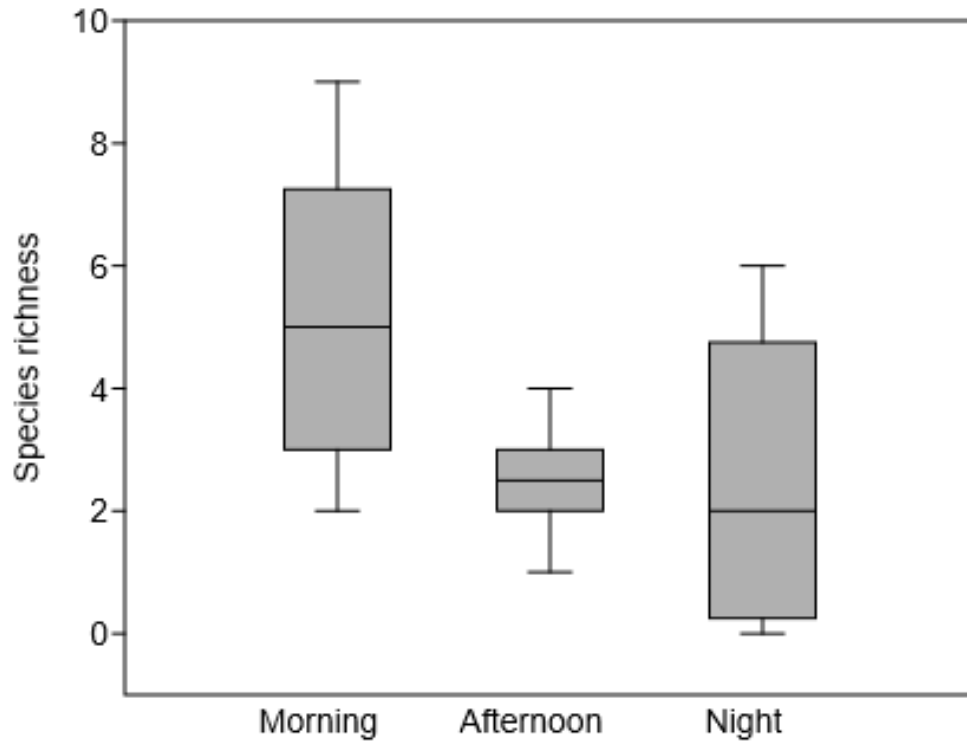
Table 15 - Species composition and activity pattern classification of terrestrial land snails recorded in the study area.

Species	Morning (%)	Afternoon (%)	Night (%)	Total	General activity trend
Achatinidae					
<i>Allopeas gracile</i> (Hutton, 1834)	3 (60.0)	2 (40.0)	0	5	Diurnal
<i>Allopeas micra</i> (d'Orbigny, 1835)	4 (30.8)	9 (69.2)	0	13	Vespertine
<i>Leptopeas bequaerti</i> (Pilsbry), 1926	13 (100)	0	0	13	Matutinal
<i>Leptinaria unilamellata concentrica</i> (Reeve, 1849)	11 (91.7)	1 (8.3)	0	12	Matutinal
<i>Leptinaria unilamellata</i> (d'Orbigny, 1838)	13 (81.2)	3 (18.8)	0	16	Matutinal
Bulimulidae					
<i>Cochlorina aurisleporis</i> (Bruguière, 1792)	1 (100)	0	0	1	IDI
<i>Cochlorina</i> cf. <i>lateralis</i> (Menke, 1828)	9 (75.0)	2 (16.6)	1 (8.3)	12	Matutinal
<i>Pseudoxychona pileiformis</i> (Moricand, 1836)	7 (20.0)	22 (62.9)	6 (17.1)	35	Vespertine
<i>Sanniostracus</i> cf. <i>obliquus</i> (Reeve, 1849)	7 (16.3)	0	36 (83.7)	43	Nocturnal
Helicinidae					
<i>Helicina variabilis</i> Wagner, 1910	14 (100)	0	0	14	Matutinal
<i>Helicina</i> sp.	2 (11.7)	0	15 (88.3)	17	Nocturnal
Cyclodontinidae					
<i>Bahiensis albofilosus</i> (Dorhn, 1853)	7 (100)	0	0	7	Matutinal
<i>Bahiensis bahiensis</i> (Moricand, 1833)	2 (20.0)	0	8 (80.0)	10	Nocturnal
<i>Burringtonia pantagruelina</i> (Moricand, 1833)	2 (100)	0	0	2	IDI
Orthalicidae					
<i>Orthalicus prototypus</i> Pilsbry, 1899	0	0	17 (100)	17	Nocturnal
Solaropsidae					
<i>Solaropsis planior</i> (Pilsbry, 1890)	3 (75.0)	0	1 (25.0)	4	Matutinal
<i>Solaropsis</i> cf. <i>rosarium</i> (Pfeiffer, 1850)	1 (100)	0	0	1	IDI
Scolodontidae					
<i>Tamayoa banghaasi</i> (Thiele, 1927)	28 (85.0)	5 (15.0)	0	33	Matutinal
Simpulopsidae					
<i>Leiostracus perlucidus</i> Spix, 1827	50 (75.8)	8 (12.1)	8 (12.1)	66	Matutinal
<i>Rhinus velutinohipidus</i> (Moricand, 1836)	5 (83.3)	0	1 (16.7)	6	Matutinal
<i>Simpulopsis</i> sp.	4 (66.7)	0	2 (33.3)	6	Matutinal
Streptaxidae					
<i>Rectartemon regius</i> (Löbbecke, 1881)	8 (42.1)	10 (52.7)	1 (5.2)	19	Diurnal
<i>Rectartemon piquetensis</i> (Pilsbry, 1930)	7 (87.5)	1 (12.5)	0	8	Matutinal
TOTAL				360	

Legend: Activity trends were assigned based on the relative frequency of records ($\geq 40\%$). IDI indicates Insufficient Data to Infer, referring to species with an insufficient number of records to reliably assign an activity pattern under the adopted criteria.

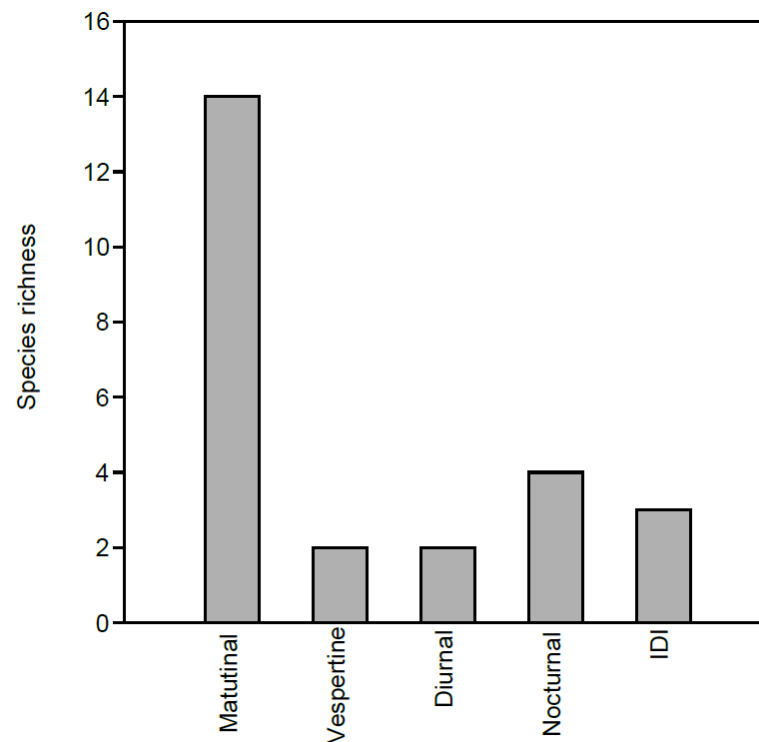
Source: Author, 2022.

Figure 28 - Variance in species richness among the different periods of the day (Kruskal-Wallis: $H = 7.732$; $p = 0.020$).



Source: Author, 2022.

Figure 29 - Distribution of species according to inferred activity patterns (matutinal, vespertine, nocturnal, diurnal, and IDI). IDI indicates species with insufficient data to infer an activity pattern.



Source: Author, 2022.

The circular statistical analysis revealed distinct temporal activity patterns among the snail species studied. The mean activity time (μ) varied widely among species, ranging from early morning to late night. The length of the mean vector (r), which measures the degree of clustering around the mean angle, also exhibited considerable variation, indicating differences in the consistency of activity periods across species (Table 16).

Table 16 - Circular statistical parameters for the activity patterns of snail species in the Sooretama Biological Reserve.

Species	Mean Vector (μ)	Length of Mean Vector (r)	Rayleigh Test (Z)	Rayleigh Test (p)
<i>Allopeas micra</i>	11:46 (176.623)	0.607	4.788	0.01
<i>Bahiensis albofilosus</i>	07:17 (109.271)	0.993	6.903	<0.0001
<i>Bahiensis bahiensis</i>	23:10 (347.61)	0.832	6.925	0.0002
<i>Cochlorina cf. lateralis</i>	06:03 (90.95)	0.604	4.374	0.0100
<i>Sanniostracus cf. obliquus</i>	22:00 (330.05)	0.681	19.456	<0.0001
<i>Helicina variabilis</i>	04:30 (67.5)	0.991	7.864	<0.0001
<i>Helicina</i> sp.	21:13 (318.482)	0.752	9.615	0.0000
<i>Allopeas gracile</i>	08:46 (131.727)	0.425	0.903	0.4270
<i>Leiostracus perlucidus</i>	07:00 (105.129)	0.494	16.094	<0.0001
<i>Leptopeas bequaerti</i>	05:55 (88.98)	0.966	12.142	<0.0001
<i>Leptinaria unilamellata</i>	09:22 (140.605)	0.701	7.872	0.0001
<i>L. unilamellata concentrica</i>	07:31 (112.904)	0.92	10.151	<0.0001
<i>Orthalicus prototypus</i>	21:34 (323.577)	0.992	6.883	<0.0001
<i>Pseudoxychona pileiformis</i>	14:46 (221.686)	0.613	13.132	<0.0001
<i>Rectartemon regius</i>	10:41 (160.485)	0.601	5.778	0.0020
<i>Rhinus velutinohispidus</i>	04:35 (68.825)	0.487	1.423	0.2500
<i>Simpulopsis</i> sp.	09:27 (141.896)	0.941	5.307	0.0010
<i>Solaropsis planior</i>	06:00 (90)	0.555	1.234	0.3120
<i>Rectartemon piquetensis</i>	07:47 (116.847)	0.893	6.374	0.0003
<i>Tamayoa banghaasi</i>	06:39 (99.998)	0.798	17.197	<0.0001

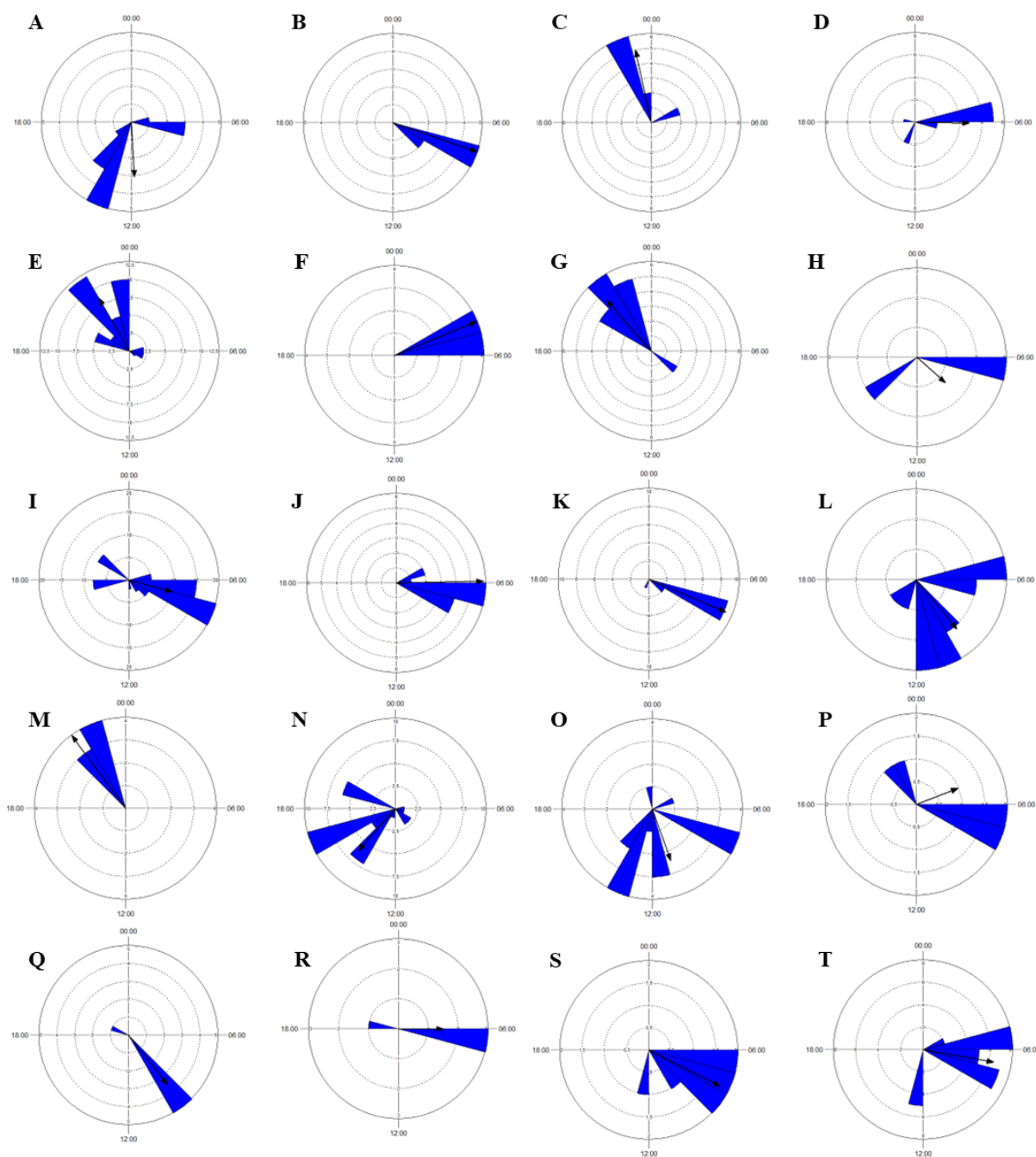
Source: Author, 2022.

Species with higher r -values (closer to 1) displayed strong temporal clustering, suggesting a well-defined period of activity. For instance, *Bahiensis albofilosus* ($r = 0.993$, $\mu = 07:17$ h) and *Helicina variabilis* ($r = 0.991$, $\mu = 04:30$ h) were highly

concentrated around specific morning periods. In contrast, species such as *Allopeas gracile* ($r = 0.425$, $\mu = 08:46$ h) and *Rhinus velutinohipidus* ($r = 0.487$, $\mu = 04:35$ h) exhibited lower clustering, indicating a broader distribution of activity times.

The Rayleigh uniformity test (Z , p -value) confirmed that most species displayed non-random temporal activity, with significant clustering around their respective mean activity periods. Overall, the results indicate that most snail species have well-defined activity peaks, predominantly in the morning and night, with a few species exhibiting broader or more dispersed activity patterns (Fig. 30).

Figure 30 - Daily activity patterns of land snail species in the Sooretama Biological Reserve, Atlantic Forest.



Legend: Each polar plot represents the temporal distribution of activity for a different species (A–V), with time displayed in a 24-hour circular format. A: *Allopeas micra*; B: *Bahiensis albofilosus*; C: *Bahiensis bahiensis*; D: *Cochlorina cf. lateralis*; E: *Sanniostracus cf. obliquus*; F: *Helicina variabilis*; G: *Helicina* sp.; H: *Allopeas gracile*; I: *Leiostracus perlucidus*; J: *Leptopeas bequaerti*; K: *Leptinaria unilamellata concentrica*; L: *Leptinaria unilamellata*; M: *Orthalicus prototypus*; N: *Pseudoxychona pileiformis*; O: *Rectartemon regius*; P: *Rhinus velutinohipsidus*; Q: *Simpulopsis* sp.; R: *Solaropsis planior*; S: *Rectartemon piquetensis*; T: *Tamayoa banghaasi*.
Source: Author, 2022.

6.3. Discussion

Our study assessed how different periods of the day influence the activity of land snails in an Atlantic Forest remnant, revealing that most individuals were recorded during the morning period. The initial hypothesis of this study proposed that land snails in the Atlantic Forest would exhibit a predominantly nocturnal activity pattern, following global trends observed in terrestrial gastropods (e.g., Sokolove *et al.*, 1977; Rayah *et al.*, 1984; Attia, 2004; Ademolu *et al.*, 2011; Schweizer *et al.*, 2019). This assumption was based on the physiological characteristics of land snails, which are highly susceptible to dehydration and are generally expected to restrict their activity to periods of higher environmental humidity, such as nighttime.

Our results partially reject the hypothesis that land snails in the studied area are predominantly nocturnal, demonstrating that the majority of species were more active in the morning than at night. Most species exhibited matutinal activity (55.8%), followed by nocturnal (16.0%), vespertine (8.0%), and diurnal (8.0%) patterns. This finding suggests that, while nocturnality is common among terrestrial gastropods, it is not a universal rule, particularly in the Atlantic Forest. The widely accepted notion that nocturnal activity in gastropods serves to minimize desiccation risk (Prior, 1985; Luchtel & Deyrup-Olsen, 2001) does not fully explain the patterns observed in this study. Instead, the high relative humidity and dense canopy of the Atlantic Forest likely provide favourable conditions for morning activity, reducing the need for strict nocturnality in many species.

When analysing the specific patterns of each species, we observed that predominantly arboreal species (*Sanniostracus* cf. *obliquus*, *Helicinas* sp., *Bahiensis bahiensis*, and *Orthalicus prototypus*) showed higher activity at night. This pattern suggests that these snails avoid sun exposure during the day, possibly seeking humid microhabitats in tree crevices and leaf axils, as previously documented for arboreal gastropods in other studies (e.g., Tattersfield *et al.*, 1998; Wronski *et al.*, 2015; Umuntunundi *et al.*, 2016).

On the other hand, terrestrial snails primarily found in leaf-litter, belonging to families such as *Achatinidae*, *Bulimulidae*, *Odontostomidae*, *Scolodontidae*, and *Streptaxidae*, exhibited more concentrated activity in the morning. The leaf-litter provides a protected microhabitat that reduces exposure to direct sunlight and desiccation, allowing these snails to become active in the early morning hours when

environmental humidity is still high. This result aligns with previous studies in which ground-dwelling species were recorded during daytime inventories in the Atlantic Forest and other tropical forests (e.g., Santos & Monteiro, 2001; Nunes & Santos, 2012; Lima *et al.*, 2015; Salvador *et al.*, 2018; Wenderbourg & Hausdorf, 2019; Nurhayati *et al.*, 2024).

Despite the increasing number of ecological studies on terrestrial gastropods worldwide, there are no previous studies evaluating the influence of different periods of the day on the activity of land snail communities in the Brazilian Atlantic Forest. In Brazil, few studies on terrestrial gastropods, whether inventories or ecological assessments, explicitly report the time of day when fieldwork was conducted. However, a noticeable trend indicates that most Brazilian field surveys occur during the daytime (e.g., Almeida, 2013; Miranda & Fontenelle, 2015; Salvador *et al.*, 2018; Rangel *et al.*, 2021). The lack of standardized sampling protocols regarding temporal activity limits our understanding of the natural circadian patterns of these communities. This gap in knowledge underscores the importance of incorporating multi-period sampling strategies to improve biodiversity assessments and avoid potential biases in species richness and activity estimates.

Our data also suggest that some species exhibit flexible daily activity patterns, with individuals recorded during both morning and night periods. This behaviour indicates that local environmental factors, such as humidity and temperature, may modulate the activity of land snails, allowing them to utilize different periods of the day for essential biological functions such as foraging and reproduction. This temporal plasticity has been observed in other land snail populations and may represent an adaptive strategy to maximize resource exploitation while minimizing desiccation risks (Schilthuizen *et al.*, 2002; Cameron & Pokryszko, 2005; Fontaine *et al.*, 2007).

Although environmental variables were not analyzed explicitly in the present study, they were systematically measured across the same sampling plots and period and have been analyzed in detail elsewhere using the same dataset. In a complementary study conducted in the Sooretama Biological Reserve, relative air humidity, soil humidity, and soil temperature were shown to significantly influence land snail abundance and species composition at fine spatial scales (Esteves *et al.*, 2025). These results reinforce that variation in environmental conditions, particularly moisture availability, likely plays an important role in modulating land snail activity patterns, including activity detected outside traditionally assumed nocturnal periods.

Additionally, variation in the mean vector length (r) in the circular statistical analyses reinforces that while some species exhibit highly clustered activity around specific time periods, others display broader temporal distributions. This variation suggests that factors such as feeding strategy, physiology, and microhabitat use significantly influence the activity patterns of different land snail species.

However, it is important to interpret these circular metrics with caution, as incomplete temporal coverage can affect estimates of activity concentration and phase. The absence of continuous sampling across the full 24-hour cycle, particularly during late-night hours, may bias circular statistical outputs by artificially increasing or decreasing apparent clustering (Willig & Presley, 2024). Accordingly, the circular analyses presented here are interpreted in relation to the sampled periods only and are not intended to infer complete diel activity cycles.

The results obtained have important implications for planning land snail surveys and monitoring programs in the Atlantic Forest. The fact that most individuals were recorded during the morning suggests that surveys conducted exclusively at night may underestimate species richness and abundance, compromising the representativeness of biodiversity assessments. Therefore, we recommend that future studies adopt sampling designs that encompass different periods of the day, ensuring a more comprehensive understanding of land snail diversity and ecology.

Furthermore, the high proportion of species recorded in the morning may indicate that local environmental conditions, such as the high humidity of Atlantic Forest, promote greater flexibility in snail activity patterns. This information is relevant for conservation strategies, as it suggests that alterations in the forest microclimate due to anthropogenic activities, such as deforestation and habitat fragmentation, may directly impact the behavioural patterns and survival of land snail species.

Our study revealed that the land snail community in the Sooretama Biological Reserve exhibits a predominantly morning activity pattern, challenging the assumption that terrestrial gastropods are strictly nocturnal. The results highlight the importance of microhabitat characteristics in shaping activity cycles, with arboreal species showing a preference for nighttime activity, while ground-dwelling species are more active in the morning. This variation in activity patterns reinforces the need for studies that consider multiple sampling periods to achieve a more accurate assessment of land snail biodiversity and ecology in the Atlantic Forest.

7. SWEET PAPAYA! ECOLOGICAL ASPECTS OF GASTROPODS ACTING AS PEST OF PAPAYA FRUIT COPS (*Carica papaya* L.) IN SOORETAMA, ESPIRITO SANTO, NORTHEASTERN BRAZIL

Esteves, R. A., Gomes, S. R., Santos, S. B., & Rocha, C. F. D. (2026). Ecological assessment of gastropods as pests in papaya (Caricaceae: *Carica papaya* L.) plantations in Brazil. *International Journal of Pest Management*, <https://doi.org/10.1080/09670874.2026.2712946>

Terrestrial gastropods, including snails and slugs, are important agricultural pests worldwide, capable of attacking plants at all growth stages (Cowie & Robinson 2003; Ismail *et al.* 2011). The number of pest gastropod species has increased in recent decades due to the expansion of agricultural frontiers, introduction of new crops, intensification of farming practices, and accidental introduction of invasive species that readily adapt to modified environments (Di Stefano 1998; Robinson 1999; Barker 2002; Gomes *et al.* 2013; Ramos *et al.* 2021).

These gastropods have been introduced across multiple continents primarily via agricultural trade, facilitated by globalization (Cowie & Robinson 2003; Robinson 2009). In Brazil, several species have been reported as pests in diverse crops such as soybean, beans, tobacco, coffee, citrus, grapes, and home gardens (Bruschi-Figueró & Veitenheimer-Mendes 2002; Ohlweiler *et al.* 2010; Baronio *et al.* 2014; Landal *et al.* 2019; Ramos *et al.* 2021).

In addition to economic losses, these mollusks may pose public health risks by serving as intermediate hosts of parasitic nematodes, such as *Angiostrongylus costaricensis* (Moreira and Céspedes 1971) and *Angiostrongylus cantonensis* (Chen 1935), responsible for abdominal angiostrongyliasis and eosinophilic meningitis, respectively (Bonneti & Graeff-Teixeira 1998; Ohlweiler *et al.* 2010; Valente *et al.* 2020; Thiengo *et al.* 2022). Human infection may occur through ingestion of raw gastropods or unwashed vegetables contaminated with mucus containing third-stage larvae (Rollins *et al.* 2023). In infested agricultural areas, especially those producing raw-consumed crops, this risk may be exacerbated (Rodriguez *et al.* 2018).

Papaya (*Carica papaya* L.) is among the top seven fruits in Brazil's export portfolio (INCAPER 2022). The state of Espírito Santo remains the country's leading producer and exporter of this fruit, with exports reaching 37 countries in 2023, primarily

Portugal, the United Kingdom, and the United States. The success of Brazilian papaya in international markets is attributed to its compliance with stringent quality and phytosanitary standards, which are increasingly demanded by global consumers.

In 2022, Espírito Santo produced approximately 426,000 tons of papaya, cultivated over an estimated area of 6,874 hectares (Espírito Santo 2023). The state's productivity, averaging 50 tons per hectare per year, surpasses the national average. Although papaya is cultivated across most Brazilian states, the main production hubs are concentrated in the Southeast and Northeast regions, with Bahia and Espírito Santo accounting for about 70% of the national production area and output.

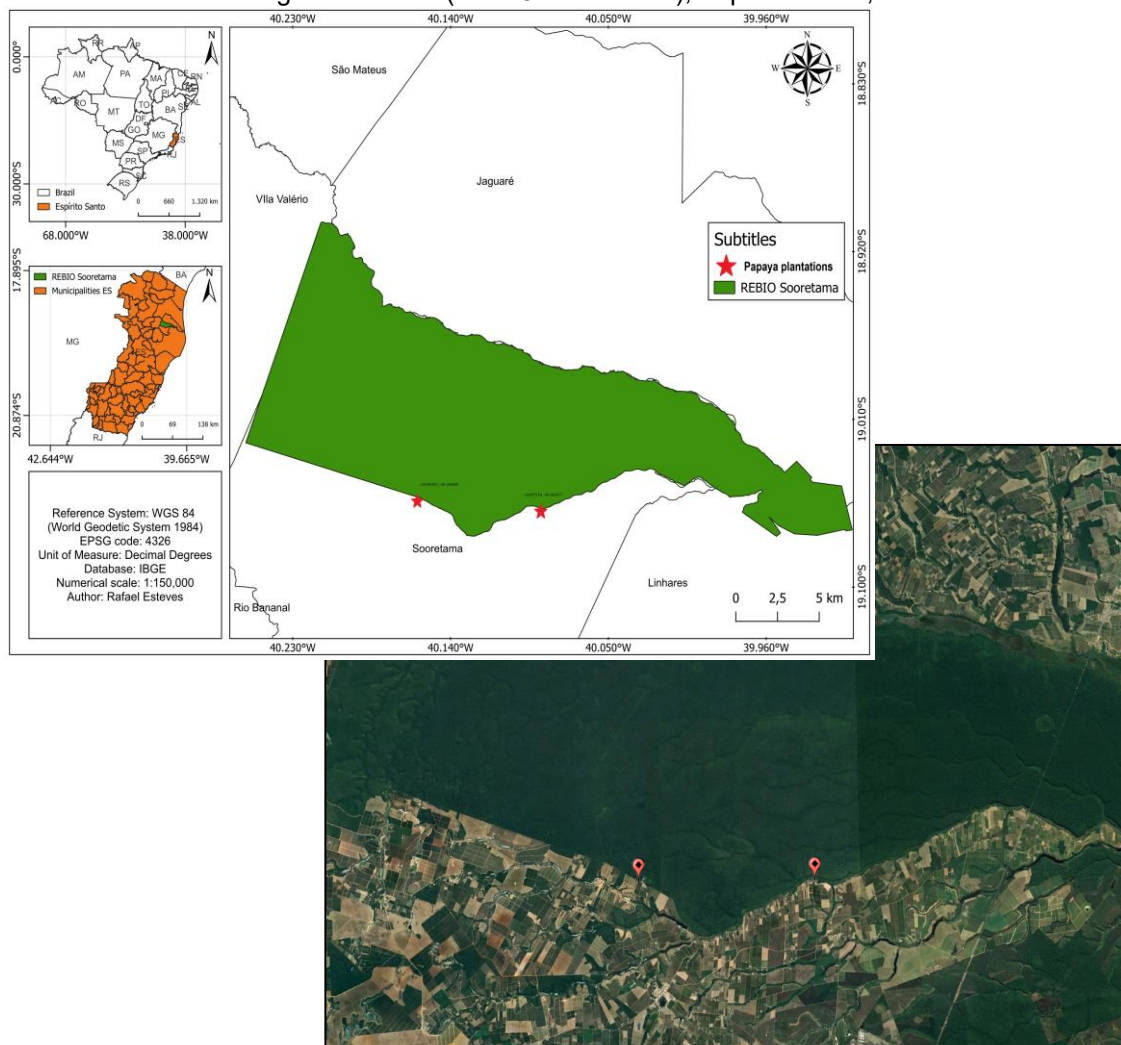
Despite the fruit's economic importance, ecological knowledge of gastropods as pests in papaya crops remains limited, especially in comparison to better-studied taxa such as insects and mites. Understanding the ecological dynamics of these pests is essential for designing effective monitoring and management strategies. Therefore, in this study, we conducted an ecological assessment of gastropod species acting as pests in papaya plantations in Sooretama, Espírito Santo, southeastern Brazil. Specifically, we aimed to: 1. Identify the gastropod species present in papaya plantations; 2. Evaluate whether their abundance differs between day and night, and between dry and rainy seasons; 3. Determine the diel activity patterns of each species; and 4. Investigate the occurrence of parasitic nematodes of public health relevance in the sampled individuals

7.1. Material and methods

7.1.1. Study area

We conducted the study in two papaya crops in the Sooretama municipality, southeastern Brazil (-19.056587, -40.148880 and -19.057154, -40.092677), of approximately three hectares each. The papaya crops are situated in an area bordered by the Sooretama Biological Reserve (REBIO Sooretama), the largest remnant of Atlantic Forest in the State of Espírito Santo (Figure 31).

Figure 31 - Study areas showing the location of two papaya (*Carica papaya* L.) plantations in proximity to the Sooretama Biological Reserve (REBIO Sooretama), Espírito Santo, Brazil.



Source: Author, 2022.

The study area is characterized by a tropical hot and humid climate (Köppen-Geiger classification: Aw), with a distinct rainy season from October to March and a dry season from April to September. The average annual temperature is approximately 23.3 °C, and the mean annual precipitation is about 1,202 mm. The region exhibits marked seasonality in rainfall, with the highest precipitation typically occurring in November and the lowest in June. This climatic pattern significantly influences the activity and abundance of terrestrial gastropods in agricultural settings. (Kierulff *et al.* 2014).

7.1.2. Data sampling

Fieldwork was conducted in 2018, with sampling events carried out in January, June, September, and December. These months were selected to represent both the dry season (April to September) and the rainy season (October to March), thereby encompassing the main climatic variation of the region.

In each of the two papaya plantations, we established ten 1 m² plots, randomly distributed with a minimum distance of 100 meters between them, totaling 20 plots (20 m² of sampled area). Time-constrained visual search surveys were conducted by two trained observers, each performing a 10-minute active search per plot. During these searches, observers recorded all active individuals - defined as gastropods exhibiting visible movement with the body extended outside the shell, including crawling, feeding, foraging, mating, or climbing.

Sampling was performed twice within each 24-hour cycle to estimate diel activity patterns: once during the daytime (05:00 - 16:00) and once at night (18:00 - 01:00). Active individuals were recorded on the plantation floor, on papaya tree stems, and on both mature and immature fruits.

7.1.3. Environmental variables

A set of five environmental variables was measured for each plot: (1) Air temperature (°C), using the Incoterm Digital Hygrometer ($0 - 50 \pm 0.1$ °C); (2) Soil temperature (°C), using the Instrutemp Digital Thermometer ($-50 - 300 \pm 0.1$ °C); (3) Relative air humidity (%), using the Incoterm Digital Hygrometer ($15 - 99 \pm 1$ %); (4) Soil humidity (%), using the PH-1000 soil pH and humidity meter ($10 - 80 \pm 1$ %), with the sensor inserted in the ground; (5) We obtained data on monthly accumulated rainfall (i.e., the total precipitation recorded each month) from the Weather Station of the Vale Natural Reserve, located near the study sites. This station is managed by Vale S.A. and provides continuous climatic monitoring. The mean distance between our sampling plots and the meteorological station was approximately 32 km, making it representative of the climatic conditions at the study sites.

The study sites are located near two important remnants of the Atlantic Forest in southeastern Brazil: The Vale Natural Reserve (RNV) and the Sooretama Biological Reserve (REBIO Sooretama). These protected areas are contiguous and together form one of the largest blocks of preserved lowland Atlantic Forest in the state of Espírito Santo. Although managed by different institutions, RNV by Vale S.A. (a private

company) and REBIO Sooretama by the Chico Mendes Institute for Biodiversity Conservation (ICMBio, a federal agency), the two reserves share ecological continuity and similar climatic conditions.

7.1.4. Data analysis

Based on the number of individuals of each gastropod species recorded per plot, we estimated species-specific abundance and density (individuals/m²). To assess whether total gastropod abundance varied between diel periods (day vs. night) and between seasons (dry vs. rainy), we applied the non-parametric Kruskal–Wallis test (Kruskal & Wallis 1952), using PAST software version 4.03 (Hammer *et al.* 2001).

To evaluate diel activity patterns, we used circular statistics, which are appropriate for temporal data due to the cyclical nature of time. The mean vector length (r) indicates the concentration of activity times around the mean angle (μ), and is used as a measure of the uniformity or dispersion of temporal activity. Values of r range from 0 (random distribution) to 1 (strong directional concentration). The statistical significance of r values was tested using Rayleigh's uniformity test (Z), which determines whether the observed activity patterns deviate significantly from a uniform distribution (Zar 1999). These analyses were performed using Oriana software version 4.02 (Kovach 2013).

Specimens were identified through conchological and morphological analysis, based on comparisons with reference materials from the Mollusc Collection of the Oswaldo Cruz Institute (CMIOC) and published taxonomic literature (Thomé 1993; Simone 2006; Ohlweiler *et al.* 2010).

To investigate the potential role of pest gastropods as intermediate hosts of parasites of public health importance, parasitological analyses were conducted using the artificial digestion method (Graeff-Teixeira & Morera 1995). These analyses were carried out at the National Reference Laboratory for Schistosomiasis – Malacology (LRNEM), Oswaldo Cruz Institute (IOC), Brazil.

7.2. **Results**

We found three species acting as pests of papaya plantations in the Sooretama municipality: the invasive snails *Bradybaena similaris* (Férusac, 1822) and the giant

snail *Achatina fulica* Bowdich, 1822, and the slug *Sarasinula linguaeformis* (Semper, 1885) (Figure 1). We recorded a total of 515 live individuals (*B. similaris* = 228 (44.4%), *A. fulica* = 191 (37.0%) and *S. linguaeformis* = 96 (18.6%)), not considering the uncountable empty snail shells at the study sites. We found live gastropods in all of the 20 plots sampled.

During the sampling period, environmental conditions varied substantially between seasons (Table 17). In the dry season, mean atmospheric and soil temperatures were 24.3 °C and 20.5 °C, respectively, while relative air moisture and soil moisture averaged 70.3% and 39.9%. Rainfall was lower in the dry season (mean = 90.4 mm) compared to the rainy season (mean = 193.2 mm). In the rainy season, relative air moisture and soil moisture increased to 86.1% and 63.8%, respectively, indicating a clear seasonal gradient in moisture availability.

Table 17 - Seasonal variation in temperature, humidity, and precipitation during the study period in papaya plantations.

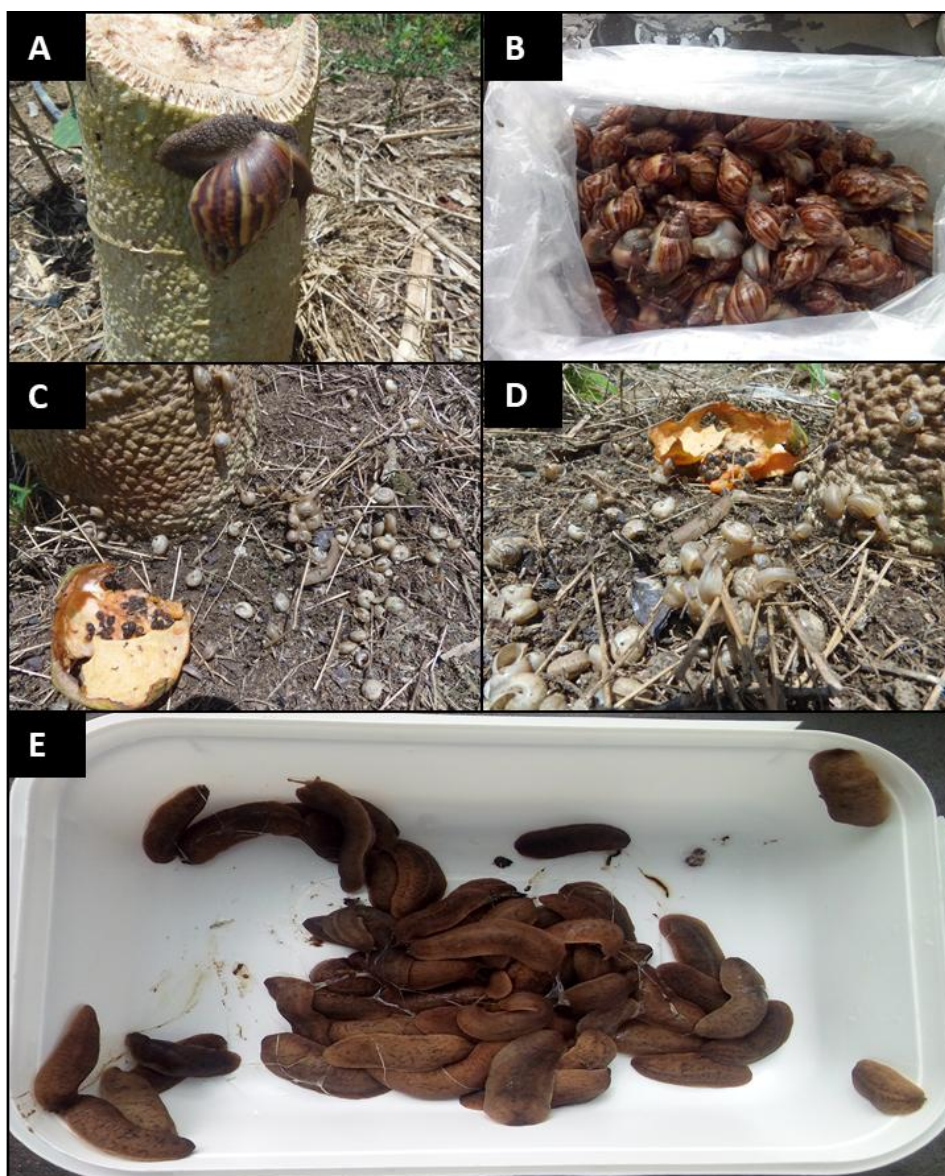
Environmental parameters	Unit	Dry season				Rainy season			
		Min	Mean	Max	SD	Min	Mean	Max	SD
Atmospheric temperature	°C	22,0	24,3	27,0	1,6	23,0	25,2	28,0	1,1
Soil temperature	°C	19,3	20,5	21,5	0,6	20,0	21,0	22,3	0,3
Relative air moisture	%	43,0	70,3	91,0	14,0	50,0	86,1	100	12,9
Soil moisture	%	17,0	39,9	53,0	10,2	28,0	63,8	100	22,1
Rainfall	mm	8,4	90,4	170,2	64,8	99,4	193,2	268,4	64,7

The highest abundance was recorded in the diurnal period (N = 280), whereas at night we recorded 235 individuals (Table 18). Only *B. similaris* was considered diurnal, with 81.6% of the individuals found during de the day. We found a significant difference in the abundance of live individuals between day and night (Kruskal-Wallis: $H = 17.13$; $p < 0.001$). On the other hand, *S. linguaeformis* was considered nocturnal, with 94.8% of the individuals found at night, showing significant difference between the periods of the day ($H = 22.15$; $p < 0.001$). Although our results considered *A. fulica* nocturnal (53.4%), we did not find a significant difference in the abundance of live individuals between day (N = 89; 46.6%) and night (N = 102; 53.4%) ($H = 0.23$; $p = 0.624$) (Table 18, Figure 33). Altogether, the overall abundance of snails and slugs did not vary among the periods of the day ($H = 0.77$; $p = 0.377$) (Table 17).

Terrestrial gastropods occurred in all months throughout the study, but the abundance of individuals varied consistently along the year with most of the individuals

active during the months of the rainy season (October to March) (N = 326; 63.3% of all individuals recorded) compared with that in the months of the dry season (April to September) (N = 189; 36.7%) (Table 19). We found significant differences in the overall abundance between the dry and rainy seasons ($H = 11.52$; $p < 0.001$) and in the specific abundance of *S. linguaeformis* ($H = 22.67$; $p < 0.001$). In contrast, we did not find significant differences in the specific abundance of *B. similis* ($H = 1.82$; $p = 0.173$) and *A. fulica* ($H = 2.50$; $p = 0.104$) (Table 19, Figure 34) between the seasons in a year.

Figure 32 - Pest-gastropods species of papaya crops in Sooretama, Espírito Santo, southeastern Brazil.



Legend: A-B: *Achatina fulica*; C-D: *Bradybaena similis* and *Sarassinula linguaeformis*; E: *Sarassinula linguaeformis*.

Source: Author, 2022.

Table 18 - Sampling frequencies (in absolute numbers and percentages in parentheses) of pest-gastropods of papaya crops during the periods of the day in the Sooretama, Espírito Santo, south-eastern Brazil, with the trend of inferred activity for each species.

Species	Day (%)	Night (%)	Total	General activity trend
Achatinidae				
<i>Achatina fulica</i> (Bowdich, 1822)	89 (46.6)	102 (53.4)	191	Nocturnal
Bradybaenidae				
<i>Bradybaena similis</i> (Férusac, 1822)	186 (81.6)	42 (18.4)	228	Diurnal
Veronicellidae				
<i>Sarasinula linguaeformis</i> (Semper, 1885)	5 (5.2)	91 (94.8)	96	Nocturnal

Source: Author, 2022.

Considering all seasons combined, the estimated overall terrestrial gastropod density in the papaya fruit crops was 12.9 ind/m² (Table 19). *Bradybaena similis* had the highest abundance and density in both dry and rainy seasons sampled (dry, N = 99, 5.0 ind/m²; rainy, N = 129, 6.4 ind/m²), followed by *A. fulica* (dry, N = 73, 3.7 ind/m²; rainy, N = 118, 5.9 ind/m²). The lower abundance (N = 17) and density (0.8 ind/m²) was recorded for *S. linguaeformis* in the dry season (Table 19).

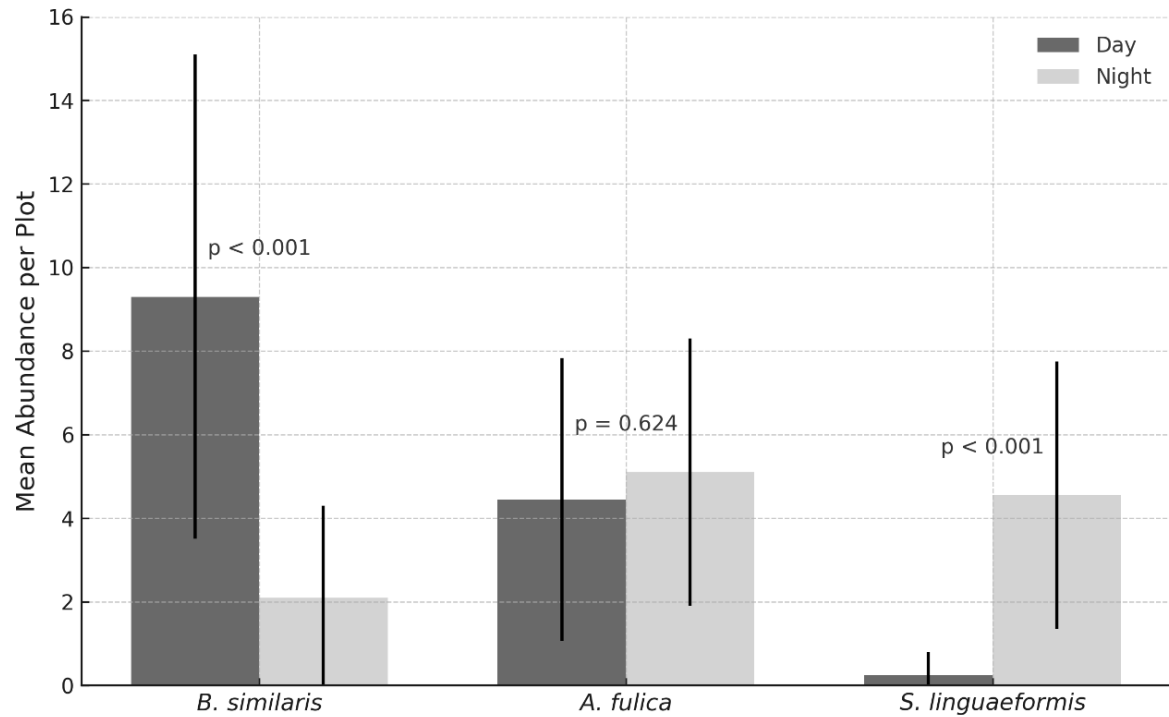
Table 19 - Abundance and density (ind./m²) of gastropods acting as pests of papaya crops at the plots in the crops during the dry and rainy seasons in Sooretama, Espírito Santo, south-eastern Brazil.

Species	Dry		Rainy		Overall	
	A	D	A	D	A	D
Achatinidae						
<i>Achatina fulica</i> (Bowdich, 1822)	73	3,7	118	5,9	191	4,8
Bradybaenidae						
<i>Bradybaena similis</i> (Férusac, 1822)	99	5,0	129	6,4	228	5,7
Veronicellidae						
<i>Sarasinula linguaeformis</i> (Semper, 1885)	17	0,8	79	4,9	96	2,4
Overall	189	9,5	326	17,2	515	12,9

Legend: A: Abundance; D: Density

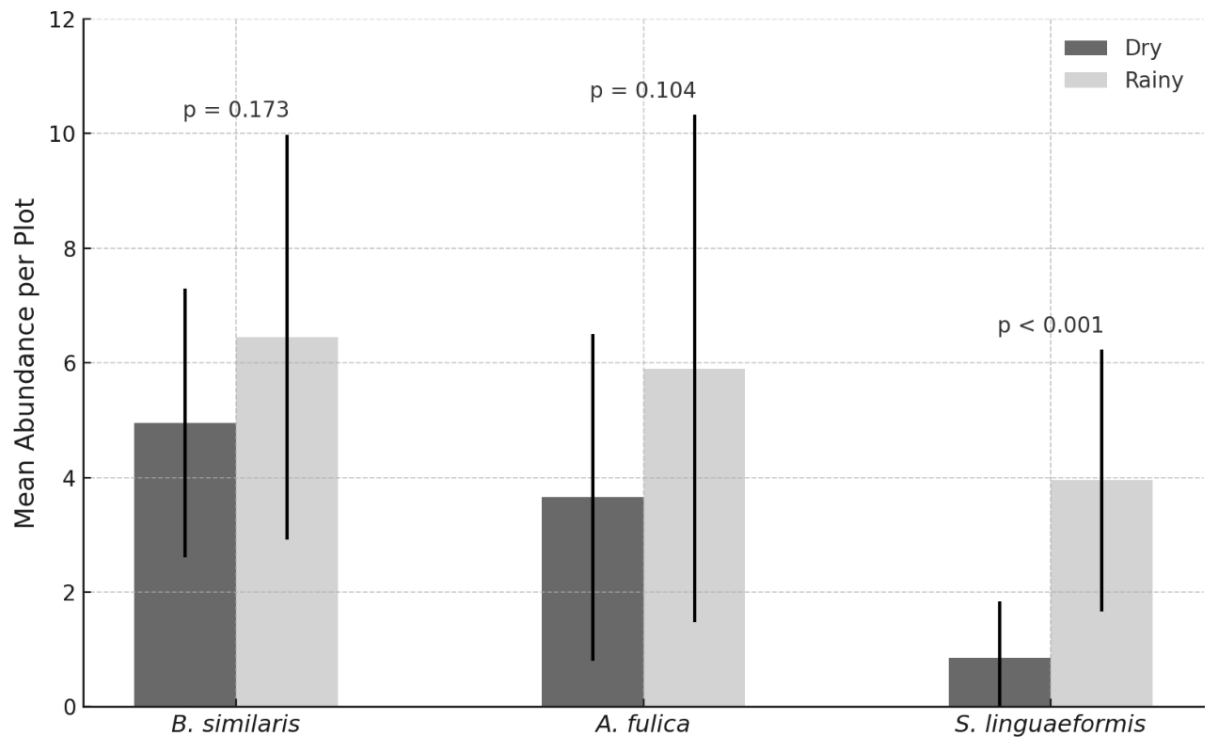
Source: Author, 2022.

Figure 33 - Differences between the periods of the day in the abundance of species acting as pest of papaya crops in Sooretama, southeastern Brazil.



Source: Author, 2022.

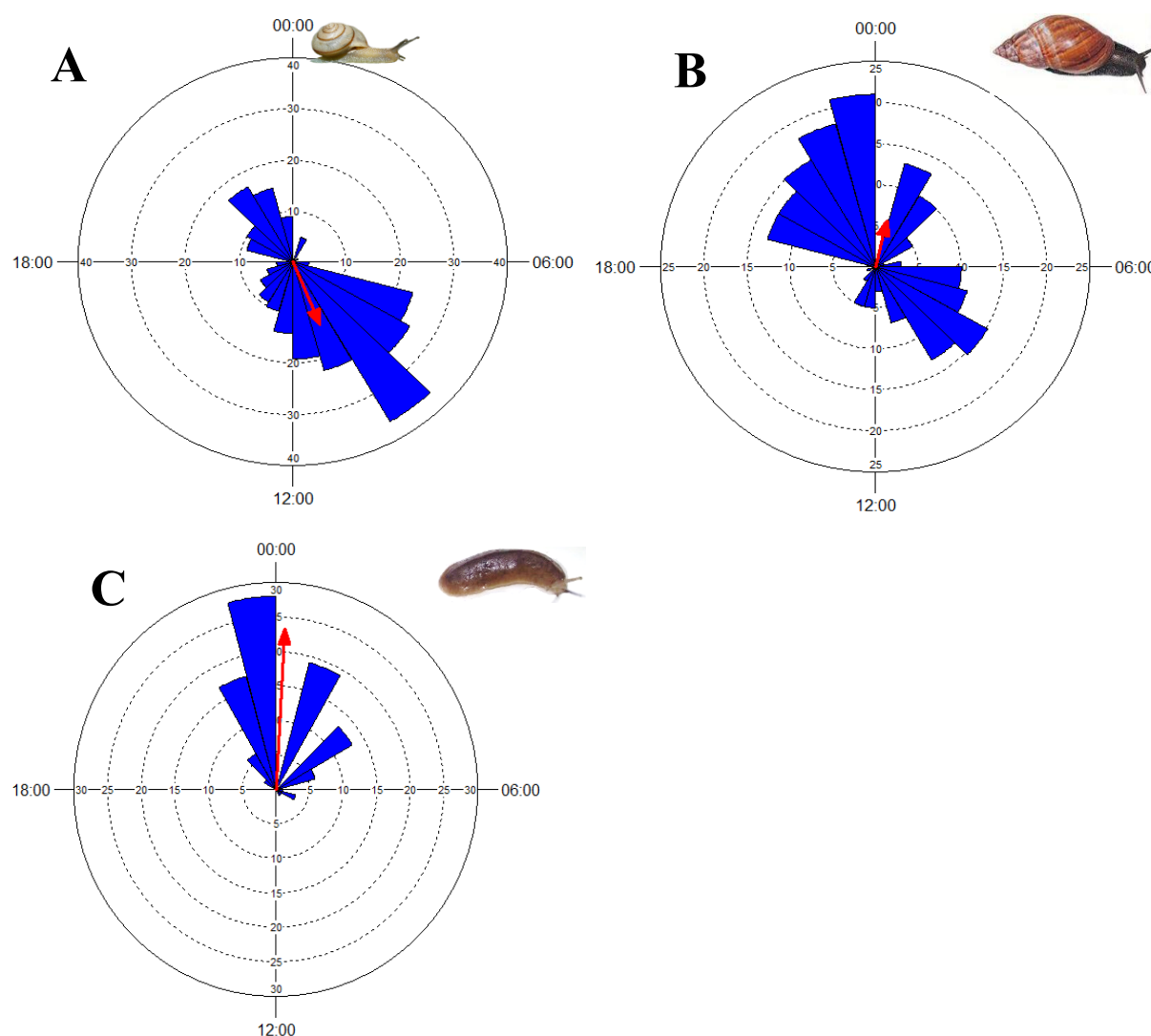
Figure 34 - Differences between the periods of the year in the abundance of species acting as pest of papaya crops in Sooretama, southeastern Brazil.



Source: Author, 2022.

Based on the site visit throughout the 24 hours cycle, most individuals of *B. similaris* were found active between 05 and 11 am, with a smaller peak of activity between 05 and 11 pm. Records of *B. similaris* had a mean vector (μ) of $157.5^\circ \pm 85.1^\circ$ (mean $\pm$ circular standard deviation), with a mean vector length (r) of 0.331, and the Rayleigh Z-test showed that the individuals' activity was not random, but that it followed a diurnal trend ($Z = 26.69$; $p < 0.001$; $N = 243$) (Figure 35-A).

Figure 35 - Daily activity pattern of the species acting as pest of papaya crops in Sooretama, Espírito Santo, southeastern Brazil.



Legend: A: *Bradybaena similaris* ($Z = 26.69$; $p < 0.001$; $\mu = 157.5^\circ \pm 85.1^\circ$; $r = 0.331$; $N = 243$); B: *Achatina fulica* ($Z = 9.96$; $p < 0.001$; $\mu = 13.1^\circ \pm 97.3^\circ$; $r = 0.232$; $N = 185$); C: *Sarasinula linguaeformis* ($Z = 58.84$; $p < 0.001$; $\mu = 3.03^\circ \pm 40.9^\circ$; $r = 0.775$; $N = 98$).

Source: Author, 2022.

Achatina fulica were recorded active during all periods of the day, showing a bimodal activity period, with two peaks of activity, one at night between 06 pm and 01

am, and another one early in the morning between 05 and 08 am. However, the records of *A. fulica* showed the nocturnal trend ($Z = 9.96$; $p < 0.001$; $\mu = 13.1^\circ \pm 97.3^\circ$; $r = 0.232$; $N = 185$) (Figure 35-B). On the other hand, the slug *S. linguaeformis* was the most restrictive species regarding the period of activity. The data showed individuals following a nocturnal trend, with peak of activity between 08 pm and 01 am ($Z = 58.84$; $p < 0.001$; $\mu = 3.03^\circ \pm 40.9^\circ$; $r = 0.775$; $N = 98$) (Figure 35-C).

7.3. Discussion

Our results showed well-established populations of the exotic snails *B. similaris* and *A. fulica*, and the native slug *S. linguaeformis* in the papaya fruit crops. The three species have been recorded as pests in different crops in Brazil (Bruschi-Figueró and Veitenheimer-Mendes 2002; Quintela 2009; Colley and Fisher 2009; Ohlweiler *et al.* 2010; Grisotti and Ávila-Pires 2011; Zawadneak *et al.* 2014; Landal *et al.* 2019). *Bradybaena similaris* is native to Asia and considered to be widely distributed in Europa, Africa, North, Central and South America, including almost the entire Brazilian territory and it has been recorded causing damage to ornamental plants, vegetables, grapes, strawberries, citrus and soybean, among other crops, being (Baker 2002; Ohlweiler *et al.* 2010; Brodier and Barker 2014; Landal *et al.* 2019, Maro *et al.* 2020). *Sarasinula linguaeformis* has been recorded causing damage to beans, soybeans and horticulture (Ohlweiler *et al.* 2010). This slug has a wide distribution in Brazil from Rio Grande do Sul to the Northeast, through Amazonas, and it is also reported to Ecuador (original description), Guyana Colombia, Peru, Paraguay and Argentina (Junqueira *et al.* 2004; Daglio *et al.* 2020). The African giant snail *Achatina fulica* is recorded as well-established pest in different parts of the world, such as Ecuador (Goldyn *et al.* 2016), United State of America (Constantinides and McHugh 2008; Capinera 2011; Nelson 2012), Samoa (Kant and Diarra 2016), India (Jayashankar *et al.* 2013; Kumar *et al.* 2018), Nepal (Budha and Naggs 2005) and Sri Lanka (Maheshini *et al.* 2019). In Brazil this species is reported to all 26 States plus the Federal District (Thiengo *et al.* 2022).

Our results indicated a clear definition on the daily activity for *B. similaris* and *S. linguaeformis* as predominantly diurnal and nocturnal habits respectively, although some individuals of both the species may remain active during the night or day. On the other hand, although the highest abundance *A. fulica* were found at night, there were

no statistically significant difference between daytime and nighttime on the species abundance, showing a high daily plasticity of the species.

Bradybaena similaris is often reported as a nocturnal species, which spends the day attached to the underside of leaves or under fallen branches and trunks, appearing active at night (Leahy 1984; Almeida and Bessa 2001). However, our data suggested a general trend habit for *B. similaris* as diurnal, once 82% of the individuals was found during the day period. Most individuals of *B. similaris* showed a peak activity in the early morning, between 05 – 10 am, with some individuals active on early evening, between 06 – 09 pm. Junqueira *et al.* (2003) studied three group of specimens of *B. similaris* (80, 40 days and newly hatched) in lab conditions and found a higher activity in the night period than in the daytime for all them. Activity patterns differed significantly according to age of mollusks and older specimens being the most active.

The scenario changes when we analyzed the *S. linguaeformis*. Our results in the field (natural environment), followed other studies that affirm the nocturnal habit of the species (e.g. Junqueira *et al.* 2004). *Sarasinula linguaeformis* showed a peak activity at night, between 7 pm – 01 am. Junqueira *et al.* (2004) also demonstrated the nocturnal behavior of *S. linguaeformis* in lab conditions. In this case, individuals were active in the period between 6 pm and 01 am, exhibiting a peak activity between 8 pm and 9 am. Slugs do not have a protective shell, having behaviors that helps to conserve moisture such as nocturnal activity and dwelling mostly in sheltered environments (Capinera *et al.* 2011). Unfortunately, studies on the activity period of terrestrial mollusks in the field are scarce and comparative data for *B. similaris* and *S. linguaeformis* were carried out under laboratory conditions. Even so, our results differed from other studies on the activity period of *B. similaris* (Santos 1982; Almeida and Bessa 2001), but our results corroborated with other authors on the activity period of *S. linguaeformis* (Junqueira *et al.* 2004).

Achatina fulica showed a bimodal distribution, with two peaks of activity. The first peak was at night, between 06 pm – 01 am, and the second in the early morning, between 05 – 09 am. Albuquerque *et al.* (2008) found similar results for the activity period of *A. fulica* also in a natural environment, in Lauro de Freitas municipality, State of Bahia, where the species started their activity at the end of the evening and stopped in mid-morning in urban areas. Almeida *et al.* (2016) indicates that young adults of *A. fulica* feed both at night and in the early morning hours, between 7 and 9 am, also indicating a long feeding period. In that study, the authors found *A. fulica* starting their

activity at the end of the evening and stopped in mid-morning. In general, most individuals of *A. fulica* have reported as nocturnal with some individuals active during daytime (Raut 1982; Raut and Baker 2002). The giant African snail is originally from East Africa, having spread to almost all continents (Africa, Americas, East and South Asia and Oceania), being considered an important agricultural and urban pest. In Brazil it is currently in 25 of the 26 States and in the Federal District (Zanol *et al.* 2010; Barbosa *et al.* 2020). It is a voracious herbivore species, having an extensive list of cultivated plants susceptible to *A. fulica* (Barker 2002). In the innumerable countries where *A. fulica* was introduced the species has been causing devastation in banana, papaya, peanut, coffee, citrus and other plantations, as well as the destruction of stored grains, gardens and home gardens (Teles *et al.* 1997).

All three pest-gastropod species studied here had higher abundance and density in the rainy season, which may result from a supposedly preference for humid climate and mild temperatures. This result is not surprising, since terrestrial gastropods are clearly dependent on humidity as they have permeable skin and move by laying down moist mucus trails, suffering high rates of dehydration (Prior 1985; Luchtel and Deyrup-Olsen 2001). Silva *et al.* (2020) demonstrated a correlation between the influence of rainfall and the frequency of *A. fulica* in a population occurrent in the Great Aracaju-SE Territory, Brazil. In other side, Almeida *et al.* (2013) investigated an urban population of *A. fulica* in a locality in Northeast of Rio de Janeiro State, where *A. fulica* suffered an oscillation in abundance during the year, being more abundant in June and February, that represent dry and wet seasons, respectively. *Achatina fulica* is considered one of the worst invasive species, preferring humid and warm conditions, but being adaptable to dry and cooler climates. Recently, Rangel *et al.* (2023) reported the highest abundances being recorded in the autumn and summer, and the presence of *A. cantonensis* in a peri-urban area in Rio de Janeiro city. These authors found snails infected with *A. cantonensis* in all analyzed plots and in the following seasons: autumn, spring and summer. Our findings are consistent with previous observations in similar tropical environments. In a study conducted in the same region, Esteves *et al.* (2025) demonstrated marked seasonal fluctuations in the activity of terrestrial gastropods, closely linked to changes in moisture availability. The increased abundance during the rainy season observed in the present study, particularly for *S. linguaeformis*, supports the idea that environmental humidity is a key driver of gastropod activity in papaya agroecosystems.

As these species were found as agricultural pests, the most important information we extract from our results, however, is the allocation of human and financial resources in the control and management of these species during planting. Snail and slugs' feces and slimy marks can also promote fungal growth, and make fruits and horticultural products unmarketable. Knowing the species seasonality variation allow efforts to combat pests to be managed in an assertive manner and aimed at solving the problem. Studies involving ecological aspects of species with devastating agricultural potential help to define more efficient loss control strategies and contribute to increase the economic productivity of plantations.

Although specimens infected with parasites of medical interest have not been found, all the three species were already found infected with natural hosts of helminths of importance to human and veterinary health (e.g., Araújo 1989; Laitano *et al.* 2001; Ramos-de-Souza *et al.* 2018; Ohlweiler *et al.* 2010; Barbosa *et al.* 2020). The presence of well-established populations of natural vectors of human disease is relevant in any agricultural activity, especially for diseases whose risk of human contamination consists of ingesting unwashed foods impregnated with the mucus of infected gastropods. Considering that papaya is a highly exported product, the presence of gastropods natural transmitter of diseases in the crops can negatively impact the commercial flow of production, affecting the trade with the final consumer.

We reported for the first the time *B. similaris*, *S. linguaeformis* and *A. fulica* as pest of papaya crops in Brazil. We concluded that in Sooretama *B. similaris* is a diurnal species, preferring to perform activity early in the morning, and *S. linguaeformis* and *A. fulica* are nocturnal species, with most individuals active during at night. For the three species the rainy season is the period of the year that most individuals are active. These results can be a starting point to support future action plans for the species, making predictions regarding the management and control of the pests in the papaya crops.

FINAL CONSIDERATIONS

- This thesis evaluated how environmental factors and ecological attributes affect the diversity, distribution, and functional and behavioral ecology of land snails in an Atlantic Forest area in Sooretama, Espírito Santo, Brazil. Taken together, the seven chapters show that the land snail fauna of the Sooretama Biological Reserve is shaped by a small set of microclimatic drivers, by the spatial configuration of the landscape, and by traits and behaviors that tie species to particular microhabitats and times of the day. These findings have direct consequences for how the group is sampled, conserved, and managed.
- The literature review (Chapter 1) showed that, despite more than a century of records, the knowledge base on leaf-litter mollusks from Brazilian preserved areas is still incipient and insufficient to reveal trends in the relationships between their populations, communities, and ecological dynamics. Only four of the reviewed studies (20%) addressed aspects of conservation, and the lack of methodological standardization limits comparisons among studies. Air and soil humidity, air and soil temperature, and leaf-litter depth recurred as factors affecting richness, abundance, and distribution, which supports the use of the standardized RAPELD sampling adopted in the following chapters and the inclusion of leaf-litter mollusks in biodiversity conservation plans.
- At the local scale, soil temperature, soil humidity, soil pH, and canopy closure were the main environmental predictors of land snail richness, abundance, and species composition (Chapter 2). Diverging from other studies, leaf-litter depth had no effect, suggesting that microclimatic conditions matter more for this community than the amount of litter. Seasonality reinforced this pattern (Chapter 3): richness and abundance were highest in the hotter and wetter rainy seasons, and the community showed a clear compositional change along a fine-scale moisture gradient even in an area without extremely dry sites. Forest-specialist species were more demanding in terms of moisture, whereas synanthropic achatinids, mostly introduced or presumably introduced, were the least demanding.

- The BR-101 highway crossing the reserve affected the main environmental predictors for land snails, with soil humidity, relative air humidity, canopy cover, and soil pH increasing, and luminosity and soil temperature decreasing, with distance from the road (Chapter 4). Species richness was strongly correlated with this distance, while abundance was only weakly correlated. Plots near the road were more homogeneous and held few species but well-established populations of non-native, generalist species, particularly Subulinidae, pointing to species turnover along the edge-interior gradient rather than simple species accumulation toward the forest interior.
- Species traits and behavior also organized the assemblage. Shell shape predicted microhabitat use (Chapter 5): 60% of species were significant indicators of a particular microhabitat, the assemblage resolved into four groups of microhabitat use closely matching shell shape, and microhabitat explained 83.8% of the variation in species composition after controlling for superfamily-level non-independence. Low-spined species were predominantly found in leaf litter, the microhabitat that differed from all others, while high-spined species occupied ground, vegetation, and arboreal microhabitats. Abundance, however, was not related to niche breadth. Activity patterns challenged a widespread assumption (Chapter 6): most species were matutinal (55.8%), only 16% were predominantly nocturnal, and leaf-litter dwellers were more active during the day, whereas arboreal species tended toward nocturnal activity. Consequently, surveys restricted to nighttime may underestimate richness and bias community-level inferences in humid forests.
- In papaya plantations bordering the reserve (Chapter 7), three species were recorded acting as pests: *Bradybaena similaris*, *Achatina fulica*, and *Sarasinula linguaeformis*. *B. similaris* was predominantly diurnal (81.6% of individuals active during the day) and *S. linguaeformis* predominantly nocturnal (94.8% at night), whereas *A. fulica* showed no significant difference between day and night. All three species were most active in the rainy season, which concentrated 63.3% of all individuals recorded. Because these species can also host helminths of medical and veterinary importance, and papaya is a highly

exported crop, this information is a starting point for management and control actions timed to species-specific activity and to seasonality.

- A common thread runs through the chapters: humidity and the microclimatic conditions that regulate it govern the occurrence, seasonal dynamics, microhabitat use, and daily activity of land snails, and the loss of canopy and the resulting drying near roads and agricultural edges favor generalist and non-native species at the expense of forest specialists. For conservation, this implies protecting canopy cover and humidity regimes, mitigating the effects of linear infrastructure on forest remnants, treating leaf litter as a key microhabitat, and standardizing sampling protocols that include daytime periods. The ongoing taxonomic inventory of the land snails of the Sooretama Biological Reserve will refine the species identifications used here and provide the baseline needed to extend these approaches to other Atlantic Forest remnants.

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