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Original Article

Seasonal variation and patterns in the land snail community along a fine-scale humidity gradient in an Atlantic Rainforest remnant, Southeastern Brazil

Variação sazonal e padrões na comunidade de gastrópodes terrestres ao longo de um gradiente de umidade em um remanescente de Mata Atlântica no Sudeste brasileiro

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Abstract

In this study, we provide the first data regarding seasonal variation and patterns along a fine-scale humidity gradient on the land snail community, including parameters such as richness and abundance, in the Sooretama Biological Reserve, Espírito Santo, Brazil. Our study was conducted from January 2017 to December 2018, covering all four seasons (summer, autumn, winter and spring). We used 24 plots of 250 m each, combined with subplots of 25 x 75 cm (to sample leaf-litter), following the RAPELD methodology. We collected 440 live specimens belonging to 35 species from 11 families. The snail species richness varied among seasons, with the highest mean values in summer and spring. The highest variation of richness occurred between summer and autumn, and the smallest variation occurred between spring and summer. Soil temperature, relative air moisture and soil moisture affected significantly the overall land snail abundance. The rainy season was hotter and wetter than the dry season and showed highest richness and abundance of species. Our results showed a clear compositional change along the moisture gradient, suggesting differences in species preference for moisture conditions even at a fine-scale.

Keywords: coastal plain forest, gastropoda, pulmonata, REBIO Sooretama, seasonality.

Resumo

No presente estudo nós fornecemos os primeiros dados sobre a variação sazonal e os padrões ao longo de um gradiente de umidade em uma comunidade gastrópodes terrestres, incluindo parâmetros como riqueza e abundância, na Reserva Biológica de Sooretama, Espírito Santo, Brasil. O estudo foi conduzido entre janeiro de 2017 e dezembro de 2018, abrangendo todas as quatro estações (verão, outono, inverno e primavera) de cada ano. Utilizamos 24 parcelas de 250 m cada, combinadas com subparcelas de 25 x 75 cm (para amostragem de serapilheira), seguindo a metodologia RAPELD. Ao todo foram coletados 440 espécimes vivos pertencentes a 35 espécies de 11 famílias. A riqueza de espécies na comunidade variou entre as estações, com os maiores valores médios no verão e primavera. A maior variação ocorreu entre o verão e o outono, e a menor entre a primavera e o verão. A temperatura do solo, a umidade relativa do ar e a umidade do solo afetaram significativamente a abundância geral das espécies. A estação chuvosa foi mais quente e úmida do que a estação seca e apresentou maior riqueza e abundância de espécies. Os resultados mostraram, ainda, uma clara mudança composicional ao longo do gradiente de umidade, sugerindo diferenças na preferência das espécies por condições de umidade, mesmo em uma escala fina.

Palavras-chave: floresta da planície costeira, gastropoda, pulmonata, REBIO Sooretama, sazonalidade.

1. Introduction

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). Regarding that the basic question of Ecology is to determine the causes of distribution and abundance of organisms (Krebs, 2001), considerable effort has been

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done to document the differences between these two aspects and understand why they occur (Pianka, 2000).

The composition and species richness of land snail communities is linked mainly to available calcium content (Dallinger et al., 2001; Juřičková et al., 2008) and humidity/moisture (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). However, in ecological studies on land snails, the humidity has rarely been directly measured (Hettenbergerová et al., 2013), but mostly only estimated (Getz and Uetz, 1994; Chiba, 2007), or the studied sites were classified into several moisture categories (Martin and Sommer, 2004). Some 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., Hylander et al., 2005; Juřičková et al., 2008; Horsák et al., 2010; Horsák et al., 2018). On the other hand, the biota of the tropical regions is less studied (Lewinsohn et al., 2005), despite often showing terrestrial gastropod communities with high values of richness and abundance (e.g., Emberton et al., 1996; Schilthuizen et al., 2003; Nunes and Santos, 2012; Wendebourg and Hausdorf, 2019).

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

2. Material and Methods

2.1. Study area

The study was conducted in the Sooretama Biological Reserve (mean coordinate: 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 1). The reserve has approximately 28,000 ha and is one of the areas with highest importance for the conservation of biological diversity of the Atlantic

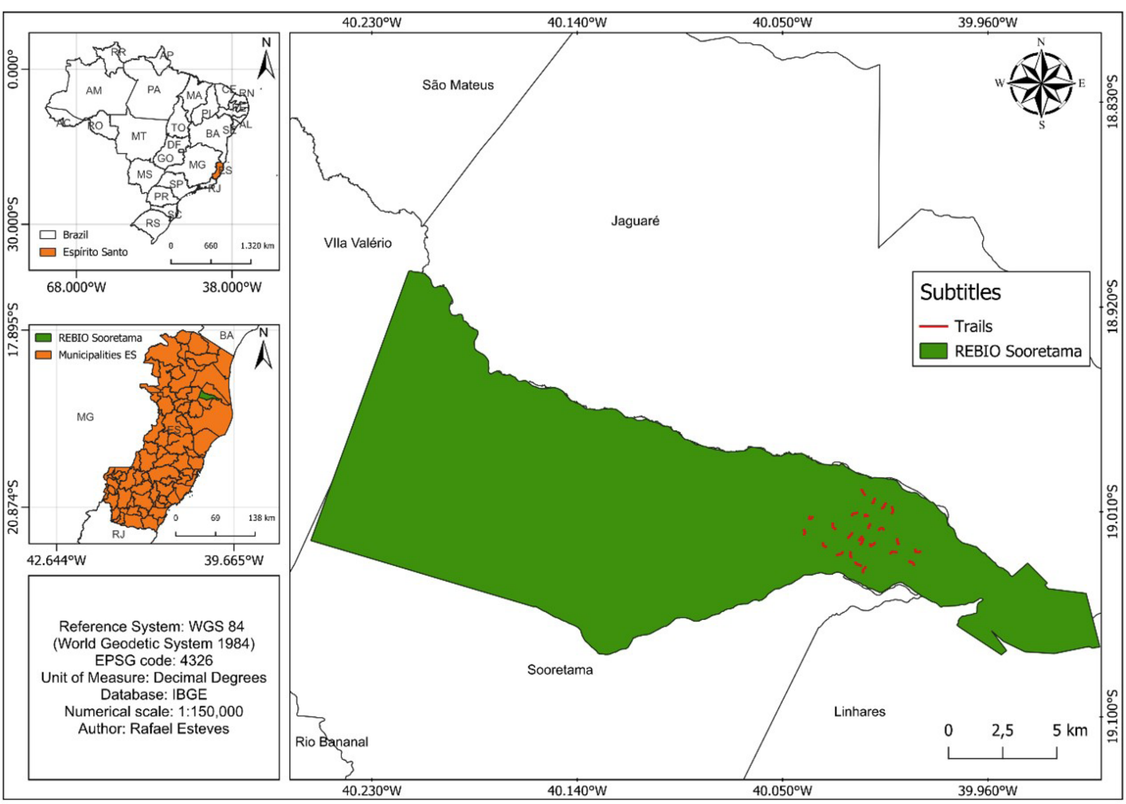

Figure 1. Study area and sampling plots at the Sooretama Biological Reserve, Espírito Santo, Brazil. The map shows the Sooretama Biological Reserve (REBIO Sooretama), highlighted in green, with the 24 sampling plots (red lines) distributed following the RAPELD methodology. The inset maps provide spatial context, indicating the location of the reserve within the state of Espírito Santo and Brazil.

Rainforest, and it is located in the Central Corridor of the Atlantic Forest Biome (Brasil, 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).

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.

2.2. 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 rainy seasons (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 method consists of permanent and standardized plots, each 250 m long, 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). Along the 250 m for each plot, the researcher moved at a slow walking pace and used the active search method, with visual sampling for macro-gastropods (> 5 mm in diameter or height) by one observer (the same person during all period of study) (Oliveira et al., 2021). 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 L each subplot). All recorded specimens were analyzed under a stereomicroscope, quantified and deposited at the Malacological Collection of Universidade do Estado do Rio de Janeiro (Col. Mol. UERJ).

2.3. Environmental variables

A set of five environmental variables was measured for each plot prior to the removal of 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 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.

2.4. Statistical analysis

The evaluation of sampling 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 the community of land snails among seasons was analyzed using a 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 humidity) on the land snail abundances ($p < 0.05$). Statistical significance between the seasons was tested using analysis of variance (ANOVA) and Tukey as a post-test. 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., 2013) for all statistical analyses.

3. Results

The species accumulation curve 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 2). We sampled 440 live specimens belonging to 35 species from 11 families (Table 1). 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% of specimens) and the most abundant species was *Leiostracus perlucidus* Spix, 1827 (22.5%).

Table 1. Abundance of the land snail species found in each season at Sooretama Biological Re3serve, Espírito Santo, using plots and subplots of 25 x 75 cm within combined sampling method (visual inspection + leaf litter).

Species	Summer	Autumn	Winter	Spring	Overall
Achatinidae					
Allopeas gracile (Hutton, 1834)	1	1	0	1	3
Allopeas micra (d'Orbigny, 1835)	0	1	1	3	5
Leptopeas bequaerti Pilsbry, 1926	2	5	4	3	14
Leptinaria concentrica (Reeve, 1849)	2	0	0	10	12
Leptinaria unilamellata (d'Orbigny, 1835)	11	0	5	0	16
Bulimulidae					
Cochlorina aurisleporis (Bruguière, 1792)	0	0	0	2	2
Cochlorina intensior (Pilsbry, 1898)	0	0	1	6	7
Pseudoxychona pileiformis (Moricand, 1836)	1	0	7	2	10
Drymaeus flexilabris (Pfeiffer, 1853)	2	3	1	3	9
Charopidae					
Radiodiscus goeldii (Thiele, 1927)	0	0	0	3	3
Lilloiconcha superba (Thiele, 1927)	0	0	1	0	1
Euconulidae					
Euconulus martinezi (Hidalgo, 1869)	1	0	0	0	1
Habroconus semenlini (Moricand, 1846)	8	3	0	2	13
Pseudoguppya aenea (Scott, 1948)	37	4	13	7	61
Helicinidae					
Helicina angulata Sowerby II, 1842	0	3	0	0	3
Helicina variabilis Wagner, 1910	4	2	0	0	6
Helicina inaequistriata Pilsbry, 1900	1	0	1	0	2
Odontostomidae					
Bahiensis albofilosus (Dohrn, 1883)	1	4	0	4	9
Bahiensis bahiensis (Moricand, 1833)	0	0	1	1	2
Burringtonia pantagruelina (Moricand, 1833)	0	0	0	3	3
Orthalicidae					
Orthalicus prototypus Pilsbry, 1899	3	0	2	2	7
Pleurodontidae					
Solaropsis amazonica (Reeve, 1854)	0	1	2	1	4
Solaropsis rosarium (Pfeiffer, 1849)	0	0	0	2	2
Scolodontidae					
Happia pilsbryi Gube, 1902	3	0	3	6	12
Scolodonta spirorbis (Deshayes, 1850)	5	10	9	7	31
Scolodonta bounobaena (d'Orbigny, 1835)	0	0	6	8	14
Systrophia circumplexa (Deshayes, 1839)	1	0	2	3	6
Happiella sp.	1	2	0	0	3
Tamayoa banghaasi (Thiele, 1927)	19	0	0	13	32
Tamayoa decolorata (Drouët, 1859)	0	0	5	2	7
Simpulopsidae					
Leiostracus perlucidus (Spix, 1827)	32	9	19	39	99
Rhinus ciliatus (Gould, 1846)	1	0	1	2	4
Simpulopsis atrovirens (Moricand, 1836)	0	0	1	4	5
Streptaxidae					
Rectartemon iguapensis (Pilsbry, 1930)	18	2	2	2	24
Rectartemon iheringi (Thiele, 1927)	2	0	3	3	8
Overall	156	50	90	144	440

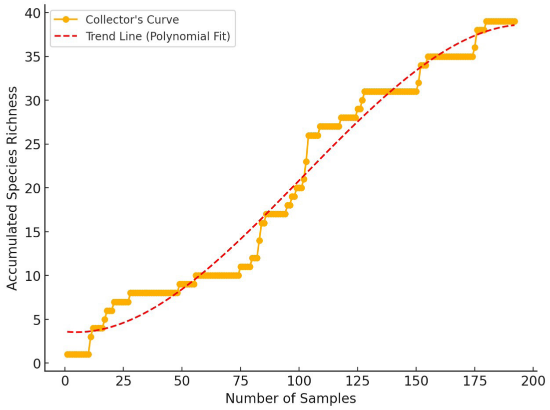

Figure 2. Cumulative curve of richness of land snails recorded at the Sooretama Biological Reserve, Espírito Santo, Brazil.

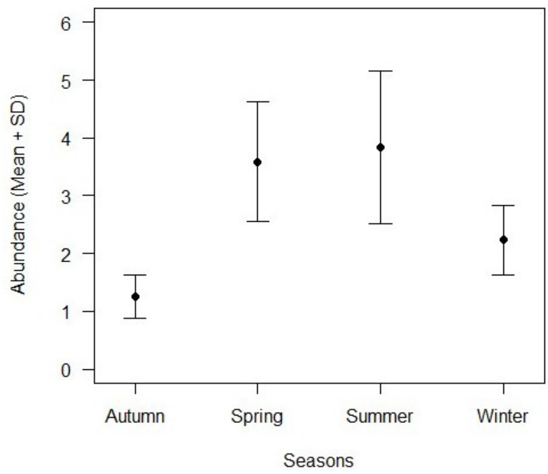

Figure 3. Boxplot with the variance of abundance between seasons of the land snail community at Sooretama Biological Reserve, Espírito Santo, Brazil (F = 3.565, p = 0.016).

Table 2. Environmental parameters analyzed at the plots in the Sooretama Biological Reserve, Espírito Santo, Brazil. Min: minimum; Max: maximum; SD: standard deviation; % Var: variation rate among each plot.

Environmental variables	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

The species richness varied among seasons (ANOVA; DF = 3; F = 3.565, p = 0.016), with the highest mean values in summer and spring (Table 2, Figure 3). The highest variation occurred between summer and autumn (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 (Table 2). There was a sharp moisture gradient between plots, 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 soil temperature (2.8% and 1.6% of variance, dry and rainy season respectively) (Table 2).

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 (Table 3). Atmospheric temperature (r^2 = 0.0953, p = 0.355) and leaf-litter humidity (r^2 = 0.0316, p = 0.692), in contrast, did not affect overall the land snail abundance (Table 3).

Table 3. Summary of the NMDS performed for seasonal variables used to characterize plots and overall land snail species distribution at the Sooretama Biological Reserve, Espírito Santo, Brazil. Bold numbers indicate p < 0.05.

	NMDS1	NMDS2	r^2	P(>r)
Atmospheric temperature	-0.99716	-0.07529	0.0953	0.355
Soil temperature	-0.86829	0.49605	0.4113	**0.008**
Relative air humidity	0.98166	-0.19064	0.7406	**0.001**
Soil humidity	0.97473	0.22338	0.5111	**0.001**
Leaf-litter humidity	-0.44584	-0.89511	0.0316	0.692

Considering the relative air and soil humidity, *Radiodiscus goeldii, Systrophia circumplexa, Scolodonta bounobaena, Solaropsis amazonica, Happiella* sp., *Solaropsis rosarium* and *Happia pilsbryi* were the species most associated with moisture environments. On the other hand, the synanthropic achatinids *Allopeas micra*, *Leptinaria unilamellata*, *Leptopeas bequaerti* and *Allopeas gracile* were the species less demanding of moisture (Figure 4).

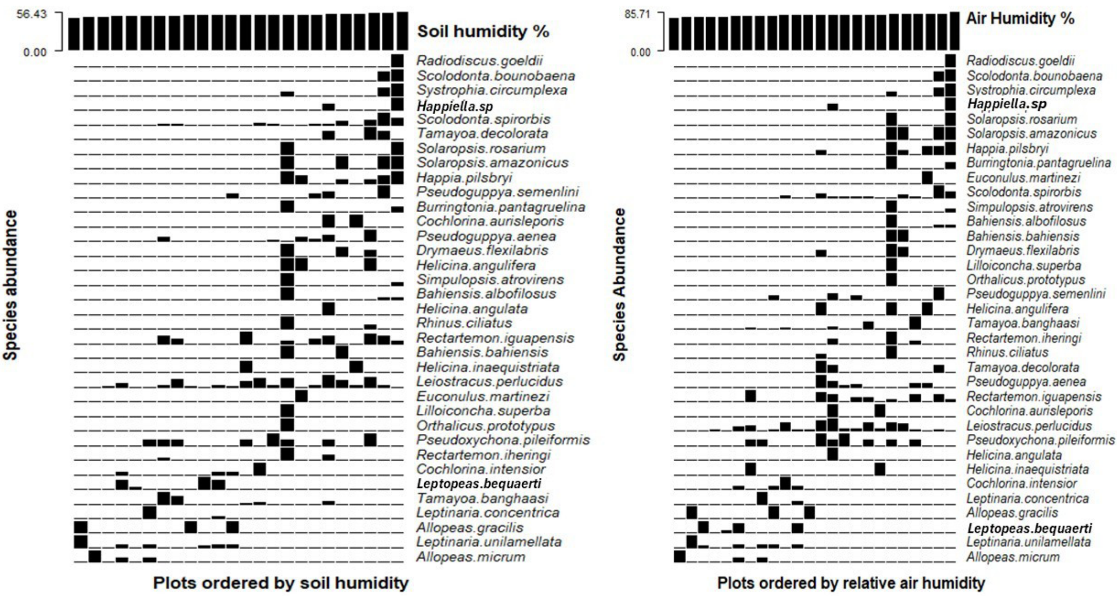

Figure 4. Species occurrences along a fine-scale moisture gradient at the Sooretama Biological Reserve, Espírito Santo, Brazil: pattern in a soil humidity gradient and in a relative air humidity gradient.

4. Discussion

Our study showed that the terrestrial snail community is relatively rich, both in terms of species richness and in variation of composition along the year. Scolodontidae was the most speciose family, with seven registered species, and *Tamayoa banghaasi* (Thiele, 1927) was the most abundant species among the Scolodontidae (Table 1). However, *Leiostracus perlucidus* Spix, 1827 (Simpulopsidae) was the most abundant species in the entire sampling period. Representatives of the family Scolodontidae (formerly Systrophiidae) can be found frequently and often abundantly across Central and South America from Mexico to Argentina and Chile (Hausdorf, 2006). Our results align with previous studies on land snail community composition in different regions, including Brazil (Ilha Grande [Santos and Monteiro, 2001; Nunes and Santos, 2012]), Peru (San Martin [Ramírez and Cordová, 1997], Cashiriani [Ramírez and Caro, 1998], Lower Urubamba Forest [Ramírez et al., 2001], Los Amigos [Ituarte et al., 2008], Panguana [Wendebourg and Hausdorf, 2019]), and Venezuela (La Fría [Baker, 1925]).

Our data revealed that the composition of the land snail community in the Sooretama Biological Reserve varied across seasons. The highest values for species richness and abundance were recorded in summer and spring (Table 1). Interestingly, we observed a grouping between spring and winter, suggesting that community parameters in these seasons are similar, indicating the influence of seasonality on the land snail community in the studied area. However, during the studied period, an atypical rainfall pattern occurred due to the El Niño phenomenon (AGERH, 2017), resulting in a comparatively drier period in the region, which may have affected species composition. Unfortunately, there are no previous studies on the seasonal variation of terrestrial gastropod communities in Brazil that allow for direct comparisons under similar climatic conditions.

Additionally, our results showed that the land snail community in the Sooretama Biological Reserve was significantly affected by relative air humidity and soil humidity ($p = 0.001$) but not by leaf-litter humidity ($p = 0.692$). These findings are consistent with Boycott's (1934) pioneering study on land snails, as well as with research conducted in various countries examining species distribution patterns across seasons, including Madagascar (Emberton et al., 1999), England (Millar and Waite, 2002), Germany (Martin and Sommer, 2004), Tanzania (Tattersfield et al., 2006), Central and Eastern Europe (Horsák et al., 2007), and Brazil (Nunes and Santos, 2012). Terrestrial gastropods, having a permeable body and moving by laying down moist mucus trails, suffer high rates of dehydration (Prior, 1985; Luchtel and Deyrup-Olsen, 2001). Terrestrial gastropods, having a permeable body and moving by laying down moist mucus trails, are highly susceptible to dehydration (Prior, 1985; Luchtel and Deyrup-Olsen, 2001). Moist conditions are essential for respiration and reproduction (Coney et al., 1982) and for mucus production, which is vital for locomotion (Cameron, 1970). However, all previous studies assessing the influence of soil humidity on land snail distribution have analyzed assemblages from isolated and distant sites, mostly on relatively large regional scales. This sampling approach may introduce bias due to site-specific characteristics unrelated to soil moisture that could also influence land snail distribution (Hettenbergerová et al., 2013).

We found a remarkable change of species composition over a moisture 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. amazonica* and *H. pilsbryi*), other four species being more abundant in drier plots (*A. micra, L. unilamellata, L. bequaerti* and *A. gracile*) and the other 26 species in an intermediary environment. In different environmental and climatic conditions, Hettenbergerová et al. (2013) found a pattern of species displacement in the humidity 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 to provide data on seasonal variation and species distribution patterns along a moisture gradient in a land snail community in Brazil, within a natural environment. Despite the climatic influence of El Niño, which led to a prolonged drought during the studied period, our results showed that the land snail community varied across seasons, particularly between summer and autumn. Although the studied period was drier than the historical average, the highest species richness and abundance were found in summer and spring, which are the rainy seasons, indicating a positive relationship between land snails and humidity. Our findings lead to important autecological insights: while our system did not include extremely dry plots, the results revealed a clear compositional shift along the moisture gradient, suggesting species-specific moisture preferences even at a fine spatial scale.

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