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Shell shape predicts microhabitat use in a land-snail assemblage from the Atlantic Forest

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Abstract. Land-snail assemblages in the Brazilian Atlantic Forest remain poorly studied despite this biome's exceptional biodiversity and high endemism. We investigated patterns of microhabitat use in a land-snail assemblage from the Sooretama Biological Reserve, southeastern Brazil, testing three predictions: (1) that more abundant species would occupy broader microhabitat ranges; (2) that species would show non-random associations with particular microhabitats; and (3) that species sharing the same microhabitat would exhibit convergent shell morphologies. We recorded 440 individuals from 30 species and 12 families across 24 standardised plots, assigning each individual to one of five microhabitat categories: ground, leaf litter, vegetation, tree trunk, and tree leaves. Species differed significantly in their distribution across microhabitat categories (*G*-test: $G = 943.51$, $p < 0.0001$), and 60% of species were significant indicators of a particular microhabitat (IndVal, $p < 0.05$). No significant relationship was detected between species abundance and standardised Levins' niche breadth (Spearman: $\rho = 0.251$, $p = 0.197$), and Prediction 1 was not supported. Hierarchical cluster analysis resolved the assemblage into four groups corresponding to distinct microhabitat-use patterns, showing strong correspondence with shell shape: groups associated with arboreal and ground microhabitats were predominantly high spired (80–100%), while the group associated with leaf litter was predominantly low spired (80%). Shell shape differed significantly among microhabitat categories (Kruskal–Wallis test: $H = 274.43$, $p < 0.0001$), with leaf litter differing from all other microhabitats in post-hoc comparisons. Phylogenetically stratified PERMANOVA confirmed that microhabitat accounted for 83.8% of the variation in species composition after controlling for superfamily-level non-independence ($F = 32.345$, $R^2 = 0.838$, $p = 0.001$). Our results extend the bimodal shell-shape framework to the Brazilian Atlantic Forest and provide a quantitative baseline for comparative studies of land-snail assemblages in this threatened biome.

Key words. Bimodal distribution, Gastropoda, microhabitat associations, shell morphology, Sooretama Biological Reserve

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Introduction

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 biomechani-

cal 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 ≈ 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 abundance of species 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.

Materials and Methods

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. 1). 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.

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–

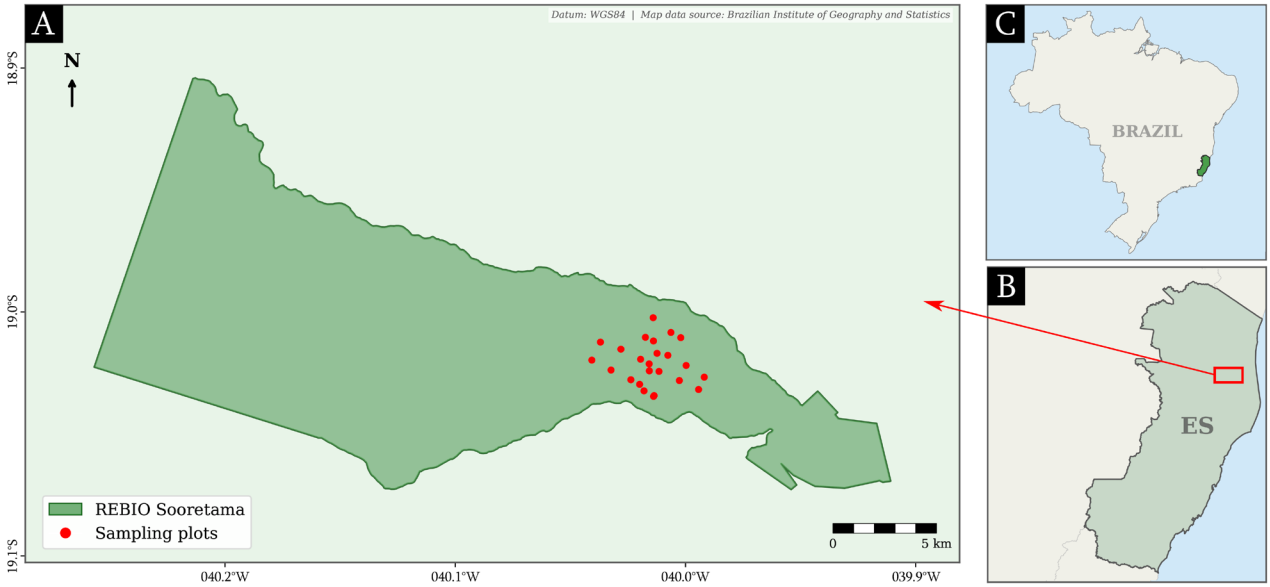

Figure 1. Location of study area (**A**) within Espírito Santo state (**B**) and Brazil (**C**). Sampling plots (trails) following the RAPELD methodology at the Sooretama Biological Reserve, Espírito Santo, Brazil.

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 microgastropods 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 considered when interpreting patterns in those microhabitats.

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).

Figure 2. Representative examples of microhabitats used by land snails in the Sooretama Biological Reserve, southeastern Brazil (not to scale). (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).

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.

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. 2).

- Ground—individuals found directly on the exposed soil surface, with no accumulated organic matter beneath them.
- Leaf litter—individuals found within or beneath the accumulated layer of decomposing organic matter on the forest floor; a distinction between ground and leaf litter was made at the time of collection: individuals resting on bare soil were assigned to ground category, while individuals found among or beneath leaf litter were assigned to the leaf-litter category.
- Vegetation—individuals found on herbaceous plants or shrubs up to approximately 1.5 m in height.
- Tree trunk—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.

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.

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 × 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).

Results

We recorded 440 individuals belonging to 30 species from 12 families across 24 plots and 64 non-empty plot × microhabitat combinations (Table 1). 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. 3).

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 1.

Eighteen species (60% of the assemblage) showed statistically significant associations with particular microhabitats (IndVal permutation test, $p < 0.05$; Table 2). 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 2).

The Spearman correlation between log10-transformed total abundance and standardised Levins' niche breadth (B') was not statistically significant ($\boldsymbol{\rho} = 0.251$, $S = 2735.7$, $p = 0.197$). The majority of species (29 of 30) showed B' values at or near zero. Individual species abundances and B' values are presented in Table 1.

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. 4): 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 1.

Shell shape (H/D ratio) differed significantly among microhabitat categories (Kruskal–Wallis: $H = 274.43$, df = 4, p

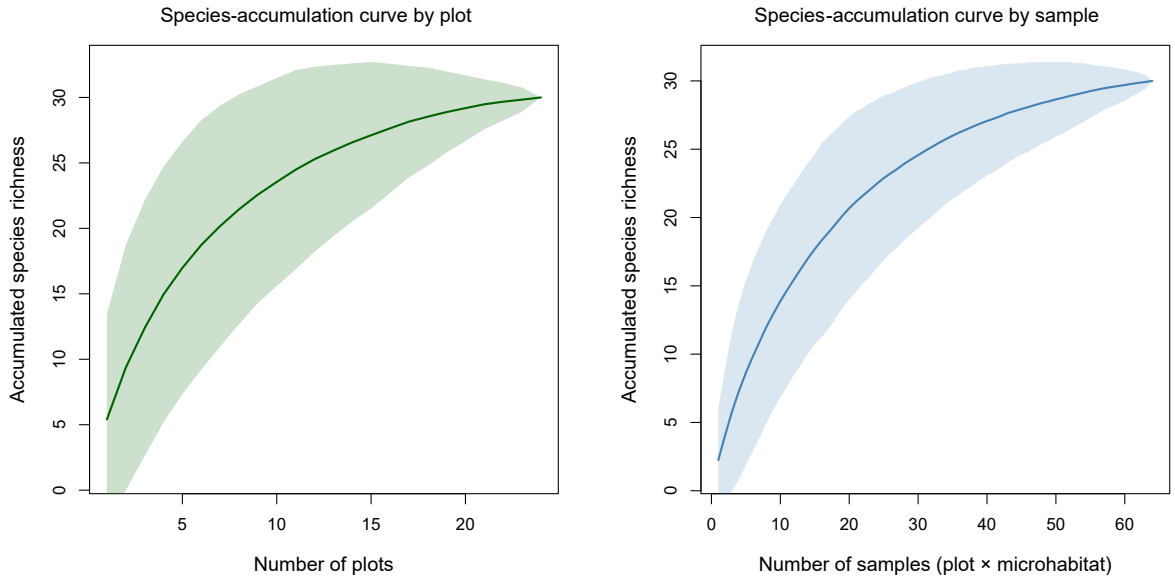

Figure 3. Species-accumulation curves for the land-snail assemblage of the Sooretama Biological Reserve, Espírito Santo, Brazil.

Table 1. Shell shape measurements and microhabitat use of land snail species recorded in the Sooretama Biological Reserve, southeastern Brazil. H: shell height; D: shell diameter; 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.

Superfamily Family Species	H (mm)	D (mm)	H/D	Shell shape	Microhabitat					*n*/plots	Habitat category*
					Ground	Leaf-litter	Vegeta-tion	Tree trunk	Tree leaves		
Helicinoidea Férussac, 1822											
Helicinidae Férussac, 1822											
Helicina variabilis Wagner, 1827	9.81	14.03	0.70	Low-spired	0	0	0	1	8	9/4	Semi-arboreal
Helicina sp.	7.06	10.94	0.65	Low-spired	0	0	0	2	0	2/2	Arboreal
Achatinoidea Swainson, 1840											
Achatinidae Swainson, 1840											
Leptinaria unilamellata (d'Orbigny, 1838)	8.04	5.49	1.47	High-spired	28	0	0	0	0	28/6	Ground-dweller
Leptopeas bequaerti (Pilsbry, 1926)	7.39	4.12	1.80	High-spired	14	0	0	0	0	14/4	Ground-dweller
Allopeas micra (d'Orbigny, 1835)	3.90	1.92	2.03	High-spired	5	0	0	0	0	5/3	Ground-dweller
Allopeas gracile (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											
Pseudoxychona pileiformis (Moricand, 1836)	17.64	13.01	1.36	High-spired	0	1	9	0	0	10/8	Semi-arboreal
Sanniostracus cf. *obliquus* (Reeve, 1849)	20.83	10.43	2.00	High-spired	0	0	0	9	0	9/3	Arboreal
Cochlorina cf. *lateralis* (Menke, 1828)	32.00	24.03	1.33	High-spired	0	0	0	7	0	7/4	Arboreal
Cochlorina aurisleporis (Bruguière, 1792)	31.48	21.45	1.47	High-spired	0	0	0	2	0	2/2	Arboreal
Cyclodontinidae Salvador & Breure, 2023											
Bahiensis albofilosus (Dohrn, 1883)	19.61	7.31	2.68	High-spired	0	0	9	0	0	9/3	Semi-arboreal
Bahiensis bahiensis (Moricand, 1834)	15.13	4.87	3.11	High-spired	0	0	0	2	0	2/2	Arboreal
Burringtonia pantagruelina (Moricand, 1833)	54.39	20.40	2.67	High-spired	0	3	0	0	0	3/2	Litter-dweller
Orthalicidae Martens, 1860											
Orthalicus prototypus Pilsbry, 1899	36.52	23.71	1.54	High-spired	0	0	0	7	0	7/1	Arboreal
Simpulopsidae Schileyko, 1999											
Leiostracus perlucidus (Spix, 1827)	15.12	9.31	1.63	High-spired	0	8	81	4	6	99/17	Semi-arboreal
Simpulopsis sp.	7.10	6.01	1.18	High-spired	0	0	0	0	5	5/2	Semi-arboreal
Rhinus velutinohispidus (Moricand, 1836)	20.56	18.45	1.11	High-spired	1	3	0	0	0	4/2	Litter-dweller

Superfamily Family Species	H (mm)	D (mm)	H/D	Shell shape	Microhabitat					*n*/plots	Habitat category*
					Ground	Leaf-litter	Vegeta-tion	Tree trunk	Tree leaves		
Punctoidea Morse, 1864											
Charopidae Hutton, 1884											
Radiodiscus sp.	2.06	2.41	0.86	Low-spired	0	3	0	0	0	3/1	Litter-dweller
Lilloiconcha superba (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											
Solaropsis planior (Pilsbry, 1890)	17.12	37.82	0.45	Low-spired	0	4	0	0	0	4/4	Litter-dweller
Solaropsis cf. *rosarium* (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											
Tamayoa banghaasi (Thiele, 1927)	1.87	3.80	0.49	Low-spired	0	39	0	0	0	39/7	Litter-dweller
Scolodonta sp. 1	1.36	3.59	0.38	Low-spired	0	31	0	0	0	37/10	Litter-dweller
Scolodonta sp. 2	2.11	4.72	0.45	Low-spired	0	14	0	0	0	14/2	Litter-dweller
"Happia" pilsbryi Gude, 1902	1.74	3.77	0.46	Low-spired	0	12	0	0	0	12/6	Litter-dweller
Systrophiella circumplexa (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											
Rectartemon regius (Löbbecke, 1881)	14.39	23.15	0.62	Low-spired	3	21	0	0	0	24/9	Litter-dweller
Rectartemon piquetensis (Pilsbry, 1930)	5.04	7.82	0.64	Low-spired	0	8	0	0	0	8/3	Litter-dweller
Trochomorphoidea Mörch, 1864											
Euconulidae Backer, 1928											
Habroconus semenlini (Moricand, 1846)	2.76	2.94	0.94	Low-spired	0	74	0	0	0	74/8	Litter-dweller
Euconulus martinezi (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	

*Ground-dweller: predominantly on bare soil; Litter-dweller: predominantly in leaf litter; Semi-arboreal: distributed across vegetation and arboreal microhabitats; Arboreal: predominantly on tree trunks.

Table 2. 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 are grouped by microhabitat.

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

< 0.0001) (Fig. 5). 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. 6). Achatinoidea was exclusively associated with ground habitats. Scolodontoidea, Streptaxoidea, Trochomorphoidea, 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.

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

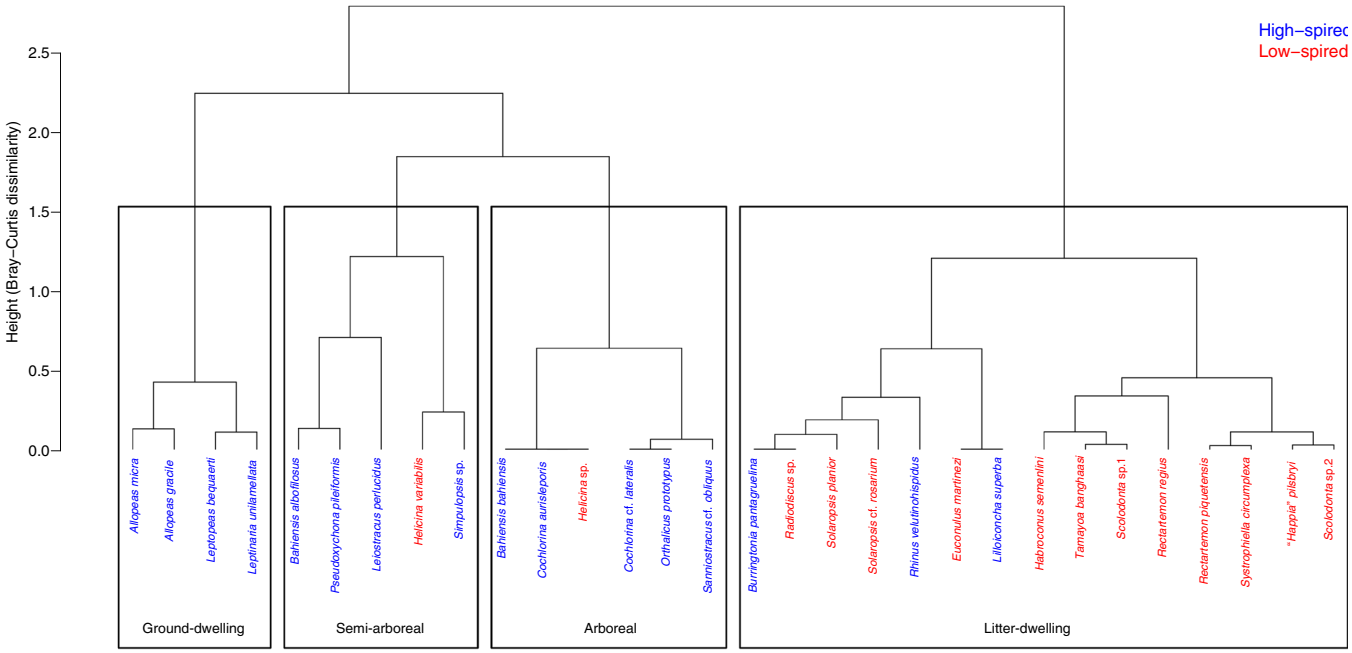

Figure 4. Hierarchical cluster analysis of land snail species from the Sooretama Biological Reserve based on microhabitat use. The dendrogram was constructed from log-transformed abundance data [log(x + 1)] using Bray–Curtis dissimilarity and the β-flexible linkage method.

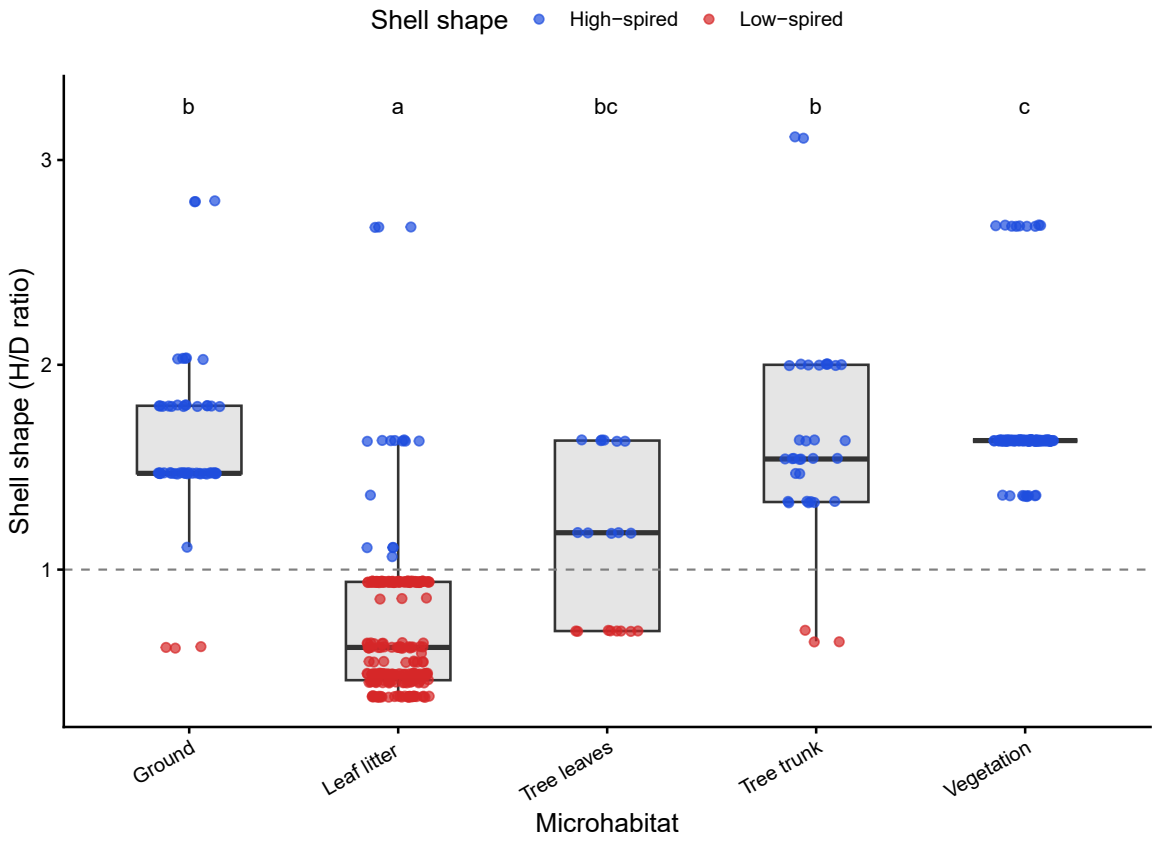

Figure 5. Shell shape (H/D ratio) across microhabitat categories in the land snail assemblage of the Sooretama Biological Reserve. Each point represents one recorded individual, with H/D ratio assigned from the species mean. The dashed horizontal line marks H/D = 1.0.

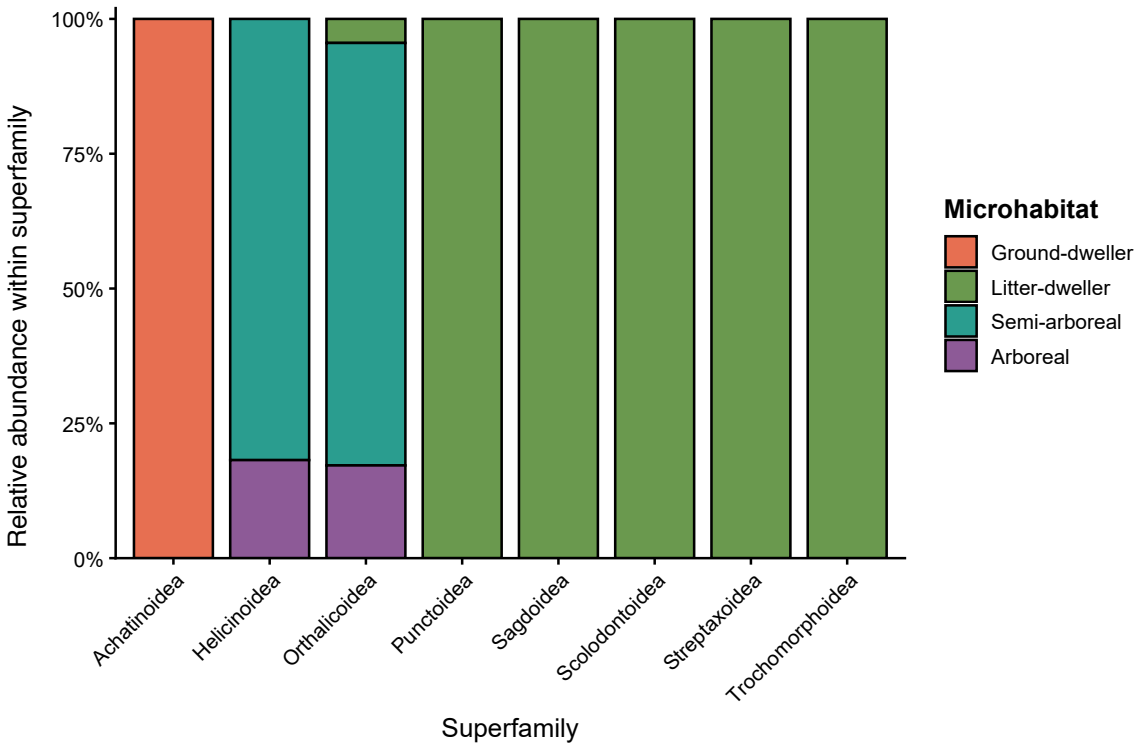

Figure 6. Relative abundance of individuals across microhabitats within each superfamily of land snails recorded in the Sooretama Biological Reserve.

associated with ground and arboreal microhabitats were composed predominantly of high-spired species (100% and 80–83%, respectively), while the litter-dwelling group was composed predominantly of low-spired species (80%). These associations are consistent with biomechanical arguments in the literature: high-spired shells confer a narrower profile and a higher centre of mass facilitating adhesion to vertical and inclined surfaces, while low-spired 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 ≈ 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 velutinohispidus* 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 Trochomorphoidea 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-spired 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: $\boldsymbol{\rho} = 0.251$, $p = 0.197$), 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.

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