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Research Article

Influence of habitat structure on the use of space by small mammals in Atlantic Forest area

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Abstract

Small mammal species may utilise different vertical strata of vegetation, and environmental characteristics may influence this utilisation. Consequently, microhabitats can provide important information regarding their role in space use. This study aimed to evaluate whether habitat structure influences the spatial use of small mammals in Sergipe, northeastern Brazil. Fieldwork was conducted monthly between August/2022 and July/2023 in the Atlantic Forest area. A total of 120 Sherman traps were baited on the ground and understory, resulting in a sampling effort of 4,320 trap-nights. Microhabitat characteristics were recorded at each capture station every three months. The Pianka index was used to check for niche overlaps, and Canonical Correspondence Analysis (CCA) was applied to evaluate associations between species and habitat variables. The marsupial *Marmosa demerarae* and the rodent *Cerradomys vivoi* significantly utilised the understory, and *Marmosops incanus* was found on the ground. The marsupial *Didelphis albiventris* did not differ in its occurrence between strata. When all four species were analysed together, the null model indicated spatial resource partitioning. The CCA explained 46 % of the total variation in species captured by habitat variables, with only litter depth being significant for the capture of *C. vivoi*. This species and *M. incanus* showed changes in their patterns of vertical stratum use, which may be related to the type of local phytophysiognomy present. Spatial segregation is an important factor that facilitates species coexistence. Locations with greater litter depths can provide shelter for *C. vivoi*, reducing the chances of detection by predators and benefiting from the consumption of invertebrates in the litter. Therefore, the distribution of species according to vertical stratification in the environment, as well as spatial segregation that can minimise interspecific competition, are important components in structuring the small-mammal community.

Introduction

Several researchers have considered the segregation of spatial resources as a factor that facilitates the coexistence of small mammals, such as marsupials and rodents (Camargo et al., 2018). This coexistence occurs in at least one dimension of the spatial niche, either vertical or horizontal (Vieira and Camargo, 2012; Cáceres et al., 2012). By partitioning spatial resources, species also make greater use of the niches available in their environment (Hannibal et al., 2020).

Small mammals are classified according to their use of vertical strata as fossorial, semi-fossorial, terrestrial, scansorial, or arboreal animals (Paglia et al., 2012). Consequently, species can select different environmental resources, which may vary according to the type of vegetation or habitat complexity (Hannibal et al., 2020; Camargo et al., 2018). For example, marsupial species have selected different vertical strata depending on the type of Atlantic Forest formation, varying between preferential use of the ground and understory (Vieira and Camargo, 2012).

When conducting a study of different phytophysiognomies in the Brazilian savanna, Camargo et al. (2018) also observed a change in space use by marsupials and rodents in relation to open areas and forest formations. In addition to phytophysiognomy, vertical complexity influences the use of space by small mammals, and the high complexity of vertical strata allows for more frequent use of above ground strata (Hannibal et al., 2020). Various environmental characteristics may influence space use, and it is possible to verify the association between some species and different environmental variables (Hannibal et al., 2020; Delciellos et al., 2016; Püttker et al., 2008). Therefore, microhabitats can provide important information about their influence on the use of space by these animals (Shepherd and Ditgen, 2016).

Terrestrial species are associated with areas of less dense undergrowth and fewer fallen trunks, which can act as obstacles to animal movement (Delciellos et al., 2016). Open areas with no canopy may favour movement, whereas ground cover can be an important factor in the distribution of terrestrial species in the environment (Benedek and Sîrbu, 2018; Rocha et al., 2011) because of their constant contact with the substrate. Herbaceous cover is mainly associated with terrestrial species (Benedek and Sîrbu, 2018; Rocha et al., 2011), acting as shelter (Briani et al., 2001) and providing foraging sites for various species.

Leaf litter is also an important factor for both terrestrial and scansorial species (Ferreira et al., 2023a; Owen, 2020), as well as fossorial and semi-fossorial species (Ardente et al., 2021). This may be related to the fact that this habitat component is used as a shelter (Briani et al., 2001) and has a large number of food resources, such as soil invertebrates (Dos Santos Oliveira et al., 2021), which corresponds to a group widely consumed by small mammals (Santori et al., 2012).

For arboreal species, dense understory and canopy facilitate movement into the higher vegetation strata (Owen, 2020; Paste and Voltolini, 2013). Arboreal and scansorial species are mainly associated with sites with greater canopy cover (Cademartori et al., 2008) and fruit availability (Owen, 2020). A greater number of lianas also contributes to the increased abundance of arboreal species in forest environments (Cobra et al., 2023). In addition, scansorial species have been associated with sites with a denser understory and a greater number of horizontal structures (Püttker et al., 2008), that is, with greater vegetation connectivity.

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Therefore, the use of vertical strata may be related to environmental characteristics, as they present a greater possibility of successful foraging, shelter, or escape from predators (Delciellos et al., 2016; Paste and Voltolini, 2013). Understanding the environmental variables that influence the habitat use of small mammals is important. This study aimed to evaluate the use of space and the influence of habitat structure on the use of space by the rodent *Cerradomys vivoi* Percequillo, Hingst-Zaher and Bonvicino, 2008, and marsupials *Marmosa demerarae* (Thomas, 1905), *Marmosops incanus* (Lund, 1840), and *Didelphis albiventris* Lund (1840) in an area in northeastern Brazil. Considering that species select vertical strata (Leiner et al., 2010), it is expected that there will be a differentiated use of the ground and understory between species. We hypothesised that the species would show segregation in at least one of the dimensions of the spatial niche, either vertical or horizontal, and associations with habitat structure variables. Thus, arboreal species such as *M. demerarae* are expected to be associated with greater use of aboveground strata and areas with higher canopy and understory cover, whereas *C. vivoi* is expected to be associated with the ground and open areas with lower understory and canopy cover. *M. incanus* and *D. albiventris* are expected to use both open and closed areas, owing to their scansorial habits.

Materials and methods

Study area

This study was conducted in Parque dos Falcões (10°44′50″ S, 37°22′40″ W), located in the municipality of Itabaiana, Sergipe. This region corresponds to a transition area between the Atlantic Forest and Caatinga, with open areas that have shrubby plants and areas with more arboreal vegetation (Dantas et al., 2010). The vegetation in the open areas did not have a continuous canopy, and the shrubs varied between half and three meters in height, under sandy-stony soil. In areas with tree vegetation, there were medium-sized trees (between 8 and 10 m), a relatively closed canopy, an understory with lianas and shrubs, a small temporary stream, and soil covered with leaf litter. The climate was characterised as tropical according to the Koppen-Geiger classification.

Capture methods

Sampling was conducted monthly for three consecutive nights between August 2022 and July 2023 using the capture-mark-recapture method. Two transects with 30 capture stations were established in the study area. The capture stations had two traps (one on the ground and the other at a height of 1.5 m) 15 m apart, for a total of 120 Sherman traps (30 × 8× 9 cm). The traps were baited with a mixture of corn flour, banana, corn, ground peanut, and sardines, checked daily in the morning, and re-baited when necessary. The animals were tagged with a numbered earring in their left ear and released at the place where they were captured, in accordance with licence n° 84157-1 to the SISBIO/ICMBio.

Habitat structure

The percentages of canopy cover, understory cover, herbaceous cover, litter cover, rock, water, and exposed soil, litter depth, number of lianas, and vegetation connectivity were measured at each capture station. Each variable (except the number of lianas and connectivity) was obtained at the point where the trap was placed and in the four directions of the cardinal points, three meters away from this central point, every three months (September and December 2022, March and June 2023).

The data used in the analysis corresponded to the average measurements obtained for each variable at each capture station, according to Freitas et al. (2002).

The percentage of canopy cover was obtained using the Canopeo app (https://canopeoapp.com/; Patrignani and Ochsner 2015), installed on a cell phone with an Android operating system, using a photograph of the canopy taken 1.5 m above the ground. The photos were automatically converted to black and white by the app, and the percentage of canopy cover at each point was obtained.

The percentage of understory, herbaceous cover, leaf litter, rock, water, and exposed soil was measured using a square 0.25 m^2 (0.50 m × 0.50 m) PVC screen, divided by nylon thread into 100 squares (adapted from Freitas et al. 2002). To determine the percentage of understory, the screen was positioned vertically at a height of 1.5 m in the centre of the capture station, and the vegetation obstruction between the screen and an imaginary wall three meters away in the direction of the four cardinal points was quantified. For the herbaceous, litter, rock, water, and exposed soil cover variables, the screen was placed parallel to the ground at a height of 60 cm, and the percentage cover was obtained at five points in each season.

The number of lianas was determined by the number of lianas present within a three-meter radius at each capture station. The depth of the leaf litter (in cm) was obtained using a millimetre ruler placed perpendicular to the ground at five points, and the horizontal connectivity of the vegetation at each capture station was measured by assigning a score from 0 to 4 (adapted from Püttker et al. 2008), considering the horizontal structures of the vegetation around the tree in which the understory trap was placed. Twigs and lianas from adjacent trees that were connected to the tree on which the trap was placed were taken into account.

Data analysis

The four species studied had at least five captures during the study, and a significance level of 5 % was used for statistical tests. For each species, the association between trap height (ground vs. understory) and capture frequency was evaluated using the chi-square test, with the expected capture proportions equal in each stratum, using Yates correction, if necessary, in the R program (R Core Team, 2022).

The Pianka index was used in the EcoSim program to verify the spatial niche overlap for each pair of species (Gotelli and Entsminger, 2005), based on the proportion of captures on the stratum of the trap (ground and understory) by each species (vertical dimension) and the number of individuals captured at each capture station (horizontal dimension). The values of this index ranged from 0 to 1, with values close to 1 indicating a high degree of niche overlap between species. Subsequently, to assess whether species exhibited resource partitioning in the vertical dimensions, a null niche overlap model was applied. The model compared the observed value of overlap with values expected by chance from 1.000 randomizations of the vertical use matrix.

To check the association between species and habitat variables, species capture was used as the dependent variable and habitat variables as the independent variable. Thus, the capture data were grouped and associated with the habitat variables of the stations for each capture in which the species were recorded. Canonical Correspondence Analysis (CCA) was used to investigate species associations (capture matrix) in relation to habitat variables in R software (R Core Team, 2022) using the vegan package (Oksanen et al., 2018). The species capture matrix was standardised using Hellinger transformation (Legendre and Gallagher, 2001), and the environmental variables were standardised using z-score transformation in R software (R Core Team, 2022). The ordistep function was used to determine which environmental variables had a significant value in relation to the capture of species (Borcard et al., 2011). To assess the significance and uncertainty of the environmental variables in the CCA, permutation tests (999) were performed using the envfit function from the vegan package (Oksanen et al., 2018), providing the correlation (r) and determination (r^2) coefficients, as well as the p-value for the relationship of each variable with the canonical axis. In addition, 95 % confidence intervals were obtained using the bootstrap resampling method. Pearson's correlation test was performed to verify the correlation and multicollinearity among the habitat structure variables. Variables with correlations greater than 0.7 were discarded.

Results

In this study, 44 captures of small mammals belonging to nine species (six marsupials and three rodents) were recorded, resulting from a sampling effort of 4,320 trap-nights, representing a capture success rate of 1 %. However, only four species were used in the analyses (Tab. 1), with a total of 36 records.

Table 1 – Records of small mammals on the ground and understory in Parque dos Falcões, Itabaiana, Sergipe, northeastern Brazil.

	Capture stations			
Species	**Ground (0 m)**	**Understory (1,5 m)**	X^2	***p*-value**
Didelphimorphia				
Didelphis albiventris	4	5	1,00	0,3681
Marmosa demerarae	3	10	16,00	< 0.0001
Marmosops incanus	4	1	36,00	< 0.0001
Rodentia				
Cerradomy vivoi	3	6	10,24	0,0019
Total	14	22	-	-

In terms of the proportion of vertical strata used, the marsupial *M. demerarae* (70 %, $X^2 = 16.00$, $p < 0.0001$) and the rodent *C. vivoi* (66 %, $X^2 = 10.24$, $p = 0.0019$) preferentially occurred in the understory. The marsupial *M. incanus* used the ground to a greater extent, with 80 % of captures ($X^2 = 36.00$, $p < 0.0001$), whereas *D. albiventris* used both strata in a similar way ($X^2 = 1$, $p > 0.05$).

High vertical spatial niche overlap was identified between *C. vivoi* and *M. demerarae* (0.99), *C. vivoi* and *D. albiventris* (0.97), and *D. albiventris* and *M. demerarae* (0.96); intermediate overlap was found between *M. demerarae* and *M. incanus* (0.61), and between *C. vivoi* and *M. incanus* (0.65) (Fig. 1). When all four species were analysed together, the null model indicated resource partitioning ($p < 0.05$). The results indicated a low horizontal overlap (high segregation) among species, with an index ranging from 0 to 0.23.

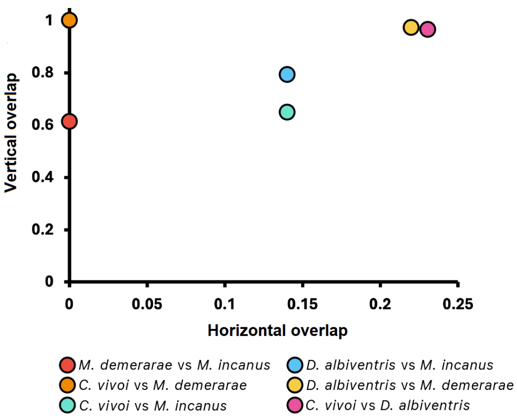

Figure 1 – Horizontal (among capture stations) and vertical (between ground and understory strata) spatial niche overlap among small mammal species was assessed using the Pianka index (ranging from 0 to 1) in Parque dos Falcões, Sergipe, northeastern Brazil.

The CCA explained 46 % of the total variation in species captures by habitat variables (Fig. 2). The first canonical axis (CCA1) explained 23.8 % ($p < 0.05$) and the second (CCA2) explained 17.6 % of the captured species-environment variation in the community. In addition, the test indicated that the environment had a significant influence on the capture of species ($F = 1.896$, $p = 0.014$, $R^2aj = 0.226$). After permutation tests for canonical axes, only the CCA1 axis ($F = 11.467$, $p = 0.015$) was significant. Forward selection identified litter depth as the only variable significantly associated with *C. vivoi* distribution ($F = 3.567$, $p = 0.008$, 999 permutations; Fig. 2), indicating an association between species and local litter depth. Only the litter layer depth showed a significant and positive correlation with CCA1 ($r = 0{,}971$, $r^2 = 0{,}327$, $p = 0{,}007$; IC 95 %: 0.352–0.728; Tab. 2). The variable “water” was excluded from the analysis because it presented a correlation greater than 0.7.

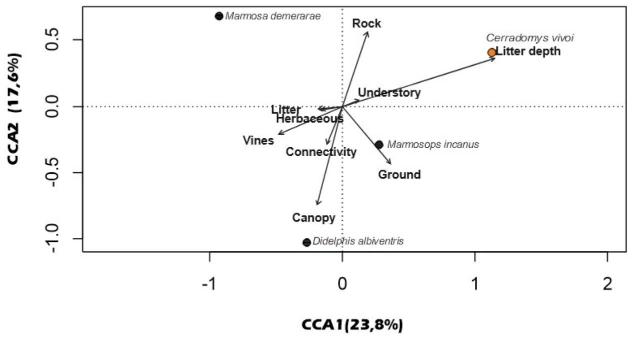

Figure 2 – Canonical Correspondence Analysis (CCA) showed the relationship between the capture of marsupials (black dots) and rodents (orange dot) and environmental variables (Canopy = canopy cover, Understory = percentage of understory cover, Herbaceous = herbaceous cover, Litter = itter cover, Litter depth = litter depth, Rock = rock cover, Ground = soil cover, Vines = number of vines, Connectivity = connectivity) at the capture stations in Parque dos Falcões, Sergipe, northeastern Brazil.

Table 2 – Results of the ordistep function in Canonical Correspondence Analysis (CCA) with canonical axes CCA1 and CCA2. Environmental variables: canopy = canopy cover, understory = percentage of understory cover, herbaceous = herbaceous cover, litter = litter cover, litter dep. = litter depth, rock = rock cover, ground = soil cover, vines = number of vines, connectivity = connectivity. The r^2 values represent the proportion of variance explained by each variable, and 95 % CI are the confidence intervals for the correlations with CCA1. Highlights in bold indicate significant values ($p \leq 0.05$) at the capture stations in Parque dos Falcões, Sergipe, northeastern Brazil.

Environment variable	CCA1	CCA2	r^2	p	IC 95 % (CCA1)
Litter dep.	0,971	0,239	0,327	**0,007**	0,352–0,728
Canopy	-0,291	-0,957	0,109	0,198	-0,378–0,309
Ground	0,728	-0,686	0,066	0,403	-0,223–0,481
Rock	0,385	0,923	0,066	0,373	-0,304–0,480
Vines	-0,946	-0,325	0,060	0,432	-0,536–0,147
Herbaceous	-0,993	-0,121	0,006	0,945	-0,390–0,267
Litter	-0,996	-0,084	0,008	0,894	-0,446–0,330
Understory	0,959	0,284	0,004	0,947	-0,302–0,401
Connectivity	-0,458	-0,889	0,018	0,789	-0,404–0,406

Discussion

Although *M. demerarae* was recorded more frequently in the understory, there was no association with variables related to arboreal vegetation (such as canopy, lianas, and connectivity). *C. vivoi*, due to its terrestrial habits, was expected to be more associated with open areas with exposed soil and herbaceous vegetation. However, this species was captured more frequently in the understory, demonstrating an association with leaf litter. *M. incanus* was recorded more frequently on the ground, although it was not associated with any of the environmental variables analysed. *D. albiventris* was the only species that showed no differences in captures between strata.

The low number of captures may be related to habitat quality. Studies on the vertical stratification of small mammals in various environments highlight the importance of sampling in different vertical strata (Camargo et al., 2018; Vieira et al., 2014), contributing to better sampling of abundance and richness (Ferreira et al., 2023a; Monticelli et al., 2021; Paste and Voltolini, 2018; Vieira and Camargo, 2012) and changes in the composition of communities (Vieira et al., 2014). By sampling in more than one stratum, there is greater coverage of the two-dimensional axis of the space used by the species (Cunha and Vieira, 2004) and a better characterisation of the sampled community.

The use of vertical strata by small mammals has been observed in different environments (Ferreira et al., 2023a; Camargo et al., 2018; Vieira et al., 2014; Caldara-Júnior and Leite, 2007) and is related to the search for and availability of food resources (Abreu et al., 2015). At Parque dos Falcões, some species studied differed in their use of strata, as has been observed in other studies (Ferreira et al., 2023a; Beltrão-Mendes et al., 2020; Passamani and Rosa, 2015; Leiner et al., 2010).

M. demerarae had the highest number of captures above the ground. Vieira and Camargo (2012) reported that this species preferentially uses the understory and canopy strata and occasionally descends to the ground. This corroborates its specialist habit of using vertical strata in relation to other species captured in the Parque dos Falcões. A study in the Atlantic Forest of Sergipe also found greater understory use by *M. demerarae* (Beltrão-Mendes et al., 2020), corroborating its arboreal habits (Arévalo-Sandi et al., 2021). In environments where it is possible to sample more than two strata of vegetation, this species is mainly found in the canopy (Vieira and Camargo, 2012).

Another species that was present in both vertical strata but preferentially used the understory was *C. vivoi*. However, the opposite pattern was observed in an area of eucalyptus forest in Sergipe (Beltrão-Mendes et al., 2020), indicating a change in the use of vertical strata by this species in different habitats. Despite being classified as terrestrial by Paglia et al. (2012), this rodent has been recorded above ground (Beltrão-Mendes et al., 2020) and preferentially uses the understory in the present study, demonstrating that it can be scansorial in relation to the use of space. Furthermore, there is a concentration of birds of prey in the area, and the use of understory vegetation may hinder the visual detection of predators. Therefore, habitat complexity and predation pressure may influence the use of vertical strata by this species, promoting greater spatial plasticity in its behaviour.

The marsupial *D. albiventris* is classified as a scansorial species that uses vertical strata in a similar manner (Camargo et al., 2018; Vieira and Camargo, 2012; Almeida et al., 2008), as observed in this study. Despite being considered a generalist in terms of space use (Almeida et al., 2008)) and diet (Paglia et al., 2012), this species has been found to use the ground most frequently in Atlantic Forest areas (Beltrão-Mendes et al., 2020; Sanches et al., 2012), showing its plasticity in the use of vertical strata. However, no adult individuals were sampled in Parque dos Falcões because of the size of the traps used, which might have influenced the results as a reflection of an ontogenetic change in the use of strata by this species. The equal exploitation of strata by subadults may indicate a reduction in competition with adults, who tend to use the ground more frequently (Sanches et al., 2012).

Among the species studied in Parque dos Falcões, *M. incanus* was the only species that preferentially used the ground. This species is classified as scansorial and is often found in Atlantic Forest environments, showing changes in the use of strata in different vegetation types (Bezerra and Geise, 2015). Studies have indicated its preferential use in the ground (Ferreira et al., 2023b; Passamani and Rosa, 2015; Leiner et al., 2010; Loretto and Vieira, 2008) and understory (Calazans and Bocchiglieri, 2019; Paste and Voltolini, 2018). Their movement on the ground and in the undergrowth helps them forage successfully and escape predators (Bezerra and Geise, 2015), as well as makes better use of two-dimensional space (Cunha and Vieira, 2004). Greater understory use by *M. incanus* has been observed in a restinga area (Calazans and Bocchiglieri, 2019) in the state of Sergipe, where it is the most abundant species found. Thus, the dominance of other species in the study area may have influenced the greater use of the ground by *M. incanus* as a way of minimising the pressure of competition. Another factor is the environment (Ferreira et al., 2023b; Bezerra and Geise, 2015; Leiner et al., 2010), since in forest formations with a more widely spaced canopy, as in the present study, the species uses the ground more often.

Studies have shown that the most locally abundant species can use the same vertical strata (Ferreira et al., 2023b; Beltrão-Mendes et al., 2020; Calazans and Bocchiglieri, 2019; Vieira and Camargo, 2012), as in the present study area, resulting in a high spatial overlap. The low overlap in the horizontal dimension probably reflects a differentiated occupation of the environment which, according to Cunha and Vieira (2004), can facilitate local coexistence between species. One of the factors that may explain this low horizontal overlap is the differentiated territoriality between species which select distinct areas (Sanches et al., 2012) and reduce competition for the environment (Caldara-Júnior and Leite, 2007).

The high vertical overlap and horizontal segregation observed in this community suggest that species coexistence is structured along several niche axes. However, significant spatial segregation was observed throughout the community. It has already been observed that, at the local scale, communities are structured by environmental heterogeneity and by interactions such as competition and predation (Liesenjohann et al., 2011). Thus, horizontal segregation may be influenced by small-scale factors such as litter depth. In this context, species such as *C. vivoi* and *M. demerarae* may use the same understory stratum but reduce competition by occupying different microhabitat patches within the sampled area.

With regard to habitat variables, a significant association was observed between leaf litter depth and the occurrence of the rodent *C. vivoi*. This habitat variable is associated with soil moisture (Mateus et al., 2013) and a high availability of invertebrates (Pereira et al., 2013), which may influence the quality of shelter and the foraging success of the species. Sites with a greater depth of leaf litter can provide shelter for the species, as rodents can be found in burrows using leaf litter as material (Briani et al., 2001), reducing the chances of detection by predators. In addition, *C. vivoi* was captured in this study at stations with more open vegetation and the presence of the tree species known as "lixeira" (*Curatella americana* L.), which had an accumulation of dry leaves on the ground around the capture stations, increasing the litter layer. Litter depth is related to habitat heterogeneity and is one of the main factors influencing species abundance (Carmignotto et al., 2022).

This study demonstrated that the partitioning of spatial resources contributes to the coexistence of species in an area. Although considered a terrestrial species, the rodent *C. vivoi* more frequently used the understory, suggesting plasticity in its use of vegetation strata according to the environmental characteristics. Although the study showed statistically significant patterns, the low number of captures at the site limited the associations between species and habitat variables.

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