

Tree cover, understory complexity and heaps shape fine-scale microhabitat partitioning in sympatric rodents

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Abstract

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Habitat heterogeneity promotes species coexistence by increasing opportunities for niche differentiation. Temperate forest small mammals provide an excellent model for investigating how fine-scale habitat structure influences spatial segregation. In this study, we examined fine-scale microhabitat associations of sympatric forest rodents, *Clethrionomys glareolus* and *Apodemus* spp., within a heterogeneous deciduous woodland in central Italy. We reanalysed a historical dataset using contemporary statistical approaches to assess habitat associations, based on a 289-trap grid (2-m spacing, 12 days) and 20 additional traps monitored for 23 days in woody debris heaps and control plots. A total of 176 individuals of *Apodemus* spp. and 65 of *C. glareolus* were captured within the trapping grid, whereas *C. glareolus* was recorded near heaps significantly more frequently (49.1%, $n = 57$ captures) than *Apodemus* spp. (32.8%, $n = 116$). Multivariate ordination (RDA), GLMMs and GLMs consistently identified vegetation structural complexity as the main driver of habitat segregation. *Clethrionomys glareolus* was associated with woody debris heaps and higher tree cover, whereas *Apodemus* spp. preferred herb-rich, open understory habitats and occurred significantly less frequently near heaps. Independent evidence from the spatial distribution of the asp viper (*Vipera aspis*), the principal ambush predator of both rodents, further indicated that heaps function as focal microhabitats, with nearly 90% of recently fed vipers recorded within 5 m of these structures. These results support the hypothesis that fine-scale habitat heterogeneity promotes coexistence by reducing spatial niche overlap. Maintaining structural complexity, including woody debris and heterogeneous understory layers, may therefore contribute to sustaining small mammal diversity in Mediterranean forest ecosystems.

Keywords

Apodemus spp., *Clethrionomys glareolus*, heap structures, Mediterranean forest ecology, microhabitat heterogeneity, niche partitioning, *Vipera aspis*

Introduction

Understanding how ecologically similar species coexist remains a central challenge in community ecology. Classical coexistence theory predicts that species with similar

resource requirements cannot persist without mechanisms reducing niche overlap, such as spatial, temporal, or trophic differentiation (AMARASEKARE, 2003, 2008; RICKLEFS et al., 2014). Habitat heterogeneity promotes coexistence by creating diverse ecological niches that species exploit

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differently (HOLT, 1984; MCPEEK, 1996; AMARASEKARE, 2003). Structurally complex temperate and Mediterranean forests are ideal systems for studying these processes because variation in canopy structure, understory vegetation, deadwood, and microtopography creates heterogeneous microhabitats (ISHII et al., 2004; SHAW, 2004; McELHINNY et al., 2015; CANNON et al., 2019; MURPHY et al., 2022; LIU et al., 2024). These features shape microclimate, predation risk, and food availability, influencing small mammal distributions (AMORI et al., 2010; WARDHAUGH, 2014; GÁMEZ and HARRIS, 2022; THOMAS et al., 2022; BALČIAUSKAS and BALČIAUSKIENĖ, 2026; RŮŽIČKOVÁ et al., 2026). Fine-scale habitat structure can promote spatial niche partitioning and reduce competition, facilitating coexistence (DENNY and NIELSEN, 2017; CAMARGO et al., 2018; BENEDEK et al., 2021; REYES-PUIG et al., 2025).

Rodent assemblages have traditionally played a major role in community ecology studies and in studies documenting species-habitat associations (e.g. BROWN, 1989; ERNEST et al., 2008; OWEN et al., 2020). Recently, the importance of microhabitat gradients in structuring rodent communities has been highlighted (STEVENS and TELLO, 2011; BENEDEK et al., 2021; ANCILLOTTO et al., 2025). For example, differences in vegetation structure, soil characteristics, or topographic conditions can generate environmental gradients along which species partition space and resources (BENEDEK and SÎRBU, 2025). Such patterns are consistent with broader ecological theory predicting that habitat heterogeneity promotes biodiversity by increasing the dimensionality of ecological niches (SWAN et al., 2020). However, despite growing interest in the role of microhabitat structure, relatively few studies have explicitly disentangled the relative importance of individual structural habitat components in promoting spatial segregation among sympatric forest rodents within the same forest stand. In Mediterranean oak forests, structural features such as canopy openness, shrub cover, coarse woody debris, litter accumulation, and ground-layer complexity are fundamental drivers of biodiversity because they generate fine-scale environmental heterogeneity, buffer temperature and moisture extremes, provide refuges from predators, and increase the availability of food and nesting resources for a wide range of organisms (HARMON et al., 1986; LASSAU et al., 2005; BLONDEL, 2010). Yet, it remains unclear which of these structural habitat elements most strongly determine the spatial segregation and coexistence of ecologically similar rodent species at fine spatial scales.

Rodent assemblages of European woodlands provide a particularly suitable model for investigating these mechanisms. Among the most widespread and abundant species in Europe are the bank vole, *Clethrionomys glareolus*, and wood mice of the genus *Apodemus* (MITCHELL-JONES et al., 2026). These taxa frequently co-occur across temperate and Mediterranean forests, where they represent key functional components of terrestrial ecosystems through seed predation, herbivory, and their role as prey for a wide range of predators (FERRARI et al., 2025). Despite their frequent sympatry, these rodents exhibit subtle yet consistent differences in ecological preferences and behavioral strategies (AMORI et al., 2015; CASULA et al., 2019), with different patterns de-

pending on the general habitat characteristics (BALESTRIERI et al., 2017; BENEDEK et al., 2026).

Previous studies suggest that such differences may translate into distinct microhabitat associations (SUCHOMEL et al., 2014; BALČIAUSKAS and BALČIAUSKIENĖ, 2026). The bank vole is typically associated with dense understory vegetation, closed canopy conditions, and structurally complex ground layers, which provide cover from predators and suitable nesting sites. In contrast, wood mice such as *Apodemus flavicollis* and *A. sylvaticus* often exploit a wide variety of forests, with the latter being more linked to open forest floors, forest edges, or herb-rich understories, reflecting their greater mobility and exploratory behavior, and the former to more densely vegetated areas (MONTGOMERY, 1978; FLOWERDEW et al., 1985). These contrasting habitat affinities suggest that fine-scale spatial segregation may reduce niche overlap, allowing both taxa to coexist within the same landscape (AMORI et al. 2010), but quantitative studies examining these small-scale habitat differences between species are scarce.

The deciduous oak forest “Macchia Grande di Manziana” in central Italy provides an ideal setting to investigate these processes. Dedicated by the Etruscans to the god Mants, from whom comes the name '*Silva Mantiana*', this is among the oldest and best preserved forests in central Italy, being inhabited by several rare taxa linked to mature forest ecosystems (CORSANICI and ANGELI, 2023; ANGELI et al., 2025). This forest still exhibits strong micro-scale variation in canopy cover, understory vegetation, and the distribution of woody debris, creating a heterogeneous mosaic of microhabitats within a relatively small spatial extent. In this study, we revisit a historical dataset originally collected in the early 1980s (AMORI et al., 1986) and reanalyse it using modern statistical approaches. Re-examining legacy ecological data offers an important opportunity to extract new insights from previously collected observations while improving statistical inference through contemporary analytical tools. Such approaches allow better quantification of uncertainty, identification of previously undetected patterns, and more robust interpretation of ecological processes, while avoiding the ecological and logistical costs associated with new field sampling. Importantly, the habitat characteristics of the study area have remained largely unchanged over the last three to four decades, indicating that the field dataset obtained by AMORI et al. (1986) is likely to remain representative of current conditions. This area was intensively surveyed for studies on rodent ecology 40 to 50 years ago, but it has not been used as a study case for this type of studies for decades.

To address these questions, we analyzed spatial patterns of captures of *C. glareolus* and *Apodemus* spp. across a trapping grid characterized by variation in canopy cover, ground vegetation, and the presence of woody debris heaps. In comparison with most other studies, the live-trapping grid design analyzed here (289 traps at 2 m intervals; see AMORI et al., 1986) is exceptional in fine-scale spatial resolution, and therefore allows a much deeper analysis of the microhabitat use patterns of the target species. Based on ecological theory and previous empirical studies, we

formulated the following testable key questions based on explicit hypotheses:

- (i) *Microhabitat partitioning hypothesis*. Do the two species exhibit significant spatial segregation along microhabitat gradients, reflecting differences in habitat preference?
- (ii) *Structural complexity hypothesis*. Does capture probability of *C. glareolus* positively associate with microhabitats characterized by tree cover and woody debris heaps, as predictable on the basis on the literature on this species (MONTGOMERY, 1978; FLOWERDEW et al., 1985) from elsewhere?
- (iii) *Open understory hypothesis*. Does capture frequency of *Apodemus* mice increase in areas with higher herbaceous vegetation cover and relatively open microhabitats, as predictable on the basis on the literature on this species (MONTGOMERY, 1978; FLOWERDEW et al., 1985) from elsewhere?

Beyond the specific study system, our findings in this paper demonstrate the value of revisiting historical ecological datasets with modern analytical tools to uncover the mechanisms through which fine-scale habitat heterogeneity promotes species coexistence, providing insights relevant for understanding and conserving biodiversity in Mediterranean forest ecosystems.

Materials and methods

The dataset

As noted above, this study is based on a re-analysis of a

historical dataset originally collected in the early 1980s (AMORI et al., 1986). In addition to the data reported in the original publication (AMORI et al., 1986), we accessed the complete original data files preserved in the personal archives of one of the study's authors (G. Amori). These previously unpublished records provided additional information that was particularly valuable for investigating the role of woody debris heaps in microhabitat partitioning among the target species (see below).

Study species

The species *Apodemus flavicollis* was identified in the original work based on morphological evidences (AMORI et al., 1986). However, subsequent investigations with genetical methods have shown that both *A. flavicollis* and *A. sylvaticus* occur in the study area, with their morphology and colouration being almost identical. Therefore, here we decided to define them a *Apodemus* spp.

As concerns the aspects studied in the present paper, AMORI et al. (2015) demonstrated the occurrence of inter-specific competition between the two species at fine spatial scales. Similar patterns have been reported in other parts of Europe (e.g., KOZAKIEWICZ et al., 1999). *Apodemus flavicollis* is generally more aggressive than *Clethrionomys glareolus* (GURNELL, 1985; GRÜM and BUJALSKA, 2000), and the two species appear to exhibit mutually exclusive daily activity patterns (WÓJCIK and WOLK, 1985; CONNOR and BOWERS, 1987). The larger-bodied and more dominant *Apodemus* mice are generally considered competitively superior to bank voles (ANDRZEJEWSKI and OLSZEWSKI, 1963; SOZIO and MORTELLITI, 2016). Differences in aggressiveness and locomotor performance are also reflected



Fig. 1. Map of Latium (central Italy), showing the study area (a) and the habitat where rodent individuals were captured (b).

in the antipredator behaviour (JEDRZEJEWSKI et al., 1993): *C. glareolus* typically exhibits a more cautious response (YLONEN et al., 1992), whereas *Apodemus* individuals are more likely to actively defend themselves.

Study area

The Macchia Grande di Manziana (approx. Latitude: 42.1300, Longitude: 12.1254) is a deciduous forest located in the municipality of Manziana (Lazio, central Italy), approximately 50 km northwest of Rome (Fig. 1). The forest covers roughly 580–600 ha and represents one of the largest remaining fragments of the ancient “Silva Mantiana”, a once-extensive woodland complex that historically connected the Monti Sabatini and Monti Cimini volcanic districts (SPADA, 1977). The area lies at an elevation of approximately 320–360 m asl. The forest is dominated by *Quercus cerris*, with co-dominance of *Quercus robur* and associated species including *Carpinus betulus*, *Acer campestre*, *Castanea sativa*. The understory is composed of typical mesophilic shrub and herb assemblages, including *Ilex aquifolium*, *Ruscus aculeatus*, and several fern species. This structural heterogeneity, combined with small open patches, seasonal wetlands, and transitional ecotones, supports a high level of local biodiversity.

In the study area, the forest (species composition, structure, canopy cover) and management practices of deadwood have not changed at all over the past four decades. Therefore, it represents one of the few mature “monumental” forests still occurring in central Italy.

Trapping design

Two complementary trapping designs were employed by AMORI et al. (1986): (a) grid trapping – a 32 × 32 m plot (1,024 m²) with 17 × 17 wood snap traps at 2 m intervals (289 total); and (b) additional 20 traps were randomly placed on five heaps (woody debris accumulations) and 20 traps were randomly placed in one control plot without heaps. Both the traps placed nearby heaps and in the control plot were positioned at about 500 m distance from the borders of the trapping grid to avoid potential interference (traps on heaps drawing animals away from the main grid). Traps (90 × 50 mm) were baited with bread, apple, oats, and hazelnut mixture and checked daily for 12 days (18–30 April, 1983). An additional 23-day session (24 April–16 May) was conducted on heaps vs. controls.

Environmental variables

At each trap station, the following variables were recorded: (i) Tree cover (% canopy), (ii) Vegetation cover (% of ground covered with grass and shrubs), and (iii) Heap presence/absence (binary). The spatial distribution of the variables in each grid cell is presented in the Appendix Tables A1 and A2. We defined the above-mentioned environmental variables as follows:

- (i) Tree cover was the proportion of the sky obscured by tree foliage directly above the trap station,

and was estimated visually (always by the same person). Because in the various grids the tree cover was always with canopy either higher than 60% or lower than 25% (no intermediate values above each positioned trap), for brevity in the Appendix Table A1 we defined the two categories as “presence” or “absence” of trees. This measurement reflects canopy density, which can influence microclimate, predation risk, and food availability for small mammals.

- (ii) Vegetation cover was characterized as the percentage of the ground surface covered by herbaceous vegetation and low shrubs (mainly *Rubus* sp.). Presence of vegetation cover was assumed when the percentage of ground surface with grass/shrubs exceeded 40% of the total. This variable was estimated within a standardized plot surrounding each trap (1 × 1 m quadrat). Ground cover provides shelter and foraging resources for rodents and can affect the accessibility of traps. Examples of two different types of vegetation cover are given in Fig. A1.
- (iii) The occurrence of natural or anthropogenic debris heaps (e.g., logs, rock piles, or leaf litter accumulations) within a defined radius of the trap station (n = 1 m) was recorded independently, during field surveys, as a binary variable (1 = present, 0 = absent). Heaps are localized microhabitat structures providing potential shelter and refuge for small mammals. Examples of heap structures are given in Fig. A1.

To obtain an independent indication of the ecological relevance of heaps, we also analysed the spatial distribution of the asp viper (*Vipera aspis*), the principal ambush predator of both rodent species in the study area (CAPULA and LUISELLI, 1990). The asp viper was considered in this study not only because it mainly feeds on these species of rodents in the study area, but also because it is an ambush predator, has a small home range, and once it has eaten its prey, it moves very little for several days, making it possible to understand the approximate predation site. During standardized field surveys conducted between March 1987 and October 2025, the linear distance from the nearest heap of each viper encountered was recorded by a tape. Individuals showing a markedly enlarged abdomen, indicative of recent prey ingestion (within approximately two days), were classified as recently fed. The proportion of vipers occurring within 2 m of a heap was calculated for the entire sample and for recently fed individuals separately. An example of a viper found nearby a heap is given in Fig. A1.

Statistical analyses

To investigate the relationship between rodent distribution and microhabitat characteristics, we applied complementary multivariate and regression-based approaches linking species occurrence to environmental variables. All analyses were performed at the level of the trapping grid cells

(17 × 17), which represented the basic spatial sampling unit. Habitat variables (tree cover and ground vegetation cover) were recorded independently for each trapping cell (Tables A1 and A2). The total number of captures of individuals of the two taxa recorded in each trapping cell was used to construct a species-by-site matrix, in which rows represented the 289 trapping cells and columns represented the number of captures of each rodent species. Capture frequencies were log(x + 1) transformed.

Differences among grid cells in vegetation cover and tree cover were analysed using Generalized Linear Models (GLMs) with a binomial error distribution and logit link function, as both variables were recorded also as binary presence/absence data at the cell level. Grid identity (cell position) was included as a fixed factor. We did not model each of the 289 cells as a predictor (that would be invalid/overparameterized). Instead, heterogeneity is tested via overall spatial variance in binomial response across cells, which is the correct ecological interpretation as spatial clustering ≠ random Bernoulli process.

To test whether rodent captures differed among grid cells, separate GLMs were fitted for each species. Because capture data were count-based and strongly zero-inflated, Poisson error structures were initially applied; model fit was assessed using residual deviance and overdispersion diagnostics. Where overdispersion was detected, negative binomial GLMs were considered more appropriate. For all models, significance of grid-level variation was assessed using likelihood ratio tests (χ^2). All analyses were conducted at the cell level (n = 289 grid cells), treating each trapping cell as an independent sampling unit.

A Detrended Correspondence Analysis (DCA, see HILL, 1979) was first performed on the species matrix to determine the length of the ecological gradient and to select the most appropriate constrained ordination method. Since the length of the first DCA axis was shorter than 3 standard deviation units (analysis not shown for brevity), indicating a predominantly linear species response to the measured environmental gradients, a Redundancy Analysis (RDA) was subsequently used to investigate the relationships between rodent distribution and habitat vari-

ables. RDA allows visualization of the main environmental gradients influencing species distribution and provides a quantitative assessment of the proportion of variance explained by environmental variables. The statistical significance of the RDA model and the explanatory variable was tested using permutation tests (999 permutations). The RDA was performed using the species abundance matrix as the response matrix and the habitat variables (tree cover and ground vegetation cover) as explanatory variables. The ordination therefore represents the variation in rodent distribution explained by the measured habitat characteristics. Because heaps represent discrete structural elements rather than the general habitat descriptors used to constrain the ordination, they were not included among the explanatory variables of the RDA.

To evaluate the effects of habitat characteristics on rodent abundance, Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution and log-link function were fitted separately for *Apodemus* spp. and *C. glareolus*. Capture frequency was used as the response variable, whereas tree cover (presence/absence) and ground vegetation cover (presence/absence) were included as fixed effects. This modelling framework is appropriate for count data derived from trapping surveys. Because trapping stations were arranged in a regular spatial grid, the row and column positions of each trapping cell were included as random intercepts to account for the hierarchical sampling design and potential spatial dependence among neighbouring cells. Model parameters were estimated by maximum likelihood, and the statistical significance of fixed effects was assessed using Wald z-tests.

Differences in capture frequency of rodent individuals near heaps and away from heaps within the trapping grid were tested using χ^2 tests. Differences in the probability of occurrence near heaps between species were tested using a binomial GLM with a logit link, with heap proximity (near vs. away) as the binary response variable and species as the explanatory variable. Differences among lines of the grid in the median number of captured rodents were assessed by Kruskal-Wallis text.

All statistical analyses were performed in R (R CORE

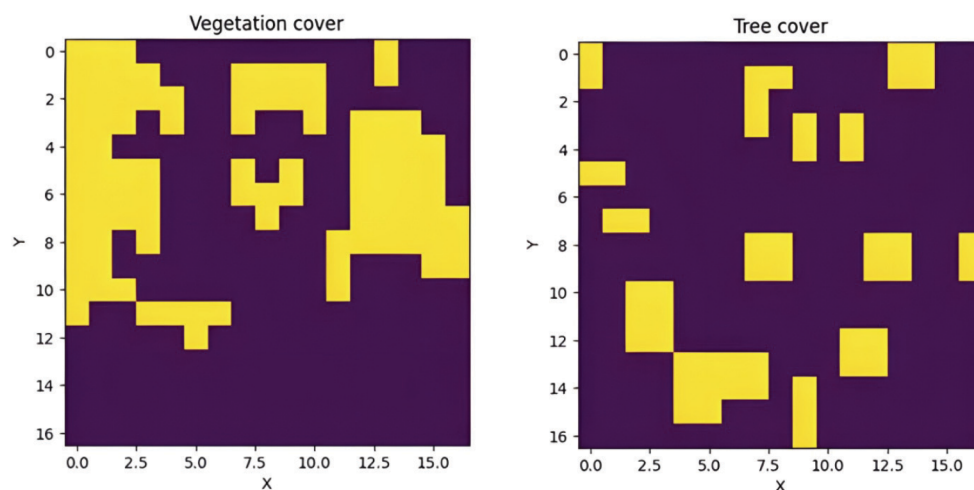


Fig. 2. Schematic distribution of cells with vegetation cover and with tree cover at the study area. Presences are given in yellow.

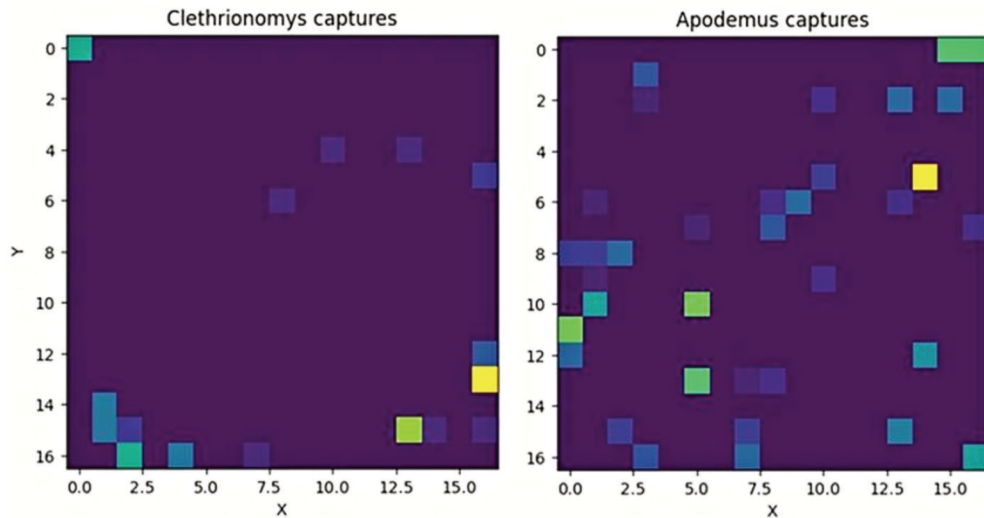


Fig. 3. Heatmap showing the frequency of captures of the target rodent taxa within the trapping grid. For the precise number of captures in each cell, see Table A3. Lighter colours indicate higher number of captures.

TEAM, 2024). DCA and RDA were carried out using the package *vegan* (OKSANEN et al., 2016), whereas GLMMs were fitted using the package *lme4* (BATES et al., 2015). Non-parametric tests were used after verification (by Kolmogorov-Smirnov test, with $P < 0.05$) of the non-normal distribution of the considered variables. Alpha was set at 5% and, in the text, means are presented ± 1 Standard Deviation.

Results

Habitat structure

Vegetation cover was present in 92 of 289 cells (31.8%), while tree cover was present in 51 cells (17.6%), indicating a heterogeneous habitat mosaic dominated by open areas. Vegetation was spatially clustered in the central and northern portions of the grid, while tree cover showed more fragmented patches (Fig. 2).

Significant spatial heterogeneity was detected across the trapping grid for both vegetation and tree cover. Binomial GLMs indicated strong variation among grid cells in vegetation presence (χ^2 , $p < 0.001$) and tree cover (χ^2 , $p < 0.001$), demonstrating pronounced habitat patchiness at the fine spatial scale. Vegetation was more widely distributed but spatially clustered, whereas tree cover occurred in distinct localized patches with large expanses of relatively open habitat (Fig. 2). These results confirm that the trapping grid represented a structurally heterogeneous environment.

Capture summary

Overall, 176 individuals of *Apodemus* spp. and 65 of *C. glareolus* were captured within the trapping grid. The heatmap showing the frequency of captures of the target taxa within the trapping grid is given in Fig. 3, with the exact

numbers of captures in each cell being given in Table A3. The synthesis of the presence-absence and capture number patterns of the two rodent species across grid cells, in relation to the microhabitat characteristics, is given in Table A4. Mean capture rate was 0.17 ind. trap⁻¹ night⁻¹. There were no significant differences in terms of number of captured rodents among the lines of the grid in the case of *Apodemus* spp. (Kruskal-Wallis H (χ^2) = 4.46, H_c (corrected) = 13,89, $P = 0.607$) whereas there was a significant difference for *C. glareolus* (Kruskal-Wallis H (χ^2) = 5.06, H_c (corrected) = 32,22, $P = 0.009$).

With respect to the rodents trapped within/nearby the heap structures versus control area, a total of 116 *Apodemus* spp. and 57 *C. glareolus* were captured (see below for the details).

Role of vegetation cover in the local distribution of rodents

Vegetation cover showed a positive association with both abundance and occurrence of *Apodemus* spp. Mean captures were higher in cells with vegetation present (0.72 captures per cell) compared to cells without vegetation (0.56 captures per cell), indicating an increase in local abundance in structurally complex habitats. Similarly, occupancy probability was higher in vegetated cells (0.163) than in non-vegetated cells (0.102). Although the effect size is moderate, the pattern is consistent across both abundance and presence-absence metrics, suggesting that vegetation cover acts as a favorable microhabitat feature for this species, likely providing shelter and foraging opportunities.

In contrast, *C. glareolus* exhibited a negative association with vegetation cover. Mean captures were substantially lower in vegetated cells (0.09 captures per cell) than in non-vegetated cells (0.25 captures per cell), indicating higher local abundance in more open habitats. This pattern was also reflected in occupancy probabilities, which were

lower in vegetated cells (0.033) compared to non-vegetated cells (0.066). Overall, *C. glareolus* appears to avoid densely vegetated cells, suggesting either preference for open ground conditions or dependence on habitat features not captured by the vegetation metric. Along the tree cover gradient, *C. glareolus* displayed a positive relationship with tree cover, with increasing capture probability as habitat structure becomes more canopy-closed, reaching a plateau at high tree cover levels.

Role of tree cover in the local distribution of rodents

Along the tree cover gradient, *Apodemus* spp. showed a negative response, with higher capture probability in low tree cover conditions and a rapid decline as tree cover increases (Fig. 4). In contrast, *C. glareolus* showed an opposing pattern, with increasing capture probability associated with higher tree cover and reduced ground vegetation, suggesting stronger affinity for forested structural conditions (Fig. 5). The joint visualization of both species within the same environmental space highlighted partial niche separation along both habitat axes (Fig. 6). While some intermediate overlap occurs in transitional habitat conditions, peak suitability regions are spatially distinct, supporting the presence of multidimensional habitat partitioning between the two sympatric species (Fig. 6).

Together, these response curves illustrate clear niche divergence along the two habitat dimensions gradient, supporting the interpretation of habitat-driven segregation between the two species within the trapping grid: *Apodemus* spp. exhibited highest predicted capture probability in areas characterized by high ground vegetation cover and relatively low tree cover, indicating a strong positive response to understory structure combined with avoidance of dense woody canopy.

Species–habitat relationships

The GLMM analysis revealed different species-area relationship patterns between the two taxa: there was a significant positive effect of tree cover and a significant negative effect of vegetation cover on captures of *C. glareolus*, whereas *Apodemus* spp. showed no significant relationship with either of these variables (Table 1).

The RDA (Table 3) further confirmed the role of tree cover as the main environmental gradient structuring the rodent assemblage, although to a lesser significance level, also the vegetation cover significantly structured the rodent assemblage (Table 2). This analysis confirmed a clear separation between the two rodent species according to the measured habitat variables (Fig. 7): *Apodemus* spp. was associated mainly with cells presenting abundant ground

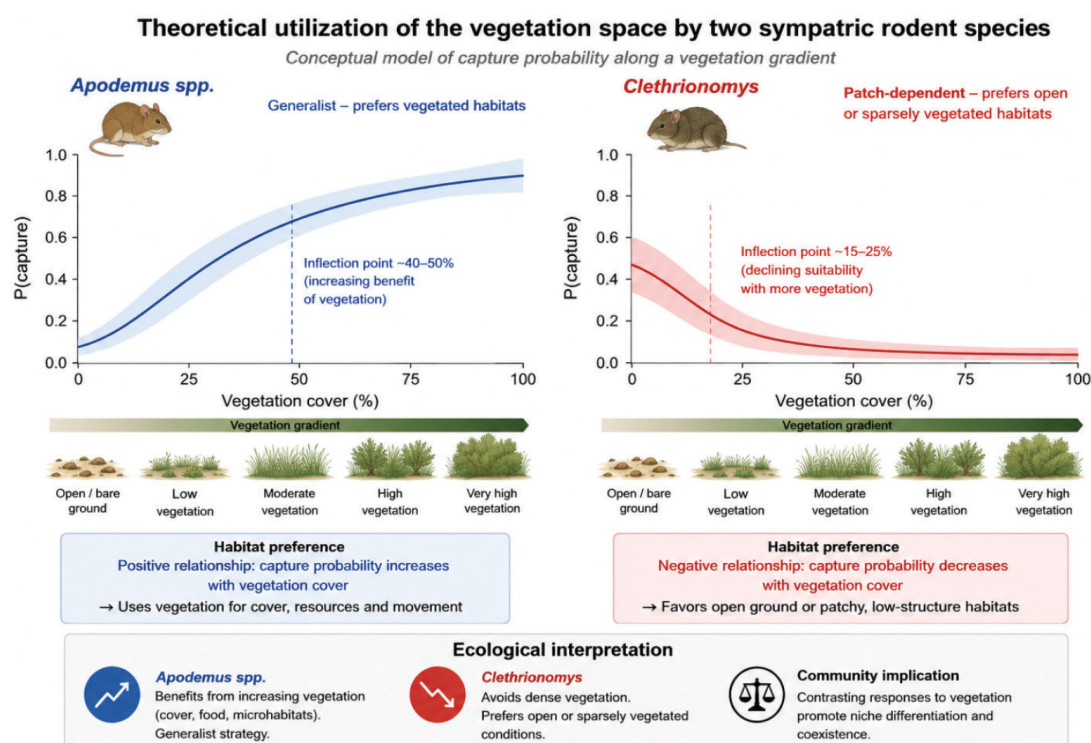


Fig. 4. Theoretical utilization of vegetation space by two sympatric rodent species. Response curves showing predicted capture probability ($P(\text{capture})$) along a gradient of vegetation cover (%) for *Apodemus* spp. (left, blue) and *Clethrionomys* (right, red). Shaded areas represent conceptual uncertainty around the response functions. *Apodemus* spp. displays a positive, saturating relationship with vegetation cover, with increasing capture probability as habitat structure becomes more complex, reaching a plateau at high vegetation levels. In contrast, *Clethrionomys* shows a negative exponential response, with higher capture probability in low vegetation conditions and a rapid decline as vegetation cover increases. The bottom panels illustrate the corresponding habitat gradient from open ground to dense vegetation and summarize inferred habitat preferences. Overall, the figure represents a theoretical niche partitioning along a fine-scale structural habitat gradient.

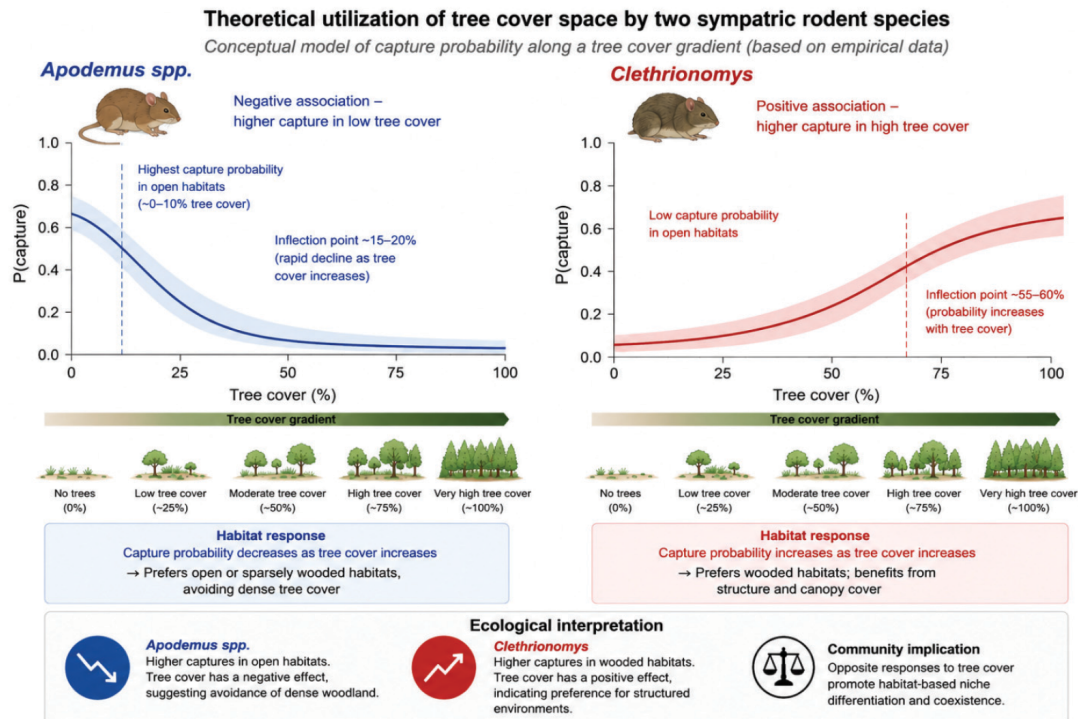


Fig. 5. Theoretical utilization of tree cover space by two sympatric rodent species. Response curves showing predicted capture probability ($P(\text{capture})$) along a gradient of tree cover (%) for *Apodemus* spp. (left, blue) and *Clethrionomys* (right, red). Shaded areas represent conceptual uncertainty around the response functions. *Clethrionomys* displays a positive relationship with tree cover cover, with increasing capture probability as habitat structure becomes more canopy-closed, reaching a plateau at high tree cover levels. In contrast, *Apodemus* spp. shows a negative response, with higher capture probability in low tree cover conditions and a rapid decline as tree cover increases. The bottom panels illustrate the corresponding habitat gradient from open tree to closed tree and summarize inferred habitat preferences. Overall, the figure represents a theoretical niche partitioning along a fine-scale structural habitat gradient.

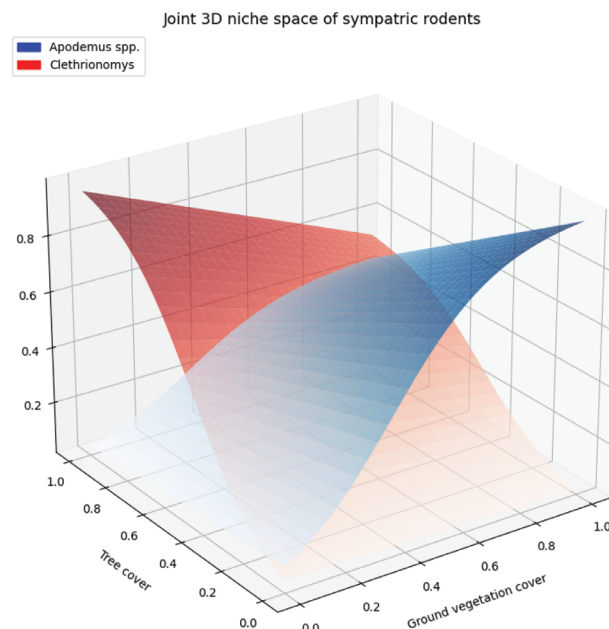


Fig. 6. Joint three-dimensional niche space of two sympatric rodent species along ground vegetation and tree cover gradients. Predicted capture probability ($P(\text{capture})$) surfaces for *Apodemus* spp. (blue) and *Clethrionomys* (red) across a bivariate habitat space defined by ground vegetation cover (x-axis) and tree cover (y-axis). Semi-transparent response surfaces illustrate species-specific habitat associations and allow visual assessment of niche differentiation in multidimensional environmental space. *Apodemus* spp. shows highest predicted capture probability in areas of high ground vegetation and low-to-moderate tree cover, whereas *Clethrionomys* reaches maximum suitability in environments characterized by high tree cover and reduced ground vegetation. The overlap between surfaces indicates partial but not complete niche separation along the combined habitat gradients.

Table 1. Effect of tree cover and vegetation cover on the capture frequency of the two species. GLMM model with Poisson distribution, log-link; row and column of the grid included as random effects. GLMM – Generalized Linear Mixed Model, SE = Standard Error.

Species	Predictor	Estimate (β)	SE	z-value	P-value
<i>Apodemus</i> spp.	Intercept	−0.529	0.08	5.12	<0.001
	Vegetation cover	+0.254	0.09	1.62	0.102
	Tree cover	−0.18	0.11	−1.64	0.101
<i>Clethrionomys glareolus</i>	Intercept	−1.312	0.15	−1.64	<0.001
	Vegetation cover	−1.045	0.12	−8.64	0.006
	Tree cover	0.62	0.12	2.95	0.003

Table 2. Results of the Analysis of Redundancy (RDA) of the species $\times$ cells matrix in relation to tree cover and vegetation cover

(A)

Component	Eigenvalue	% Variance Explained
RDA1	0.28	62.6
RDA2	0.11	37.4

(B) Significance test by means of 999 permutations:

Term	F	P-value
Tree cover	4.12	0.019
RDA1	2.98	<0.05

(C) Species scores (RDA1)

Species	RDA1 score
<i>Apodemus</i> spp.	−0.42
<i>Clethrionomys glareolus</i>	0.67

Table 3. Number of rodent individuals captured near heaps and away from heaps within the trapping grid. For statistical details, see the text.

Species	Near heaps	Away from heaps	Total
<i>Apodemus</i> spp.	38	78	116
<i>Clethrionomys glareolus</i>	28	29	57
Total	66	107	173

vegetation, whereas *C. glareolus* was positioned towards the tree-covered portion of the ordination space, indicating contrasting habitat preferences between the two sympatric rodents (Fig. 7).

Role of heaps in the local distribution of rodents

The synthesis of the data concerning the rodent individuals captured near heaps and away from heaps within the trapping grid is given in Table 3. *Clethrionomys glareolus* was recorded near heaps more frequently (49.1%, 28/57) than *Apodemus* spp. (32.8%, 38/116). A binomial GLM

revealed a significant effect of species on heap proximity (likelihood-ratio test: $\chi^2_1 = 4.29$, $P = 0.038$). The probability of occurring near heaps was higher in *C. glareolus* than in *Apodemus* spp. ($\beta = 0.686 \pm 0.333$ SE, $z = 2.06$, $P = 0.039$), corresponding to almost a two-fold increase in odds (OR = 1.99, 95% Confidence Intervals = 1.03–3.83).

To further assess the ecological importance of heaps for the two rodent species, we examined the spatial distribution of one of their principal predators, the asp viper (*Vipera aspis*), whose diet at the study area consists predominantly of *Clethrionomys glareolus* and *Apodemus* spp. (61.4% of all prey items; Table A5) (see also CAPULA and LUISELLI, 1990; LUISELLI and AGRIMI, 1991). Between March 1987 and October 2025, a total of 294 vipers were recorded within the Macchia di Manziana, of which 166 individuals (56.4%) were observed within 5 m of a heap. The association was even stronger among recently fed individuals, identified by the presence of a conspicuously enlarged abdomen indicating prey ingestion within the previous two days. Of the 113 recently-fed vipers, 101 (89.4%) were found within 5 m of a heap. This marked spatial concentration suggests that heaps represent important foraging sites for *V. aspis*, likely reflecting the local aggregation of its principal small-mammal prey around these structurally complex microhabitats.

Discussion

Overall, our trapping data suggest that *Apodemus* spp. were more abundant than *Clethrionomys glareolus* within the study area. Although the spatial extent of the study and the trapping effort (i.e. the number of trap-nights) were not sufficient to draw robust conclusions regarding the relative population sizes of the two species, this pattern is consistent with independent dietary data from their principal predators with known generalist feeding habits (e.g. CAPULA and LUISELLI, 1990; CAPIZZI et al., 2008). In particular, *Apodemus* spp. and *C. glareolus* occurred in comparable proportions in the diet of both the asp viper (CAPULA and LUISELLI, 1990) and the Aesculapian snake *Zamenis longissimus* (CAPIZZI et al., 2008), suggesting that the relative abundances observed in our trapping survey may be broadly representative of the wider study area. Nevertheless, substantial interannual fluctuations in the abundance

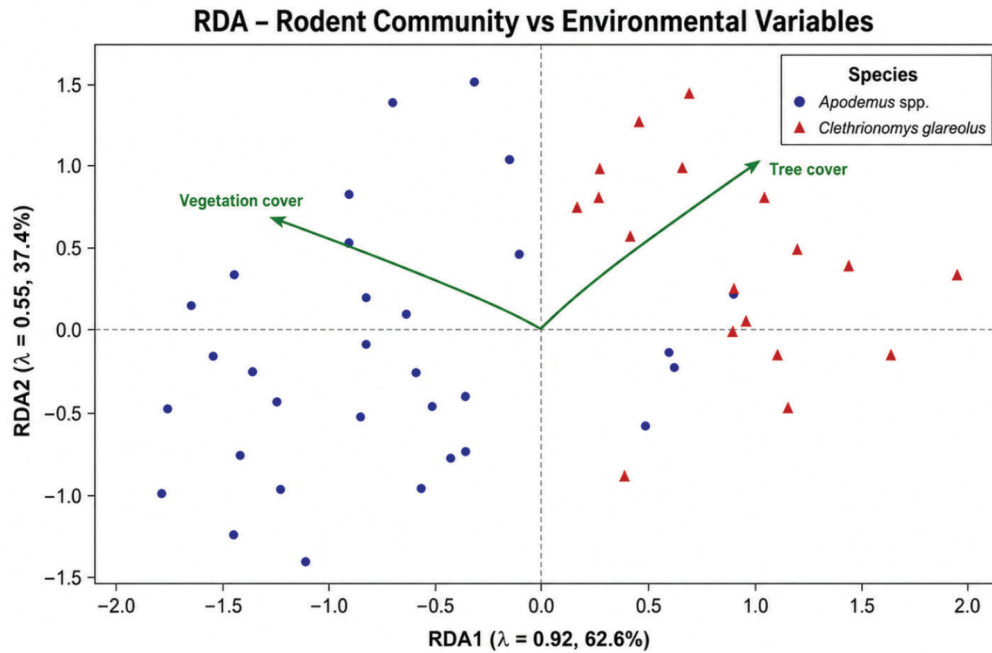


Fig. 7. RDA Ordination of rodent taxa and environmental variables. This graphic visualizes the separation of *Apodemus* spp. and *Clethrionomys glareolus* along ecological axes.

of both rodent species cannot be excluded.

Our results provide evidence that fine-scale habitat heterogeneity structures the spatial distribution of sympatric forest rodents in the deciduous woodland of the study area. Patterns of capture frequency and ordination scores indicate that *C. glareolus* and *Apodemus* spp. occupy partially distinct microhabitats within the same forest stand. Overall, these findings support the broader ecological prediction that environmental heterogeneity facilitates species coexistence by reducing niche overlap and promoting spatial differentiation among ecologically similar species (AMARASEKARE, 2003). Relatively similar results were also obtained, for instance, by CAREY and WILSON (2001) in the Pacific Northwest of the U.S.A., OWEN et al. (2020) in Paraguay, and CHOCK et al. (2022) in California, indicating that the fine-scale segregation mechanisms observed by us may be a general niche partitioning strategy for sympatric rodents worldwide.

Evidence for microhabitat partitioning

The microhabitat partitioning hypothesis predicted spatial segregation along microhabitat gradients (LEIMGRUBER et al., 2014), and both ordination and capture data support this expectation. Indeed, the two species were distributed along distinct positions in the DCA space, showing the relevance of habitat structure plays in shaping their spatial arrangement within the trapping grid. Model-based analyses reinforced this interpretation: GLMM results showed that captures of *C. glareolus* were positively associated with tree cover, whereas *Apodemus* spp. showed no significant relationship with this variable. This suggests that canopy-related structural complexity is particularly important

for *C. glareolus*, a species typically linked to forest interiors and sheltered environments. In contrast, the broader distribution of *Apodemus* spp. indicates greater ecological flexibility and the ability to exploit more heterogeneous or open microhabitats. The RDA results were consistent with these findings, identifying tree cover as a primary gradient separating the two species.

Although both taxa co-occurred within the same area, their preferential use of different portions of the microhabitat spectrum suggests partial niche segregation. This pattern is consistent with classical niche theory, which predicts that coexistence among similar species is stabilized by differentiation in habitat use or resource exploitation (BOEYE et al., 2014). Even modest differences in habitat preference can reduce competitive interactions in structurally complex environments.

Comparable patterns have been documented in European forest systems, where small mammal distributions are strongly influenced by microhabitat features such as vegetation structure, litter depth, and canopy cover (PUCEK et al., 1993; BENEDEK et al., 2021; CHOCK et al., 2022). Our results therefore reinforce the role of fine-scale heterogeneity as a mechanism maintaining local rodent diversity.

The second hypothesis predicted that *C. glareolus* would be associated with structurally complex microhabitats. This was supported by the higher capture frequency of the species in areas with woody debris and greater tree cover. Deadwood likely represents a key structural component for bank voles, providing shelter, nesting sites, and protection from predators while contributing to microclimatic stability and food availability (BULL, 2002; RADU, 2006; KAJITA and KAJIMURA, 2024). This association is consistent with previous studies describing the species as

strongly linked to forest interiors and dense ground cover (SUCHOMEL et al., 2014). From a functional perspective, these habitats increase structural complexity and reduce predation risk while maintaining access to resources. As predicted by habitat-mediated coexistence theory (VAN ALLEN and RUDOLF, 2015), species dependent on complex structures may become spatially segregated from more generalist competitors.

The third hypothesis predicted that *Apodemus* spp. would be associated with herbaceous and relatively open microhabitats, which was supported by our ordination analysis of the data. Wood mice are generally more mobile and exploratory than voles, with larger home ranges and a greater capacity to exploit spatially variable resources (MONTGOMERY, 1980; MAZURKIEWICZ and RAJSKA-JURGIEL, 1998). These traits likely facilitate the use of open habitats where food availability may be higher but structural protection is reduced. Behavioral flexibility may compensate for increased exposure to predation.

Implications for coexistence in forest rodent communities

Notably, our data suggest that interspecific segregation occurs at very fine spatial scales within a single trapping grid (~0.1 ha), highlighting the importance of meter-scale habitat variation for sympatric forest rodents. This suggests that even in relatively homogeneous forests, microhabitat structure can strongly influence community organization. These results are consistent with theoretical models predicting that environmental heterogeneity increases niche dimensionality and allows ecologically similar species to coexist (AMARASEKARE, 2003; CHESSON, 2000). Structural elements such as deadwood, canopy cover, and understory vegetation thus contribute directly to maintaining biodiversity.

From a management perspective, maintaining structural heterogeneity is essential for supporting diverse small mammal communities. Practices such as deadwood retention, promotion of understory variability, and preservation of fine-scale habitat mosaics are particularly important (LINDENMAYER and FRANKLIN, 2013; SEIBOLD et al., 2015). Rodents such as *C. glareolus* and *A. flavicollis* play key ecological roles as seed predators, dispersers, and prey for higher trophic levels (e.g. JENSEN, 1985; FERRARI et al., 2025). Conserving the microhabitat features that support their coexistence may therefore have cascading effects on forest ecosystem functioning and resilience.

Study limitations and future research

Despite these insights, some limitations should be acknowledged. First, the data represent a single sampling period and therefore capture only a temporal snapshot of rodent activity. Seasonal and interannual changes in vegetation structure, food availability, and population dynamics could modify habitat associations over time (ROCHA et al., 2017). Second, the environmental variables available for analysis were relatively coarse and did not include more detailed measures of litter depth, deadwood volume,

or three-dimensional vegetation structure. Incorporating such variables in future studies could improve the mechanistic understanding of habitat selection. Finally, the present study does not directly test the role of interspecific competition or behavioral interactions between species. Experimental approaches or long-term monitoring would be necessary to disentangle the relative contributions of habitat preference and biotic interactions to the observed patterns of spatial segregation.

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Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

The dataset presented in the Appendices is available online at <https://osf.io/q3pf5>

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