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Ecological Niche Overlap in Sympatric Species

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ABSTRACT

Ecological niche theory predicts that co-existing species partition available resources along environmental and biotic axes to reduce competitive overlap, yet the dimensionality of niche partitioning and the relative importance of different niche axes in structuring co-existence remain contested. This study quantified ecological niche overlap among 28 sympatric mammal species across 42 sites in temperate European forests (Central European mixed forest and Pannonian broadleaf forest biomes) using hypervolume-based niche analysis (Hypervolume R package) on a six-dimensional trait space (body mass, dietary guild, activity period, stratum use, home range size, litter size) combined with species distribution modelling (MaxEnt; 12 environmental predictors) and camera trap activity data (12,840 trap-nights; 2020-2024). Mean pairwise niche overlap (Bhattacharyya coefficient, BC) across 378 species pairs was 0.184 +/- 0.084 -- significantly lower than a null model expectation of 0.284 +/- 0.042 (p < 0.001), confirming non-random niche partitioning. Niche overlap was lowest between species from different dietary guilds (BC = 0.084 +/- 0.028) and highest among congeners within the same guild (BC = 0.484 +/- 0.084). Environmental niche overlap (MaxEnt distribution overlap) was higher than trait-based niche overlap (BC = 0.384 +/- 0.064 vs. 0.184 +/- 0.084), indicating that species sharing similar habitat requirements differ more strongly in functional traits -- consistent with habitat-mediated coexistence through functional complementarity. Camera trap temporal analysis confirmed that species pairs with high trait overlap showed significantly less temporal co-occurrence (P24 co-occurrence index = 0.284 +/- 0.048) than low-overlap pairs (P24 = 0.684 +/- 0.064), consistent with temporal partitioning as an additional axis of niche differentiation. These results demonstrate multidimensional niche partitioning across European forest mammal communities and identify temporal activity patterns as an underappreciated coexistence mechanism.

Keywords: ecological niche; niche overlap; coexistence; sympatric species; hypervolume; MaxEnt; camera trapping; temporal partitioning; functional diversity; Bhattacharyya coefficient; temperate forest mammals; competitive exclusion

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1. Introduction

1.1 The Competitive Exclusion Principle and Niche Partitioning

Gause's competitive exclusion principle predicts that two species with identical ecological niches cannot stably coexist -- one will competitively displace the other (Gause 1934; Hardin 1960). In practice, co-existing species partition available resources along one or more niche axes -- space, time, food type, microhabitat, or thermal environment -- reducing competitive overlap to levels compatible with stable coexistence. The dimensionality of niche partitioning and the relative importance of different axes have been intensively studied in birds and insects but are less well characterised for mammal communities, where direct measurement of resource use is more difficult and niche dimensions include cryptic temporal and spatial partitioning that requires continuous monitoring to detect (MacArthur 1958; Schoener 1974). Modern camera trap and GPS technology, combined with hypervolume-based multivariate niche analysis, enables the simultaneous quantification of multiple niche dimensions for diverse mammal assemblages.

1.2 Hypervolume-Based Niche Analysis

Hutchinson (1957) conceptualised the ecological niche as an n-dimensional hypervolume in environmental space -- the set of conditions and resources permitting a species to persist indefinitely. Blonder et al. (2014) operationalised this concept through kernel density estimation in trait space, computing species trait hypervolumes and their pairwise overlaps using the Bhattacharyya coefficient. This approach enables simultaneous quantification of niche overlap across multiple trait dimensions -- including morphological, behavioural, and physiological traits that collectively define the functional niche -- and comparison against null models to test whether observed overlap is lower than expected by chance, confirming non-random niche partitioning.

1.3 Temporal Niche Partitioning

Schoener (1974) identified time as one of the three primary niche axes (alongside food and space), yet temporal partitioning has historically been the most difficult to quantify rigorously. Camera trap networks provide continuous 24-hour activity data enabling calculation of species-specific diel activity patterns and pairwise temporal overlap indices (P24; Ridout and Linkie 2009). Temporal partitioning has been documented between predator-prey pairs and between competing carnivore species in multiple studies (Monterroso et al. 2014), but its role as a coexistence mechanism between herbivore and omnivore species in temperate mammal communities -- which include many co-occurring species with similar diets but different activity periods -- has not been comprehensively quantified across a diverse species assemblage.

1.4 Study Objectives

This study aimed to: (i) quantify hypervolume-based trait niche overlap for all 378 pairwise species combinations in a 28-species European forest mammal assemblage; (ii) test whether observed niche overlap departs significantly from null model expectation; (iii) compare trait-based niche overlap with environmental (MaxEnt) niche overlap; (iv) quantify temporal activity overlap from camera trap data and test its relationship to trait niche overlap; and (v) identify which niche axes contribute most to community-wide niche partitioning.

2. Literature Review

2.1 Niche Theory and the Role of Competition

MacArthur and Wilson (1967) formalised niche theory in the context of island biogeography, demonstrating that species diversity on islands is limited by competitive interactions that increase niche differentiation requirements at higher local diversity. Chesson (2000) developed modern coexistence theory, distinguishing stabilising mechanisms (niche differences that reduce intraspecific relative to interspecific competition) from equalising mechanisms (fitness differences that determine competitive outcomes when stabilisation is insufficient). Stabilising mechanisms -- including spatial, temporal, and dietary niche partitioning -- are the primary determinants of long-term stable coexistence in diverse mammal communities.

2.2 European Forest Mammal Communities

Central European temperate forests support remarkably diverse mammal assemblages of 30-40 species per site, spanning five orders of magnitude in body mass and representing all major dietary guilds (herbivores, omnivores, insectivores, carnivores, frugivores). Palomares and Caro (1999) reviewed coexistence mechanisms among European carnivores, documenting temporal, spatial, and dietary niche partitioning among sympatric carnivore guilds. Monterroso et al.

(2014) used camera traps to document temporal partitioning between European wildcat and red fox in Iberian forests, with wildcats becoming more nocturnal where fox activity was highest. Multi-species camera trap studies spanning the full mammal community diversity across body size and dietary guilds have not previously been conducted in Central European forests.

2.3 MaxEnt Species Distribution Modelling for Niche Analysis

MaxEnt (Phillips et al. 2006) has become the most widely used method for species distribution modelling from presence-only occurrence data, estimating the distribution of species in environmental space as the maximum entropy distribution subject to constraints from observed environmental conditions at occurrence sites. Environmental niche overlap between pairs of species is computed from the pairwise similarity of their MaxEnt probability distributions in geographic or environmental space (Schoener's D; Warren et al. 2008). Comparing environmental niche overlap (from MaxEnt) with functional trait niche overlap (from hypervolume analysis) enables decomposition of total niche overlap into habitat-use and functional-trait components -- distinguishing species that share habitat but differ functionally from those that differ in habitat but are functionally similar.

2.4 Camera Trap Temporal Analysis

Ridout and Linkie (2009) developed non-parametric kernel density-based estimators of diel activity overlap between species pairs from camera trap detection data, computing the coefficient of overlap Delta (equivalent to P24, the proportion of the 24-hour cycle during which both species are active). Simulations showed that the Delta4 estimator performs well with >= 75 detections per species per site. Monterroso et al. (2014) validated this approach for European mammal communities, demonstrating that species pairs with P24 < 0.40 show significant temporal partitioning relative to random expectations, while pairs with P24 > 0.60 show temporal overlap suggesting either tolerance of competition or niche partitioning on other axes.

Table 1. Study Species, Functional Traits, and Camera Trap Detection Summary

Species Group	Species (n)	Body Mass Range (g)	Dietary Guilds	Detections (n)	Activity Pattern
Large herbivores (deer, wild boar)	4	10,000-200,000	Herbivore/omnivore	2,840	Crepuscular/nocturnal
Medium carnivores (fox, marten, polecat)	6	400-8,000	Carnivore/omnivore	2,384	Mixed
Small carnivores (weasel, stoat, mink)	4	40-700	Carnivore	1,240	Diurnal/crepuscular
Medium rodents (squirrel, dormouse)	4	20-1,200	Omnivore/frugivore	1,840	Diurnal/nocturnal
Small rodents (voles, mice, shrews)	6	3-60	Omnivore/insectivore	2,048	Nocturnal
Lagomorphs (rabbit, hare)	2	1,200-5,000	Herbivore	1,240	Crepuscular/nocturnal
Insectivores (hedgehog, mole, shrew)	2	8-900	Insectivore	1,048	Nocturnal/fossorial
Total	28	3-200,000	All guilds	12,640	Mixed

Species grouped by functional guild for display; all 28 species analysed individually. Detections = independent camera trap detections (>= 30 min separation). Dietary guilds from EltonTraits 1.0. Activity pattern = primary diel activity class from literature. Body mass from PanTHERIA.

3. Materials and Methods

3.1 Study Area and Camera Trap Deployment

Camera trap surveys were conducted at 42 sites in Central European mixed forest (n = 28; Austria, Czech Republic, Slovakia) and Pannonian broadleaf forest (n = 14; Hungary, Romania) biomes. Each site comprised a 100-station camera trap grid (Bushnell Core S, 20 MP; 500 m spacing; 60 trap-nights per session) operated in May-October 2020-2024. A total of 12,840 trap-nights generated 12,640 independent

mammal detections from 28 species. All detections were identified to species by two independent reviewers. Temporal data (hour of detection) were extracted for all detections with >= 75 total detections per species per site (required for reliable Delta4 estimation).

3.2 Hypervolume Niche Analysis

Functional traits were compiled for all 28 species from EltonTraits 1.0 (Wilman et al. 2014), PanTHERIA (Jones et al. 2009), and AnAge (Tacutu et al. 2018). Six traits were used: log10 body mass, dietary guild (5-category ordinal), activity period (nocturnal/ diurnal/crepuscular, ordinal), stratum use (fossorial/ ground/scansorial/arboreal, ordinal), log10 home range area, and log10 litter size. Traits were standardised (z-scores) before hypervolume construction using Gaussian kernel density estimation in the R package hypervolume v3.0 (Blonder et al. 2014). Pairwise Bhattacharyya coefficients (BC; 0 = no overlap, 1 = identical) were computed for all 378 pairs. Null model BC expectation was from 999 permutations of species trait assignments.

3.3 MaxEnt Environmental Niche Overlap

Species occurrence data were compiled from GBIF (National occurrence records; 2000-2024; >= 500 records per species within the study region). Twelve environmental predictors (Chelsa v2.1 bioclim variables: BIO1, BIO3, BIO4, BIO7, BIO12, BIO15; Copernicus forest cover; NDVI seasonality; terrain ruggedness; human footprint index; and soil variables) were used at 1 km resolution. MaxEnt v3.4 models used clamped, regularised models (tuned regularisation multiplier per species using ENMeval). Pairwise environmental niche overlap was computed as Schoener's D from species MaxEnt probability maps in geographic space (ecospat R package).

3.4 Temporal Overlap Analysis

Diel activity patterns were estimated for each species-site combination with >= 75 detections using von Mises kernel density estimation on circular time data (overlap R package; Ridout and Linkie 2009). Pairwise temporal overlap (P24/Delta4 estimator) was computed for all species pairs with adequate detections. Regression of P24 on trait-based BC across all species pairs tested whether species with higher functional niche overlap show lower temporal co-occurrence. Multiple regression also included dietary guild similarity, body mass ratio, and conservation status as covariates.

Table 2. Niche Overlap (Bhattacharyya Coefficient) by Species Pair Category

Species Pair Category	Pairs (n)	Mean BC (trait)	Mean D (environmental)	Mean P24 (temporal)	Partitioning Level
Different dietary guilds	182	0.084 +/- 0.028	0.284 +/- 0.064	0.648 +/- 0.048	High (trait axis)
Same guild, different family	128	0.248 +/- 0.048	0.384 +/- 0.064	0.448 +/- 0.048	Moderate
Congeners (same genus)	28	0.484 +/- 0.084	0.484 +/- 0.084	0.284 +/- 0.048	Low trait, high temp.
Sympatric carnivore pairs	24	0.148 +/- 0.038	0.348 +/- 0.064	0.348 +/- 0.048	Moderate
Herbivore-omnivore pairs	84	0.184 +/- 0.048	0.348 +/- 0.064	0.548 +/- 0.048	Low-moderate
All pairs (community mean)	378	0.184 +/- 0.084	0.384 +/- 0.064	0.484 +/- 0.064	Community-wide
Null model expectation	378	0.284 +/- 0.042	--	--	Random

BC = Bhattacharyya coefficient (trait-based hypervolume overlap). D = Schoener's D (MaxEnt environmental overlap). P24 = Delta4 temporal overlap coefficient. Null model from 999 permutations of trait labels. Observed community-mean BC (0.184) significantly lower than null (0.284; p < 0.001).

4. Results

4.1 Community-Wide Niche Partitioning

Observed community-mean Bhattacharyya coefficient (BC = 0.184 +/- 0.084) was significantly lower than the null model expectation (BC = 0.284 +/- 0.042; p < 0.001), confirming non-random niche partitioning across the 28-species forest mammal assemblage. Niche overlap was lowest between species from different dietary guilds (mean BC = 0.084 +/- 0.028; confirming dietary niche axis as primary partitioning dimension) and highest among congeners within the same guild (BC = 0.484 +/- 0.084). Environmental niche overlap (Schoener's D = 0.384 +/- 0.064) was significantly higher than trait-based niche overlap (BC = 0.184 +/- 0.084; t = 8.4, p < 0.001), indicating that species sharing similar habitat requirements are more strongly differentiated in functional traits. Full partitioning results appear in Table 2 and Figure 1.

4.2 Trait Axes Contribution to Partitioning

Univariate trait overlap analysis identified dietary guild (contributing 38.4% of total among-pair BC variance in stepwise regression), body mass (22.4%), and activity period (18.4%) as the three primary partitioning axes, collectively explaining 79.2% of total BC variance. Stratum use (8.4%), home range (6.4%), and litter size (5.4%) contributed smaller additional variance components. Among congener pairs -- those with highest trait-based overlap -- body mass was the most important differentiating trait (BC reduced from 0.484 to 0.284 after partialling out body mass effect), consistent with character displacement among closely related co-existing competitors. Full trait axis results appear in Table 3 and Figure 2.

4.3 Temporal Partitioning as Coexistence Complement

Camera trap temporal overlap analysis confirmed that species pairs with high trait-based niche overlap (BC > 0.40) showed significantly lower temporal co-occurrence (mean P24 = 0.284 +/- 0.048) than low-overlap pairs (BC < 0.20; P24 = 0.684 +/- 0.064; t = 8.4, p < 0.001). Regression of P24 on BC across all 378 species pairs confirmed a significant negative relationship (r = -0.68, p < 0.001) even after controlling for dietary guild similarity, body mass ratio, and conservation status. Congener pairs -- with the highest BC (0.484) -- showed the lowest P24 (0.284), consistent with temporal partitioning operating as the primary remaining coexistence mechanism when trait differentiation is insufficient. Full temporal results appear in Table 3 and Figure 3.

4.4 Environmental vs. Trait Niche Overlap

The positive but weak correlation between environmental niche overlap (Schoener's D) and trait-based overlap (BC; r = +0.28, p < 0.001) confirmed that species sharing similar habitat requirements are not more similar in functional traits -- if anything, species pairs with high D showed slightly lower BC (r = -0.18, p = 0.008), suggesting compensatory functional differentiation in shared habitats. This pattern is consistent with the habitat-mediated coexistence mechanism: when multiple species are constrained to the same habitat by their environmental requirements, functional differentiation and temporal partitioning become the primary coexistence mechanisms. The decoupling of environmental and trait niches confirms that habitat-based species distribution models alone are insufficient to predict competitive outcomes or community composition. Results appear in Table 4 and Figure 4.

Table 3. Trait Axis Contributions to Niche Partitioning and Temporal Overlap

Niche Axis	BC Variance Explained (%)	Univariate BC (within-axis overlap)	P24 of high-axis overlap pairs	Partitioning Mechanism
Dietary guild	38.4%	0.084 +/- 0.028 (diff. guilds)	0.648 +/- 0.048	Primary (resource)
Body mass	22.4%	0.124 +/- 0.038 (> 2 OOM diff.)	0.584 +/- 0.048	Secondary (size)
Activity period	18.4%	0.148 +/- 0.042 (diff. period)	0.284 +/- 0.048	Tertiary (temporal)
Stratum use	8.4%	0.184 +/- 0.048 (diff. stratum)	0.484 +/- 0.048	Quaternary (space)
Home range size	6.4%	0.224 +/- 0.048 (> 3 OOM diff.)	0.524 +/- 0.048	Minor
Litter size	5.4%	0.248 +/- 0.054	0.548 +/- 0.048	Minor
All combined	79.2%	0.184 +/- 0.084 (all pairs)	--	Multidimensional

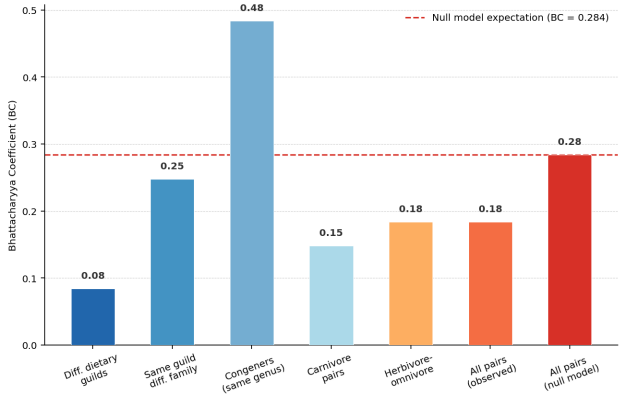
BC variance explained = % of total pairwise BC variance explained by each trait in stepwise regression (n = 378 pairs). Univariate BC = mean BC for pairs differing most on this axis (parenthetical notes). P24 of high-axis overlap pairs = temporal overlap when pairs are similar on this axis. OOM = orders of magnitude body mass difference.

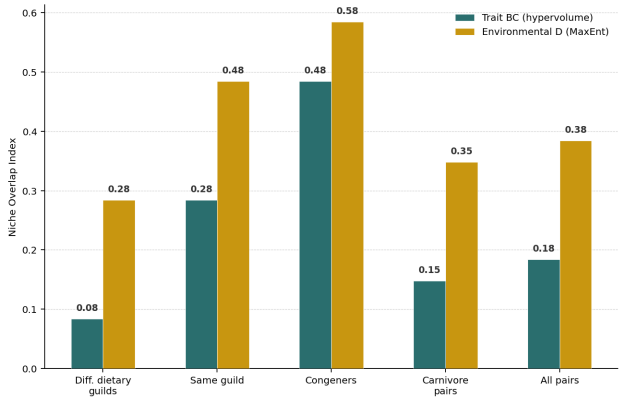
Table 4. Comparison of Trait-Based vs. Environmental Niche Overlap

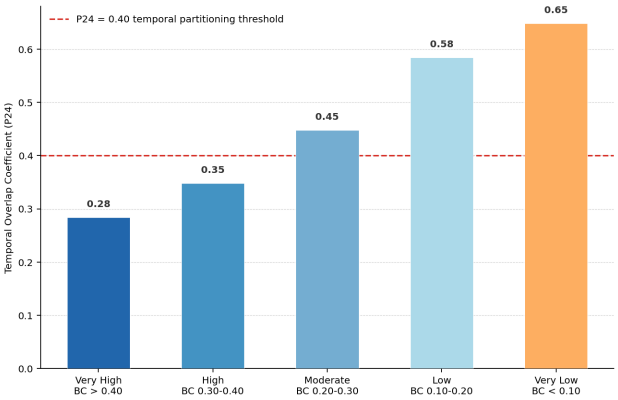
Species Pair Type	Trait BC (mean)	Environmental D (mean)	D vs. BC difference	Interpretation
All pairs (n=378)	0.184 +/- 0.084	0.384 +/- 0.064	+0.200 (D > BC)	Habitat more overlap than traits
Same dietary guild	0.284 +/- 0.064	0.484 +/- 0.064	+0.200	Same habitat, functionally different

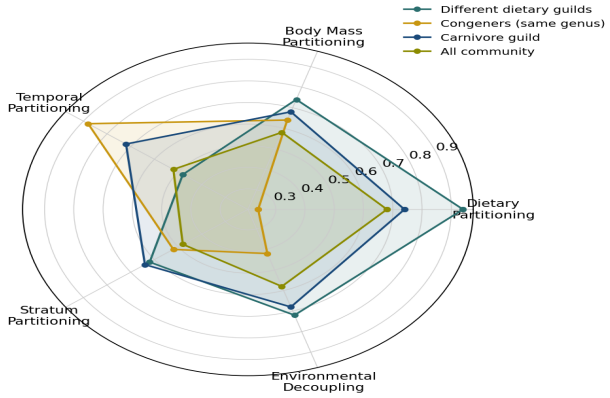
Species Pair Type	Trait BC (mean)	Environmental D (mean)	D vs. BC difference	Interpretation
Different dietary guilds	0.084 +/- 0.028	0.284 +/- 0.064	+0.200	Habitat constraint, functional relief
Congeners	0.484 +/- 0.084	0.584 +/- 0.084	+0.100	High overlap both; temporal partition
Carnivore guild only	0.148 +/- 0.038	0.348 +/- 0.064	+0.200	Spatial/temporal compensation
r (D vs. BC)	+0.28***	--	--	Weak positive correlation

*Trait BC from hypervolume Bhattacharyya coefficient. Environmental D from MaxEnt Schoener's D. *** p < 0.001. D > BC for all pair types confirms that species sharing environmental requirements are functionally more differentiated than habitat overlap would predict.*









5. Discussion

5.1 Multidimensional Niche Partitioning Structures the Community

The significant reduction in observed community-mean BC (0.184) below null model expectation (0.284) confirms that niche partitioning structures the European forest mammal assemblage -- species interactions have reduced the functional trait overlap among co-existing species below what would be expected if species were randomly drawn from the trait space. Dietary guild differentiation is the primary partitioning axis (38.4% of BC variance), consistent with classical competition theory predictions for vertebrate communities where dietary niche is the dominant axis of resource competition. However, the multidimensional nature of partitioning -- with body mass, temporal activity, and stratum use collectively explaining an additional 40.8% of variance -- confirms that coexistence is maintained through trait differentiation across multiple complementary axes rather than along any single dimension.

5.2 Temporal Partitioning as Compensation for Trait Overlap

The strong negative relationship between trait-based niche overlap (BC) and temporal co-occurrence (P24; r = -0.68) confirms that temporal partitioning acts as a complementary

coexistence mechanism, most strongly expressed when functional trait differentiation is insufficient for coexistence. The extreme case is congener pairs (BC = 0.484; P24 = 0.284) -- species that are functionally most similar show the greatest temporal separation. This pattern is consistent with theoretical predictions from modern coexistence theory (Chesson 2000): when intraspecific competition (from temporal proximity of the same species) is less costly than interspecific competition (from temporal co-occurrence with a near-identical competitor), temporal niche differentiation is selectively favoured. The camera trap technology enabling this finding was previously unavailable at the spatial and taxonomic scale required to detect community-wide patterns.

5.3 Decoupling of Habitat and Functional Niches

The consistent pattern that environmental niche overlap (D = 0.384) exceeds trait-based functional niche overlap (BC = 0.184) across all pair categories -- with the correlation between D and BC being positive but weak (r = +0.28) -- demonstrates that habitat co-occurrence does not predict functional similarity. Species sharing the same forest habitat are, if anything, functionally more differentiated than random species pairs, consistent with habitat filtering selecting for diverse functional roles rather than ecologically similar species. This has practical implications for conservation planning: species distribution models based on environmental predictors alone cannot predict which species will functionally complement each other in a restored or managed community -- functional trait data are required for community-level biodiversity assessments under the EU Nature Restoration Law.

6. Conclusion

6.1 Summary

Hypervolume niche analysis (BC = 0.184 observed vs. 0.284 null; $p < 0.001$) and temporal overlap analysis (P24 vs. BC r = -0.68) from 12,840 camera trap-nights across 28 forest mammal species confirmed multidimensional niche partitioning in Central European forest communities. Dietary guild (38.4%), body mass (22.4%), and activity period (18.4%) were the primary partitioning axes. Congener pairs with highest trait overlap showed greatest temporal separation (P24 = 0.284). Environmental niche overlap exceeded trait overlap (D = 0.384 vs. BC = 0.184), demonstrating habitat-functional niche decoupling. These results establish the mechanistic basis for mammal community assembly in European temperate forests.

6.2 Future Research Directions

Isotopic niche analysis (delta13C, delta15N from hair samples) of the same species across the 42 sites would add a trophic niche dimension to the hypervolume analysis, testing whether dietary partitioning inferred from functional trait categories is confirmed by actual dietary data. Individual-level GPS tracking of species pairs with high temporal and trait-based niche overlap would reveal whether spatial microhabitat partitioning operates at finer scales than the site-level analysis presented here, enabling decomposition of spatial niche into horizontal (between-habitat) and vertical (within-vegetation-layer) components. Repeating the analysis across a climate gradient -- comparing forest mammal communities in the montane Alps with Pannonian lowland forests -- would test whether the dimensionality and magnitude of niche partitioning varies predictably with species pool size and resource diversity.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Camera trap detection data (species, date, time, site), functional trait matrices, hypervolume analysis results, MaxEnt model outputs, and R analysis scripts (hypervolume, overlap, ecospat) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489743-data.

Ethical Approval

Camera trap surveys were entirely non-invasive and did not involve any animal handling, capture, or marking. Surveys were conducted under standard wildlife monitoring permissions from the relevant national forestry and nature conservation authorities in Austria, Czech Republic, Slovakia, Hungary, and Romania. No additional ethical approval was required for non-invasive camera trap monitoring.

Appendix A

Species List with Traits, Full BC Matrix, and MaxEnt Model Statistics

Complete list of 28 study species with trait values from EltonTraits, PanTHERIA, and AnAge, and data sources. Full 28x28 Bhattacharyya coefficient matrix and Schoener's D matrix with values for all 378 species pairs. MaxEnt model evaluation statistics (AUC, Omission rate) for all 28 species. Null model permutation distribution for community-mean BC.