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**Habitat-mediated reassembly of rodent assemblages along an urban–suburban–rural gradient**

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**Abstract:** Urbanization profoundly alters habitats and biological communities; however, its impacts on rodent assemblages and functional traits across varying habitat types remain inadequately understood. We surveyed rodents across 81 subplots encompassing woodland, farmland, and residential habitats along an urban-suburban-rural gradient in Wuhan, a rapidly urbanizing megacity of central China. We collected data on species composition, external morphology, organ traits, and local environmental covariates, analyzing them via multispecies count models, beta-diversity partitioning, community-weighted mean trait decomposition, ordination, path analysis, and nested cross-validation. In 9,720 trap-nights, we captured 246 individuals representing six species across four genera. Capture success increased from urban to rural sites and was significantly higher in farmland and woodland than in residential areas. Rodent assemblage composition varied significantly with urbanization, habitat type, and their interaction, with habitat explaining a substantially greater proportion of the variation. Residential assemblages were characterized by larger body-sized *Rattus* spp., whereas farmland and woodland were dominated by the smaller *Apodemus agrarius* and *Niviventer confucianus*, respectively. Among-site variation in community-level body size was primarily driven by species turnover and shifts in dominance, whereas organ traits exhibited high intraspecific heterogeneity that was not consistently explained by the measured environmental variables. Furthermore, human activity intensity was significantly associated with assemblage composition. These findings suggest that urbanization shapes rodent functional composition predominantly through habitat-mediated species turnover and dominance shifts, rather than through uniform intraspecific responses. This study underscores the necessity of habitat-specific rodent monitoring and management strategies in rapidly urbanizing landscapes.

**Keywords:** urbanization; rodent assemblage; habitat filtering; community-weighted mean traits; species turnover

## 1. Introduction

Urbanization is a major driver of global environmental change, involving the conversion of natural and semi-natural ecosystems into human-dominated built landscapes (Johnson and Munshi-South, 2017; González-Morales et al., 2025). At a broader socioeconomic–environmental scale, urbanization exerts contrasting spatial effects on ecological efficiency, as evidenced by provincial-level data from China (Yao et al., 2021). Although urbanization has fostered socioeconomic progress, it has engendered widespread ecological degradation, including biodiversity decline, habitat fragmentation, intensified urban heat island effects, and impaired ecosystem functioning (Grimm et al., 2008). Through environmental filtering and species turnover, urbanization reshapes community structure and imposes directional selection on organismal morphology, behavior, and physiology, thereby driving rapid adaptive evolution (McKinney, 2006; McKinney, 2008; Alberti et al., 2017).

Growing empirical evidence has validated urban-driven phenotypic shifts across a wide range of taxonomic groups. For example, at the ecosystem level, artificial light at night in urban environments can increase leaf toughness and reduce herbivory, thereby decreasing food availability for herbivorous insects and potentially triggering cascading effects on predatory insects and insectivorous birds (Cao et al., 2024). At the community level, birds frequently show reduced species richness and increasing compositional similarity (Sidemo-Holm et al., 2022). At the population level, Munshi-South and Kharchenko (2010) found that spatial isolation among urban green spaces result in genetic differentiation among white-footed mouse (*Peromyscus leucopus*) populations in New York City parks. At the individual level, long-term records from North America indicate that small mammals generally declined in body size as temperatures increased during urbanization (Searing et al., 2023). Previous studies have well documented the ecological impacts of urbanization across multiple scales, ranging from ecosystem processes and community structure to population genetics and individual phenotypes. Nevertheless, integrative

research on this topic remains limited (Łopucki et al., 2013; Łopucki and Kitowski, 2017; Wang et al., 2023).

Rodents are characterized by remarkable species diversity, broad geographic distributions, high reproductive potential, and pronounced environmental plasticity to environmental variation. As primary consumers and important prey for a wide range of predators, they play an important role in some key ecological processes, including seed dispersal, vegetation regeneration, soil disturbance, and nutrient cycling (Dong and Zhang, 2008; Kay and Hoekstra, 2008). At the same time, rodents serve as important reservoirs and vectors for numerous zoonotic pathogens. Frequent human-rodent contact, especially in urban and peri-urban settings, may elevate public health risks (Zhang et al., 2010; Himsworth et al., 2013; Han et al., 2015). As rodent community composition, population dynamics, and phenotypic variation are sensitive to habitat modification and anthropogenic disturbance, they are ideal model systems for assessing both the ecological consequences of urbanization and public-health risks (Zhao et al., 2024; Zhang et al., 2026).

The adaptability of urban rodents has garnered increasing attention in urban ecology and evolutionary biology. Synanthropic species such as *Rattus norvegicus* and *Mus musculus* exhibit urban-associated shifts in behavior, physiology, and phenotype, encompassing altered human avoidance, activity patterns, stress responses, immune function, metabolism, and traits related to locomotion or body size (Harpak et al., 2021; Fardell et al., 2021). These responses are likely driven by multiple urban selective pressures, including anthropogenic food resources, habitat fragmentation, altered predator and pathogen regimes, pollution, and chronic human disturbance (Becker et al., 2015; Blasdell et al., 2022). However, most existing studies have focused on highly modified residential or built-up habitats (Byers et al., 2019). Few of them have compared rodent responses across urban gradients spanning natural, semi-natural, and human-modified systems, or examined gradient-dependent responses at community, population, and individual levels (Mazza et al., 2020; Larson and Sander, 2025). Furthermore, the patterns and mechanistic basis of trait

divergence along urbanization gradients remain poorly understood, particularly regarding the integrated links among community reassembly, population differentiation, and individual morphological trait syndromes. It remains unclear whether urbanization effects on rodents are driven more by broad urbanization gradients or local habitat filtering, whether community-level trait shifts reflect species turnover/dominance or intraspecific variation, and whether rodent metrics can serve as repeatable sentinels across habitat contexts.

Wuhan, a rapidly urbanizing metropolis in central China, exhibits a distinct urban–suburban–rural gradient (Zhao et al., 2025). Remnant woodlands, farmlands, and residential areas are interspersed across this landscape. This spatial configuration enables comparisons of urbanization intensity and habitat types within a shared regional species pool, facilitating tests of the consistency in rodent assemblage responses to varying urbanization and habitats.

Here, we analyzed species composition, capture rates, taxonomic diversity, morphology of dominant species, community-weighted mean (CWM) traits, and local environmental conditions to assess rodent's responses at both community and population levels. Specifically, we addressed four key questions: (1) Do rodent diversity and assemblage composition vary primarily along the urbanization gradient, or are they more strongly structured by habitat type (woodland, farmland, and residential area)? (2) What are the primary drivers of shifts in community-weighted traits: species turnover and changes in dominance, or intraspecific trait variation? (3) Which local environmental factors best explain the variation in rodent assemblage structure and trait composition across different habitat types? By integrating taxonomic, functional, morphological, and environmental data, this study evaluates the potential of rodent communities to serve as sensitive indicators of habitat-mediated ecological change in rapidly urbanizing landscapes.

## 2 Methods

### 2.1 Study Area

This study was carried out in the Wuhan Metropolitan Area and its adjacent regions (29°58′–

31°22′ N, 113°41′–115°05′ E), situated in the eastern Jianghan Plain along the middle reaches of the Yangtze River (Fig. 1). The area features a subtropical monsoon climate, characterized by ample thermal resources, plentiful rainfall, and precipitation–temperature synchronization. Mean annual temperature is 16.9 °C, and annual precipitation is about 1300 mm. As the largest metropolis in central China, Wuhan has undergone rapid and ongoing urbanization over recent decades. This city has a permanent population of over 13.8 million and an urbanization rate of approximately 85.0%, while its built-up area has more than doubled since 2000. The administrative region spans approximately 155 km north–south and 134 km east–west, covering a total area of more than 8 570 km². Wuhan hosts tens of thousands of forest patches, including plantations, semi-natural forests, and natural forests. Together with urban zones, farmlands, lakes, rivers, and wetlands, these patches form a heterogeneous mosaic landscape that supports high biodiversity. Detailed descriptions of the study region have been described in detail in our previous publications (Zhao et al., 2024; Chen et al., 2025; Zhang et al., 2026).

**2.2 Trapping plots and habitat factor measurement**

Using ArcGIS Pro 3.1 (Esri, Redlands, CA, USA), we delineated a circular study area with a radius of 100 km, centered on the Wuhan Municipal Government (30°35′44″ N, 114°17′56″ E). A composite urbanization index was constructed from impervious surface proportion, population density, and built-up area. Based on this index, the study area was divided into urban (0 – 40 km), suburban (40 – 70 km), and rural zones (70 – 100 km) based on distance from the center, reducing the potential bias associated with distance-based classification alone. The core area encompassed Wuhan, while the peripheral reference areas included Tongshan County in Xianning and Zhaoshan Town in Ezhou, Hubei Province (Fig. 1).

Three habitats, including woodland, farmland, and residential habitats, were surveyed within each urbanization gradient. Nine trapping subplots were established for each habitat type in each zone, giving a total of 81 subplots (three urbanization zones × three habitat types × nine subplots).

Adjacent subplots were separated by at least 1 km wherever possible to reduce spatial autocorrelation. Woodland and farmland subplots covered at least 1 000 m², while each residential subplot included at least ten households. Sites that had undergone large-scale rodent control or vegetation clearance during the preceding year were excluded or replaced by a similar neighbor patch. The locations and characteristics of all subplots are provided in Supplementary Table S1.

The environmental variables included land surface temperature, normalized difference vegetation index (NDVI), population density, and the proportion of built-up land. Land surface temperature data were derived from Landsat 8/9 imagery obtained from the United States Geological Survey and the Geospatial Data Cloud (https://www.usgs.gov/). Images corresponding to the two rodent-trapping seasons in 2024 were selected, with four scenes retained for each season. Land surface temperature was retrieved in ENVI 5.6 using the STB10 thermal infrared band. Temperature values were then extracted for each sampling location in ArcMap 10.6 and used in subsequent analyses. NDVI data were obtained from the MOD13A3 Version 6.1 monthly vegetation-index product released by the National Aeronautics and Space Administration. Monthly NDVI data for 2024 were extracted and quality controlled. A pixel-wise maximum-value composite was then used to derive the annual maximum NDVI, representing peak vegetation growth within each sampling area. Population data were obtained from the 2024 LandScan population-distribution dataset produced by Oak Ridge National Laboratory. Population density was extracted according to the spatial location of each sampling subplot and used as an indicator of human activity intensity. Land-cover information was obtained from the Wuhan University 30 m land-use dataset covering 1985–2025 (https://zenodo.org/records/15853565). Built-up land was extracted for 2024. Its proportion within the buffer surrounding each sampling subplot was calculated and used as an indicator of surface urbanization. All spatial datasets were projected to a common coordinate reference system (CRS), spatially aligned, and clipped to the study area. Environmental variables were then extracted using the coordinates of each subplot and its

surrounding buffer.

**2.3 Animal trapping and data collection**

Rodent trapping was conducted during spring (March–May) and autumn (September–November) of each experimental year, corresponding to peak rodent activity, to ensure representative sampling of community composition. Standard live-trapping procedures were applied across all sites, while trap layout was flexibly adapted to habitat conditions. In woodland and farmland habitats, traps were deployed along linear transects at a density of 20 live traps per transect with a 5-m spacing. In residential habitats, 20 traps were installed per site, with two traps placed at each selected household and approximately 5 m apart. All traps (25 × 12 × 12 cm) were made of wire-mesh and covered with wooden boards to shield captured individuals from direct sunlight and rain. Traps were set between 17:00 and 19:00 daily, inspected the following morning during 07:00 to 09:00, and operated for three consecutive days. Traps were baited with peanuts and fermented soybean cake, supplemented with cucumber slices as a food and water source. Cotton was placed inside each trap to provide thermal insulation, reduce stress, and keep warming (Torre et al., 2023). Pregnant females and juveniles (body mass < 50% of adult mass) were recorded and released immediately. Adult individuals were transferred individually to the laboratory in cloth bags for further processing without accidental mortality. For each specimen, capture location, date, species, sex, and age groups were documented. Animals were assigned to four age groups based on body mass and tooth wear to ensure sample homogeneity (Yang 2016). Capture rate [(captured individuals / effective trap-nights) × 1,000] and relative abundance [(number of captured individuals each species / Total number of captured individuals) × 100%] were calculated to reflect rodent abundance.

Only adult rodents were transported to the laboratory and no accidental mortality occurred before planned euthanasia. All individuals were humanely euthanized via carbon dioxide ($CO_2$) inhalation in compliance with AVMA guidelines (American Veterinary Medical Association,

2020). For each individual, body mass (g) and carcass mass (g) were measured using an electronic balance to the nearest 0.01 g. Body length (mm), tail length (mm), ear length (mm) and hind foot length (mm) were measured using a stainless-steel ruler to the nearest 0.1 mm, following standard methods (Yang, 2016). Lee's index (body mass^(1/3) / body length × 1,000) was calculated as an indicator of body compactness. The liver, spleen, lungs, kidneys, and epididymis were dissected, cleaned of adipose and connective tissues, blotted dry, and weighed using an analytical balance to the nearest 0.001 g. Visceral coefficients (organ mass / body mass × 100%) were calculated to evaluate relative organ development and physiological status. Morphological analyses were performed separately for each species to account for interspecific differences in body size (Zhang et al., 2026).

**2.4 Data analysis**

Rodent assemblage composition, external morphology, organ traits, and environmental variables collected in spring and autumn were analyzed at three levels: community, population, and trait-environment coupling. We also evaluated the potential of rodent metrics as candidate ecological sentinels. Annual capture abundance was compared among urbanization gradient and habitats using negative-binomial generalized linear models (GLM). NB1 and NB2 variance structures were compared, and the main model was selected based on AIC values, model convergence, and residual diagnostics (Brooks et al., 2017). Capture occurrence was compared using mean bias-reduced logistic regression (Kosmidis et al., 2021). Poisson, negative-binomial, and Conway-Maxwell-Poisson generalized linear models were conducted for species richness comparison (Sellers and Shmueli, 2010). Shannon diversity and Pielou evenness were calculated as descriptive metrics (Shannon, 1948; Pielou, 1966). Simpson dominance was used to describe dominance structure (Simpson, 1949). For coverage-standardized effective number (Hill diversity), all 246 adult rodents were pooled separately by urbanization gradient and habitat type. Hill numbers were then estimated for assemblages pooled by urbanization gradient or habitat

(Hill, 1973; Chao and Jost, 2012). All groups were standardized to a common sample coverage of 0.973. Hill diversity was estimated at three different orders: q = 0 denotes species richness, q = 1 denotes exponential Shannon diversity, and q = 2 denotes inverse Simpson diversity.

Assemblage composition was analyzed using the species abundance matrix from all sites. Negative-binomial many-GLM was conduct to test the effects of urbanization gradient, habitat type, and their interaction (Wang et al., 2012). Species-level tests used the corresponding resampling-adjusted results (Warton et al., 2017). β-diversity and spatial species turnover were assessed using Bray-Curtis dissimilarity (Baselga, 2010). Bray-Curtis dissimilarity was calculated for occupied sites with at least one rodent captured (Bray and Curtis, 1957), followed by principal coordinates analysis to display patterns shaped by urbanization gradients and habitats (Gower, 1966). To interpret the assemblage differences based on Bray-Curtis dissimilarity, differences in assemblage centroids were tested using permutational multivariate analysis of variance (PERMANOVA), whereas differences in within-group multivariate dispersion were tested using permutational multivariate dispersion test (PERMDISP) (Anderson, 2001, 2006).

Within each urbanization gradient and habitat type, multiple-site Sørensen dissimilarity was calculated and partitioned into species-turnover and nestedness-resultant components (Baselga, 2010). Indicator-species analysis used IndVal.g to test associations of individual species with urbanization gradients or habitat types (De Cáceres and Legendre, 2009).

Separate PCAs were conducted for external morphology and organ trait dataset (Hotelling, 1933; Jolliffe and Cadima, 2016). External morphological variables included body mass, carcass mass, body length, tail length, ear length, and hind-foot length. Organ traits included liver, spleen, lung, and total kidney coefficients. The variables were log10-transformed, centered, and standardized before PCA. The direction of each principal-component axis was aligned according to the loadings of key traits. Morphological PC1 and organ PC1 and PC2 were retained for later analysis. Observed CWM used the observed mean trait value of each species within each site.

Fixed CWM used the species grand means from the full dataset. Both components used the same weights based on the number of individuals with valid trait measurements. Intraspecific trait variation (ITV) was defined as Observed CWM minus Fixed CWM (Ricotta and Moretti, 2011; Lepš et al., 2011).

Among-site variance in observed CWM was further partitioned into fixed CWM variance, ITV variance, and their covariation component. The covariation component was twice the covariance between fixed CWM and ITV. Positive values indicate reinforcement between the two components, whereas negative values indicate compensation (Lepš et al., 2011). Uncertainty (95% CI) was estimated using 5 000 sampling site-level bootstrap resamples. Associations between CWM and the environment were analyzed using linear models with anthropogenic intensity, habitat type, the anthropogenic intensity × habitat interaction, and NDVI. HC3 heteroscedasticity-robust standard errors were used. Both anthropogenic intensity and the response variables were standardized. Simple slopes for the three habitat types were adjusted for FDR within each trait-component test family (MacKinnon and White, 1985).

Supplementary individual-level analyses were conducted for the dominant species. These analyses examined morphological PC1, organ PC1, organ PC2, and selected allometric relationships. Assemblage data from occupied sites were Hellinger-transformed. A global Redundancy Analysis (RDA) was then fitted using anthropogenic intensity, NDVI, and habitat type. Partial RDA and variation partitioning were used to separate independent and shared fractions of explained variation (Legendre et al., 2011).

Statistical significance was set at 0.05. Multiple tests were controlled within prespecified test families using the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995). Data were organized in Microsoft Excel 2021. Statistical analyses and the main visualizations were completed in R 4.5.2.

**2.5 Ethical approval**

All animal handling was approved by the Animal Ethics and Welfare Committee of Central China Normal University (Permit No. SYXK (E) 2022-0052). All experiments were conducted in strict accordance with international ethical guidelines for wildlife research and the institutional standards for the care and use of laboratory animals in China.

## 3 Results

### 3.1 Rodent community

We captured 246 rodents in a total of 9 720 effective trap-nights, giving an overall capture rate of 25.3‰ (Table 1). The captures represented six species in four genera of the family Muridae. *Apodemus agrarius* and *Niviventer confucianus* was the dominant species, contributing to 132 and 85 individuals and 53.7% and 34.6% of the total catch. *Rattus norvegicus* and *Rattus tanezumi* were captured mainly in residential habitats, with 20 and 6 individuals recorded, respectively. *Mus musculus* and *Niviventer fulvescens* were rare, with only two and one individuals recorded. Capture rate increased along the urban-suburban-rural gradient, from 17.9‰ in urban sites to 25.9‰ in suburban sites and 32.1‰ in rural sites. Across habitat types, capture rate was highest in farmland (34.9‰), followed by woodland (30.2‰) and residential habitat (10.8‰).

The AIC of the annual NB1 model (350.02) was smaller than that of the NB2 model (358.46). Capture abundance was significantly associated with the urbanization gradient ($\chi^2$ = 7.12, $P$ = 0.028) and habitat type ($\chi^2$ = 18.86, $P$ < 0.001). By contrast, the zone × habitat interaction exerted no significant effect on capture abundance ($\chi^2$ = 7.85, $P$ = 0.097). The observed capture rate in urban woodlands was 8.33‰, which was considerably lower than that in suburban (37.04‰) and rural woodlands (45.37‰; Fig. 2A). Rodent alpha diversity varied substantially across habitat types and exhibited no consistent monotonic trend along the urban-suburban-rural gradient. Annual rodent occurrence was significantly shaped by habitat type ($\chi^2$ = 10.79, $P$ =

0.0045), whereas neither the urbanization gradient ($P = 0.486$) nor its interaction with habitat type exerted a significant influence (Fig. 2B). Species richness displayed divergent patterns across combinations of urbanization levels and habitat types, with no consistent increasing trend from urban to suburban and rural sites (Fig. 2C). Additionally, urban rodent assemblages harbored a lower estimated effective number of species (Fig. 2D).

Community differences were distributed across several ordination dimensions (Fig. 3A, B). The first two axes of the Bray-Curtis PCoA for occupied sites accounted for 22.6% and 9.6% of the ordination variation, respectively (Fig. 3A, B). In the additive PERMANOVA, after controlling for the other factor, the marginal $R^2$ values for urbanization gradient and habitat type were 4.6% and 38.9% ($F = 2.23$, $P = 0.037$ for urbanization gradient, and $F = 18.89$, $P < 0.001$ for habitat type). In the model containing the interaction, the zone × habitat term accounted for 12.1% of the variation ($F = 3.50$, $P < 0.001$). Negative-binomial manyGLM detected significant associations of assemblage composition with urbanization gradient, habitat type, and their interaction across all sites [Fig. 3C, summed deviances were 29.25 ($P = 0.0038$), 117.22 ($P < 0.001$), and 22.86 ($P = 0.010$) accordingly].

Pairwise comparisons revealed significant differences in assemblages between urban and rural sites after adjustment ($P = 0.025$), whereas other pairwise comparisons along the urbanization gradient were non-significant. After accounting for the urbanization gradient, assemblage composition differed significantly across the three habitat types. Bray-Curtis dispersion was homogeneous along the urbanization gradient ($P = 0.287$) but varied significantly among habitat types ($P = 0.0018$). Jaccard dispersion also differed significantly across the urbanization gradient ($P = 0.010$). Accordingly, habitat-associated variation in distance-based assemblage structure arises from both shifts in group centroids and changes in within-group heterogeneity (Fig. 3D).

Beta-diversity partitioning varied in spatial assemblage structure. Within the urban, suburban,

and rural zones, total multiple-site dissimilarity was 0.800, 0.866, and 0.886, respectively. The turnover components were 0.720, 0.808, and 0.838, whereas the nestedness-resultant components were 0.080, 0.058, and 0.048 respectively (Fig. 3E). Total dissimilarity in woodland was 0.815, including a turnover component of 0.733 and a nestedness-resultant component of 0.081. The corresponding values in residential habitat were 0.796, 0.686, and 0.110. Farmland showed a different pattern, with a total dissimilarity of 0.635, a turnover component of 0 and a nestedness-resultant component of 0.635 (Fig. 3E).

After FDR correction, indicator-species analysis did not identify any species that consistently indicated urban, suburban, or rural zones. Habitat associations were far more distinct, with *A. agrarius* was significantly associated with farmland ($P = 0.001$), *N. confucianus* with woodland ($P = 0.003$), and *R. norvegicus* with residential habitat ($P = 0.001$, Fig. 3F).

**3.2 Community functional-trait variation and intraspecific responses of dominant species**

Principal component analysis showed that morphological PC1 explained 81.49% of the individual variation in external morphology and mainly represented overall body size. Organ PC1 and PC2 explained 34.92% and 26.43% of organ-trait variation, respectively. Liver coefficient had the largest positive loading on organ PC1, which was also related to variation in total kidney and spleen coefficients. Organ PC2 mainly contrasted a higher lung coefficient with a lower spleen coefficient.

Among occupied sites, variance partitioning of morphological PC1 showed that species turnover, ITV, and turnover-ITV covariation contributed 86.50%, 13.33%, and 0.17%, respectively. The corresponding values were 11.54%, 86.69%, and 1.78% for organ PC1, and 23.68%, 71.14%, and 5.19% for organ PC2 (Fig. 4A). Community functional-trait variation was mainly driven by species turnover, although intraspecific associations also existed within habitats. Farmland assemblages had a smaller body-size profile, residential ones had a larger profile, and woodland ones were intermediate. The distributions of observed and fixed morphology were

consistent with the distribution of dominant species.

After controlling for NDVI and allowing habitat-specific slopes, both observed morphological PC1 and fixed morphological PC1 were negatively associated with anthropogenic intensity in woodland. The standardized slopes were -1.421 and -1.142, respectively, with FDR-adjusted *P* values below 0.001. Morphological ITV also showed a negative association in woodland ($\beta$ = -0.983, 95% CI: -1.733 to -0.233, FDR-adjusted $P$ = 0.031, Fig. 4B). However, the source of overall organ-trait variation did not fully match its response along the gradient. In woodland, the anthropogenic-intensity slope was -1.054 for Fixed organ PC1 and 1.320 for Fixed organ PC2. Both FDR-adjusted P values were below 0.001. Organ ITV was not significant in any of the three habitat types.

Individual-level analyses focused on the three dominant rodent species (i.e., *A. agrarius, R. norvegicus*, and *N. confucianus*) across different habitats (Fig. 4C). No consistent urbanization-associated shifts in morphological or organ composite axes were detected in *A. agrarius*. Only the standardized total kidney coefficient was significantly higher in rural individuals relative to urban conspecifics (95% CI: 0.07–1.24, $F$ = 8.42, FDR-adjusted $P$ = 0.002).

Intraspecific analyses were performed for *A. agrarius, N. confucianus*, and *R. norvegicus*. However, robust cross-gradient comparisons were primarily restricted to *A. agrarius*, due to the limited overall sample size of *R. norvegicus* and the capture of only a single *N. confucianus* individual in urban zones. Collectively, the three dominant species exhibited no directionally consistent variations in morphological or organ composite axes along the urbanization gradient. For *A. agrarius* specifically, the urbanization gradient exerted no significant overall effects on morphological PC1, organ PC1, and organ PC2.

### 3.3 Anthropogenic gradient, local environment, and assemblage-trait associations

The continuous anthropogenic-intensity PC1 was constructed from population density and impervious-surface proportion. It explained 90.88% of their joint variation, and both variables had

high loadings of approximately 0.707. The global RDA was significant ($P < 0.001$), with an adjusted $R^2$ of 0.580. RDA1 and RDA2 explained 70.3% and 28.3% of the constrained variation, respectively (Fig. 5).

Marginal RDA tests showed that habitat type was the stronger explanatory term ($F = 29.63$, $P < 0.001$). Continuous anthropogenic intensity had a weaker independent association ($F = 3.42$, $P = 0.032$), whereas NDVI was not significant ($P = 0.942$). In the partial RDA, habitat type independently explained 44.54% of the variation after adjustment. The fractions explained by continuous anthropogenic intensity and NDVI were both very small. In the habitat-stratified analysis, the marginal effect of NDVI was significant within woodland ($P = 0.045$).

## 4 Discussion

### 4.1 Urbanization mainly caused habitat-mediated assemblage reassembly

McKinney (2006, 2008) and Deng (2024) proposed that urbanization simplifies small-mammal assemblages, reduces habitat specialists and urban avoiders, and favors generalists, urban adapters, and urban exploiters. Our study only partially supports this view. Hill diversity metrics that give greater weight to common and dominant species were generally lower in urban sites than in suburban and rural sites. Species richness did not show a monotonic increase along the urban-suburban-rural gradient. Although for assemblage composition, the manyGLM showed significant effects of urbanization gradient, habitat type, and their interaction, habitat type had a much stronger multivariate signal than the broad urbanization gradient. Thus, the answer to our first research question is that the primary ecological consequence of urbanization is the alteration of dominant species across different habitats. Diversity indices exhibited weaker responses to urbanization than compositional metrics, indicating that shifts in species composition or dominance serve as more sensitive indicators.

Our results suggest that species richness or the Shannon index alone may underestimate the effects of urbanization. PCoA and PERMANOVA also showed that the three habitat types

supported distinct species assemblages. Different sites with similar numbers of species may still vary in species identity and dominance. Such species changes may affect resource use, dispersal ability, trophic roles, and the potential for pathogen carriage. Previous studies have also shown that small-mammal responses to urbanization are often shaped by species-specific requirements for land cover, habitat fragmentation, and vegetation structure (Gomes et al., 2011; Larson and Sander, 2025).

Indicator-species analysis and beta-diversity partitioning provided further evidence of assemblage reassembly. Farmland dissimilarity was entirely attributable to species turnover-ITV covariation (nestedness). This pattern may reflect the widespread dominance of *A. agrarius* in farmland. The beta-diversity partitioning in other habitat types and the urbanization gradient was dominated by species turnover, showing that differences among sites mainly reflected replacement in species identity. In our study, *A. agrarius*, *N. confucianus*, and *R. norvegicus* were indicators of farmland, woodland, and residential habitat, respectively, but none consistently indicated all three habitat types. Therefore, habitat type appeared to be more closely associated with ecological filtering than the urbanization gradient.

**4.2 Community-level morphological differences were mainly driven by species turnover**

Community-weighted mean (CWM) traits are affected by species composition, relative abundance, and intraspecific trait variation (Ricotta and Moretti, 2011; Lepš et al., 2011). In our study, observed and fixed CWM showed similar habitat patterns. Farmland assemblages had smaller body-size profiles, residential assemblages had larger profiles, and woodland assemblages showed intermediate profiles. This pattern can be explained by the distribution of dominant species across habitats: farmland was dominated by the smaller-bodied *A. agrarius*, residential habitats contained a higher proportion of the larger-bodied *R. norvegicus*, and woodlands were mainly occupied by the intermediate-bodied *N. confucianus*. This result suggests that, for our second research question, CWM variation was stemmed primarily from shifts in rodent species

composition and alterations in the relative dominance of species with distinct body sizes. Nevertheless, localized intraspecific morphological adjustments may still occur in woodland habitats. Organ traits showed high heterogeneity among individuals and populations. Organ mass and organ coefficients can be affected by age, reproductive stage, nutritional condition, parasite or pathogen infection, contaminant exposure, and short-term stress. Their variation may therefore reflect individual physiological condition more than a uniform response to urbanization (Fardell et al., 2021).

The dominant-species analysis also revealed inconsistent urban morphological and organ syndromes among *A. agrarius*, *N. confucianus*, and *R. norvegicus*. Urban environments can drive genetic and phenotypic change, but the direction of these responses often depends on species' evolutionary history, resource use, and local selective pressure (Alberti et al., 2017; Johnson and Munshi-South, 2017). In our study, intraspecific responses were likewise species- and trait-specific, and the differences in community-level morphology were mainly shaped by replacement among dominant species.

**4.3 Habitat type was the main dimension of environmental filtering**

The anthropogenic-intensity index did not significantly explain the total rodent captures, capture occurrence, or species richness (McKinney, 2006; Aronson et al., 2016). It did, however, explain multispecies assemblage composition (Alvarez Guevara and Ball, 2018; Ofori et al., 2022). This again suggests that, for our third research question, urbanization pressure firstly changes species identity and dominance.

The global RDA identified habitat type as the clearest environmental dimension of rodent assemblage composition. Woodland, farmland, and residential habitat exhibit systematic differences in vegetation structure, food resources, shelter, and human disturbance, representing diverse local conditions that could directly affect rodent assemblages. Habitat type was the primary axis structuring both assemblage and CWM trait composition. Continuous urbanization

intensity exerted the secondary effects on body size traits mainly in woodlands, whereas the influence of NDVI was restricted to this habitat.

## 5 Summary

Our findings demonstrate that urbanization in Wuhan drives habitat-mediated reassembly of rodent communities. Urbanization did not produce a simple monotonic decline in species richness; instead, it primarily reorganized assemblage in species composition and dominance. For body-size-related morphology, community-level shifts were driven mainly by species turnover and dominance shifts; organ traits showed higher intraspecific heterogeneity, but no consistent environmental signal. Variation partitioning further revealed that habitat type independently accounted for assemblage variation. These results demonstrate that urbanization restructures rodent communities through habitat-filtered species turnover rather than uniform intraspecific responses, providing a mechanistic framework for predicting community reassembly under rapid urbanization, and highlighting rodent assemblages as sensitive indicators of habitat-mediated ecological change. Future studies should incorporate additional factors and broader spatiotemporal scales to verify the generalizability of these findings.

## Informed consent statement

Not applicable.

## CRediT authorship contribution statement

Zekai Ren conducted the field works and wrote the manuscript, Hongyu Niu and Hongmao Zhang produced the original ideas, designed the experiments and revised the manuscript, and the other coauthors partially contributed to the field works and manuscript revision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The raw data supporting the findings of this study are not publicly available because they are subject to sensitive ecological location information, privacy protection requirements and institutional data-management policies. Researchers may submit a reasonable request for data access to the corresponding author, subject to applicable laws, data-use agreements, and institutional requirements. Requests will be evaluated based on their intended purpose, data-protection requirements, and the availability of the necessary authorization.

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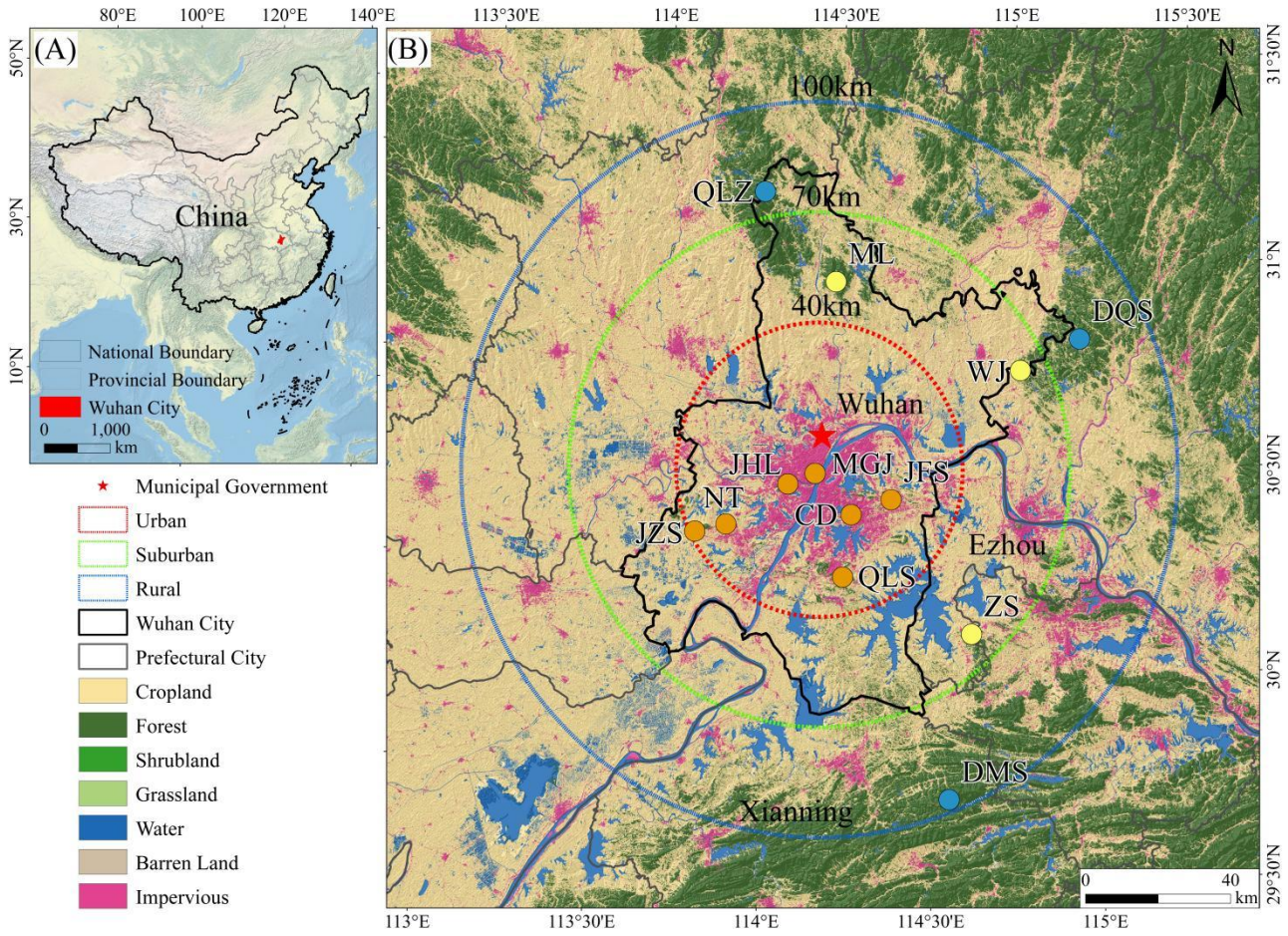



Figure 1. The study area and sampling sites in Wuhan, central China. Urban woodlands are Jiufengshan (JFS), Jiuzhenshan (JZS), Qinglongshan (QLS), urban residential habitats are Zhengyuan residential neighborhood (CD), Jianghanlu residential neighborhood (JHL), and Longyang boulevard (MGJ), and urban farmland plots coded NT, including Daji street, Jinkou street, Yangluo street, and Cangbu street. Suburban plots are Zhaoshan mountains (ZS), Wenjin Academy (WJ), and Mulanshan mountains (ML). And rural plots are Damushan mountains (DMS), Daqishan mountains (DQS), and Qingliangzhai mountains (QLZ).

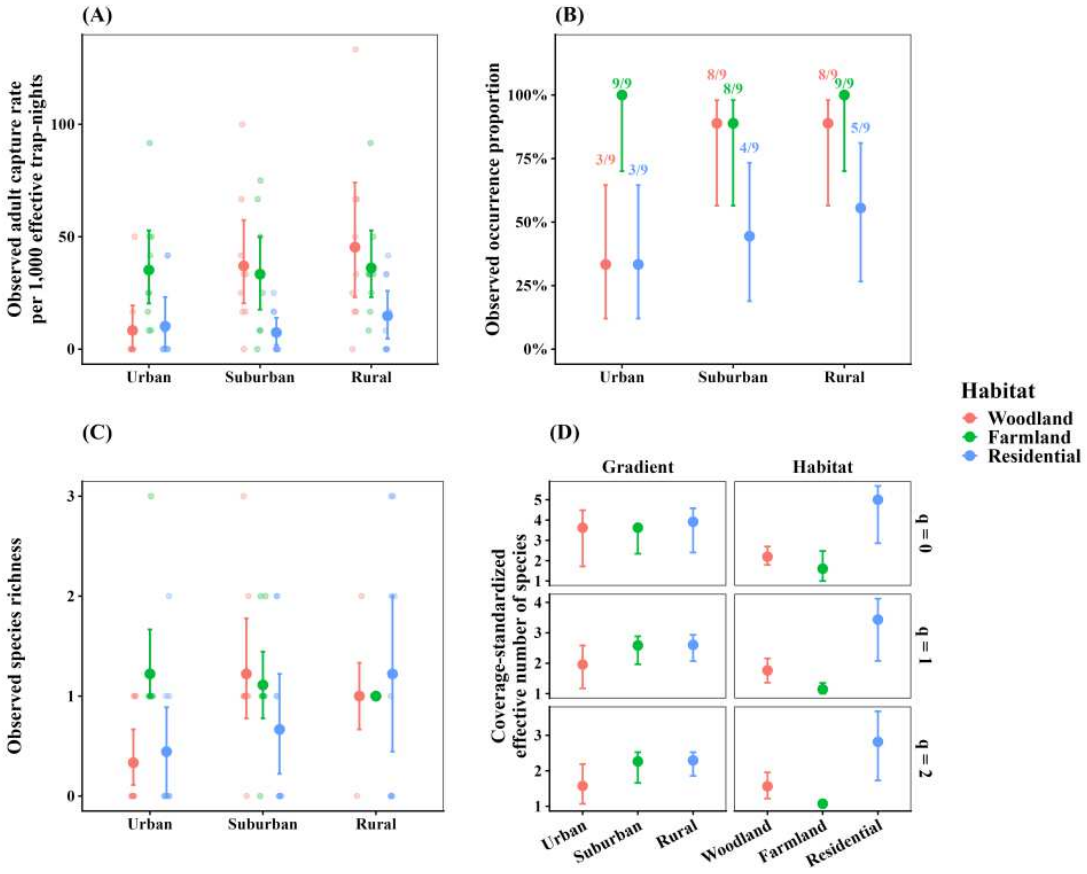



Figure 2. Variation in rodent abundance, occupancy, and diversity metrics across the urbanization gradient. The figures are capture rate (per 1,000 effective trap-nights) (A), occupancy rate (B), species richness (C), and coverage-based rarefied Hill numbers (q = 0, 1, 2) for assemblages pooled by Gradient or Habitat (standardized to 97.3% coverage) (D). q = 0 is species richness, q = 1 is exponential Shannon diversity, and q = 2 is inverse Simpson diversity.

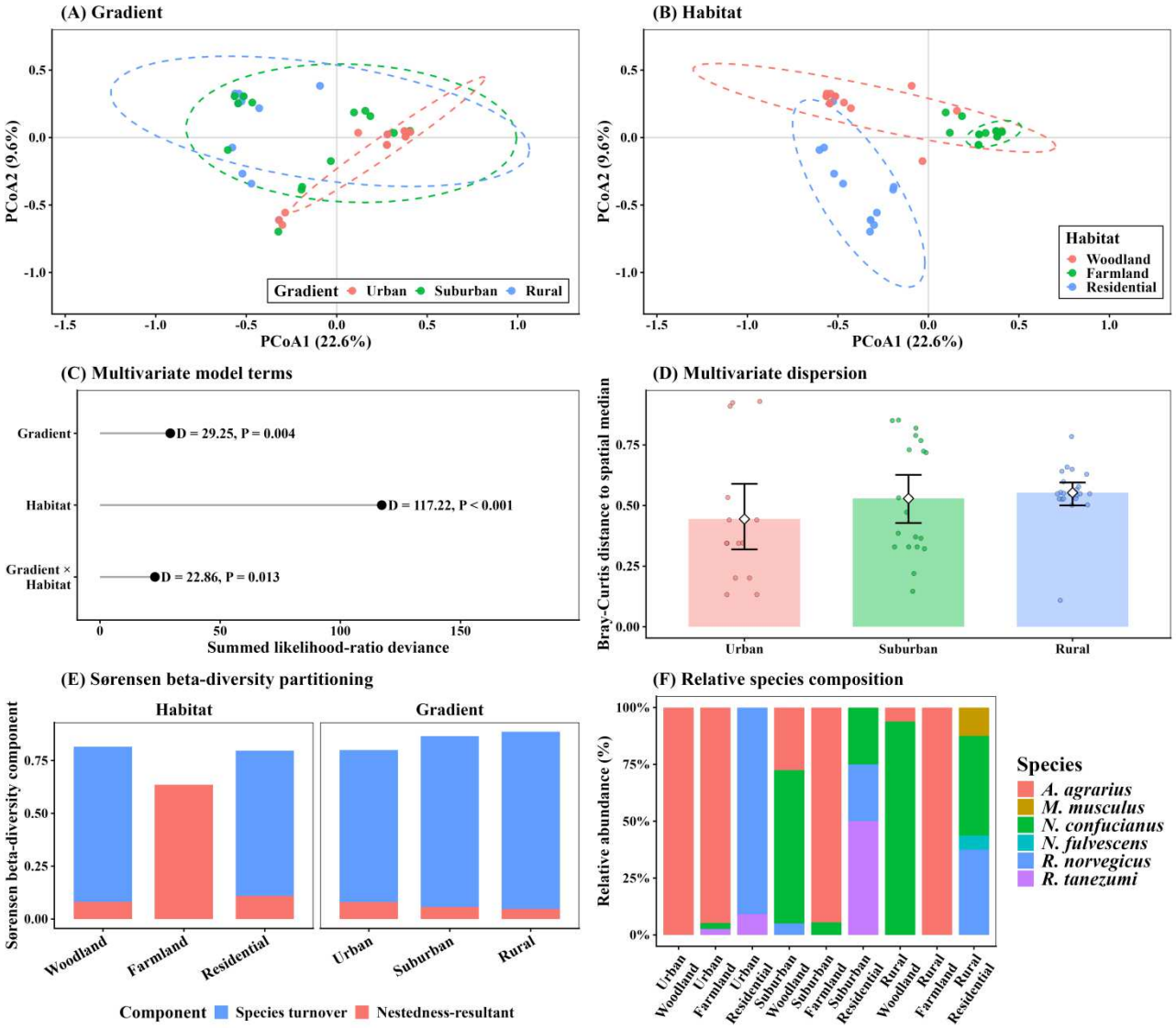



Figure 3. Rodent assemblage reassembly across the urbanization gradient and habitat types. The figures are Bray–Curtis principal coordinates analysis (PCoA) of the 57 occupied annual sampling sites across urbanization gradients (A), and habitats (B), overall terms from the negative binomial manyGLM (C), Bray-Curits distance to spatial median in different urbanization gradient (D), multiple-site Sørensen beta diversity within each gradient or habitat group (E) , and relative species composition across the nine Gradient × Habitat groups (F).

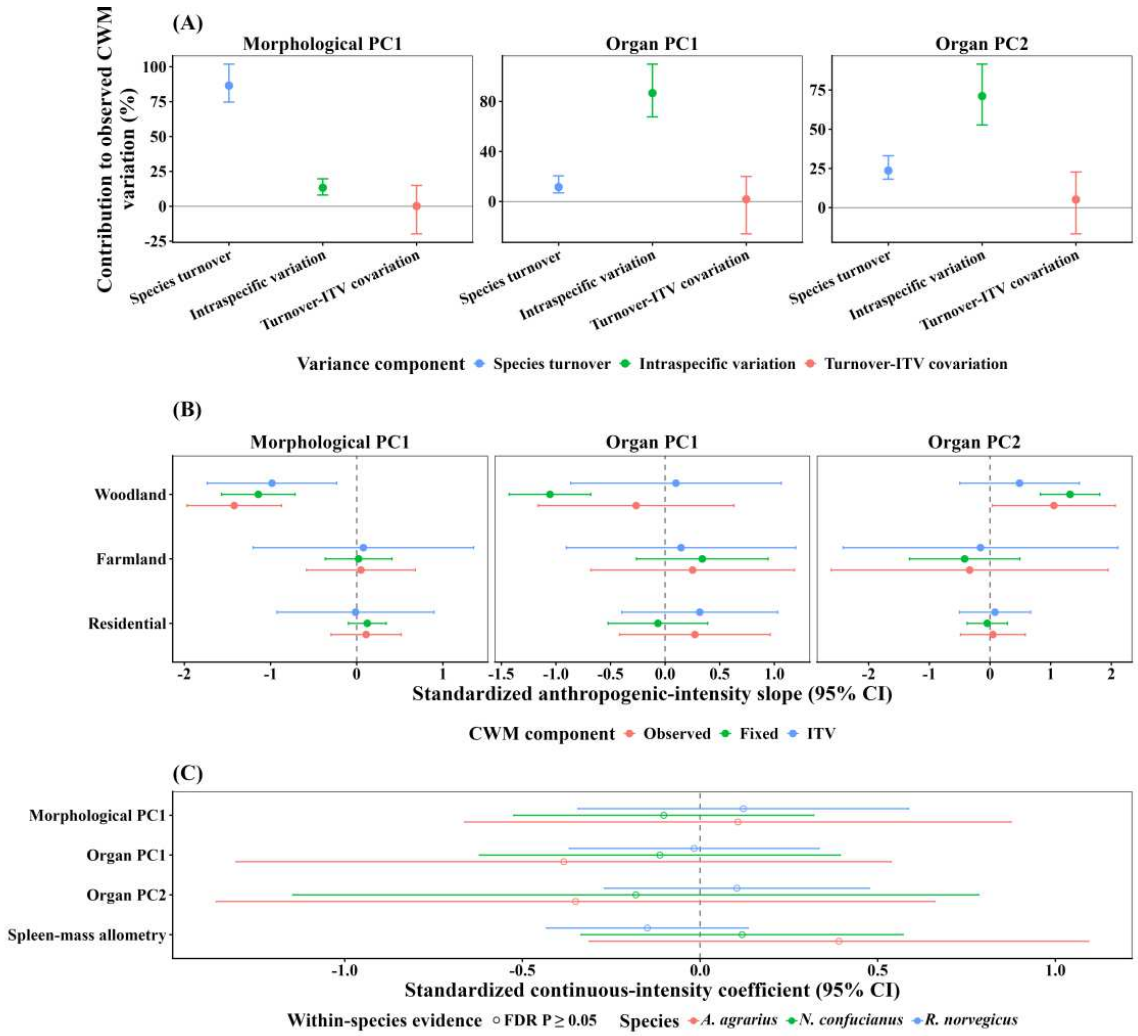
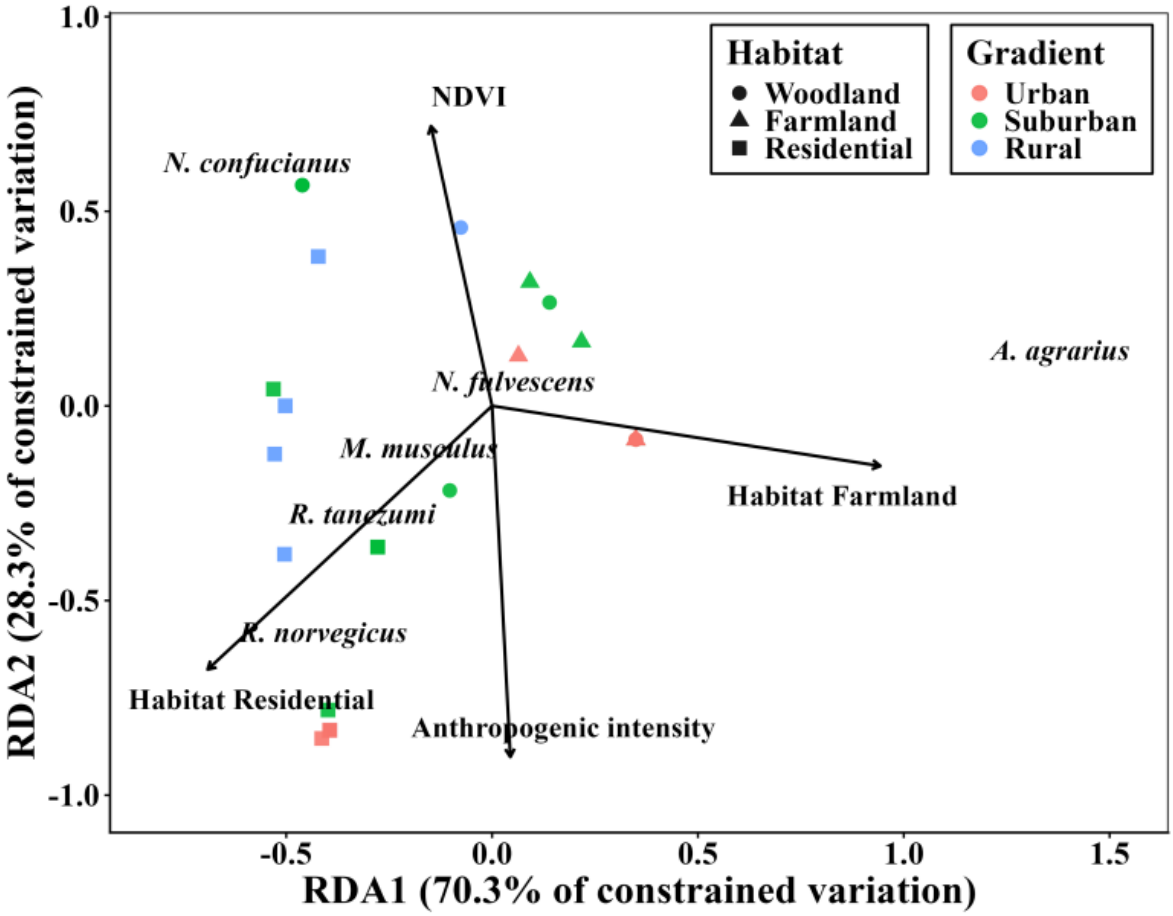



Figure 4. Sources of variation in community-weighted mean (CWM) traits and trait responses to anthropogenic intensity. The figures are contributions of species turnover, intraspecific trait variation (ITV), and their covariation to the total variation in observed CWM (A), standardized slopes of anthropogenic intensity for observed, fixed, and ITV components across habitats (B), and standardized coefficients of continuous anthropogenic intensity derived from within-species analyses for *Apodemus agrarius, Niviventer confucianus,* and *Rattus norvegicus* (C).




691

692 Figure 5. Redundancy analysis (RDA) of rodent assemblage composition in relation to

693 anthropogenic intensity, NDVI, and habitat type.

694

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