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# Soil animal communities demonstrate simplification without homogenization along an urban gradient

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**Abstract**

Urbanization profoundly impacts biodiversity and ecosystem function, exerting an immense ecological filter on the flora and fauna that inhabit it, oftentimes leading to simplistic and homogenous ecological communities. However, the response of soil animal communities to urbanization remains underexplored, and it is unknown whether their response to urbanization is like that of aboveground organisms. This study investigated the influence of urbanization on soil animal communities in 40 public parks along an urbanization gradient. We evaluated soil animal abundance, diversity, and community composition and related these measures to urban and soil characteristics at each park. The most urbanized parks exhibited reduced animal abundance, richness, and Shannon diversity. These changes were influenced by many variables underscoring the multifaceted influence of urbanization on ecological communities. Notably, contrary to our expectation, urbanization did not lead to community homogenization; instead, it acted stochastically, creating unique soil animal assemblages. This suggests that urban soil animal communities are concomitantly shaped by deterministic and stochastic ecological processes in urban areas. Our study highlights the intricate interplay between urbanization and soil animal ecology, challenging the notion of urban homogenization in belowground ecosystems and providing insight for managing and preserving belowground communities in urban areas.

**KEYWORDS**

belowground biodiversity, soil ecology, soil fauna, urban ecology, urban homogenization, urbanization

## INTRODUCTION

Urbanization, the process of modifying landscapes for dense human habitation and use (Britannica, 2022), exerts significant and chronic pressure on ecosystem connectedness, structure, and vitality (Forman, 2014). Many facets of the urban environment, such as increased population density (Shochat et al., 2006) and impervious surface (Ma et al., 2014), reductions in landscape connectedness (Bergsten et al., 2014; Id et al., 2020), highly variable socioeconomic status (Kinzig et al., 2005; Schell et al., 2020), and geographic gradients (McDonnell & Pickett, 1990), are known to be detrimental to native taxa and to lead to homogenization of ecological communities, environmental characteristics, and processes, even among spatially independent urban areas (Delgado-Baquerizo et al., 2021; Groffman et al., 2014; Groffman et al., 2017; McKinney, 2006; Pearse et al., 2018; Ryan et al., 2022). Urbanization is increasing rapidly, with an estimated 70% of the global population expected to live in urban areas by 2050 (Kotze et al., 2013). Therefore, continued study into the effects of urbanization on biodiversity patterns and community assembly mechanisms is crucial.

Within urban environments, greenspaces can function as sanctuaries for biodiversity, creating habitat refuges and corridors for organisms to traverse within an otherwise inhospitable urban landscape (Id et al., 2020; Kendal et al., 2017). One specific urban greenspace, public parks, offers unique opportunities as experimental arenas because they encompass diverse landscapes, and often receive consistent management from a centralized municipality (Aronson et al., 2017; Byrne, 2022; Byrne et al., 2016). This has made them prime areas to study various topics in ecology, especially because these studies can often be easily translated to management recommendations and applied conservation strategies for these public areas (Faeth & Kane, 1978; Leveau & Leveau, 2016; Milano et al., 2017; Peng et al., 2020; Smetana & Crittenden, 2014).

Within public parks and urban greenspaces more broadly, soils play a foundational role in urban ecosystems by maintaining biogeochemical processes, water cycles, and ecosystem services essential for human health and well-being (Guilland et al., 2018; Kaye et al., 2006; Lehmann & Stahr, 2007; O'Riordan et al., 2021; Riordan et al., 2021; Ryan et al., 2022; Setälä et al., 2017). They serve as reservoirs of carbon, nutrients, and biodiversity, harboring a diverse range of microorganisms, invertebrates, and small vertebrates. Soil invertebrate communities are known to be highly diverse in urban greenspaces (Huang et al., 2020; Szlavecz et al., 2020), but have received limited attention in most habitats, including urban areas (Hamblin et al., 2017; Kotze et al., 2013; Smith et al., 2014). Cryptic taxa like soil mesofauna are particularly understudies despite their fundamental role in many soil ecological processes (Bock & Wickings, 2023; Huang et al., 2020; Szlavecz et al., 2020; Tresch et al., 2019; Wardle et al., 2004). Therefore, understanding how soil mesofauna communities are impacted by urbanization is essential to understanding the belowground ecology and the ecosystem service provisioning of urban greenspaces.

Belowground invertebrates, collectively referred to hereafter as "soil animals," undergo constant ecological filtering from the surrounding soil environment. Soil water content (SWC), nutrient and resource availability, and soil physical structure all influence the presence and abundance of soil animals (Anderson, 1975, 1977; Antunes et al., 2023; Potapov et al., 2022; Wolters, 2001). These environmental filters tend to converge across urban environments, both locally and at a landscape level, even across seemingly disparate locations (Groffman et al., 2014; Trammell et al., 2020). However, these soil animals are also known to be highly susceptible to stochastic processes, especially in urban areas (Caruso et al., 2017) which inherently generate ecological randomness (Sattler et al., 2010) or "hotspots" of activity and abundance (sensu Kuzyakov & Blagodatskaya, 2015; Palta et al., 2014). This dichotomy presents an ecological conundrum: does urban homogenization deterministically shape soil animal communities in the same way it is known to alter aboveground communities and processes? While urban homogenization is known to create uniform soil biophysical properties and soil microbial communities (Delgado-Baquerizo et al., 2021; Pouyat et al., 2015; Ryan et al., 2022), it is not obvious that soil animal communities will be similarly homogenized (Joimel et al., 2019). Further, the landscape scale at which urban homogenization is typically observed is many orders of magnitude greater than the scale of soil animal communities ($10^6$ m vs. $10^{-3}$ m; Bock, personal observation), and it is unclear whether homogenization will manifest at the scale relevant for soil animals.

There have been a range of investigations into the effects of ecological disturbance on spatial patterns of biodiversity and the underlying community assembly mechanisms in native ecosystems (Chase et al., 2011; Chase & Myers, 2011). However, there is little understanding of these mechanisms belowground (e.g., Chen et al., 2019), with virtually no parallel studies in urban soils. Studies in urban parks provide an opportunity to expand the scope of research on the fundamental processes shaping "the little things that run the world" (Wilson, 1987). Further, understanding interactions between soil animals and urbanization is crucial for effective urban ecosystem management. Knowledge of soil biodiversity hotspots can inform strategies to manage urban soil health, promote ecosystem resilience, and sustain the equitable provisioning of ecosystem services in the face of rapid urbanization, such as identifying urban soils to focus management and conservation efforts, or areas that may be especially vulnerable to further degradation.

In this study, we utilized 40 public parks along an urban gradient to understand how urbanization shapes soil animal communities. Specifically, we addressed the following questions:

1. Does urbanization negatively impact soil animal community composition?
2. What are the most important urban site characteristics shaping soil animal community composition?
3. Does urbanization act as a deterministic or stochastic ecological force on soil animal communities?

We hypothesized that urbanization would generally act as a disturbance which would diminish soil animal richness, abundance, and diversity in parks (sensu Catano et al., 2017). Second, we hypothesized urban soil fauna community composition would be driven by unique aspects of urbanization (e.g., impervious surfaces, populations density, distance from geographic city center), whereas in less urban areas, factors like soil texture, bulk density, and soil moisture would be key drivers. Finally, we hypothesized that urbanization acts as a deterministic driver of decreased diversity and increased similarity (homogenization) among soil animal communities.

# METHODS

## Study sites

Our study was conducted in Rochester, New York, USA, which has a yearly mean temperature of 13.9°C and a mean precipitation of 87 cm (NOAA, 2020). The city has a population of 211,321 residents, with a total population of 1,090,135 in the greater metropolitan area, making it the 52nd most populous metro area in the United States based on the 2020 U.S. census (U.S. Census Bureau 2022). We selected 40 public parks across 11 municipalities (comprising the Rochester metropolitan area) as our study sites, located from 0.22 to 20 km from the geographical city center (Appendix S1: Figure S1). The parks were chosen based on their orientation around the metropolitan area to capture the urban gradient along each cardinal direction. Soils across the study sites were characterized by soil texture, bulk density, carbon and nitrogen content, pH, soil water holding capacity (WHC), soil moisture (Appendix S2: Table S1). A qualitative assessment of soil types reveals that parks were dominated by alluvial soils, mainly sandy loam and gravelly loam (e.g., Alton gravelly loam) as is common among the glaciated regions of central New York (NRCS Web Soil Survey, 2024). Vegetation was sampled using a 1-m$^2$ quadrat at each sampling point within a park at each timepoint. We noted all plant species within a quadrat such that we generated a presence/absence matrix for each sampling point at each sampling event. We identified all plants using keys and descriptions found in Weeds of the Northeast (Uva et al., 1997) and Turfgrass Management (Turgeon & Kaminski, 2020).

## Geospatial analysis and site characterization

Before sampling, we collected geospatial data for each park using the open-source Geographic Information System (GIS) software QGIS (QGIS 2023). Using existing maps from sources such as Google Earth (earth.google.com/web/) and cross-referencing with governmental records from each municipality, we created a shapefile polygon encompassing the area of each park. After completing the park maps, we used the polygon tool in QGIS to calculate the Perimeter (m), Area (m$^2$), and Perimeter:Area ratio (unitless) for each polygon, the latter being a metric correlated with increased probability of encounter by dispersing organisms (Fahrig, 2017). Additionally, we used the buffer tool to calculate a 500-m buffer around the perimeter of each park polygon (the park boundary) to calculate the percentage of impervious surface within 500 m of the park boundary (Homer et al., 2020; Trammell, 2021).

To establish individual sampling points within each park, we randomly assigned four points to the park polygon using the random points in rgw layer bounds algorithm in the vector creation tool in QGIS. We manually reviewed and adjusted the randomly assigned points to address any placement issues, such as points placed on sidewalks, buildings, or in water, in which case we moved the points to the closest suitable location that could be sampled. We also ground-truthed each microplot to ensure adequate spatial separation within the park. Once the microplots were established, we recorded the coordinates for each microplot using a handheld GPS device to 1-m accuracy. We considered a 3-m area around each GPS coordinate as the boundary for the microplot. Population density, median household income, and median resident age were determined for each park from 2020 census tract data provided by US Census Bureau TIGER/Line shapefiles (US Census Bureau, 2020), where parks that were entirely within one census tract were assigned values from the given tract, and parks that occupied more than one census tract were assigned a mean value of the census data.

## Soil sampling

We sampled each of the 40 public parks in spring and fall of 2021 and 2022. At each timepoint, we collected seven paired soil cores using a 1.75 cm diameter Oakfield soil sampler to a depth of 7 cm. Seven larger, 6 cm diameter cores were also taken to a depth of 7 cm using a turfgrass "plugger" to collect a more representative soil fauna community than would be possible in the Oakfield sampler. Cores of each type were placed in separate plastic bags and stored in a cooler during transport. Oakfield cores were stored at 5°C and sieved within 24 h of collection (2 mm mesh) to obtain a completely homogenous sample. From each sieved Oakfield sample, we collected multiple subsamples for soil physical and chemical properties. We extracted one 10 g aliquot from each sample for calculating SWC, soil WHC, and soil saturation. SWC was determined by weighing soils before and after drying in a ventilated drying oven at 80°C for 3 days. Soil WHC was calculated gravimetrically using saturated soil samples placed in filter paper-lined funnels (Zheng et al., 2019). Soil saturation was calculated as the percentage of WHC within each soil at the time of collection, by dividing SWC by WHC. Soil pH was determined via a pH electrode (Mettler Toledo FiveEasy Benchtop F30) using Milli-Q water (Millipore, Germany) at a fresh soil to solution ratio of 1:2.5. A second 10 g aliquot of oven-dried soil from each sample was ball milled (MM200, Retsch, Germany) for total organic C and N analyses by an Elemental Analyzer (Carlo Erba 1110, CE Instruments) coupled to a DeltaPlus Isotope Ratio Mass Spectrometer (Finnigan MAT, Germany) via a Conflo III interface (Thermo Fisher, Austria). We collected a third 10 g aliquot from each sieved soil sample and performed a modified hydrometer method to determine soil texture (Gee & Or, 2002). Soil bulk density was measured by extracting one additional 6 cm × 7 cm core in spring 2021 using a modified Cornell Soil Health protocol (Moebius-Clune et al., 2016). Both soil texture and bulk density were measured once during the study due to the relatively short experiment timescale compared with the expected rate of change for these properties (Helmberger et al., 2018). Both measures were based on the Cornell Comprehensive Assessment of Soil Health protocol (Moebius-Clune et al., 2016). These soil characteristics are noted in Appendix S2: Table S1.

## Soil mesofauna

We employed modified Berlese funnels to extract soil fauna from the turf-plugger cores. Cores from each microplot were combined, resulting in four extractions per park per timepoint (Bray et al., 2019). Soil fauna were initially extracted into 70% ethanol and then transferred to 90% ethanol for long-term storage. After extraction, the dried turf-plugger cores were weighed to calculate the number of individuals per kilogram of dry soil.

Initial identification of soil fauna was done at the major taxonomic group level, using the Borror and Delong Key for Insects (Triplehorn et al., 2005) for insects and collembola, and by following the taxonomy described in Coleman et al. (2004). Due to their significance as subterranean insects, we further identified ants to species using Ants of North America: A Guide to the Genera (Fisher et al., 2007) and Urban Ants of North America and Europe (Klotz, 2008).

Three orders of soil mites, Oribatid, Mesostigmata, and Prosigmata were further identified and separated by morpho-species, then identified to genera when possible using the Key to Major Mite Taxa (Walter, 2006), Dindal Key (Dindal, 1990), and a key to northern North American oribatid mites (Behan-Pelletier & Lindo, 2023).

## Data analysis

### Urban classification

We used an automatic clustering approach (k-means) which considered 13 site characteristics which represent various facets of the urban environment (Appendix S1: Table S1) to determine urbanization "groups" for analysis. Clusters were created using the kmeans function in base R with 999 permutations. This analysis split our 40 sites into two groupings, henceforth referred to as "high-urban" and "low-urban." Notably, these groupings do not totally correlate to the geographic idea of "urban" (toward the city center) and "rural" (away from the city center). Instead, they capture a high-dimensional characterization of local urbanization based on our measured site characteristics.

### Calculating community composition

We calculated organism abundance, species richness, Shannon diversity, and Bray–Curtis dissimilarity indices for each park for spring and fall season, where each season consisted of two consecutive years of sampling (2021–2022). Species abundance per kg soil was calculated for each park at each sampling timepoint by summing all organisms across the four microplots in each park, then dividing by the total weight of soil from the plots. Species richness was calculated by creating a presence–absence matrix of the community data, then summing the number of unique species across each park's four microplots at each timepoint. Park Shannon diversity [H′] was calculated using the "vegan::diversity" function, which considers the species richness and each species relative abundances across the four microplots. Finally, we calculated the Bray–Curtis dissimilarity index between parks using the "vegan::vegdist" function, where values of zero indicate complete community overlap, and values of one indicate completely unique communities (Chase et al., 2011). We then used a two-way analysis of variance (ANOVA) to compare community composition between urbanization classes and timepoints. When an ANOVA indicated significant effects, we used a Tukey pairwise comparison to determine significant differences between groups.

## Multivariate analysis of urbanization effects on soil animal community composition

We investigated the effects of individual environmental variables and site characteristics on soil animal species composition using a two-way permutational multivariate analysis of variance (PERMANOVA, 9999 permutaions), and an Adonis pairwise comparison (pairwiseAdonis::pairwise.adonis in R) to test for differences in clustering in a Euclidean distance species abundance matrix of soil animals. We investigated the correlation between individual urban environmental variables, site characteristics and species composition using nonmetric multidimensional scaling (NMDS) ordination on the same species matrix. Final NMDS solutions were considered acceptable if they had stress values <20. The relationship between axes of the NMDS and urban environmental variables was explored with the function "vegan::envfit" (Oksanen, 2015; Oksanen et al., 2007).

## Ranking urban environmental variables

We used a random forest (RF) modeling approach to explore which site characteristic variables most influenced soil animal community composition metrics (da Silva et al., 2022). We used the "randomForest::randomForest" function in R to conduct the analysis. We randomly divided our soil animal community data into two categories: training data, which contained 70% of the original data matrix and was used for training the RF model, and test data, which contained 30% of the original data matrix and was used to validate the model (Liaw & Wiener, 2002). We trained a separate model for low-urban and high-urban data for each of the four community metrics (abundance, species richness, Shannon diversity, Bray–Curtis dissimilarity), leading to eight models in total, with 5000 replications of each model. To estimate the importance of different site characteristics on soil animal communities, we used the percent increases in mean square error (MSE%) of each variable, where higher MSE% values indicates that the omission of a variable from the RF would increase model error. The significance of each model was assessed using the "rfUtilities" package (Evans & Murphy, 2018) and the importance of each predictor variable was determined using the "rfPermute" package (Archer, 2019). We included all significant variables in the model analysis, but we emphasized variables which exceed 20% MSE due to the relative likelihood that they are both statistically significant and ecologically meaningful in the system (Prasad et al., 2006). To further illuminate the types of environmental and site characteristics which play the greatest role in shaping urban soil animal communities, we qualitatively grouped site characteristics into four main categories: "Socioeconomic," "Soil," "Spatial," and "Time," which we used in conveying variable prioritization in the results.

## Null model analysis for measuring urban homogenization

Urban homogenization is traditionally tested by comparing CV among variables between urban and native areas (e.g., Groffman et al., 2014). However, we assert that comparing the CV in β-diversity across soil animal communities may have created an experimental artifact where differences in α-diversity could conflate our interpretation and conclusions (Chase et al., 2011; Li et al., 2022; Ning et al., 2019). Thus, in addition to CV calculations (Appendix S3: Table S1), we employed a null model analysis where we compare observed community β-diversity to a null distribution to partially remedy this issue. Our null model was based on the Raup–Crick metric in "vegan::raupcrick" (Chase et al., 2011), where species are randomly selected from a known total "species pool" for each urbanization class and each timepoint. We repeated this randomization 9999 times to generate a null distribution of β-diversity ordered under the assumption of total neutrality (stochasticity) and compared our observed similarity among two urbanization groups against this null distribution. We then analyzed our observed and simulated distributions using the functions "vegan::betadisper" and "vegan::adonis2" to compare differences between point dispersion, which would indicate changes in community overlap, and differences in the permutation of points across time, which could be linked to mechanisms temporally driving community composition, respectively (Caruso et al., 2017; Maaß et al., 2014).

Based on previous literature, we considered communities that were significantly more clustered (i.e., a dissimilarity value close to 1) than the null model to be ordered by deterministic processes, and communities that were equally or more dispersed than the null model to be stochastic (Chase, 2010; Chase et al., 2011; Chase & Myers, 2011). In our analysis, we saw significant differences in point permutation, but no differences in point dispersion. Therefore, we discount this finding because of known errors that can occur in continuing the analysis when point dispersion is not significant (Anderson & Walsh, 2013).

# RESULTS

## Soil animal community response to urbanization

In total, we collected 121,178 individual specimens across all parks and sampling timepoints, with each park community containing between 30 and 67 individual taxa (Appendix S4: Table S1) and organism densities between 26.74 and 471.65 organisms per kilogram dry soil. Across both urbanization classes, soil animal communities were dominated by Acari, with Oribatida and Mesostigmata making up 10%–21% (3–14 taxa) and 30%–34% (9–23 taxa) of the total community, respectively. While we observed a nominal negative effect of urbanization on soil animal abundance, richness, and Shannon diversity, differences between urban classes were only statistically significant in the fall sampling timepoint (Table 1). The one notable exception to the negative relationship between urbanization and soil animal community composition was in comparisons of community evenness (i.e., Bray–Curtis dissimilarity) between urbanization classes. We observed that high-urban parks had significantly more dissimilar soil animal communities than low-urban parks at the fall timepoint ($0.63 \pm 0.02$ vs. $0.54 \pm 0.02$, respectively; mean ± se; Table 1; $F_{3,151} = 5.37$, $p < 0.01$).

## Plant community response to urbanization

Across all timepoints, total plant richness ranged from 2 to 10 species present per plot, with a mean of 5.4 species, and a median of 5 species. Of the species observed, *Trifolium repens* (white clover) was the most common forb, occurring in 74.3% of sites across all sampling points, while *Poa pratensis* (Kentucky bluegrass) was the most common grass, occurring in 80.9% of sites across all sampling points. The correlation between plant richness and soil animal richness was low ($R^2 < 0.01$, $p = 0.78$), and a preliminary comparison of soil characteristics (Pearson's correlation) did not yield any significant relationships ($p > 0.05$). Therefore, we chose to not include the plant community data in this manuscript due to the lack of relationships between plant communities, soil characteristics, and soil animal communities.

## Community composition responses to urbanization and environmental factors

The NMDS analysis of soil animal community composition utilized three dimensions to achieve a stress of 0.1415 (Figure 1; Table 2). Soil animal communities showed distinct compositional shifts between urban clusters ($R^2 = 0.10$, $F_{3,151} = 12.09$, $p = 0.001$) and timepoints ($R^2 = 0.04$, $F_{3,151} = 7.18$, $p = 0.001$) according to a two-way PERMANOVA. However, we did not observe an interactive effect between urban clusters and timepoint ($R^2 = 0.01$, $F_{3,151} = 2.02$, $p = 0.099$). Many environmental variables were significantly related to soil animal community composition ($R^2 = 0.05$, $p = 0.059$; Figure 1; Table 2). The most significant community separation occurred along axis 2, where park spatial (such as impervious surface and Perimeter:Area) and socioeconomic (such as population density) variables increased along the axis, while many of the variables related to soil water availability decreased along this axis (Figure 1). Additionally, other socioeconomic factors, like median household income and resident age, played a role in this axis. Notably, the variables most highly related to soil animal community composition, as indicated by their correlation

**TABLE 1** Average community measures for high- and low-urban sites in both spring and fall sampling timepoints.

| Urbanization level | Season | Abundance | Species richness | Shannon index | Bray–Curtis dissimilarity |
|---|---|---|---|---|---|
| Low-urban | Spring | 143.85 ± 16.83 b | 35.15 ± 1.08 ab | 2.51 ± 0.059 a | 0.626 ± 0.022 a |
| | Fall | 242.80 ± 17.01 a | 38.53 ± 1.10 a | 2.50 ± 0.060 a | 0.539 ± 0.022 b |
| High-urban | Spring | 157.13 ± 13.57 b | 33.84 ± 0.92 b | 2.40 ± 0.071 ab | 0.668 ± 0.024 a |
| | Fall | 168.82 ± 20.17 b | 33.40 ± 1.31 b | 2.20 ± 0.072 b | 0.626 ± 0.026 a |

*Note*: Values are displayed as mean ± SE, with letters denoting a significance of $p < 0.05$ according to pairwise comparisons.

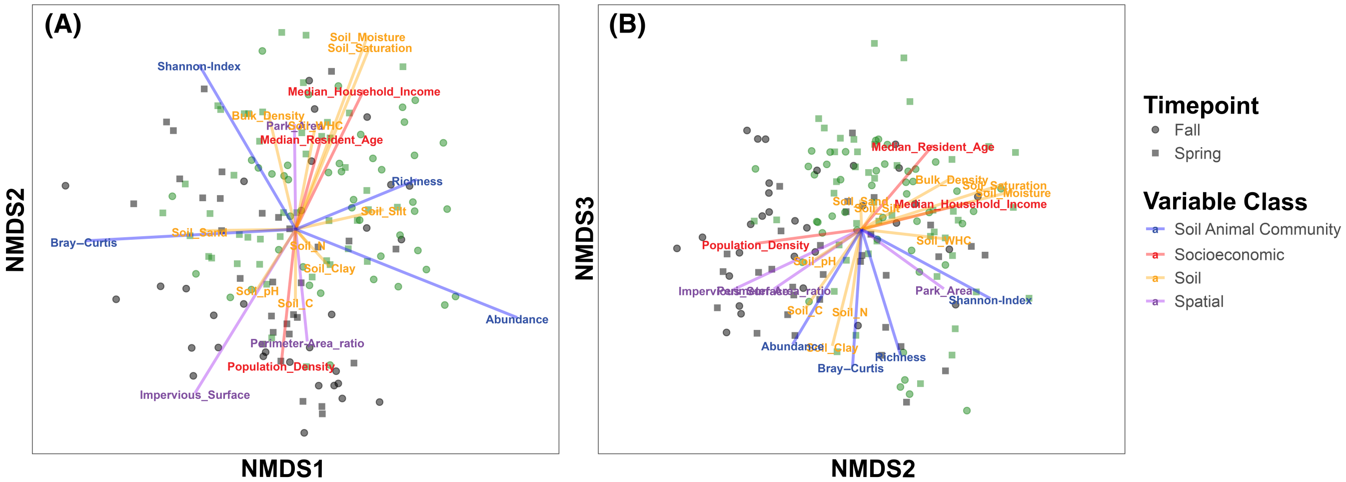


**FIGURE 1** Nonmetric multidimensional scaling (NMDS) plot of soil animal community structure (stress = 0.1415) and the environmental variables fitted on the NMDS spaces. (A) Relationship between NMDS axis 1 and axis 2. (B) Relationship between axis 2 and axis 3. Environmental variable vector color denotes qualitative groupings of community measures, socioeconomic, soil, or spatial variables, while dot shape and color denote the urban class and sampling timepoint of each park, respectively.

**TABLE 2** Site characteristic variable importance according to nonmetric multidimensional scaling (NMDS).

| Variable | NMDS1 | NMDS2 | NMDS3 | $r^2$ | *p* value |
|---|---|---|---|---|---|
| Median household income | −0.52386 | −0.83636 | −0.16146 | 0.1915 | 0.001 |
| Park area | 0.01342 | −0.8703 | 0.49235 | 0.1006 | 0.001 |
| Perimeter area ratio | −0.11627 | 0.87676 | 0.46667 | 0.1128 | 0.001 |
| Population density | 0.13494 | 0.98545 | 0.10336 | 0.1303 | 0.001 |
| Impervious surface | 0.5935 | 0.75544 | 0.2776 | 0.3237 | 0.001 |
| Soil WHC | −0.2355 | −0.96797 | 0.08698 | 0.0815 | 0.004 |
| Bulk density | 0.26566 | −0.88094 | −0.39162 | 0.1181 | 0.001 |
| Soil N | −0.18739 | 0.17612 | 0.96637 | 0.0488 | 0.059 |
| Soil C | 0.00324 | 0.67339 | 0.73928 | 0.0794 | 0.012 |
| Soil pH | 0.59098 | 0.7206 | 0.36261 | 0.0477 | 0.045 |
| Median resident age | −0.25604 | −0.71069 | −0.65526 | 0.1138 | 0.001 |
| Soil sand | 0.97193 | 0.01173 | −0.23499 | 0.1098 | 0.001 |
| Soil silt | −0.96596 | −0.16885 | −0.19598 | 0.0938 | 0.002 |
| Soil clay | −0.33301 | 0.28864 | 0.89766 | 0.1162 | 0.002 |
| Soil saturation | −0.45006 | −0.86655 | −0.21572 | 0.3073 | 0.001 |
| Soil moisture | −0.4229 | −0.8892 | −0.1746 | 0.3273 | 0.001 |
| Abundance | −0.89021 | 0.27725 | 0.36146 | 0.6979 | 0.001 |
| Richness | −0.75353 | −0.24166 | 0.61138 | 0.2925 | 0.001 |
| Shannon diversity index | 0.56924 | −0.75798 | 0.31849 | 0.3252 | 0.001 |
| Bray–Curtis dissimilarity | 0.8899 | 0.03843 | 0.45453 | 0.6271 | 0.001 |

*Note*: NMDS1–3 columns indicate the relationship of the environmental variable with each axis via coordinates of the vector head on given ordination axes, assuming that the vector is of a length = 1 unit. *R*-squared column indicates variation explained by the model of multiple regression and indicates vector length, where higher $r^2$ indicate longer vectors. *p* value column denotes significance of the multiple regression, where significant values indicate that a variable was related to ordination axes more than random chance, according to a permutation test (999 permutations).
Abbreviation: WHC, water holding capacity.

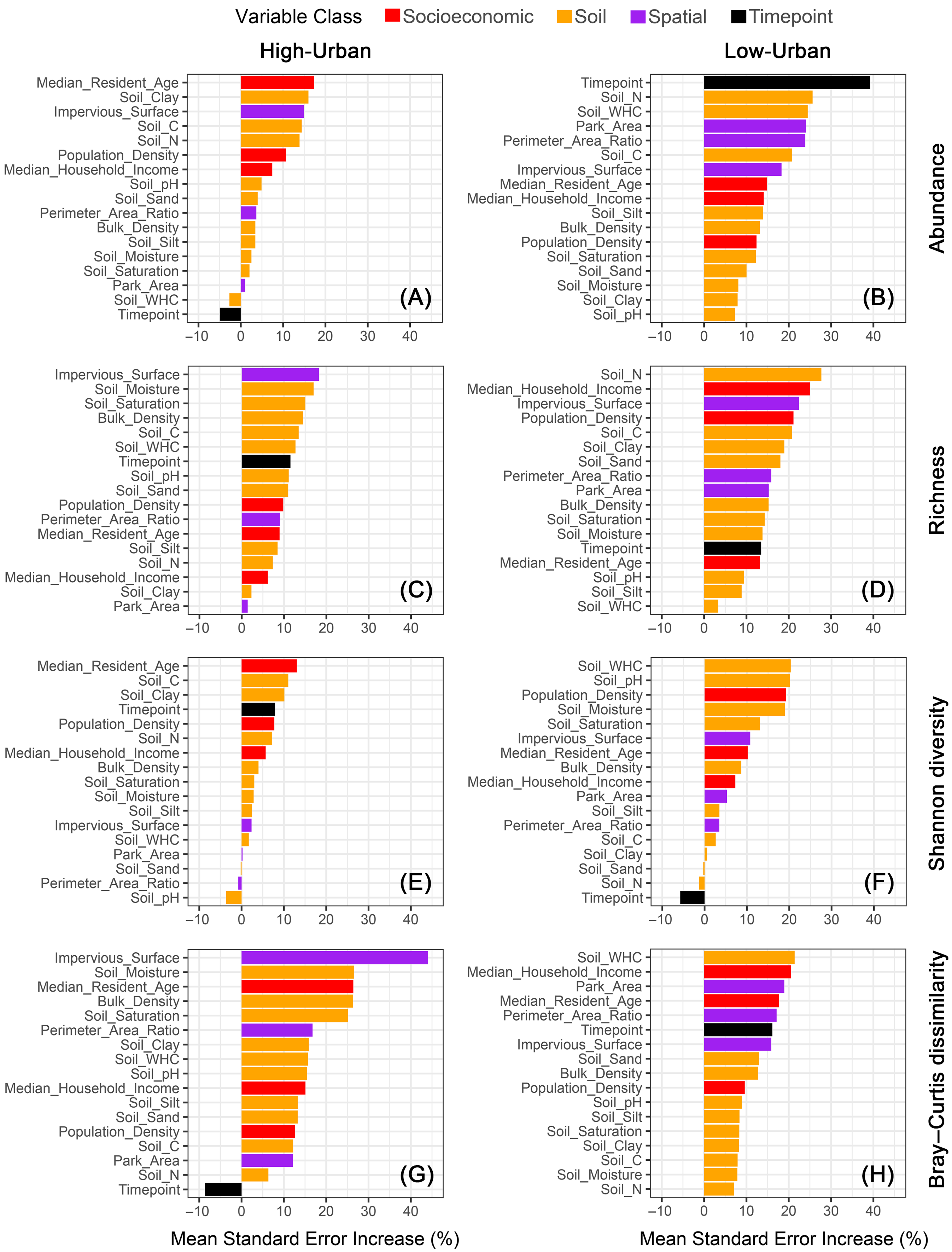


**FIGURE 2** Legend on next page.

coefficients, were correlated with axis 2: soil moisture ($R^2 = 0.33$; Table 2), impervious surfaces surrounding the park ($R^2 = 0.32$; Table 2), and soil saturation ($R^2 = 0.31$; Table 2).

We utilized RF to highlight the most important site characteristics driving each community's abundance, species richness, Shannon diversity, and Bray–Curtis dissimilarity indices. The analyses showed that the main drivers of soil animal community composition varied widely across the four community metrics (Figure 2). Additionally, we observed that for any one community metric, urbanization class led to a different variable prioritization and magnitude. Percent MSE increase of each variable was consistently higher in low-urban parks (Figure 2B,D,F,H) than high-urban parks, meaning that a greater number of variables played a substantial role in shaping the soil animal communities in low-urban parks. Only five variables in the high-urban Bray–Curtis dissimilarity RF model exceeded a MSE of 20% (Figure 2G), whereas low-urban RF models had variables surpass 20% MSE for the abundance, richness, Shannon diversity, and Bray–Curtis dissimilarity models (Figure 2B,D,F,H). In low-urban parks, richness, Shannon diversity and Bray–Curtis dissimilarity were all predominantly driven by soil factors, with abundance being most influenced by sampling timepoint (Figure 2B,D,F,H). In contrast, in the high-urban parks, community metrics were most heavily driven by "Socioeconomic" and "Spatial" variables (Figure 2A,C,E,G).

## Measuring urban homogenization

Our null model analysis detected no significant difference in point dispersion between urban clusters or timepoints between our null model and observed community dissimilarity ($F_{3,76} = 1.42$, $p = 0.243$) according to a PERMANOVA analysis. To further substantiate our results, we calculated the CV for all site characteristics and community metrics (Appendix S3: Table S1). CV was similar for Bray–Curtis dissimilarity across all parks, indicating that the communities were not exhibiting homogenization.

# DISCUSSION

Understanding patterns of community assembly and the ecological forces shaping it are crucial to the long-term sustainability of urban greenspaces. It is especially important to understand the forces shaping soils and belowground communities, as they are implicated or directly provision a disproportionate quantity of ecosystem services in urban areas (O'Riordan et al., 2021). To this end, our study demonstrates the intricate and sometimes counterintuitive nature of urban soil animal communities, which can serve as useful insight to directing conservation and management efforts to at-risk urban soils and their ecosystem services, and preserving those soil communities which are exceptionally rich and numerous.

We found that abundance, richness, and Shannon diversity metrics were consistently lower in high-urban than low-urban parks, but this trend was only statistically significant in the fall timepoint. These findings partially support our hypothesis that urbanization exerts negative forces on soil animal communities. This observed pattern was most apparent in soil mites, where both omnivorous Oribatida (Behan-Pelletier & Lindo, 2023; Cordes et al., 2022) and the predominantly predatory Mesostigmata (Minor & Cianciolo, 2007) decreased in abundance and richness in the presence of high urbanization pressure (Appendix S4: Table S1). The detected seasonal variation in soil animal communities suggests that urbanization does not exert a simple linear negative relationship on soil animal communities, but instead shows dynamic variability, driven by seasonality in environmental conditions.

Based on work in other systems and the biology of most soil animals, we suggest that the urbanization effects that we observed are governed largely by variability in soil water availability across parks (Kirichenko-Babko et al., 2020; Liao et al., 2021) which was seemingly accentuated by urban development. We observed that high-urban park soils were substantially drier (less saturated) than low-urban parks in the fall (44.77% ± 4.27 vs. 60.77% ± 2.36, mean ± SE, Appendix S2: Table S1) with CV values greater in high-urban parks for soil saturation and soil moisture (Appendix S3: Table S1). Soil water often dictates resource accessibility and habitat suitability in soil animal communities, with water becoming increasingly important as soil animal body size decreases (Lindberg et al., 2002; Tsiafouli et al., 2005). Therefore, the decreasing and highly variable SWC we observed in high-urban parks likely exacerbated the negative effects of urbanization on soil animal communities. While we did not test this experimentally, from these

**FIGURE 2** Effect of site variables on (A, B) abundance, (C, D) richness, (E, F) Shannon diversity, and (G, H) Bray–Curtis dissimilarity community measures of (left column) high-urban and (right column) low-urban parks. Bars denote variable contribution to increasing model mean squared error (MSE) where higher MSE value implies more important variables. Dashed lines, where present, denote the MSE 20% threshold, where variables that surpassed this threshold were deemed to be especially critical to determining a given community measure.

observations, we suggest that practices which sustain soil moisture, increase SWC in dry conditions, or diminish other socioecological disturbances (e.g., management or heavy foot traffic) during vulnerable, low moisture periods, may be an effective strategy to lessen the urbanization-induced decreases in soil animal communities. Future research aimed at exploring the underlying mechanisms driving seasonal variation in soil animal responses to urbanization would benefit these recommendations. Additionally, longitudinal studies and experiments manipulating specific stressors, such as soil moisture and habitat isolation can provide deeper insights into the causal relationships between urbanization and soil animal communities.

Our multivariate analysis of soil animal communities underscores the significance of environmental variables in shaping community structure. We observed that nearly all the individual variables measured correlated significantly with our ordination, demonstrating the high-dimensional complexity of urban ecosystems (Elmqvist et al., 2013), and the corresponding challenges faced by the people tasked with managing them (Aronson et al., 2017; Nilon, 2011). Our ordination analysis elucidated this complex urbanization gradient in our study system, where park spatial variables and socioeconomic factors were juxtaposed with soil water parameters (Figure 1). How individual parks related to these site characteristics effectively represents the belowground urbanization gradient in our study system, which is shown through its correlation to community richness and Shannon diversity, and to a lesser extent, abundance. Interestingly, this gradient is not aligned with the subjective or geographical categorization typical of urban–suburban–rural (McDonnell & Pickett, 1990), meaning that effectively diagnosing belowground disturbance in urban systems is potentially less intuitive than for aboveground systems.

RF modeling revealed the key factors influencing soil animal communities, supporting our hypothesis that these drivers change with urbanization intensity. Among eight models, five unique variables emerged as primary drivers (Figure 2). The variation in variable importance across each of the models highlights the complexity of the relationships we studied and suggests that the most limiting factor to soil animal communities shifts along urban gradients. In low-urban parks, soil factors were the predominant drivers of soil animal communities, whereas socioeconomic and spatial variables were more influential in high-urban parks, outweighing soil factors. Further, variables of all kinds (soil, urban, or other) impacted low-urban soil animal communities to a greater degree (number of variables exceeding 20% MSE; Figure 2) suggesting that low-urban communities are shaped predominantly by a select few variables, whereas in high-urban communities, the weak influence of many of the factors measured, as well as unmeasured factors or random processes appear to be stronger. These findings generally agree with urban ecological literature (du Toit & Cilliers, 2011; Gong et al., 2023; Grimm et al., 2017; Güler, 2020) and suggests that the highly complex nature of urbanization overwhelms the effect of any individual environmental or site characteristic on soil animals, thus creating a more unpredictable interplay between urban and environmental characteristics.

Arguably, the most surprising aspect of our study was the apparent lack of soil animal homogenization across highly urbanized parks. We hypothesized that urbanization would act deterministically, leading to a predictable simplification of soil animal communities, as is observed in many contemporary comparisons between urban and nearby native areas (Aronson et al., 2014; Gong et al., 2023; Pearse et al., 2018). However, β-diversity, which we measured through Bray–Curtis dissimilarity, was consistently higher in high-urban parks (Table 1). The lack of difference between the null model and our observed data leads us to conclude that in our study, urbanization acted stochastically, leading to random population fluctuations and dispersal patterns (Figure 3).

The lack of consistent simplification that we observed is at odds with the idea that urbanization acts to homogenize ecosystems, which has been observed in studies showing that variation in flora, fauna, and ecological processes across urban ecosystems is less than variation in these variables across the natural ecosystems that they replaced (Groffman et al., 2014; Groffman et al., 2017; McKinney, 2006; Wheeler et al., 2017). In addition to our null model results showing a lack of consistent simplification, our comparison of CV across our measured urbanization variables and community metrics showed that while urbanization homogenizes many of the site variables we measured, it does not appear to homogenize the soil animal community (Appendix S3: Table S1). We propose that our observations may be a result of the minute size of soil animals in comparison to the urban landscape (sensu Blowes et al., 2024). The relative size of soil animals, being at least six orders of magnitude smaller than our study system's spatial scale (millimeter vs. kilometer) means that each park contains immense variability in soil conditions, and entire metacommunities of animals (Caruso et al., 2017; Ettema & Wardle, 2002; Frey, 2015; Lindo et al., 2023; Maaß et al., 2014). Soils are known to be inherently patchy environments (Kuzyakov & Blagodatskaya, 2015; Palta et al., 2014), and there are many facets of urbanization, especially spatial, socioeconomic, and patterns of human use inherent in our study system which can be linked to increases in soil heterogeneity.

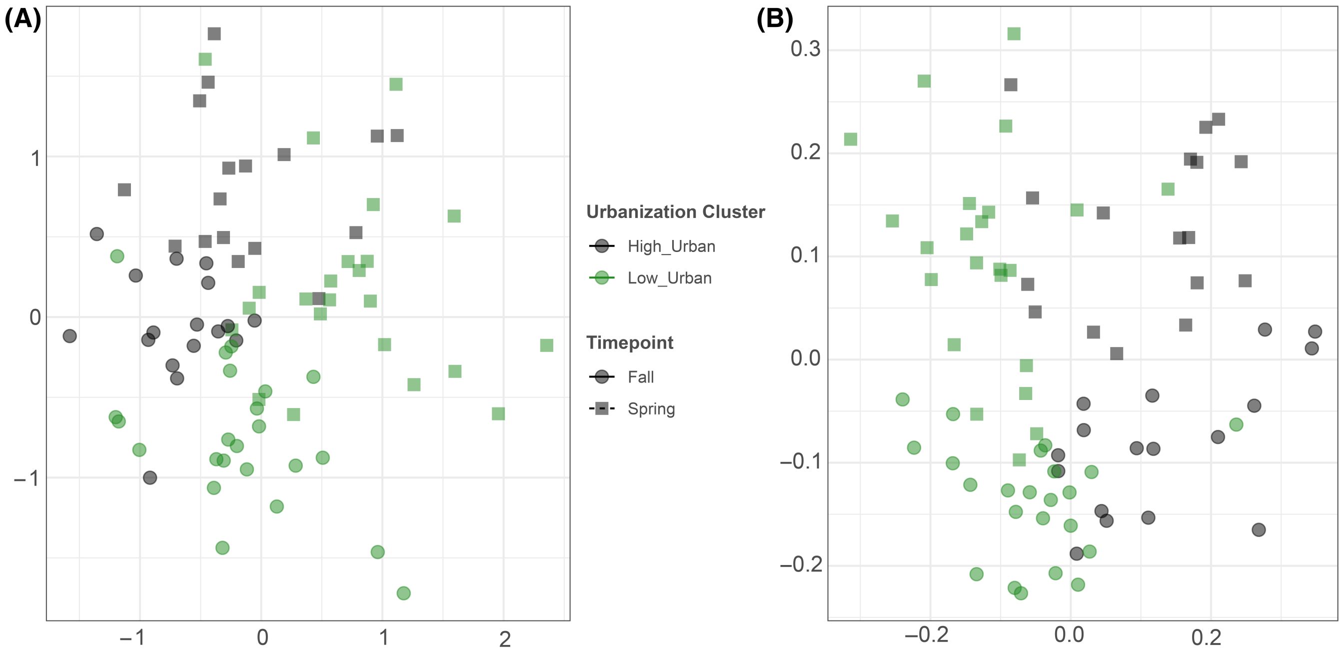


**FIGURE 3** Nonmetric multidimensional scaling (NMDS) plot of soil animal Bray–Curtis dissimilarity (beta diversity) based on (A) Raup-Crick and (B) Jaccard's index. (A) represents simulated data following the protocol outlined in Chase et al., 2011, while (B) shows observed beta diversity among park urban classes (point shape) and sampling timepoint (point color). Ellipses (solid and dashed lines) indicate one standard deviation about the centroid of each point cloud.

Thus, urbanization can be said to plausibly enhance community dissimilarity and be a force of ecological heterogenization belowground, especially at the scale of soil animals. The literature on the homogenization of soil animals is sparse, but generally suggests that soil animals may be influenced less by urbanization than other flora and fauna and may be, instead, tightly coupled to local soil geochemistry and climatic conditions (Joimel et al., 2022; Yao et al., 2022; Yu et al., 2022). It is important to note that we did not compare urban versus natural reference ecosystems as has been done in other tests of the urban homogenization idea. Our "less urban" reference sites have considerable soil and vegetation disturbance compared with natural forests, which would be the native reference condition in our study area. Still, our finding warrants further consideration of the urban homogenization hypothesis, especially how urbanization may have differential effects at the scales of continents, cityscapes, individual greenspaces, and microsites within urban greenspaces. In order to best protect these urban soil animal communities, it seems essential to move beyond a one-size-fits-all management strategy and toward a tailored approach which considers the unique context of each urban greenspace (Aronson et al., 2017). As our results show, this may not involve an exhaustive consideration of every single urban factor of a greenspace, but perhaps considering factors based on where a greenspace is located. As evidenced by our RF model, a nonspecific approach to management may suffice for less urbanized areas, while more heavily urbanized greenspaces may benefit from a more nuanced and conscientious management plan.

In conclusion, our study highlights the intricate dynamics at play in urban soil animal communities and prompts a reconsideration of urban ecology paradigms as they apply to belowground ecosystems. It implicates the need for tailored soil conservation and management strategies that considers the many layered factors of urban areas, rather than only the geographical location of a soil along the urbanization gradient. Understanding how soil animal communities respond to urbanization is important in creating resilient urban ecosystems which preserve the biodiversity and ecosystem functions in the face of current and future global change.

## AUTHOR CONTRIBUTIONS

Hayden W. Bock, Kyle G. Wickings, Peter M. Groffman designed the study. Hayden W. Bock collected data and performed statistical analyses. Hayden W. Bock and Kyle G. Wickings wrote the manuscript, with critical feedback from all authors. All authors approved the final manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Bock, 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.10625395.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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