

SHORT COMMUNICATION

Urbanization has opposing effects on the trophic niche of three ubiquitous soil animal taxa**Hayden W. Bock^{1,2}, Jed P. Sparks³, Stefan Scheu^{4,5}, Peter M. Groffman^{6,7}, Frank S. Rossi⁸ and Kyle G. Wickings^{1,*}**

¹ Department of Entomology, Cornell Agritech, Cornell University, 324 Barton Laboratory, 15 Castle Creek Dr., Geneva, New York 14456, United States

² Department of Plant Science, The Pennsylvania State University, 313 Tyson Building, University Park, Pennsylvania 16803, USA

³ Department of Ecology and Evolutionary Biology, Cornell University, E409A Corson Hall, Ithaca, New York 14853, USA

⁴ Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Untere Karspüle 2, 37077 Göttingen, Germany

⁵ Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

⁶ Advanced Science Research Center at the Graduate Center, City University of New York, 85 St Nicholas Terrace, New York 10031, USA

⁷ Cary Institute of Ecosystem Studies, 2801 Sharon Turnpike, Millbrook, New York 12545, USA

⁸ School of Integrated Plant Science, Horticulture Section, 106 Academic Surge Facility A, Ithaca, New York 14853, USA

* Corresponding author, E-mail: Kgw37@cornell.edu

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Abstract

Soil microarthropods comprise diverse trophic groups and contribute to many soil functions, including carbon and nutrient cycling. However, there is little known about how these organisms and their trophic ecologies respond to urbanization, which is a predominant force shaping modern soil ecosystems. In this study, we tested whether urbanization constrains or otherwise alters the trophic niches of three representative microarthropod taxa (Collembola, Oribatida, and Mesostigmata) across an established urbanization gradient in Rochester, New York, USA. We used stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) as a tool to study this phenomenon, and we found that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shifted slightly within and between the microarthropod taxa in response to urbanization. However, we saw more stark contrast between these taxa groups when we compared isotopic niche space between the taxa and found that Oribatida and Collembola experienced a diminishment in their isotope niche area. In contrast, Mesostigmata experienced an expansion in their niche area because of urbanization. Collectively, these findings underscore that microarthropod taxa respond uniquely to urbanization depending on their underlying biology and ecology, and the trophic niche of some organisms may even be enlarged by urbanization pressures. Thus, our study highlights that the functional roles of these organism communities may shift with urbanization pressure and demonstrates the need to further understand the link between soil animal community composition, function, and the facilitation of soil ecosystem services in urban areas.

Keywords Soil microarthropods | urban ecology | urbanization | stable isotopes

1 Introduction

Soil microarthropods are some of the most abundant and diverse arthropods in terrestrial ecosystems and represent a key component of belowground biodiversity (Coleman & Wall 2017). Their diversity spans numerous functional groups, including fungal and detrital feeders, omnivores, and predators, and they play essential roles in ecological processes such as nutrient cycling, soil formation, and the regulation of microbial communities (Brussaard 1998; Coleman et al. 2004; Coleman & Wall, 2017; Grandy et al. 2016; A. Potapov 2022). Their ecological functions are provisioned in part through their community's high functional similarity (Anderson 1975; Anthony et al. 2023; Bock et al., 2024; Briones 2014; Eisenhauer et al. 2023; Hosler et al. 2024), which acts to safeguard ecosystem processes even when certain taxa or functional guilds decline in abundance or richness (Setälä et al. 2005). This similarity is further reflected in their feeding strategies, where many of them are broadly considered detritivores or microbivores (Lussenhop 1992; A. M. Potapov et al. 2019) although the nuances of their feeding biology are admittedly understudied. Microarthropod functional roles, which encompass decomposition, nutrient mineralization, microbial community regulation, and energy transfer, are strongly linked to their diet (Bardgett & Van Der Putten 2014; Coleman et al. 2004; Crowther 2012; Liang 2020; Moore 1988; Ruess & Chamberlain 2010). Thus, determining the feeding habits and trophic positions of soil microarthropods is essential for evaluating their contributions to key ecosystem functions. Moreover, we must also understand how environmental context shifts diet and trophic position in microarthropods; doing so will enable us to predict how microarthropod-driven ecosystem functions, such as nutrient cycling and decomposition, may change in response to environmental disturbances.

Urbanization is a pervasive disturbance and ecological filter that defines the Anthropocene (Elmqvist & McDonald 2014). It is a top-down ecological disturbance that restructures ecosystems through habitat fragmentation, pollution, changes in microclimate, and alterations to the flow of energy and resources in food webs (Elmqvist et al. 2013; Kaye et al. 2006; Kotze et al. 2013; M. J. McDonnell & Pickett 1990). Urbanization acts as an ecological filter that typically homogenizes ecosystems (Aronson et al. 2014; Faeth et al. 2005, 2011; Groffman et al. 2014; McKinney 2006; Shochat et al. 2006), though there is some evidence that it may enhance biodiversity at small, local scales (Bock et al. 2024; Hosler et al. 2024). Aboveground studies demonstrate that urban environments consistently reduce species diversity, decrease trophic complexity, and simplify ecological

interactions (Aronson et al. 2014; Faeth et al. 2005, 2011; Groffman et al. 2014; McKinney 2006; Shochat et al. 2006). However, despite extensive research on the impacts of urbanization on aboveground systems, comparatively less attention has been paid to the responses of soils and their biotic communities (Huang et al. 2020; Whitehead, Hempel et al. 2022; Whitehead, Roy et al. 2022). The few studies on urban microarthropod communities suggest that their communities may respond differently to urbanization compared to other fauna and may even benefit from urbanization in some instances (Bock et al. 2024; Huang et al. 2020; Szlavecz et al. 2020). However, there is a clear literature gap in understanding how microarthropod diet and trophic position responds to urbanization. These organisms underpin many essential urban soil ecosystem processes, and understanding how urbanization influences their feeding ecology and trophic niche is critical for sustaining the function of urban soils (Bray & Wickings 2019).

Directly measuring the function of soil microarthropods is challenging due to the complexity of belowground food webs (Bardgett & Van Der Putten 2014; Briones 2014) and discrepancies over the preferred methods to link microarthropod diet to ecological function (Berg et al., 2004; A. Potapov et al., 2020). However, stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) is increasingly used in soil ecology as a means to understand diet and trophic position in belowground food webs (Chahartaghi et al. 2005; Crotty et al. 2012; Maraun et al. 2011; Pollierer & Scheu 2021; A. M. Potapov et al. 2019) and how they may shift under varying ecological conditions (Krause et al. 2021; Marshall et al. 2019; A. M. Potapov et al. 2014). Thus, stable isotopes may provide a means to understand how urbanization influences the diet and trophic position of microarthropods.

The primary objective of this study was to investigate whether urbanization leads to a similar reduction in ecological niches across microarthropods as it does to aboveground flora and fauna.

Specifically, we tested three hypotheses: (1) Urbanization increases trophic overlap among soil microarthropod taxa, as measured through $\delta^{15}\text{N}$, due to stronger top-down pressures in disturbed urban environments; (2) Urbanization broadly diminishes niche breadth among microarthropods, as measured through $\delta^{13}\text{C}$, with the greatest reductions observed in taxa closely associated with fungal resources (Hedlund et al. 2004; A. Potapov 2022; A. M. Potapov et al. 2019, 2022; Whitehead, Roy, et al. 2022); and (3) Niche overlap is greatest in urban areas, as urban microarthropod communities represent a simplified subset of less disturbed communities due to the filtering effect of urbanization. To test these hypotheses, we studied three distinct communities of microarthropod

taxa along an urban gradient: Collembola, Oribatida, and Mesostigmata. These are all highly ubiquitous taxa known to occupy multiple trophic roles (fungivore/detritivore and primarily tertiary consumers, respectively) in soils (Coleman et al. 2004; Coleman & Wall 2017; A. Potapov 2022; A. M. Potapov et al. 2019).

2 Materials and Methods:

2.1 Study Site and Organisms

To study the impact of urbanization on belowground ecological niche breadth, we studied three soil animal taxa: Collembola, Oribatida, and Mesostigmata, across an established urbanization gradient of 40 public parks in Rochester, NY, USA. Briefly, these public parks ranged from <0.5km to 20km from the city's geographic center and had a mix of woody (trees and shrubs) and herbaceous (grass lawns and planted forbs) vegetation. We measured a suite of soil (e.g. bulk density, C:N, pH, water holding capacity), spatial (e.g. percentage impervious surface, park area, park perimeter:area), and socioeconomic (e.g. median household income, median resident age, population density) factors for each park, which were collectively analyzed using a kmeans clustering algorithm to group each park into "low-urban" or "high-urban". The full methodology is described in Bock et al., 2024.

We collected a total of 160 soil samples across the parks in May 2021; we selected four random sampling locations within the grass lawn of each park, where each sampling location consisted of seven pooled 6 cm x 5 cm soil cores which were extracted over 72 hours using modified Berlese funnels. The extracted microarthropod samples were then stored in 95 % ethanol for later identification (Bock et al. 2024). The four samples belonging to each park were then pooled, so that we had one representative sample from each park. We then removed and separated Collembola, Oribatida, and Mesostigmata, from each pooled sample, so that we had a representative community of each taxa for each park, totaling 118 samples ($n = 40$ Collembola, $n = 38$ Oribatida, $n = 40$ Mesostigmata). We identified soil fauna at the major taxonomic group level, using the Borror and Delong Key for Insects (Triplehorn et al. 2005) for Collembola. We separated Oribatida and Mesostigmata by morpho-species, then identified to family and 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). We collected a total of 5, 21, and 40 morpho-species of Collembola, Oribatida, and Mesostigmata in high-urban parks. We collected

6, 24, and 41 morpho-species of these groups in high-urban parks. Fine-scale taxonomic data is detailed in the supplemental materials of Bock et al. 2024.

2.2 Isotope Analysis

Collembola, Oribatida, and Mesostigmata were individually weighed into tin capsules, so that the entirety of the taxa collected in each park were included in the analysis to ensure at least 10 μg of animal dry mass per sample. The tin capsules were then dried at 60° C for 24 h and weighed with a microbalance to determine animal dry weight. Stable isotope analysis was conducted using a coupled setup of an elemental analyzer (Eurovector, Milano, Italy) and a mass spectrometer (Delta Vplus, Thermo Fisher Scientific, Bremen, Germany) adjusted for small sample sizes (Langel & Dyckmans 2014). We expressed variations in stable isotope ratios (including baseline correction) using delta notation with $\delta X = (R_{\text{SAMPLE}} - R_{\text{STANDARD}}) / R_{\text{STANDARD}} \times 1000$ and X representing the target isotope (^{13}C , ^{15}N), and R_{SAMPLE} and R_{STANDARD} the ratios of the heavy to the light isotope ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) of the sample and the standard, respectively. We used Pee Dee Belemnite for the ^{13}C standard, and atmospheric air for the ^{15}N standard (Coplen et al. 2002). Acetanilide was used for internal calibration. We use $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as proxies for basal resource and trophic position (increase in $\delta^{15}\text{N}$ by $\sim 3.4\text{‰}$ (± 1 SD) per trophic level) to allow for relative comparisons of trophic position between taxa and urban classes (de Carvalho et al. 2021; Fry 2008)

2.3 Statistical Analysis

We used a suite of geospatial, soil, and United States Census (U.S. Census Bureau 2019) data to characterize the urbanization of each park (Table S1) in conjunction with a k-means clustering algorithm to designate "high-urban" and "low-urban" parks, which serves as a high-dimensionality urbanization classification that we used for later statistical comparisons. This process is detailed more thoroughly in (Bock et al. 2024). Due to the unbalanced sample size of our study ("high-urban" $n = 17$; "low-urban" $n = 23$), we used a nonparametric Kruskal-Wallis test to measure the effects of urbanization and taxa identity on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. When p-values were significant ($p < 0.05$), we used Fisher's least significant difference for post hoc comparisons between groups.

We calculated and visualized the isotope niche size of each taxa using the R package SIBER (Jackson et al. 2011). To compare niche breadth between the two urbanization classes of each taxon, we used the "rjags"

package with Markov Chain Monte Carlo (MCMC) sampling and posterior distributions for the isotopic values of each species, which were then used to generate Bayesian multivariate normal distributions to each taxon across both urban classes, using prior settings of length, number and iteration of sampling chain, and distribution parameters as recommended by the SIBER package (Parnell & Jackson 2019). These probability distributions were then used to calculate Bayesian standard ellipse areas corrected for small sample sizes (SEA-c) and plotted using the function `siberDensityPlot()` including 50%, 90%, and 95% credible intervals. We then compared probability distributions from the Bayesian standard ellipses with 95% credible intervals for each taxon to determine differences in isotopic niche breadth. To measure isotopic niche overlap, we used the `bayesianOverlap()` function set to 10 draws to calculate 95% credible intervals for percent ellipse overlap for $P(\text{high-urban} \cap \text{low urban})$ and $P(\text{low-urban} \cap \text{high-urban})$. The percent overlap was calculated as the percent of the overlapping area divided by the total area covered by the two ellipses. The mean of these overlapping areas was calculated for each region. An increased overlapping area represents increased isotopic niche overlap (Krumsick & Fisher 2019).

3 Results

Our univariate analysis showed an enhancement in $\delta^{13}\text{C}$ in the low-urban communities compared to high-urban communities when comparing average values of the two urban classes across taxa ($-26.44 \pm 0.13\text{‰}$ vs. $-26.90 \pm 0.12\text{‰}$, mean \pm SE; $\chi^2 = 17.41$, $p = 0.003$). However, there was not a similar enrichment between urban classes for $\delta^{15}\text{N}$ ($4.37 \pm 0.31\text{‰}$ vs. $4.28 \pm 0.24\text{‰}$, mean \pm SE; $\chi^2 = 0.10$, $p = 0.75$). Of the three taxa, Collembola exhibited the greatest difference in $\delta^{13}\text{C}$ values between high-urban and low-urban classes, respectively ($-26.37 \pm 0.21\text{‰}$ vs. $-27.20 \pm 0.24\text{‰}$, mean \pm SE). Oribatida and Mesostigmata did not respond similarly and showed no difference between urban classes (Figure 1). However, we did observe that in high-urban parks, Mesostigmata were significantly enriched in $\delta^{13}\text{C}$ compared to Collembola and Oribatida ($-26.34 \pm 0.19\text{‰}$ vs. $-27.20 \pm 0.24\text{‰}$ and $-27.15 \pm 0.18\text{‰}$) respectively. This difference was absent in low-urban parks (Figure 1). We did not observe any notable differences in $\delta^{15}\text{N}$ between taxa or urban classes (Figure 1).

Comparing isotopic ellipse area (i.e., SEA-c) allowed us to further discern how urbanization may alter belowground niche breadth (Jackson et al. 2011). Urbanization reduced Collembola SEA-c by 1.22–

1.90‰ and similarly reduced Oribatida by 1.20–2.27‰ (95% CI; Figure 3, Table S2). There was not a similar diminishment in Mesostigmata niche breadth; on the contrary, urbanization enhanced Mesostigmata SEA-c by 0.35–1.79‰, according to 95% CI (Figure 3; Table S2). For Collembola and Oribatida, high-urban communities had nominally more community overlap with low-urban communities (i.e., high-urban communities fell within a portion of the low-urban ellipse), while Mesostigmata had the opposite trend, with urbanization diminishing niche overlap by 21% (Table 1).

4 Discussion

Our study aimed to elucidate the impacts of urbanization on microarthropod trophic niches along an urban gradient, focusing on three functionally distinct but ubiquitous taxa: Collembola, and Oribatida and Mesostigmata mites. We hypothesized that these microarthropods would exhibit reduced trophic level separation (i.e., increased overlap in $\delta^{15}\text{N}$) under high urbanization pressures due to the known role of urbanization as a top-down control on terrestrial food webs. Within each taxa, there were no clear shift in their $\delta^{15}\text{N}$ signature between urbanization classes (Figure 1). However, what may be more illuminating to our hypothesis is the range in median $\delta^{15}\text{N}$ between taxa groups. In low-urban areas, Collembola and Oribatida occupy a similar $\delta^{15}\text{N}$ space, while Mesostigmata occupy a higher trophic level. In contrast, high-urban parks show distinct $\delta^{15}\text{N}$ values between each taxa, which suggests that urbanization may enhance trophic differentiation belowground. Similar patterns of niche partitioning in urban settings have been documented aboveground (Aronson et al., 2014; Faeth et al., 2011), but these results add to the growing literature showing microarthropod community structure and function are shaped by urbanization (Bock et al., 2024; Huang et al., 2020).

In line with our second hypothesis that urbanization reduces niche breadth (i.e. range of $\delta^{13}\text{C}$), we observed that Collembola and Oribatida became significantly depleted in $\delta^{13}\text{C}$ in high-urban parks (Figure 1), with their narrowed isotopic ellipse areas suggesting that in the presence of urbanization, these taxa experience a constrained range of food resources (Figure 2 & 3). Since Collembola and Oribatida often function as mediators of decomposition and microbial processes (Bock & Wickings 2023; T. W. Crowther et al. 2012), a narrowing of their resource base may diminish the efficiency or stability of these processes in urban soils (Elmqvist et al. 2013; Setälä et al. 2005). This finding

agrees with the broader urban ecology literature, which suggests urbanization both structurally and functionally homogenizes plant and microbial communities (Aronson et al. 2014; Wheeler et al. 2017; Whitehead, Roy et al., 2022) which may limit dietary options for these taxa. However, given that urbanization is known to lower soil C:N (Yang et al. 2020) and litter quality (McDonnell et al. 1997) which can change urban carbon cycling dynamics (Groffman et al. 1995), we cannot definitively attribute our results to shifts in diet, as there may have been changes in $\delta^{13}\text{C}$ signatures of the resources themselves that led to these observations.

Conversely, while these primary decomposers experienced diminished niche breadth, Mesostigmata predators showed an expansion of their niche breadth as urbanization increased (Figure 2 & 3). This finding was surprising to us, as it suggests that urbanization may relatively benefit this specific taxa. Mesostigmata are highly mobile and generalist predators (Coleman et al. 2004; Klarner et al. 2013; Minor & Cianciolo 2007). Therefore, their life history may enable them to exploit shifting resources in urbanized soils, such as changes in bacteria:fungi ratios (Hedlund et al. 2004; Lee Taylor & Sinsabaugh 2015; Whitehead, Roy et al. 2022), which

Table 1. Mean predicted posterior estimates for isotope ellipse overlap between taxa for each urbanization class. The “High” column indicates the overlap the High-Urban taxa shares with the Low-Urban taxa. The “Low” column indicates the overlap the Low-Urban taxa shares with the High-Urban taxa. The “Both” column indicates the mutual overlap between High-Urban and Low-Urban taxa. 95% credible intervals for each overlap combination are displayed in the CI column.

Taxa	High		Low		Both	
	mean \pm se	CI (95%)	mean \pm se	CI (95%)	mean \pm se	CI (95%)
Collembola	81.69 \pm 4.02	62.09, 101.8	61.7 \pm 1.98	53.50, 76.70	35.52 \pm 16.26	28.16, 45.68
Oribatida	76.18 \pm 5.05	4.20, 97.13	65.71 \pm 5.58	37.08, 98.10	32.39 \pm 2.07	22.58, 42.00
Mesostigmata	68.34 \pm 5.12	45.97, 90.06	89.53 \pm 3.11	75.31, 104.48	18.70 \pm 1.10	13.36, 23.41

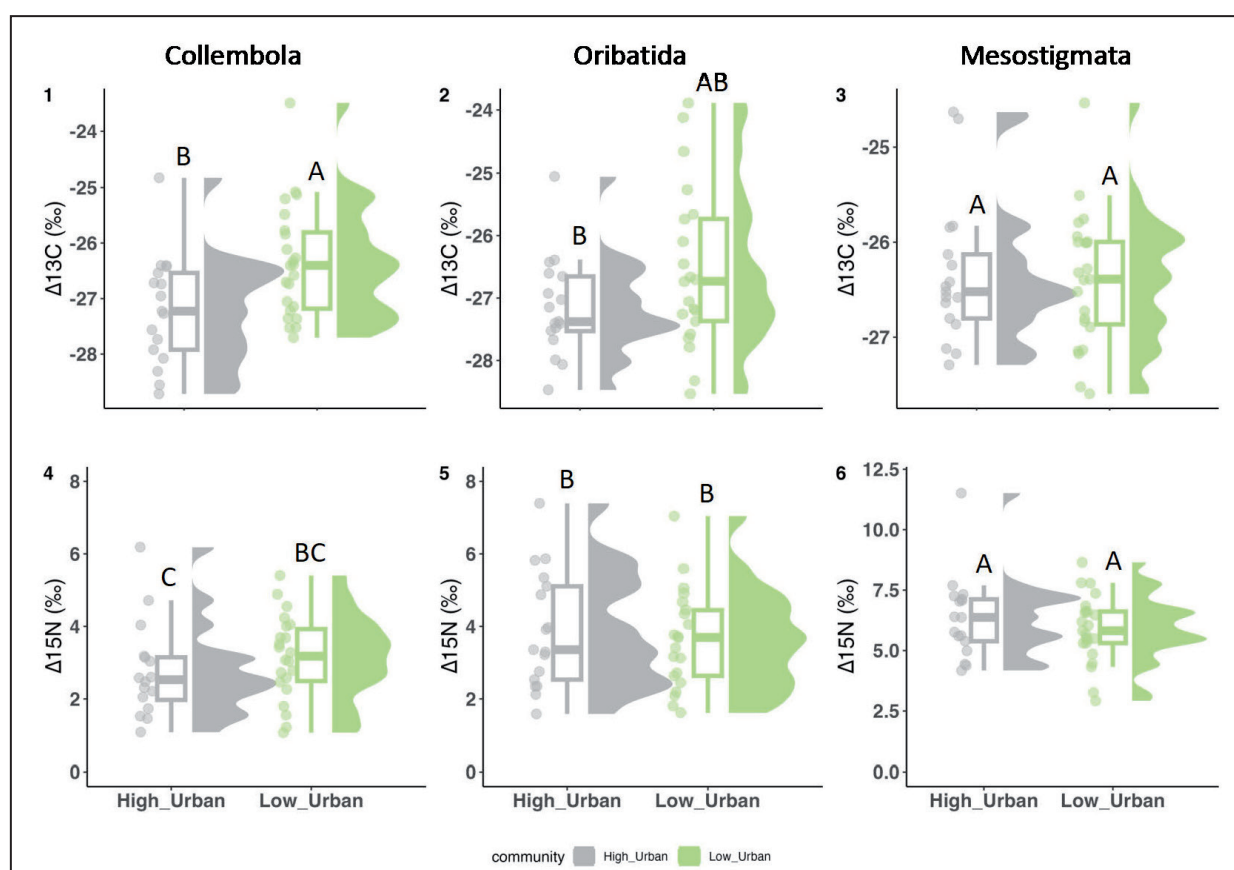


Figure 1. Box and whisker plot showing the median (central line in box), interquartile range (IQR; upper and lower bounds box) and 1.5 times the IQR (whisker) of $\delta^{13}\text{C}$ (panel 1-3) and $\delta^{15}\text{N}$ (panel 4-6). Scatterplots and distribution plots are provided alongside each boxplot to better convey visual differences in data distribution. Significance between urbanization classes across taxa denote significant differences according to Fisher's least significant difference test.

may provide new food resources to Mesostigmata via increases to bacterial grazer populations (e.g. Nematodes). While this finding suggests that organisms with flexible feeding strategies may sometimes benefit from anthropogenic changes, we again acknowledge that without isotopic baseline data from soil, litter, or prey resources, we cannot definitively attribute these isotopic shifts exclusively to diet changes (Fry 2008). Thus, further comprehensive research is necessary to elucidate these relationships in urban soil ecosystems.

Finally, we hypothesized that urban microarthropod communities would represent a subset of the niche space found in low-urban areas due to the filtering effect of urbanization. Collembola and Oribatida in high-urban parks largely overlapped with the low-urban ellipse (Figure 3, Table 1). This finding aligns with our hypothesis and supports the idea of a belowground “filtering” mechanism. In heavily urbanized soils, the community of Collembola and Oribatida become sparse,

resulting in a narrowing of the original niche space (Setälä et al. 2005). Mesostigmata showed the opposite pattern: their niche expanded in high-urban parks compared to low-urban parks, as measured by declining niche overlap in high-urban settings (Figure 3). This suggests that as a community, the Mesostigmata found in highly urban soils may be contributing a disproportionately large amount to belowground function, and even occupying new functional roles, compared to Mesostigmata in less urbanized areas (Figure 3, Table 1). Overall, these findings demonstrate that the impacts of urbanization on trophic niches are likely taxon-specific and intimately tied to feeding strategies. By altering resource availability (e.g., fungal biomass, litter diversity) and changing prey communities, urbanization can substantially reshape the diets and trophic positions of soil microarthropods. Future research should integrate direct resource measurements, molecular gut analyses, or compound-specific isotopic approaches to pinpoint the precise dietary channels

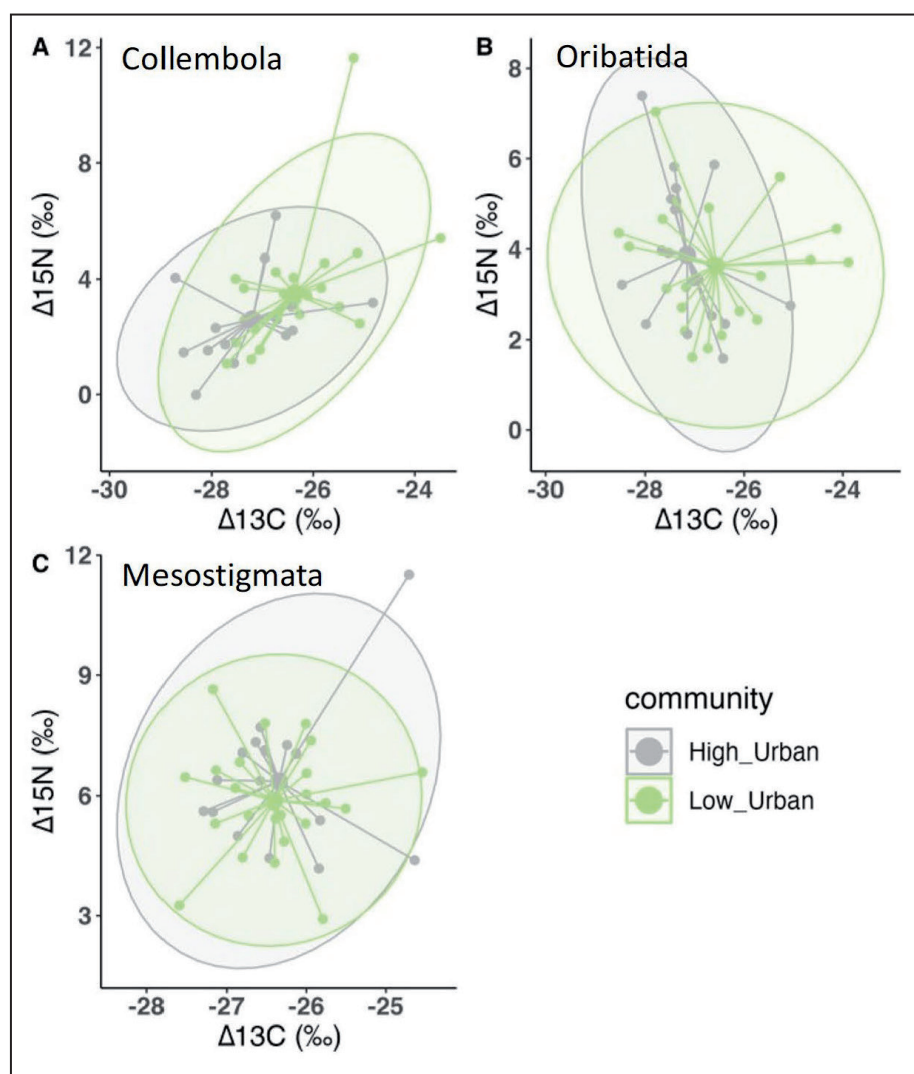


Figure 2. Scatter plot showing two-dimensional isotopic niche space along $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes. The central point of each scatterplot denotes mean value by community, while the smaller, connected points denote observed values. Ellipses denote 95% confidence interval of each taxa group.

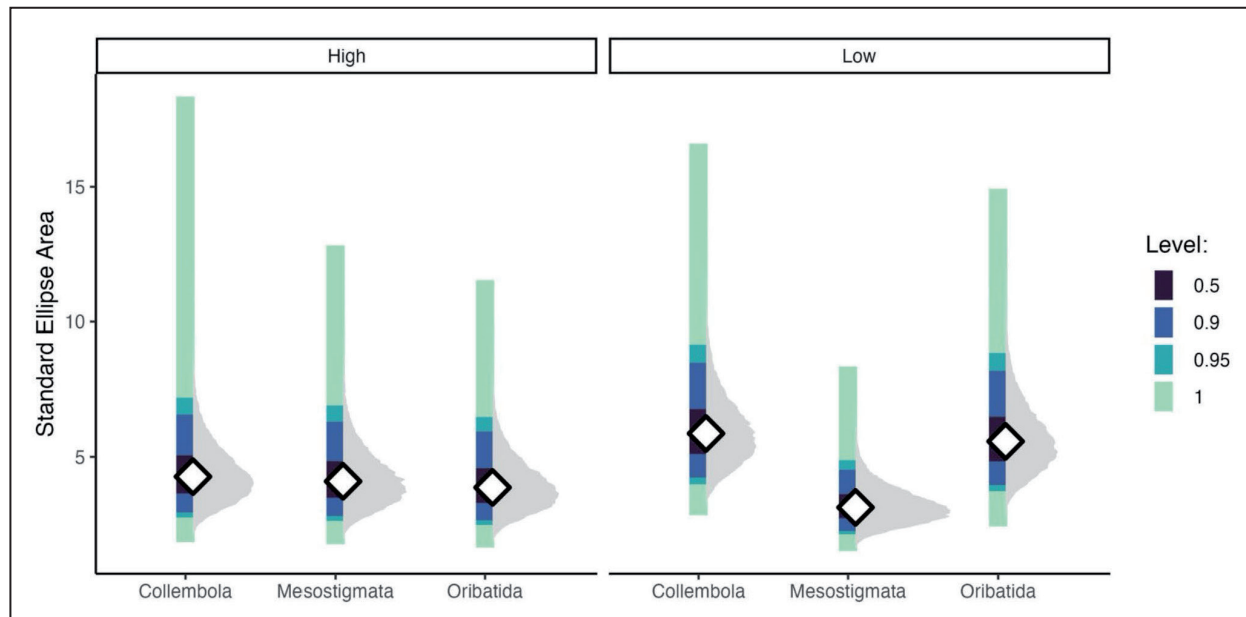


Figure 3. Distribution plot showing predicted corrected standard ellipse areas (SEA-c) for each taxa and urbanization class. White diamonds show posterior estimates of the Bayesian standard ellipse area with 50%, 90 %, 95 %, and 100 % credible intervals (according to legend colors).

underpinning these patterns. Such mechanistic understanding will be essential for developing effective urban land-management strategies aimed at preserving soil health and sustaining the critical ecosystem services mediated by belowground communities. As urban land area continues to expand globally, understanding the resilience or sensitivity of these belowground systems toward urbanization will be pivotal for sustaining soil health and ecosystem function in the built environment.

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