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Research article

Soil microarthropod distribution on the urban–rural gradient of Riga city: a study with robust sampling method application

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Abstract

To address the new challenge of bringing more nature into the urban environment and developing adequate green infrastructure management methods, it is necessary to clarify the regularities of the distribution of the main ecosystem components—soil organism communities on the urban gradient. Microarthropods—collembolans and mites—are the most diverse soil animals and bioindicators of soil conditions. However, no suitable approaches exist so far to help reduce the high workload of soil zoological studies and make the data acquisition for soil assessment faster. To get closer to a solution to this problem, we propose a robust sampling approach using one pooled sample per site with surface area 58 cm^2. This was tested in a microarthropod distribution study on the urban gradient of Riga city (Latvia) in six urban habitat types at 21 sites. The use of classical statistical methods for the processing of soil microarthropod data is limited because these data do not meet model requirements on which classical methods are based, first of all, conformity to the normal distribution. These problems are circumvented by bootstrapping methodology, which thanks to increasing computer performance now is implemented in the most modern program packages. We tested a set of such methods: one-way bootstrap-based analysis of variance, nonmetric multidimensional scaling (NMS), nonparametric multiplicative regression (NPMR), multi-response permutation procedure and Chao bootstrap-based rarefaction curves. NMS in combination with NPMR gave the best results providing statistically significant species distribution curves along the urban gradient which were broadly in line with species traits found by other studies.

Key words: urban habitats, green infrastructure, soil microarthropods, nonparametric multiple regression, sample size

Introduction

The term ‘urbanization gradient’ refers to the spatial variation of environmental factors in relation to the intensity of urbanization, from natural landscapes to the most heavily urbanized areas (McDonnell and Hahs 2008). The concept of urban gradient and urban habitat classification was coined in the 1980s by German researchers (Sukopp and Werner 1983; Klausnitzer 1987). Later, the concept was advanced by McDonnell and Pickett (1990), providing a basis for intensified studies of urban biodiversity

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(Guilland et al. 2018). The idea of generalization of urban gradients is currently relevant, which would make it possible to quantify and compare urban gradients in different cities (McDonnell and Hahs 2008). However, its implementation is hindered by insufficient knowledge about the distribution of different groups of living organisms on the urban gradient. Mostly, these studies are biased towards larger organisms, such as plants (Aronson et al. 2015), birds (Blair 1996; Alberti, Botsford, and Cohen 2001) and some insect groups (Avondet et al. 2003), but almost nothing is known about less noticeable groups such as soil fauna (McDonnell and Hahs 2008).

Soil biodiversity is a key factor providing the functioning of a soil ecosystem (Barrios 2007; Wagg et al. 2014) and therefore the study of the distribution of these organisms on the urban gradients is of particular importance. Among soil animals the microarthropods—collembolans and soil mites represent the most taxonomically diverse group, demonstrating significantly high variability in abundance and species diversity. Collembola play an important role in the plant litter decomposition and regulation of soil microscopic fungi (Hopkin 1997). Collembola have relatively high reproduction rates and they respond sensitively to environmental fluctuations (Pollierer and Scheu 2017). Oribatid mites are the most abundant group of all arthropods in the organic horizons of most soils, especially in boreal forests, and are essential for breaking down organic detritus and distributing fungi (Behan-Pelletier and Lindo 2022). As typical litter decomposers and mycetophages they have relatively low reproduction rates (Behan-Pelletier and Lindo 2022). Mesostigmata mites include mostly predatory species feeding on Collembola, other mites, enchytraeids, insect eggs and nematodes (Koehler 1999; Ruf and Beck 2005). Thus, these three groups of microarthropods represent a very wide range of ecological traits and may provide a comprehensive assessment of changes in soil ecosystems under the influence of urban environmental factors (McIntyre 2000; Santorufo et al. 2012).

Until now, studies on microarthropods in urban environments have been mainly focused on the comparison of communities from 2 to 3 habitats under different anthropogenic pressures: oribatid mites from soils of street lawns, parks, gardens, wastelands, urban and natural forests (Niedbała et al. 1982; Eitminaviciute 2006; Manu and Honciuc 2010; Andrievskii and Syso 2012; Vacht et al. 2019), Mesostigmata from parks and urban forests (Telnov and Salmane 2015; Manu et al. 2019; Manu et al. 2021) and Collembola from parks and street lawns (Sterzyńska 1982; Kuznetsova 1994; Krestyaninova and Kuznetsova 1996; Fiera 2009; Milano et al. 2017, 2018). Considering the aggregated spatial distribution of microarthropods, to provide a statistically reliable result at least 10–30 soil samples from each sample site should be collected (MacFadyen 1962). The total number of soil samples in the above-mentioned studies counted from several dozen to hundreds. In order to construct the urban gradient axis, it is necessary to include more than three types of urban habitats differing in anthropogenic pressure (Klausnitzer 1987). Keeping the above-mentioned number of soil samples to be collected at each site, the total number of samples increases steadily making the analysis extremely labour intensive. It is not surprising that there are still very few studies (Niedbała et al. 1990) showing the distribution of microarthropod community characteristics on an urban gradient. At the same time, it should be noted that in addition to gradient methods, there are also other approaches to soil condition assessment by soil animals based on specially developed indices (Parisi et al. 2005; Accattoli and Salazar Martínez 2012).

In general, labour intensity of analysis of microarthropod samples is the main obstacle for the introduction of these animals in quality control of urban soils (Landeiro et al. 2012).

It is necessary to note also that urban habitats are highly fragmented and often fragments of green areas such as lawns along streets and flower beds are occupying only a few square metres (Yli-Pelkonen and Kohl 2005; Zigmunde and Nitavska 2013). In order not to destroy the site, the conventional sampling approach in such cases cannot be used.

It is therefore important to work on the development of adequate sampling methods.

During recent years, some studies of soil microarthropods in urban habitats already have turned to small sample sets containing 3–5 soil samples with a total surface of 60–100 cm^2 and 5–10 cm depth (Menta et al. 2011; Santorufo et al. 2014; Rzeszowski, Zadrożny, and Nicia 2017; Sterzyńska et al. 2018; Yu et al. 2021). During our earlier comprehensive studies on the effects of soil pollution (Melecis 1985; Lapiņa and Melecis 1989) and climate change (Jucevica and Melecis 2006; Koehler and Melecis 2010) on soil microarthropods, a series of small soil samples ($n = 100$, 5 cm^2 × 10 cm, with the total area 500 cm^2) were used, thus providing a large data pool for comparative analysis of species–area curves from various habitats. It was shown that species–area curves never flatten off even at the sample size $n = 100$. Thus, if our goal was to obtain the values of the species richness s, as an estimate of the real number of species in the studied habitat, the required number of soil samples would make the study too labour intensive. At the same time, it was demonstrated (Melecis et al. 2018) that by increasing the total surface area of the sample to 60 cm^2, it covered 38–50% of Collembola species, 61–66% of Oribatida and 42–50% of Mesostigmata species found in 500 cm^2. Of course, the species richness indirectly indicates the adaptive capacity of the ecosystem (Gunderson 2000). however, the main role in ecosystem functioning may play the dominant/subdominant species (Coleman and Whitman 2005), which due to their higher density always are present even in the small sample series and so can be used for the assessment of soil conditions.

Based on this analysis, a robust approach was developed (Melecis et al. 2018) for extensive sampling of small urban green areas. It recommends limiting the number of urban habitats included in the study to six and setting the total number of sample plots close to 20. To minimize the data variation due to the aggregated spatial distribution of microarthropods, as well as to reduce time and equipment for microarthropod extraction, a pooled sample consisting of three random soil cores (20 cm^2 × 10 cm) was collected from each study site with a total area about 60 cm^2.

The use of classical statistical methods for the processing of soil microarthropod data is limited because these data do not meet the model requirements on which the classical methods are based, first of all, conformity to the normal data distribution. These problems are circumvented by bootstrapping methodology, which thanks to increasing computer performance is recently implemented in the most modern program packages (Manly 2007), We tested a set of such methods and used several bootstrapping-based data analysis programs to analyse the data. The purpose of this paper was to evaluate the selected sampling approach along with the assessment of effectiveness of these bootstrap-based methods in studies of microarthropod distribution on an urban gradient.

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Materials and methods

Novel ecosystems

Riga city is located along the Baltic Sea at the southern coast of the Gulf of Riga (56°58′18.2″N, 24°07′42.3″E) on the Rigava coastal plain. The historical core of Riga is situated on the right bank of the Daugava River, near the place where the Daugava flows into the Gulf of Riga. The natural terrain of this area is a flat and sandy plain, about 1–10 m above sea level.

The climate in Riga is humid continental (*Dfb* according to Köppen 1936). It is affected by the moderate latitude air masses of the Atlantic Ocean and its proximity to the sea. Yearly mean temperature is +7.9°C. Average precipitation is measured 700–720 mm a year. Summers are comparatively cool and cloudy, with an average temperature in July of +16.9°C; on the hottest days, the temperature can exceed 30°C. Winters are comparatively warm with frequent thaws. The average temperature in January is 4.7°C, but temperatures as low as −20 to −25°C can last up to 8 days (LEGMC 2020; Riga City Council 2017).

The area of Riga covers 307.17 km^2. The city stands on the glacial and post-glacial Baltic Ice Lake accumulations, as well as post-glacial dunes. Latvia has relatively newly developed soils, only starting to exist during the Quaternary period's last glacier retreat, before 15 000 years. So far, no special studies have been performed on Riga soils. The development of soils depends on the climate, when precipitation dominates over evaporation, influence of vegetation of Boreonemoral zone and a large variety of granulometric and mineral compositions of the bedrock (Nikodemus 2019).

Soils in Riga have formed on poor dune sand bedrock. At the elevated terrain zones, podzol soils are formed. In the valleys where precipitation waters accumulate sediments, peaty low marsh soils are formed (Danka and Stiprais 1973). It has been estimated that only 30% of the city's space refers to residential areas and 28% is considered as the 'green space' (e.g. public and private lawns, city parks and urban forests) leaving the remaining 42% for city waterbodies, roads and technogenic or industrial spots (Riga City Council 2012, 2017). Undeveloped parts and suburban areas are covered by pine forests subjected to different levels of human pressure (Latvia's State Forests 2018). The patches of the green infrastructure of Riga are implemented as isles in an anthropogenic landscape. Natural soils are unsustainable for gardens, parks, or greenery. To improve the topsoil in green areas of the city, since the 18th-century fertile soil, mostly gained from wet river floodplains had been implemented, in some parts adding up to 20-cm-thick horizons. Soils in the central part of Riga can be characterized as artificial, sandy, highly heterogeneous and compacted. In general, the top layer of the studied street soils (0–35 cm) contains 8.58% clay, 13.32% silt, 78.09% sand and organic matter from 3.55 to 12.27%, park soils are richer containing 10.38% clay, 24.2% silt, 65.5% sand and 5.70% organic matter (Cekstere and Osvalde 2013).

Sampling sites

Klausnitzer (1987) distinguishes several types of urban gradients: R-H gradient (from Latin rusticus—rural, hortus—garden), R-M gradient (rupes—rock, murus—wall), C-C gradient (caverna—cave, cella—chamber) and A-E gradient (arbor—tree, eremus—desert). The A-E gradient characterizes the transition from forest through perennial grasslands to rocky landscape. The A-E gradient is the most characteristic of the city of Riga, which was formed in a forested area. Later on in this article, we will simply use the term urban gradient. Within this gradient, Klausnitzer (1987) distinguishes smaller urban habitats, which differ mainly in the impact of soil management and potential pollution: street edge areas and squares, larger parks, cemeteries and botanical gardens and suburban gardens of private houses, urban forests with the high anthropogenic load. The distal end of the gradient is marked by suburban forests with little human-modified soils.

The following six types of urban habitats (according to the classification of Klausnitzer 1987) typical of the city of Riga were selected on the urban–rural gradient to the NE border from the city center: street surrounding lawns (Str), park lawns (PaL), private house garden lawns (PrL), cemetery lawns (Cem), urban forests (UrF) and suburban forests (SubUrF) (Fig. 1). According to the city map, 4 random plots were selected within each classification unit, except for street edges and cemeteries, where the number of selected plots was 3 and 2, respectively. To reduce as much as possible the potential influence of the internal spatial heterogeneity of the specific urban habitat (fragments of bare soil, animal digs, paths, flower beds, micro-hollows, burial grounds, etc.) on the microarthropod sampling data, homogeneous elements of the spatial structure were chosen for sampling plots—perennial lawns, which can be found in practically all urban habitats, with the exception of urban and suburban forests, where the spatial structure is mainly formed by moss cover. In forest habitats, sample plots were selected in patches of moss in the inter-crown space of trees.

Urban habitats are subjected to numerous human pressures. However, considering the specifics of their management in the city of Riga, the mentioned habitats could be ranked on the urban–rural gradient, in the following order according to the spectrum of dominant anthropogenic factors and its intensity: Str, PaL, PrL, Cem, UrF and SubUrF (Table 1). Two groups can be distinguished among these habitats. UrF and SubUrF represent the human least affected habitat group with natural soils and some elements of natural vegetation, while in all the other habitats, soils are totally transformed by substrates brought from other places. Habitats of the last group have a specific set of governing pressures. Str suffers from the most intense anthropogenic influences—pollution, regular litter removal and soil compaction. PaL suffer from less pollution; however, they are subjected to compaction by heavy tractors during lawn mowing and removal of tree litter. PrL do not suffer from heavy compaction. Cem lawns have less frequent mowing and litter removal. Urban and suburban forests differ mostly by the level of anthropogenic influence. The vegetation covering urban forest soil is less dense than in suburban forests. Herbs like *Vaccinium myrtillus* may cover the soil in suburban forests unlike the urban forests with less dense coverage predominantly consisting of Gramineae spp. plants. Soil of urban forests is more affected by humans containing human walked paths or even asphalted paths whereas in suburban forests there are only traces of mushroom picking (see Supplementary Appendix A).

Soil sampling

Soil samples were taken at the end of September/beginning of October 2017. In total, 21 sample plots (~5–10 m^2 each) were rounded along the urban–rural gradient (Fig. 1). Steel soil corer (*D* 50 mm, surface area 19.6 cm^2 depth 10 cm) was used according to Melecis et al. (2018). In each plot, three soil samples were taken with a soil corer as to not cause damage to the small urban habitat fragments. The total area sampled equalled 58.8 cm^2. In sample plots with specific topography, e.g. street

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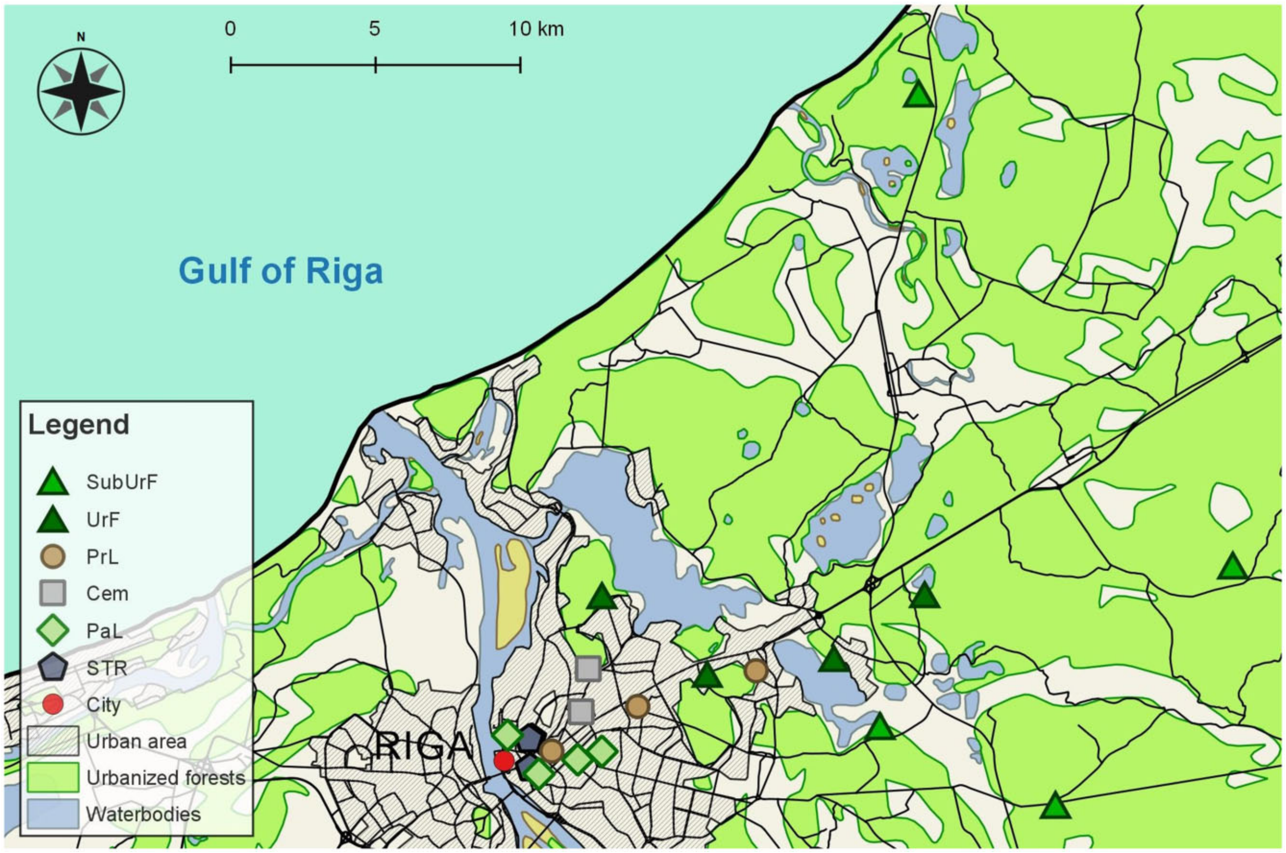

Figure 1: Sample plot locations in Riga city centre and periphery. Urban habitats: Str—street surrounding soil, PaL—park lawn soil, PrL—private lawn soil, Cem—cemetery soil, UrF—urban forest soil, SubUrF—suburban forest soil.

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Table 1: Expert ranking of urban habitat types along the urban gradient of Riga city with the prevailing kinds of human disturbance

Human influence	Urban habitats					
	Street surrounding lawns (Str)	Park lawns (PaL)	Private lawns (PrL)	Cemetery lawns (Cem)	Urban forests UrbF	Suburban forests (SubUrF)
Expert ranks	1	2	3	4	5	6
Pollution	X					
Soil compaction	X	X	X			
Mowing	X	X	X	X		
Tree litter removal	X	X	X	X		
Vegetation trampling	X	X	X	X	X	

surrounding soil (Str), soil samples were distributed in a row at 1-m intervals. In areas with city lawns (see PaL and PrL in Table 1), samples were assigned in the middle of the examined lawn area with most homogenous vegetation. If present, lawn edges, sidewalks and human trails were avoided so that the possibility of significant local mechanical disturbance on the soil structure was minimized. Urban forest sample plots were selected in the inter-crown space of trees, in a spot with most homogenous forest litter and moss cover. At each plot, the vegetation cover was characterized, including the registration of nearby tree species, micro-relief and litter conditions, distance from the road surface or footpath, signs of trampling and gardening (Supplementary Appendix A).

Soil microarthropod extraction and identification

In the laboratory samples from each habitat were pooled and microarthropods were extracted from them using Berlese-Tullgren funnels equipped with 25 W bulbs as a heat and light source for two weeks (Dunger, Fiedler, and Fiedler 1997).

Microarthropods were counted and sorted under the stereo microscope *Motic SMZ-17* and microscopic slides were prepared for the identification of species using oven *Memmert* UN75, light microscope *Olympus BX41* and keys of Collembola (Fjellberg 1998, 2007), Oribatida (Weigmann 2006; Krantz and Walter 2009) and Mesostigmata (Bregetova 1977; Hyatt 1980; Begljarov 1981; Karg 1993). Microarthropods were identified at the species level.

Chemical analysis

Soil pH was measured with three replicates using KCl solution (ISO 2021) and pH meter. The content of the organic matter (%) was determined based on Tyurin (1951) method, three replicates were executed for each sample. Soil moisture was not measured because the soils had accumulated a large amount of moisture due to prolonged rains prior and during the collection period, therefore this environmental factor could not be considered as limiting for soil organisms (Liu et al. 2017).

Data analysis

With the improvement of computer performance, the application of statistical analysis programs based on bootstrap and Monte Carlo methods in ecology has grown rapidly (Manly 2007). We tested several bootstrap-based data analysis methods with the aim to find out their applicability in community and species-level analysis of changes in microarthropods on the urban gradient.

A first approach, which traditionally is being used in comparative analysis, is testing of group means by analysis of variance (ANOVA). To have an insight into the distribution of microarthropod community characteristics on the urban gradient, we analysed differences between abundance and species richness of the selected urban habitat types by bootstrap-based one-way ANOVA from the IBM SPSS Version 22 software package. Post hoc multiple comparison of group means was performed by Tukey test and only microarthropod species showing significant peaks on the urban gradient were considered.

However, the urban–rural gradient is formed by many interrelated technogenic, microclimatic and ecological factors. When selecting urban habitat types for the study, we initially arranged them on an urban–rural gradient, based on the expert assessment of the potential intensity of urban factors within the selected habitat groups. However, the ranking of habitats by human experts may differ from the 'ranking' of those habitats by soil animals. This can be ascertained by ordination of sample plots in the axes obtained by the multidimensional analysis of species data. Nonmetric multidimensional scaling (NMS) was used to find out the latent factors determining the community structure, sample plots were assigned to the NMS axes using the PC-ORD software package (McCune and Mefford 1999; McCune and Grace 2002). Prior to the analysis species with frequency $P < 0.1$ were excluded from the main data matrix and data were log-transformed. Sørensen similarity measure was used for the calculation of species similarity matrix. Random starting configuration and 250 runs with real data were used for selecting dimensionality and Monte Carlo test with 250 runs was executed to assess whether the extracted dimensions differ from random ones ($P < 0.05$). To facilitate the interpretation of the obtained axes, a second matrix containing measurement data on soil pH and content of organic matter was included in the analysis.

We also checked how much our preliminary ranking of study sites on the urban–rural gradient match with ranking obtained by NMS ordination by calculation of Kendall's correlation coefficient between the axis scores describing the gradient and the dummy variable containing the preliminary ranks.

Considering the non-compliance of the data with the normal distribution, it is not possible to use classical linear or nonlinear regression methods for calculating the microarthropod distribution curves on the urban gradient. Therefore, for this purpose, we used the hitherto less popular method nonparametric multiplicative regression (NPMR), a class of statistical techniques with several variants developed by McCune (2006, 2011). Nonparametric regression finds relationships between a response variable and one or more predictors. It tries to optimize fit to the data circumventing the problem of assumptions about the shape of a species response to environmental variables, so it calculates no regression coefficients, and the obtained curve is not described by a mathematical equation.

Calculations were performed by the HyperNiche 2 program package (McCune and Mefford 2004). We had only one predictor integrating all the partial effects of anthropogenic factors influencing microarthropod communities on the urban gradient. Such a predictor is represented by the NMS axis describing an integrated effect of the urban environment on the microarthropods.

The use of small sample series raises the question about how fully they reflect community level changes of microarthropods on the urban gradient. In choosing this approach, we assumed in advance that the sample set would represent mainly dominant species and thus the total species diversity would be significantly reduced. To answer the question whether there are statistically significant differences between different types of urban habitats, the multi-response permutation procedure (MRPP) from the PC-ORD program package was used developed by (McCune and Grace 2002). MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups of entities The PC-ORD program calculates average distance between groups of species, performs a series of permutations each time calculating the distance between the groups and finally estimating the probability P that distances do not differ from random ones. The MRPP also calculates T value which describes separation between groups. The more negative is T, the stronger the separation. Sørensen similarity measure was used for distance calculation.

Since in our study we had only one combined sample per study site, it was not possible to analyse the community structure using collector's curves, which model the dependence of the species richness from the number of samples (Fisher, Corbet, and Williams 1943). Instead, rarefaction curves should be used, which describe changes in species numbers from the total number of individuals in the sample (Crist and Veech 2006). An integrated sampling, rarefaction and extrapolation methodology was proposed (Chao and Jost 2012) which provided the method for calculation and comparison of rarefaction curves for the sampled species communities. The calculations were performed by R program iNEXT (Hsieh, Ma, and Chao 2016). The program also computes bootstrap confidence intervals around the diversity for rarefied/extrapolated samples, facilitating the comparisons of diversities across multiple sites. The estimated asymptote along with a 95% confidence interval for each of the three diversity measures is also provided (Hsieh et al. 2016). We compared rarefaction curves based on Shannon's species diversity index for microarthropod communities of the studied sites.

Results

General characteristics of the collected material

A total of 59 species of Collembola, 109 species of Oribatida and 48 species of Mesostigmata were identified in the collected material. Typical saprophages and mycetophages represented by springtails and oribatid mites predominated, accounting for 92% of the total number of individuals. Oribatid mites were the most abundant group among microarthropods (52%), their

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density ranged on average from 2000 to 58 000 ind./m^2 and species richness from one to 45 species per sample plot. Collembola were less abundant (36%), its mean density ranged from 14 000 to 24 000 ind./m^2 and species richness from 1 to 15 per sample plot. Predatory Mesostigmata mites were the least abundant (8%) group with the average density ranging from 3000 to 6000 ind./m^2 and species richness from 1–16 species per sample plot.

Two Oribatida species *Microppia minus* and *Oppiella nova* and three Collembola species *Parisotoma notabilis*, *Mesaphorura macrochaeta* and *Cryptopygus bipunctatus* dominated in the collected material (Table 2). A relatively high percentage among microarthropods had also the Collembola species *Hypogastrura manubrialis*, *Sphaeridia pumilis*, *Folsomia fimetaria* and *Friesea mirabilis*, the oribatid species *Minunthozetes semirufus*, *Tectocepheus velatus*, *Punctoribates sellnicki*, *Achipteria coleoptrata* and *Brachychthonius bimaculatus* and the mesostigmatid species *Rhodacarellus silesiacus*. Relative abundance of these species exceeded 5% in at least one sample site. The presence of the rest of the species in any site did not exceed 5%. Habitats strongly and moderately affected by humans did not differ in numbers of dominant species (5–6 species), while the composition of these species varied considerably not only among habitats but also among different sample plots. In contrast, the least affected forest habitats had only 2–3 dominant species (Table 2).

Comparison of species density between urban habitat types

Collembola had a maximum density in Cem but it did not differ significantly from Str and PrL (Fig. 2A). The mean densities for most habitats did not differ significantly. Hemiedaphic forms predominated among Collembola but there were no striking visible differences in the distribution of life forms among urban habitat types, except in PaL where springtails had the lowest density of hemiedaphic species. Mesostigmata mites showed the highest density in UrF and SubUrF and the lowest density in PaL (Fig. 2B). Both Collembola and Oribatida mean densities at Str were low but at the same time did not differ significantly from most other habitats with higher densities (Fig. 2A and C) due to very high variation in numbers of microarthropods among individual sample plots of this habitat. Oribatid mites showed a gradual increase from the lowest density in soils strongly affected by technogenic factors (Str) up to suburban forests (SubUrF) (Fig. 2C). Notably, the UrF and SubUrF soils had significantly higher mean Oribatida densities in comparison with the other urban habitats.

Comparison of average species richness across urban habitats had statistically significant differences only for Oribatida (Fig. 2D) and Collembola (Fig. 2E). Oribatid mites had a significantly higher species richness only in forest soils, in other habitats it did not differ significantly (Fig. 2D). For Collembola the lowest species richness, which differed significantly from other habitats, was found only in Str (Fig. 2E).

Of all the microarthropod species that were screened by one-way ANOVA to examine their mean density differences between various urban habitat types, statistically significant results yielded only six oribatid, three mesostigmatid and five collembolan species (Table 3). For almost all of them, maximum densities were found in forest soils, except two Collembola species, *F. fimetaria* and *S. pumilis*, which had highest density in the park soils.

Comparison of species composition and species diversity between habitat types

MRPP analysis did not find statistically significant differences between Str, Cem and PrL as well as between urban forest PrL and Cem (Table 4). The largest negative T-values describing separation between habitats were found between PaL, UrF and SubUrF between Cem and UrF.

The method of rarefaction curves, which in our case was based on only one pooled sample unit per site, allowed us to compare not only species diversity per se, but also its internal structure, described by the shape of rarefaction curves. The levelling up of the curves (see UrF2, SubUrF2 and Cem2) may

Table 2: Relative abundance (%) and occurrence (figures in parentheses) of dominant species of microarthropods in urban habitats of Riga city (abbreviations for the habitats are given in Table 1)

Species/habitats	Str	PaL	PrL	Ce	UrF	SubUrF	Total
Collembola							
Cryptopygus bipunctatus	30.2 (1)	–	19.7 (2)	12.8 (1)	–	–	6.3 (4)
Hypogastrura manubrialis	20.3 (1)	–	10.8 (1)	–	–	–	2.8 (2)
Mesaphorura macrochaeta	17.1 (2)	16.2 (4)	12.5 (4)	14.2 (2)	2.6 (4)	0.3 (2)	6.5 (18)
Sphaeridia pumilis	–	15.4 (4)	–	–	0.2 (2)	0.2 (2)	1.2 (8)
Parisotoma notabilis	–	0.2 (1)	13.5 (3)	0.6 (1)	11.5 (4)	6.4 (4)	7.3 (13)
Folsomia fimetaria	–	8.5 (3)	0.5 (2)	–	0.1 (1)	–	0.7 (6)
Friesea mirabilis	–	1.3 (2)	–	6.8 (1)	1.8 (2)	1.2 (1)	1.8 (6)
Isotomiella minor	–	–	–	3.5 (1)	2.1 (4)	7.1 (4)	3.3 (9)
Isotoma anglicana	0.6 (2)	3.7 (4)	2.2 (2)	2.2 (2)	0.7 (1)	0.1 (1)	1.1 (12)
Oribatida							
Minunthozetes semirufus	–	12.9 (1)	–	–	–	–	0.9 (1)
Microppia minus	2.1 (1)	–	1.8 (1)	27.0 (1)	4.8 (3)	0.3 (2)	5.2 (8)
Oppiella nova	–	0.8 (2)	0.1 (1)	2.3 (1)	26.9 (4)	26.4 (4)	16.4 (12)
Tectocepheus velatus	5.6 (3)	6.9 (4)	2.9 (3)	0.9 (1)	0.8 (3)	3.8 (4)	2.8 (18)
Punctoribates sellnicki	–	5.0 (2)	0.5 (3)	0.4 (2)	–	0.03 (1)	0.5 (8)
Achipteria coleoptrata	0.4 (2)	0.7 (2)	6.8 (2)	0.1 (1)	1.6 (2)	–	1.5 (9)
Brachychthonius bimaculatus	–	–	–	5.6 (1)	0.1 (1)	–	0.7 (2)
Mesostigmata							
Rhodacarellus silesiacus	5.3 (3)	1.7 (3)	4.7 (3)	1.0 (1)	0.04 (1)	0.03 (1)	1.3 (12)

Only species having relative abundances >5% in at least one sample plot of the particular urban habitat are included.

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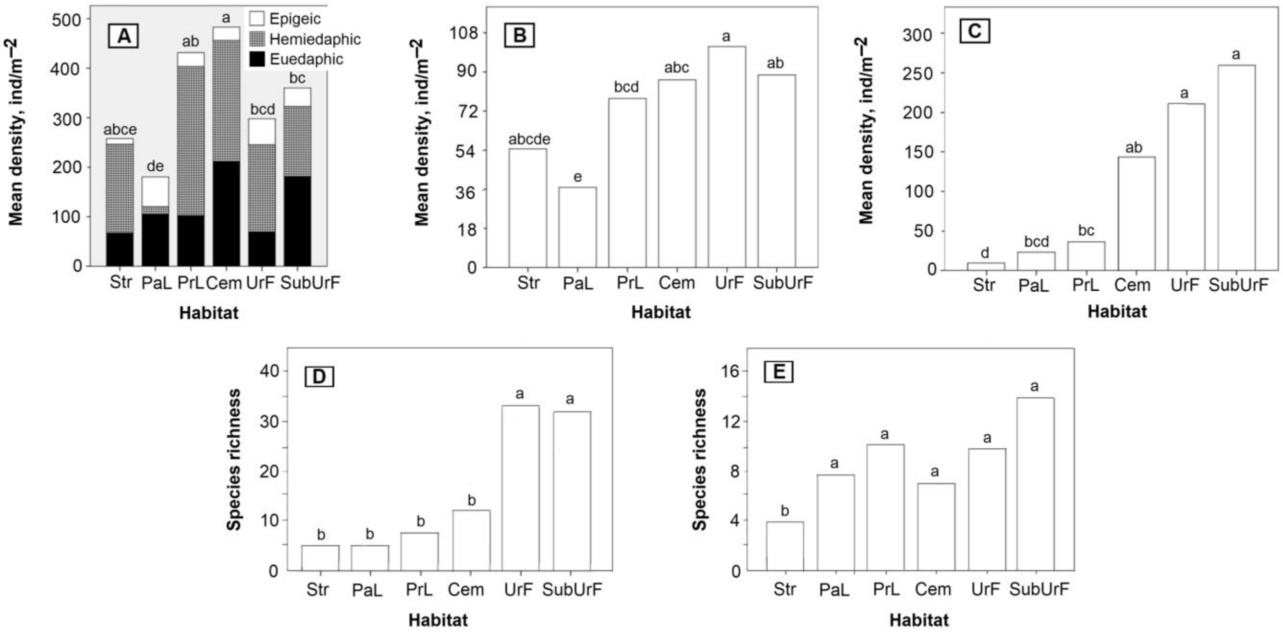

Figure 2: Distribution of mean densities and species richness of the main taxonomic groups of microarthropods in sample plots of different habitats along the urban-rural gradient. Groups of habitats marked with the same letters do not differ statistically significantly (one-way ANOVA, post hoc Tukey test with bootstrapping; abbreviations for the habitats are given in Table 1). A, E—Collembola, B—Mesostigmata, and C, D—Oribatida.

Table 3: Mean densities (ind./sample) of Collembola, Oribatida and Mesostigmata species in the urban habitats of Riga city

	Urban habitats						P	F
Species	Str	PaL	PrL	Cem	UrF	SubUrF		
Collembola								
Folsomia fimetaria	0 b	12.8 a	1.5 a	0	0.5 b	0 b	0.006	5.12
Isotomiella minor	0 b	0 b	0 b	20.5 a	13.5 a	53.0 a	0.007	4.963
Lepidocyrtus lignorum	0 c	0 c	0 c	0 c	13.5 a	2.8 b	0.016	4.066
Neanura muscorum	0 b	0 b	0 b	0 b	0.75 a	1.25 a	0.046	2.974
Sphaeridia pumilis	0 b	23 a	0 b	0 b	1.5 b	1.5 b	0	11.401
Oribatida								
Adoristes ovatus	0 c	0 c	0 c	0 c	4.75 a	2 b	0	10.343
Oppiella nova	0 b	1.25 b	0.25b	13 b	164.3 a	194.8 a	0.022	3.704
Scheloribates initialis	0 b	0 b	0 b	0 b	5 a	1.75 a	0.005	5.441
Steganacarus carinatus	0 b	0 b	0 b	0 b	7.25 a	4.25 a	0.022	3.696
Suctobelbella falcata	0 c	0.25 b	0 c	0 c	6.75 a	34.25 a	0.006	5.241
Suctobelbella subtrigona	0 b	0 b	0 b	0 b	15 a	28.5 a	0.019	3.877
Mesostigmata								
Pergamasus lapponicus	0 b	0.5 b	0 b	0 b	9.75 a	4.5 a	0.024	3.605
Parasitus sarekensis	0 b	0 b	0 b	0 b	6.75 a	7.25 a	0.024	3.62
Veigaia excigua	0 b	0 b	0 b	0.5 a	2 a	0.25 a	0.037	3.197

Only those species for which one-way ANOVA showed statistically significant differences ($P < 0.05$) of mean densities are included. Mean density values for the species followed by different letters are statistically different (post hoc Tukey's test with bootstrapping). Abbreviations for the habitats are given in Table 1.

indirectly indicate that the pooled sample as a whole covers the potential species diversity of the given research site. The application of bootstrapping with calculation of 95% confidence intervals allows one to visually interpret the differences in the structure of species diversity between different study sites. Without going into detail, two important conclusions can be drawn: (i) there are statistically significant differences between the microarthropod species of urban (UrF) and suburban (SubUrF) forests and the species diversity structure of all other urban habitats and (ii) the structure of species diversity varies significantly within individual urban habitat types (Fig.3, see Cem1 and Cem2, SubUrF1 and SubUrF2, Str2 and Str1, Str3).

Data ordination and calculation of urban–rural gradient vector

NMS ordination of the microarthropod community data yielded three statistically significant ($P < 0.05$) axes explaining 89.1% of the total data variation with stress value 9.2. This value should be regarded as fair to good according to Kruskal (1964) and

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Clarke (1993) rules of thumb. The first axis captures 58.3% of this variation, second and third axes each only 23.3% and 11.1% of variation. Only the first axis was clearly interpretable as the effects of the urban–rural gradient while the two others reflected some internal variation of community composition within the habitats caused by unknown environmental factors. The hidden meaning of the first axis was best manifested by combining it in a biplot with the third one (Fig. 4).

The biplot showed distinct non-overlapping clusters of urban habitats. Axis 1 clearly separated two groups of habitats. UrF and SubUrF represent the least human-affected habitat group with semi-natural soils, and Str, PaL, PrL and Cem habitats—with soils affected by urban influence. Axis 3 separated Str and PaL from Cem and PrL and PrL from PaL.

Clusters PrL and Str were stretched along Axis 3, indicating certain variation in species structure within the habitat type. Axis 1 negatively correlated with organic matter content ($r = -0.877$, $P < 0.001$) and positively with soil pH ($r = 0.621$, $P < 0.01$). Axis scores were strongly correlated with sequence numbers taken as dummy variates assigned to habitat types on the gradient (Kendall's Tau = 0.947, $P < 0.001$). This is well matched with our preliminary expert arrangement of habitats along the urban–rural gradient based on our notions of the potential distribution of the intensity of urban factors on the gradient (Table 1).

Table 4: Similarity matrix between urban habitat groups calculated by MRPP

	Str	PaL	PrL	Cem	UrF	SubUrF
Str	X	0.049			0.009	0.010
PaL	−1.884	X	0.025	0.040	0.006	0.006
PrL		−2.311	X		0.010	0.005
Cem		−1.800		X	0.036	0.005
UrF	−3.407	−4.109	−2.744	−2.104	X	0.005
SubUrF	−3.584	−4.242	−3.756	−3.756	−3.756	X

Symbols of habitats see in Table 1. Only statistically significant *P*-values are shown on the right side of the matrix. *T*-values describing separation between habitat groups are shown on the left side of the matrix.

Twenty Oribatida species, four Mesostigmata species and six Collembola species had the highest negative correlations (Kendal's Tau >0.4) with this axis (Table 5). Respectively, these species seem to be negatively affected by the urban environment. Noticeably, 68% of oribatids were found only in UrF and SubUrF. Only one mesostigmatid species *R. silesiacus* had positive correlation with Axis 1. *Rhodacaris mandibularis*, *Leioseius halophilus*, *S. pumilis*, *Isotoma anglicana Achiptera coleoptrata* and *P. sellnicki* had the highest correlations with Axis 2 or 3. Most of them were rare in forests but were scattered throughout the other urban habitats.

Response curves of microarthropod density and species richness to the urban–rural gradient

For all major microarthropod taxonomic groups, nonparametric regression curves increased towards the forest habitats (Figs 5–7). A stepwise curve was observed for changes in the mean densities of oribatid mites. Changes in species richness curves are S shaped, but Mesostigmata had a small peak towards forest habitats (Fig. 6).

For most microarthropod species, the NPMR gave either slightly nonlinear or S-shaped curves, reflecting a gradual or rapid increase in density towards forest UrF and SubUrF habitats (Figs 5–7).

Collembola had nine such species *Entomobrya* sp., *F. mirabilis*, *P. notabilis*, *Micraphorura absoloni*, *Willemia anophthalma*, *Isotomiella minor*, *Micranurida pygmaea*, *Neanura muscorum* and *Pogonognathellus flavescens* (Fig. 5). *Lepidocyrtus lignorum* had a density maximum towards forest habitats and *I. anglicana* in its middle part of the gradient. Only three species *Mesaphorura macrochaeta*, *S. pumilis* and *F.*

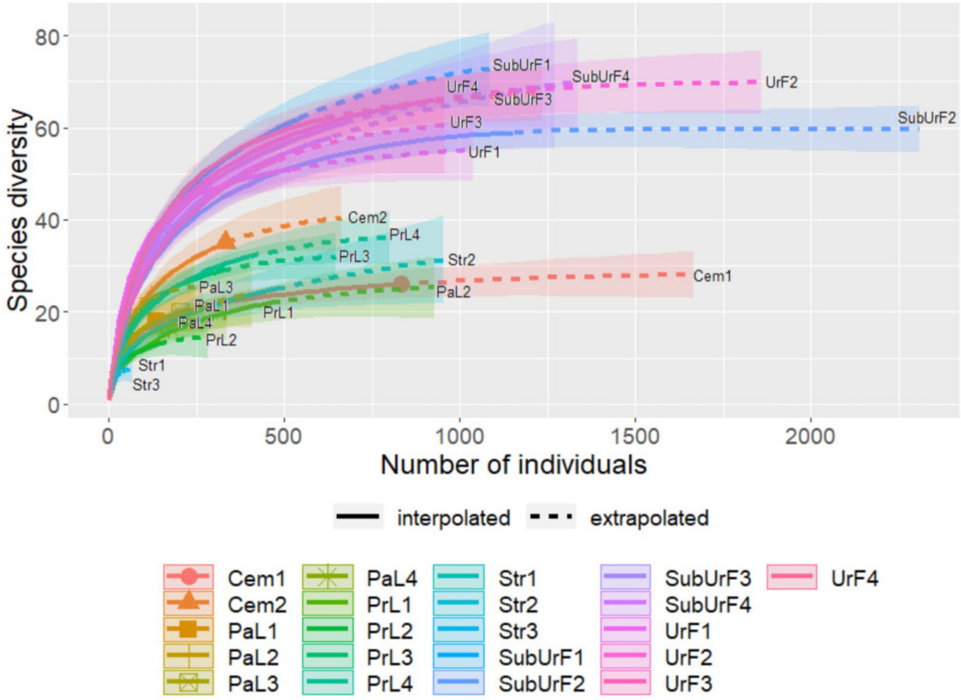

Figure 3: Coverage-based rarefaction/extrapolation curves with 95% confidence intervals (shaded areas, based on a bootstrap method with 200 replications) comparing microarthropod species diversity in 21 sites distributed along the urban gradient of Riga city.

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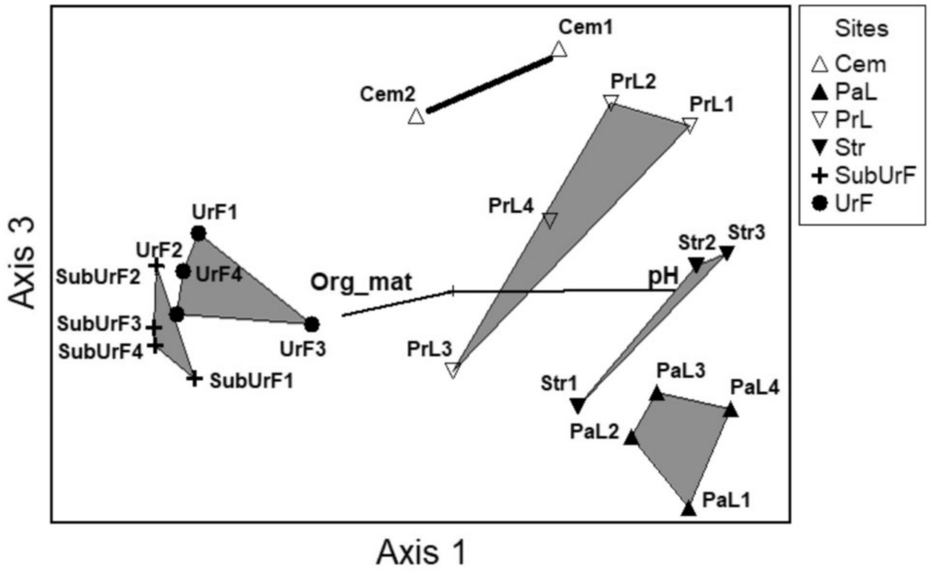

Figure 4: Distribution of urban sites in NMS ordination axes. Abbreviations for the habitats are given in Table 1. Polygons represent urban habitats. Vectors symbolize the correlations of soil pH and organic matter content (Org_mat) with NMS axes.

fimetaria showed the opposite trend—a decrease in density demonstrating their adaptability to heavily modified urban soils.

Most oribatid species (26) showed sharp density increase towards the forest habitats on the urban–rural gradient (Fig. 7). Two species *Rhysotritia ardua* and *Hypochthonius rufulus* had a slight increase of density in the UrF to compare with the SubUrF. *A. coleoptrata*, *Brachychthonius berlesei*, *Nothrus anauniensis* and *P. sellnicki* have maximum density in the middle part of the gradient. *Platynothrus peltifer* has distinctly bimodal curve.

Of the Mesostigmata found in the study, statistically significant gradient curves were found for 11 species (Fig. 6). Six species *Pergamasus vagabundus*, *Parazercon sarekensis*, *Veigaia nemorensis*, *Veigaia excigua*, *Pergamasus lapponicus* and *Parasitus kraepelini* tended to increase in their density towards UrbF and SubUrF. Three species *R. silesiacus*, *Trachytes aegrota* and *L. halophilus* showed an increase towards highly influenced urban habitats. For two species, *R. mandibularis* and *Pergamasus mirabilis*, maximal densities were observed in the middle part of the gradient.

Discussion

The need to perform a soil biodiversity assessment of green infrastructure of the urban environment is increasing (Guilland et al. 2018; Minixhofer and Stangl 2021). To ensure the effective assessment of urban soil biodiversity, the time-consuming standard methods are not appropriate. In habitats such as street edge, park and square greenery, the study sites often are too small for intensive sampling consisting of at least 10–20 soil samples per site. Many of our sampling sites were not larger than 10 m^2 and classical sampling schemes would have destroyed these sites. The suggested approach used in our study aims to overcome problems connected with high labour intensity of soil zoological studies and potential negative effects of intensive sampling on the urban habitats. Despite the relatively small sample size, the total number of 216 microarthropod species found proved to be large enough—from 9 to 66 species per site. Also, the mean density values obtained for the main groups of microarthropods were found to correspond to the average densities observed in Latvian soils (Eglitis 1954). The sample included dominant species from each site; the number of species in the group with relative abundance >5% appeared to be higher in heavily or moderately affected urban habitats (5–6 species) in comparison with less affected urban forest habitats (2–3 species). This can be explained by the significant decline in the number of individuals and species in strongly and moderately affected urban habitats, especially at the expense of oribatid mites. At the same time, great variability in the dominant and subdominant species groups demonstrates a compensative reaction occurring within the community (Supp and Ernest 2014) by substitution of species tolerant to the urban environment. Decrease in the density of microarthropods and species richness in urban habitats exposed to direct pollution from vehicles have also been noted in Moscow (Kuznetsova 1994) and Vilnius (Eitminaviciute 2006).

Two approaches were compared for analysing species distribution on an urban gradient: (i) a standard approach, using ANOVA for assessment of species distribution along the expert-defined habitat groups on the urban gradient, and (ii) application of nonparametric regression on the urban gradient axis obtained by ordination techniques (NMS) from species data matrix. In the first case, due to the large variation of data inside the expert-defined habitat groups, pairwise comparison of group means in most cases did not give a statistically reliable result. Only 11 species were found to have statistically reliable peak distributions on the urban gradient (Table 6). Analysis performed by MRPP and coverage-based rarefaction curves also indicated inhomogeneity in the within-group community structure. To improve the statistical reliability of the results, it would be necessary to increase the sample size, which would contradict the purpose of our methodological approach.

Using NMS and NPMR, it was possible to replace the expert-defined urban gradient with an urban gradient ‘interpreted’ by the microarthropods.

Application of the NPMR yielded challenging results. From 216 species of microarthropods, statistically significant gradient curves were found for 57 species comprising the pool of dominant and subdominant species (Table 6). It should be noted,

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Table 5: Presence of microarthropod species in sample plots from various urban habitats (presence abbreviated with ‘1’; abbreviations for the habitats are given in Table 1) and their correlations with NMS axes

Urban habitats	Str			PaL				PrL				Cem		UrF				SubUrF				Kendall’s correlation with NMS Axes		
Sample plots	STR1	STR2	STR3	PaL1	PaL2	PaL3	PaL4	PrL1	PrL2	PrL3	PrL4	Cem1	Cem2	UrF1	UrF2	UrF3	UrF4	SubUrF1	SubUrF2	SubUrF3	SubUrF4	Axis 1	Axis 2	Axis 3
Oribatida																								
Sellnickochthonius sp.1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	·	**−0.607**	−0.373	0.241
Porobelba spinosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	·	**−0.563**	−0.329	0.271
Suctobelbella sp.6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	1	**−0.631**	−0.384	0.155
Steganacarus carinatus	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	1	·	1	1	1	**−0.559**	−0.290	0.034
Nothrus silvestris	·	·	·	·	·	·	·	·	·	·	·	·	·		1	·	1	·	1	1	1	**−0.607**	0.080	0.066
Suctobelbella sp.5	·	·	·	·	·	·	·	·	·	·	·	·	·		1	1	1	1	1	1	1	**−0.680**	−0.337	0.184
Eupelops torulosus	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	·	·	**−0.492**	−0.155	0.182
Galumna lanceata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	1	1	1	·	**−0.525**	−0.259	0.244
Ceratozetes minimus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	·	1	**−0.567**	−0.335	0.145
Suctobelbella subcornigera	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	1	**−0.697**	−0.300	0.144
Suctobelbella sp.2	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	1	**−0.642**	−0.254	0.121
Suctobelbella sp.4	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	1	**−0.661**	−0.312	0.156
Rhysotritia ardua	·	·	·	·		·	·	·	·	·	·	·	1	·	1	1	1	1	1	1	·	**−0.542**	−0.236	0.019
Adoristes ovatus	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	·	1	1	1	**−0.553**	−0.222	0.002
Scheloribates initialis	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	·	·	1	1	**−0.524**	−0.211	0.075
Suctobelbella sp.3	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	1	1	**−0.487**	−0.128	0.026
Brachychthoniidae spp.	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	1	1	·	·	**−0.453**	−0.070	−0.019
Quadroppia quadricarinata	·	·	·	·	·	·	·	·	·	·	1	·	·	1	1	·	1	1	·	·	1	**−0.424**	−0.061	−0.074
Suctobelbella spp.	·	·	·	·	1	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	1	**−0.664**	0.306	0.179
Suctobelbella falcata	·	·	·	·	1	·	·	·	·	·	·	·	·	1	1	·	1	1	1	1	·	**−0.597**	−0.356	0.241
Microppia minus		·	1	·	·	·	·	·	1	·	·	1	·	1	1	·	1	1	1	·	·	**−0.541**	−0.347	0.234
Oppiella nova	·	·	·	·	1	·	1	1	·	·	·	1	·	1	1	1	1	1	1	1	1	**−0.603**	−0.310	0.110
Achipteria coleoptrata	·	1	1	·	·	1	1	·	·	1	1	·	1	1	·	1	·	·	·	·	·	0.059	**0.458**	−0.117
Punctoribates sellnicki	·	·	·	·	·	1	1	1	·	1	1	1	1	·	·	·	·	·	·	·	1	0.180	**0.417**	−0.355
Mesostigmata																								
Trachytes aegrota	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	·	1	1	**−0.496**	−0.165	0.000
Parazercon sarekensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	**−0.644**	−0.376	0.134
Veigaia nemorensis	·	·	·	·	·	·	·	·	·	1	·	·	1	1	1	1	1	1	1	1	1	**−0.728**	−0.224	0.045
Asca bicornis		·	·	·	·	·	·	1	·	·	·	1	·	·	1	1	1	1	1	1	·	**−0.471**	−0.202	0.006
Rhodacarellus silesiacus	1	1	1	1	1	·	1	1	1	·	1	·	1	·	·	1	·	·	·	·	1	**0.589**	−0.101	−0.122
Rhodacarus mandibularis	·	1	·	·	·	1	·	·	·	1	1	1	1	·	·	·	·	·	·	·	1	0.038	**0.457**	**−0.457**
Leioseius halophilus	·	1	·	1	1	1	1	·	·	·	·	·	·	·	·	·	·	·	·	1	·	0.309	0.254	**0.433**
Collembola																								
Neanura muscorum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	1	1	1	·	**−0.595**	−0.327	0.223
Lepidocyrtus lignorum	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	·	1	1	1	·	**−0.474**	−0.149	0.176
Pogonognathellus flavescens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	**−0.610**	−0.292	0.216
Isotomiella minor	·	·	·	·	·	·	·	·	·	·	·	·	1	1	1	1	1	1	1	1	1	**−0.594**	−0.306	−0.087
Micraphorura absoloni	·	·	·	·	·	·	·	·	1	·	·	·	1	·	1	1	1	1	1	1	1	**−0.514**	**−0.456**	−0.029
Parisotoma notabilis	·	·	·	·	1	·	·	1	·	1	1	·	1	1	1	1	1	1	1	1	1	**−0.528**	0.005	−0.108
Sphaeridia pumilis	·	·	·	1	1	1	1	·	·	·	·	·	·	·	·	1	1	1	·	·	1	0.084	0.276	**0.529**
Isotoma anglicana	·	1	·	1	1	1	1	·	·	1	1	1	1	·	·	1	·	1	·	·	·	0.081	**0.622**	−0.049

The table contains only species having Kendall’s Tau >0.400 for at least one NMS axis.

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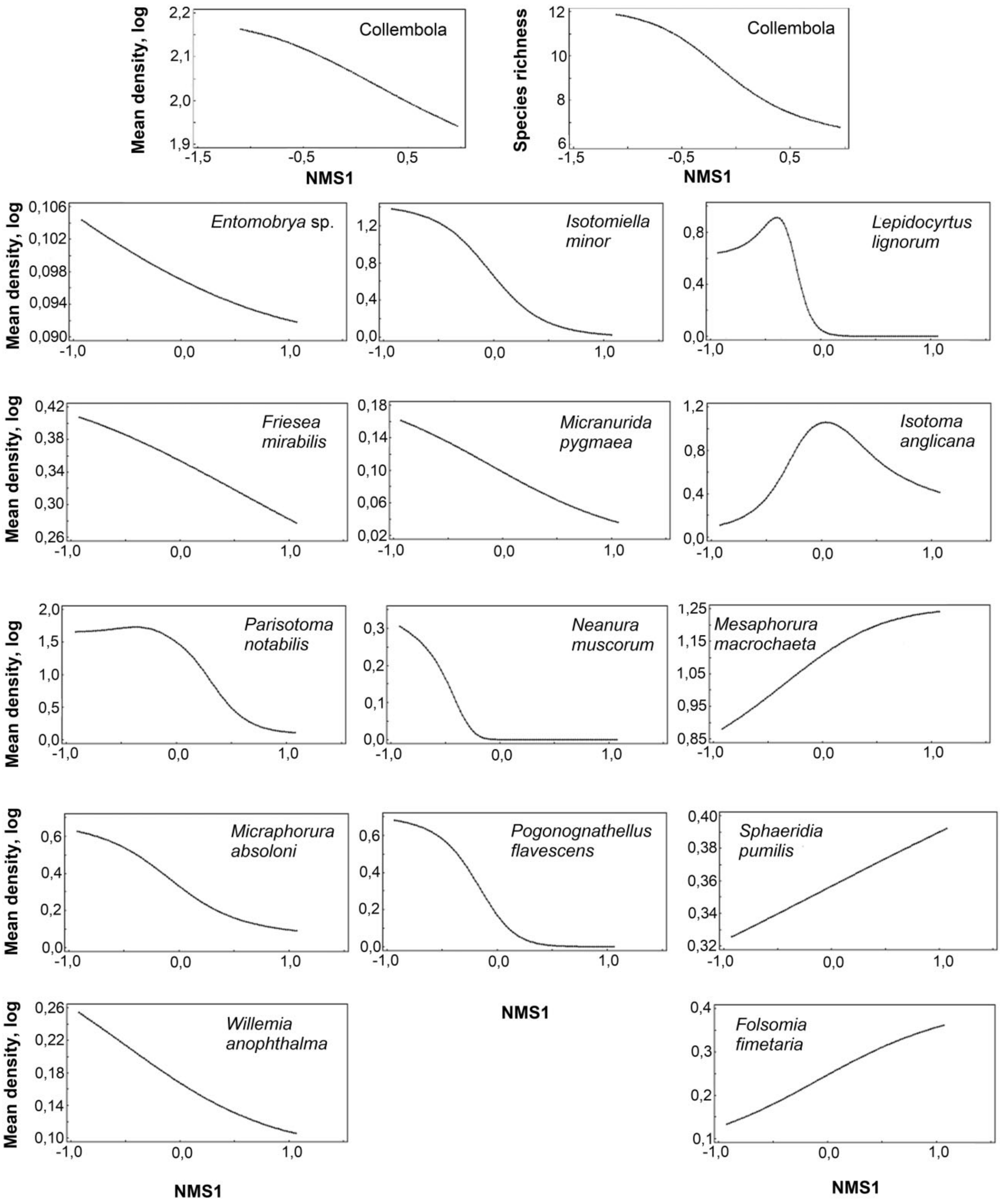

Figure 5: Nonparametric regression curves along the urban-rural gradient (NMS 1 axis) calculated for mean density and species richness data of Collembola species. Only statistically significant curves are shown ($P < 0.01$).

however, that these curves should not be used for interpolation of density values for a particular urban habitat like in parametric regression. These curves are robust characteristics of the general density trends. The analysis of the data allowed us to distinguish four types of curves: curves describing density decrease from the periphery to the city center (urban negative species curves—36), curves describing density increase towards the city center (urban-positive species curves—5), curves with density peak in the middle segment of the urban gradient (unimodal species curves—12) and curves with two maxima along the urban gradient (bimodal species curves—2).

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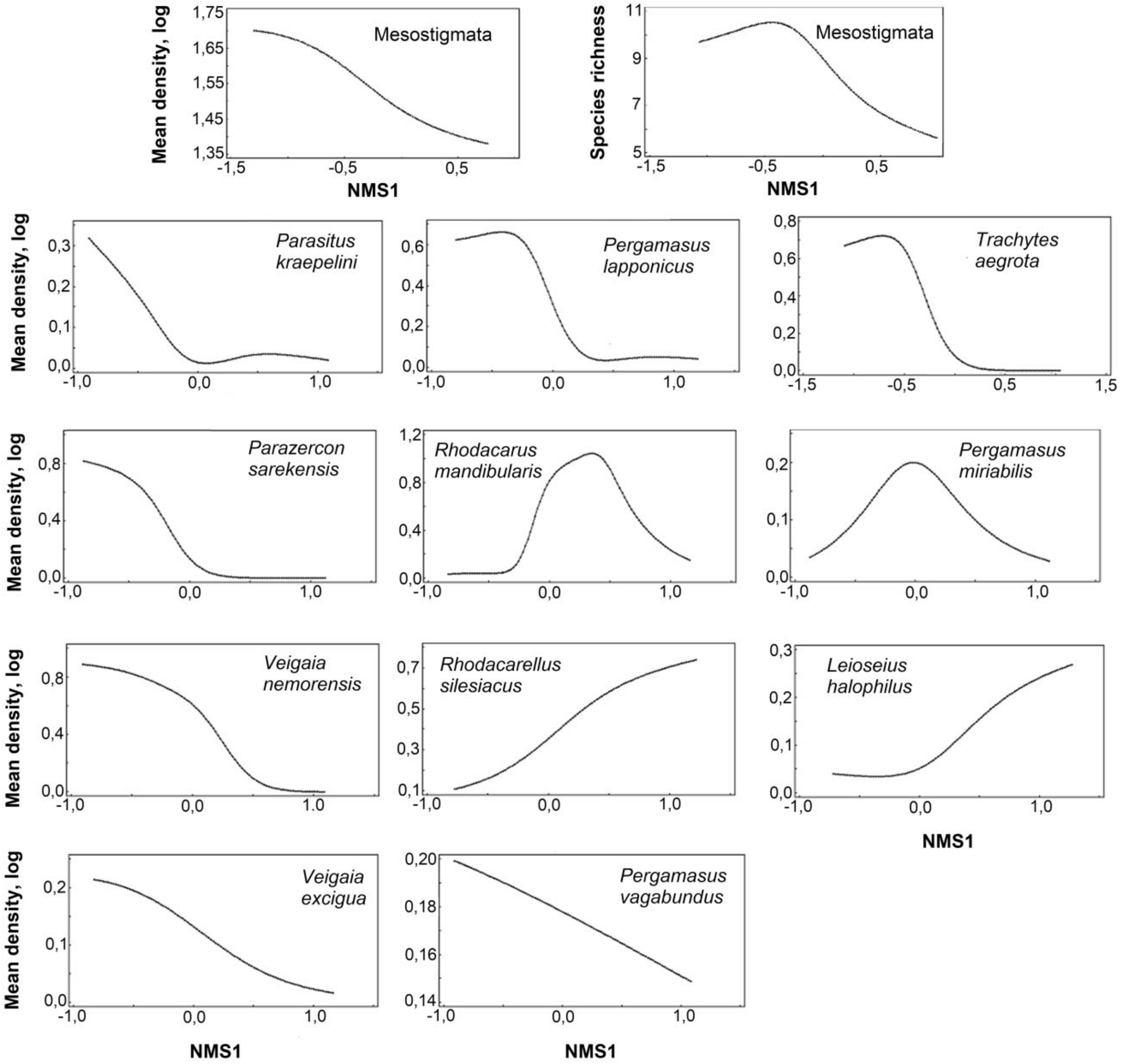

Figure 6: Nonparametric regression curves along the urban-rural gradient (NMS 1 axis) calculated for mean density and species richness data of Mesostigmata species. Only statistically significant curves are shown ($P < 0.01$).

The urban–rural gradient of the Riga city stands out with a particularly sharp transition from urban habitats with strongly modified soils to the pine forests as a semi-natural regional ecosystem with poor acidic podzol soils. Hundreds of years of human activity have led to the irreversible degradation of natural soils and the formation of new urban soils by enriching the topsoil with loam and manure, which, under conditions of abundant precipitation and good infiltration, were permanently losing the introduced organics (Nikodemus 2019). On the urban gradient, this manifested itself as a rapid jump from an acidic soil rich in organic matter to soils with significantly increased pH values and reduced organic matter content.

Urban–rural gradient represents an integrated factor made up of many different environmental variables including pollution, temperature gradients, mechanical impacts a. o. and interactions among them. It would be misleading to try to explain the changes in microarthropod communities solely by changes in soil pH and organic matter content on the urban gradient while, of course, not denying those factors as being important for microarthropods. Sterzińska et al. (2018) found a statistically significant correlation of collembolan abundance with soil pH. The decrease in soil acidity in urban soils of the Riga city is primarily related to the presence of carbonate materials, in the layer on which these soils were formed (construction materials, war debris), a higher pH level in the soil substrates deposited over the years and effects of fertilization.

Many authors studying microarthropod distribution in the urban habitats (Niedbała et al. 1982; Sterzyńska 1982; Rzeszowski and Sterzyńska 2016; Joimel, Jules, and Vieublé-Gonod 2022) focus on the impoverishment of urban habitats in comparison to the natural ones and the decrease in species numbers and density, in particular for oribatid mites (Niedbała et al. 1982). At the same time, there are some indications of an increase in springtail abundance and species richness in the

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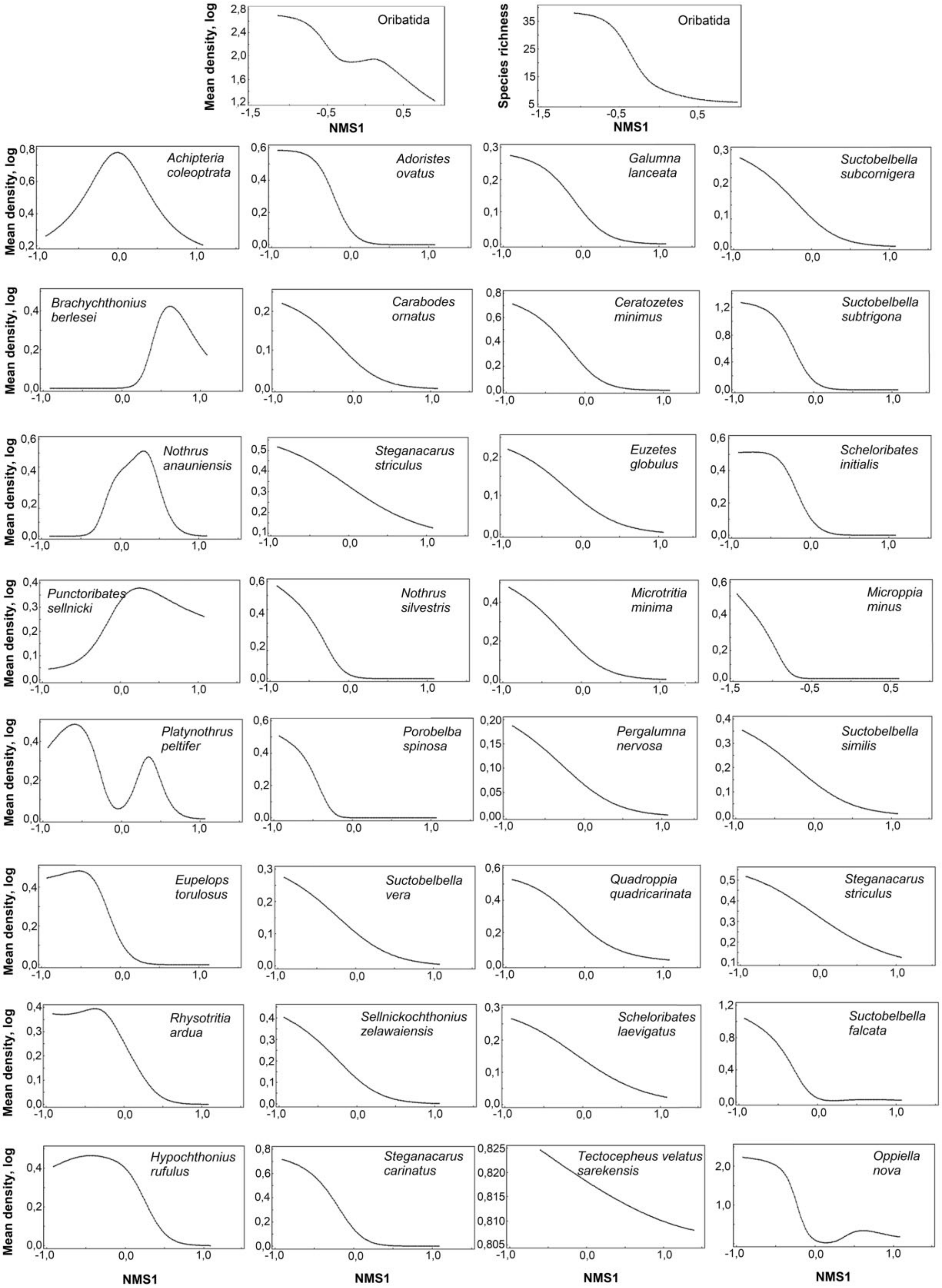

Figure 7: Nonparametric regression curves along the urban-rural gradient (NMS 1 axis) calculated for mean density and species richness data of Oribatida species. Only statistically significant curves are shown ($P < 0.01$).

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Table 6: Comparison of the results of the study of the density distribution of the dominant and subdominant microarthropod species on the urban-rural gradient using ANOVA and nonparametric multiple regression NPMR

Species	Dominance class according to Margolis et al. (1982)	ANOVA	NPMR
Collembola			
Cryptopygus bipunctatus	D		
Hypogastrura manubrialis	D		
Mesaphorura macrochaeta	D		\
Sphaeridia pumilis	D	X	\
Folsomia fimetaria	D	X	\
Isotomiella minor	D	X	/
Parisotoma notabilis	D		/
Friesea mirabilis	D		/
Isotoma anglicana	D		Λ
Lepidocyrtus lignorum	SD	X	Λ
Neanura muscorum	R	X	/
Micraphorura absoloni	SD		/
Micranurida pygmaea	R		/
Pogonognathellus flavescens	SD		/
Willemia anophthalma	SD		/
Entomobrya sp.	SD		/
Oribatida			
Minunthozetes semirufus	D		
Brachychthonius bimaculatus	D		
Microppia minus	D		/
Tectocepheus velatus sarekensis	D		/
Punctoribates sellnicki	D		Λ
Achipteria coleoptrata	D		Λ
Oppiella nova	D	X	ΛΛ
Adoristes ovatus	R	X	/
Scheloribates initialis	R	X	/
Steganacarus carinatus	SD	X	/
Suctobelbella subtrigona	SD	X	/
Suctobelbella falcata	SD	X	/
Nothrus anauniensis	SD		Λ
Brachichthonius berlesei	SD		Λ
Hypochthonius rufulus	SD		Λ
Platynothrus peltifer	SD		ΛΛ
Ceratozetes minimus	SD		/
Steganacarus striculus	SD		/
Nothrus silvestris	SD		/
Eupelops torulosus	SD		/
Suctobelbella vera	SD		/
Quadroppia quadricarinata	SD		/
Sellnickochthonius zelawaiensis	SD		/
Suctobelbella similis	SD		/
Porobelba spinosa	R		/
Pergalumna nervosa	R		/
Galumna lanceata	R		/
Euzetes globulus	R		/
Carabodes ornatus	R		/
Rhysotritia ardua	R		/
Scheloribates initialis	R		/
Mesostigmata			
Rhodacarellus silesiacus	D		\
Leioseius halophilus	SD		\
Rhodacarus mandibularis	SD		Λ
Trachytes aegrota	SD		Λ
Pergamasus vagabundus	SD		/
Pergamasus lapponicus	SD		/
Parazercon sarekensis	SD		/
Veigaia nemorensis	SD		/
Pergamasus mirabilis	R		Λ
Veigaia excigua	R		/
Parasitus kraepelini	R		/

D, dominant species with relative abundance >5%; SD, subdominant species with relative abundance 1–5%; R, recedent species with relative abundance <0.5–1%; X, statistically significant density peaks on the urban-rural gradient found by ANOVA;/, statistically significant curves obtained by Nonparametric Multidimensional Regression (NPMR) describing density decrease from the periphery to the city center (urban negative species curves);\, curves obtained by Nonparametric Multidimensional Regression (NPMR) describing density increase towards the city center (urban-positive species curves); Λ, unimodal curves obtained by Nonparametric Multidimensional Regression (NPMR)with density peak in the middle segment of the urban gradient (unimodal species curves); ΛΛ, curves obtained by Nonparametric Multidimensional Regression (NPMR) with two maxima along the urban gradient (bimodal species curves).

middle part of the urban gradient in parks and gardens, where moderate human activity is likely to create favourable environmental conditions for the development of these invertebrates (Guilland et al. 2018; Joimel et al. 2022). Our data provided similar results. Most of microarthropod species increased their density towards forest habitats and Collembola slightly increased in private garden and cemetery soils.

Nonparametric multiple regression showed that most microarthropod species are negatively affected by the urban environment. At the same time, it should be noted that some species show specific changes in density on the urban–rural gradient, indicating their capacity to adapt to the anthropogenic environment. Three Collembola species of Collembola *F. fimetaria*, *M. macrochaeta* and *S. pumilis* were urban positive. The data available for these species are partly indicative of their anthropotolerance. *F. fimetaria* is widely distributed in Holarctics mainly in disturbed sites and organic debris (GBIF 2016a). Like in our study, this species was reported to be present only in central urban sites (Fiera 2009). There is no data on ecology of *M. macrochaeta*, it is a cosmopolitan species found in forests (GBIF 2016b). In our study, its density was higher in street lawns, parks and gardens than in urban forests. We never found this species during a twenty-year study in pine forest soils of Latvia LTER site (Jucevica, pers. comm.). *S. pumilis* is a widely distributed species and was recorded from different habitats in Latvia, including polluted ones (Melecis 1985).

Two species of Collembola *L. lignorum* and *I. anglicana* had unimodal curves. *L. lignorum* has been recorded from the range of natural habitats (GBIF 2016c). In our study, this species had the highest density in urban forests. *I. anglicana* prefers parks and garden lawns, this species is characteristic for open habitats with rich soils (Filser 1999). Observations in the Warsaw Central Park (Rzeszowski and Sterzyńska 2016) suggested that this species may be a newcomer to the urban habitats for an extended period of time. In our study, it had a maximum in the

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middle part of the urban–rural gradient, corresponding to park and garden habitats (Supplementary Appendix A).

No urban-positive species were found among the oribatid mites. Five species *A. coleoptrata*, *B. berlesei*, *N. anauniensis*, *P. sellnicki* and *H. rufulus* had unimodal distribution curves on the urban–rural gradient. The species *A. coleoptrata* and *H. rufulus* can be found in a wide range of habitats starting from oligotrophic meadows and forests to mesotrophic deciduous forest litter and soil (Willmann 1931; Stefaniak and Seniczak 1976). However, supporting data on the ecology of these species are sparse, which makes it difficult to interpret the observed changes. All five species have been reported from various types of forest and meadow soils in Latvia. However, *B. berlesei* has also been recorded in Latvian arable soils (Eglitis 1954), Japanese (Suzuki 1979) and Polish (Niedbała et al. 1990) urban soils showing the pattern of a relatively high anthropotolerance.

Two species *P. peltifer* and *O. nova* had bimodal curves. *P. peltifer* is widely distributed in Europe, mostly in wet habitats (Jalil 1972). In Latvia, this species had been registered in semi-wet and wet habitats, along the coastal zone of the Baltic Sea and calcareous fens (Viksne 1959; Kagainis and Spungis 2011). *O. nova* in large numbers was recorded from Warsaw parks and gardens (Niedbała et al. 1982). This species can be considered to be an indicator of very high pollution and compaction of the soils (Andrievskii and Syso 2012). In our study, the *O. nova* had an increase in park and garden soils and in forest habitats. Interpreting bimodal response curves is a challenge considering our poor knowledge on the species traits. Bimodal species response curves may occur in the following cases: (i) when the species is limited by physical or biological conditions that vary in parallel with the measured gradient, (ii) in case of competitive exclusion and (iii) in case of environmental discontinuities (Terborgh 1971). McCune (2006) has demonstrated the first case on spruce species; still, there are no available examples on other living organisms in literature.

Most Mesostigmata species were urban negative. However, for two species *R. silesiacus* and *L. halophilus*, density increased towards the city center and *R. silesiacus*, appeared as the dominant species in our investigation (Table 3). *R. silesiacus* is a common species in grassland, urban and dune habitats in Latvia (Salmane and Brumelis 2010). This species is characteristic for a range of both natural and anthropogenic habitats, such as meadows, arable lands, dunes, urban parks, arable fields, pastures, prairies, derelict industrial and mining areas (Bregetova 1977; Manu and Honciuc 2010; Castilho, de Moraes, and Halliday 2012; Manu and Onete 2016; Manu et al. 2021). *R. silesiacus* is also known as a pioneer species, inhabiting mineral soils and soils undergoing secondary succession processes (Koehler 2000; Gulvik et al. 2008; Kaczmarek et al. 2012; Manu et al. 2017). *L. halophilus* in Latvia has been found in grasslands, agricultural and dune habitats and is known from a wide range of habitats in Europe (Binns 1974; Bregetova 1977; Salmane and Brumelis 2010). *L. halophilus* was recorded as a pioneer species in industrial wastelands and spoil areas having the ability to colonise early successional habitats because of its high reproduction rate, short developmental time and phoresy, as well as high tolerance to the chemical contamination in the soil (Manu et al. 2019). *T. aegrota* and *R. mandibularis* had distinctly unimodal distribution curves with peaks in the middle part of the gradient where urban parks and gardens are located. *T. aegrota* have a wide ecological tolerance and is common in various habitats, still it is the most abundant in deciduous forests (Mašán 2003). Cultivated recreational grasslands were recorded as preferable habitats for *P. mirabilis* and *R. mandibularis* (Huhta, Penttinen, and Pitkänen 2012). Soils of manor gardens, cottages and dune habitats were common for *R. mandibularis* in Latvia (Salmane and Brumelis 2010). Namaghi (2010) as the most abundant in urban habitats recorded Amblyseiidae mites (Parasitiformes, Mesostigmata).

Microarthropod species can be divided into four groups according to their type of response curves on the urban gradient. The largest group included species with a negative reaction to urban factors. However, the species of greatest interest are those whose density tends to increase in the middle part of the urban gradient as well as in the habitats most affected by urban environmental factors. The emergence of such species is essentially indicative of the formation of new microarthropod communities in urban habitats. In this respect, the investigation of species responses to the urban gradient using NPMR is a suitable tool for exploring these issues.

Our approach dealing with small sample sizes allowed us to find out the properties of the microarthropod distribution curves, thereby significantly reducing the investment required for research as well as the impact of the sampling process on the study site. In this respect, the approach is a step closer towards working out an express method for assessing soil biodiversity in urban environments. It should be noted that there are some other alternative approaches deserving particular attention. These include the use of soil indexes (Parisi et al. 2005; Menta et al. 2018) and soil e-DNA (Orgiazzi et al. 2015; Kirse et al. 2021). The first method stands out particularly for it does not require the identification of soil animals to the species level. The second method is based on the detection of the presence of species from the e-DNA extracted from the soil sample. Both methods are a major challenge in the assessment of soil ecological state and its biodiversity; however, further research is needed to improve them.

Supplementary data

Supplementary data are available at *JUECOL* online.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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