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Urban effects on saprophagous macroarthropods are mainly driven by climate: A global meta-analysis

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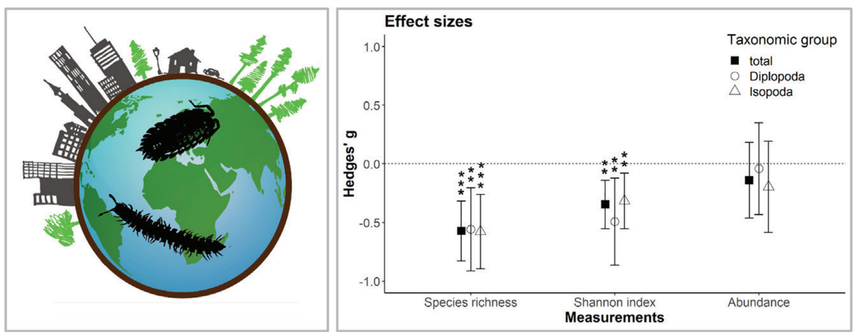
HIGHLIGHTS

- A meta-analysis was performed to assess the urban effects on millipedes and woodlice.
- Urbanization decreased species diversity of both macrodecomposer taxa.
- Their abundance response to urban disturbance was neutral.
- The urban effects on saprophagous macroarthropods were mainly driven by climate.

GRAPHICAL ABSTRACT



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ABSTRACT

Macrodecomposers provide important ecosystem services even in human dominated habitats including urban ecosystems, but the effect of urban land conversion on their species diversity and abundance has not been explored at global scale. Here, we present the first meta-analysis to quantify the general response of two major arthropod taxa, terrestrial isopods and millipedes to urbanization and to reveal the underlying mechanisms. Climatic (temperature, precipitation, growing season length), edaphic (pH, organic carbon, $CaCO_3$ and clay content of surface soils), urban (population density, city age, vegetation cover and mean actual evapotranspiration) parameters and methods of study (duration, sampling technique, replications) were used as moderators. We used a hierarchical meta-analytic approach to consider the dependence of multiple effect sizes obtained from one study. Altogether 156 paired observations were extracted from 59 urban studies conducted between 1980 and 2020. Urbanization had a negative effect on species diversity (species richness and Shannon index) of both macroarthropod taxa. However, both the direction and strength of their abundance response varied to a greater extent, resulting in a neutral effect of urban disturbance on them. The key drivers influencing the urban effects on macroarthropods were mean annual temperature and precipitation, absolute minimum temperature and length of growing season. The study also highlighted the importance of sampling methods: direct sampling (hand collecting) resulted in stronger urban effects presumably due to several sources of sampling bias. Our global synthesis highlighted that urbanization is a threat to soil arthropods, particularly to litter-dwelling detritivores, which potentially alters plant residue processing and ultimately soil biogeochemical cycles.

1. Introduction

Global biodiversity loss is a major environmental concern that is confirmed by increasing scientific evidence (e.g., Butchart et al., 2010;

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Dirzo et al., 2014). Although historically less attention has been paid to invertebrates, in recent years several studies have reported data on declining global population trends of arthropods (e.g., Sánchez-Bayo and Wyckhuys, 2019; van Klink et al., 2020), and the multitude of environmental stressors leading to this trend (Wagner et al., 2021). As the most abundant and diverse group of animals, arthropods play key roles in ecosystem functioning (pollination, pest control, nutrient cycling, soil formation, etc.) and provide ecosystem services critical to human well-being (Brussaard, 2012).

Soil is habitat for an enormous diversity of organisms such as microbes (i.e. bacteria, fungi) and invertebrates (micro-, meso-, macrofauna) ranging from 1 to 10^5 μm in size (Swift et al., 1979). About 25% of known species inhabit the soil at least part of their life cycle (FAO, ITPS, GSBI, SCBD, and EC, 2020). In addition to taxonomic and morphological diversity, soil fauna exhibits high functional diversity and, together with microorganisms, form a complex belowground food web.

The majority of soil fauna are detritivores, playing important roles in transforming plant detritus, animal carcasses, feces and other dead organic matter (Brussaard, 2012). Some taxa are fungal and bacterial feeders, regulating the composition of microbial communities, while others are predators. Large macroinvertebrates live on or close to soil surface and provide food for wildlife, such as birds, lizards and small mammals (Brussaard, 2012).

Among macroarthropods, woodlice (Crustacea: Isopoda, Oniscidea) and millipedes (Myriapoda: Diplopoda) are considered important litter transformers (Brussaard, 2012; David, 2014). The latter group is the more species rich: globally, over 12,000 species of millipedes have been described (Brewer et al., 2012), while the number of known terrestrial isopod species is over 3700 (Sfenthourakis and Taiti, 2015). In natural, semi-natural environments, diplopods occur mostly in forests (Golovatch and Kime, 2009), but can be found in unique and/or extreme habitats, such as canopy (arboreal), caves and deserts (Hopkin and Read, 1992). Woodlice inhabit a wider range of ecosystems from littoral to arid zones, tropical and temperate forests, shrublands and grasslands, preferring cryptozoic microsites (Richardson and Araujo, 2015). Species in both groups can be associated with other organisms; for example, living in the nests of wood rats, termites and ants, or in built structures (Hopkin and Read, 1992; Richardson and Araujo, 2015). Both groups are mainly surface active and feed on a variety of plant detritus; some species are specialized to live and feed on decaying wood (i.e. the millipede *Cylindroiulus boleti*), or create deep burrows in the soil (i.e. the desert woodlice *Hemilepistus reaumuri*).

Urbanization is often listed as a major threat to biodiversity in general, including soil biodiversity (e.g., Orgiazzi et al., 2016). This is expected, given that urban land use change disturbs soil structure and soil sealing disrupts the exchange of organisms and materials between the surface and belowground (EASAC, 2018; Pouyat et al., 2019). Additional filtering mechanisms include pollution, pesticide use, and habitat fragmentation (parcelization) hindering dispersal. Human management practices may counterbalance these negative effects. For example, soil transport, associated with landscaping, overcomes physical barriers, while irrigation and soil amendments create favorable conditions (Szlavecz et al., 2020). In urban environments, local species are often replaced by synanthropic, often non-native species, which have wider tolerances and thrive in even novel habitats (Bogyó et al., 2015; Kotze et al., 2011; Szlavecz et al., 2018). The relative magnitude of these contrasting drivers may result in different patterns of local species richness and species turnover (Swan et al., 2011); thus city scale biodiversity can be higher or lower than the surrounding areas. Comparisons on species richness in urban and rural habitats produced inconsistent results (reviewed by McKinney, 2008; Saari et al., 2016).

Urban soil invertebrate assessments are often local, i.e. focus on one city or even on a particular land use type, such as park, remnant forest, residential lawn, which hinders our ability to make general inferences about major drivers determining abundance and community composition of soil invertebrates. Multi-city research is still rare, although some comparative studies have been carried out, e.g., for springtails (Collembola, Joimel et al., 2019), woodlice (Isopoda: Oniscidea, Szlavecz et al., 2018; Vilisics et al., 2012), millipedes (Diplopoda, Vilisics et al., 2012), ground beetles (Carabidae, Niemelä and Kotze, 2009), and earthworms (Oligochaeta: Megadrili, Tóth et al., 2020). Most of these efforts involve only a specific region, and/or a handful of locations.

Meta-analyses systematically search and collect the existing literature in a given topic, and use quantitative procedures to gain a general insight to a scientific phenomenon. In soil ecology, this approach has been used to summarize the current state of knowledge on the effects of invasive earthworms (Ferlian et al., 2018), forest and agricultural management (Felton et al., 2010; Rowen et al., 2020), and global change (Zhou et al., 2020) on biodiversity, among others. Meta-analyses, addressing the effects of urbanization are still rare (but see Fenoglio et al., 2020; Filazzola et al., 2019), and, to date, have not been performed for specific soil invertebrate groups.

Here we first performed a global synthesis of urban studies to quantify the general response of two major macrodecomposer arthropod taxa (Diplopoda, Isopoda: Oniscidea) to urbanization and reveal the underlying mechanisms at global scale. We aimed to (i) assess the effects of urban disturbance on diversity and abundance of millipedes and woodlice; (ii) compare their responses to urbanization; and (iii) identify the most relevant factors (climatic, edaphic, and urban parameters, and research methods), influencing these responses.

2. Materials and methods

2.1. Literature search and selection

To obtain studies of how soil macrodecomposer arthropods (millipedes and woodlice) respond to urban disturbance, a systematic literature survey was conducted (search timespan August-November 2020) in the databases Google Scholar, Scopus and ISI Web of Science, without any restriction on publication year, using the following combination of the keywords: (millipede* OR diplopod* OR myriapod* OR woodlice OR isopod* OR oniscid* OR macroarthropod* OR detritivor*) AND (urban* OR city OR cities). The search results were screened for titles, abstracts and finally for full publication content according to the following selection criteria. To be included in the meta-analysis, the studies had to:

1) provide quantitative data (mean, standard error or standard deviation, and sample size) on species diversity and/or abundance of target taxa in urban environments;
2) compare more urbanized habitats with less disturbed or undisturbed ones, representing the two ends of an urban gradient;
3) have at least an English abstract.

In order to find additional relevant papers, reference lists of suitable publications were also checked. Grey literature studies (e.g., theses, dissertations) were also included in our database to increase the sample size and minimize the effect of publication bias. In the end, 59 studies were selected and used in the meta-analysis (Table S1).

2.2. Data extraction and characterization of urban areas

For each paper included in the meta-analysis, all necessary outcome parameters (mean, standard error/deviation, and sample size) on diversity and abundance of soil macrodecomposers were extracted from text, tables, supplementary materials or figures using WebPlotDigitizer software (version 4.3; Rohatgi, 2020). To capture more aspects of biodiversity, where available, we included Shannon (H'), the most commonly used diversity index, in addition to species richness. When diversity indices were not directly reported, we calculated them from raw data provided in the studies. If only the standard error (SE) was given, it was converted to standard deviation (SD) by multiplying the squared sample size. For studies where relevant information could not be directly extracted, corresponding authors were contacted. If the SD/SE values were not reported and the authors did not respond, we estimated SD values as 10% of the means (e.g., Luo et al., 2006). Multiple observations from several years (i.e., Arndt and Mattern, 1998) or cities (Rota et al., 2015) were treated as individual study. In one case (Bachvarova et al., 2015), when the data represented several time points within one year, we took the mean value of multiple dates.

Climatic (Köppen-Geiger climate class, mean annual temperature and precipitation, mean annual absolute minimum temperature, growing season length, number of rainy days) and edaphic (dominant soil group, pH, soil organic carbon, $CaCO_3$ and clay content of surface soil) data were extracted from the original studies, if reported. For missing climate and soil data, freely available databases, the Power Data Access Viewer (NASA, 2021) and Harmonized World Soil Database (FAO, 2012) were consulted. City age and population density were used to characterize the degree of urbanization; data were obtained from national webpages of Wikipedia. Vegetation cover was quantified by means of the enhanced vegetation index (EVI). EVI has several advantages (i.e., better saturation, sensitivity, filtering of canopy background and atmospheric noise) over the most widely used normalized difference vegetation index (NDVI), and is more appropriate for assessing urban vegetation (e.g., Dallimer et al., 2011; Zhou et al., 2016). For EVI calculation, the EOS LandViewer web interface (https://eos.com/landviewer/) was applied based on the Sentinel-2 images (spatial resolution: 10 m) of total area of cities during the growing season (2019-2020). Actual evapotranspiration (ETa) data were included to gain insight to local moisture conditions, as ETa combines water losses by both transpiration and surface evaporation. Monthly data during the growing season (2019-2020) were requested from the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS, 2020). From each article, we also extracted the following information: study duration, sampling method, type of urban gradient and replications. All data with references are summarized in Table S1.

2.3. Statistical analysis

All statistical analyses were carried out in R 4.0.3 software (R Development Core Team, 2020) by using 'ggplot2' (Wickham, 2016), 'metafor' (Viechtbauer, 2010) and 'esc' (Lüdecke, 2019) packages. Hedges'g unbiased standardized mean difference (Hedges and Olkin, 1985) was calculated as a measure of effect size using 'escalc' function, representing the urban effects on diversity and abundance of soil macrodecomposers. In one case (Gross, 2015), the effect size was computed from the F value of the one-way ANOVA using 'esc_f' function. Positive values for Hedges'g indicate positive impacts of urban disturbance whereas negative values imply adverse effects.

Data were analyzed by fitting weighted random-effects models using the 'rma.mv' function and restricted maximum likelihood (REML) estimation. Hedges' g effect sizes were used as response variables in the models. The effect sizes were weighted by the number of replications, giving greater weight to studies with larger sample size:

$$Wr = \frac{Nt \times Nc}{Nt + Nc},$$

where Nt and Nc are the number of replications in treated (here more urbanized habitats) and control (here less disturbed or undisturbed habitats) categories, respectively.

Several studies with unusually extreme effect sizes (see Section 3.1) were visually (boxplot inspection) identified as outliers and were excluded from the analyses. To consider pseudo-replication, 'study' and 'observation ID' variables were included in all models as random factors. First, we ran intercept-only models to estimate overall mean effect size of urbanization (with 95% confidence intervals, CI) on diversity and abundance of soil macrodecomposers. The urban effect was considered significant at $p < 0.05$, if CI did not overlap with zero. Second, we tested whether climatic, edaphic, city and study characteristics influence the response of soil macrodecomposers to urban disturbance; and whether effect sizes were different between millipedes and woodlice. These variables were used as moderators in the meta-analysis. Continuous moderators were: mean annual temperature (MAT, °C) and precipitation (MAP, mm), mean annual absolute minimum temperature (Tmin, °C), growing season length (GSL, day), number of rainy days, pH, soil organic carbon (SOC, m/m%), $CaCO_3$ (m/m%) and clay content (%) of surface soils, population density (inhabitants/km^2), age of human settlements (year), enhanced vegetation index (EVI) and mean actual evapotranspiration (ETa, mm). GSL was calculated as the number of days between the first 5-day period with average temperatures above 5 °C to the first 5-day period with temperatures below 5 °C (Mueller et al., 2015). Rainy day is a period of 24 h in which at least 0.2 mm precipitation was recorded. Discrete moderators included study duration (short: samples from one season, medium: samples from two seasons within a year, long: samples from >1 year), sampling method (direct, extraction, pitfall, other and combined), type of urban gradient (intraurban, rural-urban, natural-urban, other) and replications (sample, plot, site, city, time). In subgroup comparisons, two means were considered significantly different if their 95% CIs did not overlap. Moderator levels with small sample size (<4) were excluded from these analyses to obtain robust estimates. The heterogeneity of effect sizes was assessed by QE and QM tests (Hedges and Olkin, 1985). To examine the influence of moderators on urban effects, we applied *p*-values associated with QM that describe the variation in effect size related to a continuous variable or in the case of categorical moderators, differences between categories.

The presence of publication bias in our meta-analysis was checked by a combination of three different methods. We calculated the Rosenthal's fail-safe numbers (Rosenthal, 1979) using 'fsn' function. If this number > 5 N + 10, where N is the number of original studies, the results can be considered robust and reliable (Rosenthal, 1979). Publication bias was visually tested via funnel plots and then quantified by using Kendall rank correlation test (Begg, 1994). Symmetrical funnel plots indicate no publication bias.

3. Results

3.1. Overview of the selected studies

Our search resulted in 59 articles published between 1980 and 2020, with over 80% after in the past two decades (Fig. 1). The selected studies represent 49 cities and towns across 25 countries (Fig. 1; Table S1). The majority of study sites for both macrodecomposer taxa were located in Europe and North America characterized by temperate climate, while tropical and subtropical regions (Asia, Africa and South America) were underrepresented. A total of 156 paired observations were extracted: 24 observations from 17 studies for diversity of millipedes, 53 observations from 30 studies for diversity of woodlice, 32 observations from 27 studies for abundance of millipedes, and 47 observations from 40 studies for abundance of woodlice. Abundance was reported most frequently (79 of 156 effect sizes), followed by species richness (49 effect sizes) and Shannon diversity (28 effect sizes). During outlier detections, we found several studies, showing unusually low or high Hedges' g values, which were removed from our dataset to minimize sample bias. For species richness, five observations from four studies (Cauduro et al., 2015; Kuehnelt, 1989; Mwabvu, 2006; Tischler, 1980); for Shannon diversity, three observations from three studies (Cauduro et al., 2015; Tischler, 1980; Vilisics et al., 2007); and for abundance, five observations from four studies (Barratt et al., 2015; Cauduro et al., 2015; Gorgievska et al., 2008; Lee and Kwon, 2015) were excluded, retaining

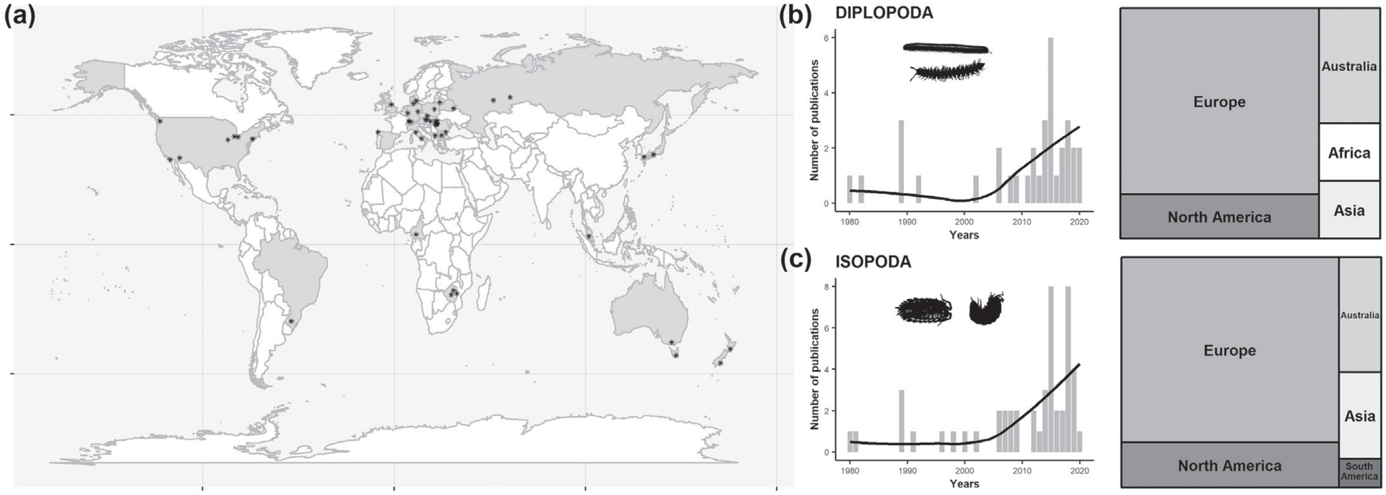

Fig. 1. Geographical location of cities and towns included in the meta-analysis (a), and the temporal and spatial distribution of publications on millipedes (b) and woodlice (c).

a total of 143 comparisons for statistical analyses. Hedges'g effect sizes of all original studies are shown in Fig. S1-6.

3.2. Urban effects on diversity of soil macrodecomposers

At global scale, negative urban effects on diversity of soil macrodecomposers were observed in this study. Shannon diversity and species richness of both taxa significantly decreased with urbanization (Fig. 2a,b). However, we found no significant relationship between the urban effects and the studied variables (Table 1).

3.3. Urban effects on abundance of soil macrodecomposers

The overall effect of urban disturbance on abundance of studied arthropods was neutral. Neither taxa showed a clear negative or positive response to urbanization (Fig. 3a). The direction and magnitude of urban effects on macrodecomposer abundance depended on climatic factors, such as mean annual temperature (MAT) and precipitation (MAP), mean annual absolute minimum temperature (Tmin) and growing season length (GSL). All the above moderators negatively correlated with effect sizes (Fig. 3c-f, Table 1), indicating favorable or less adverse effects of urbanization on soil macrodecomposers in cities from colder (e.g., Nizhnekamsk and Yekaterinburg, Russia) and drier (e.g., San Diego and Phoenix, USA) regions. Sampling method was also a critical factor influencing the effects of urbanization on abundance of soil macrodecomposers (Fig. 2b, Table 1). Although the subgroup analysis showed no significant differences among sampling methods, direct sampling (hand collecting) revealed a significantly stronger negative urban effect (Fig. 2b).

3.4. Publication bias

Rosenthal's fail-safe number, which is the estimated number of additional studies that are required to make the observed urban effect non-significant, was 931 for species richness (5 N + 10 = 185), 105 for Shannon diversity (5 N + 10 = 100), and 0 for abundance (5 N + 10 = 220). Since fail-safe numbers were higher than the critical values (see in parentheses), except for abundance which was not affected significantly by urbanization in this study, we concluded that there is no publication bias in our meta-analysis. Funnel plots showed some skewness (Fig. S7-9), but Kendall rank correlation tests indicate non-significant relationships between the standardized effect sizes and

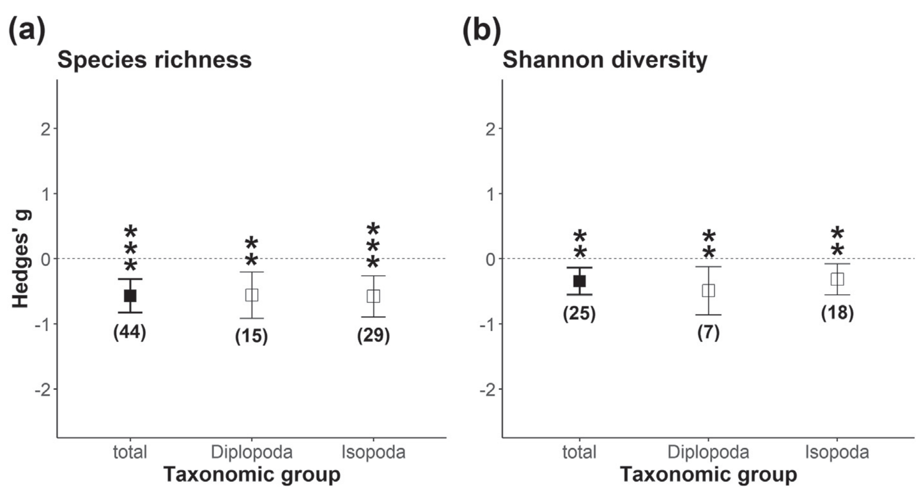

Fig. 2. Effects of urbanization on species richness (a) and Shannon diversity (b) of soil macrodecomposers. Horizontal grey dashed lines indicate that urbanization has no effect. Error bars represent 95% confidence intervals (CIs). Urban effects were considered significant if the 95% CI did not cover zero. Two groups were considered significantly different if their 95% CIs did not overlap. Sample sizes are given in parentheses. Asterisks denote significant urban effects (** < 0.01, *** < 0.001).

Table 1
Summary statistics resulting from random-effects models of the Hedges' g that include test values of moderators with the corresponding residual heterogeneities (in parentheses) for diversity and abundance of soil macrodecomposers. Significant results are highlighted in bold. Abbreviations: MAT-mean annual temperature, MAP-mean annual precipitation, Tmin-mean annual absolute minimum temperature, GSL-growing season length, SOC-soil organic carbon, EVI-enhanced vegetation index, ETa-actual evapotranspiration.

Characteristics	Moderators	Diversity						Abundance		
		Species richness			Shannon index					
		df	Q	p	df	Q	p	df	Q	p
	Taxonomic group	1 (42)	0.01 (77.76)	0. 937 (<0.001)	1 (23)	0.64 (30.92)	0.424 (0.125)	1 (72)	0.43 (306.77)	0.514 (<0.001)
Climatic	MAT	1 (42)	0.55 (73.15)	0.459 (0.002)	1 (23)	1.24 (28.25)	0.265 (0.206)	**1 (70)**	**11.92 (199.39)**	**<0.001 (<0.001)**
	MAP	1 (42)	0.99 (67.51)	0.319 (0.008)	1 (23)	0.59 (29.29)	0.443 (0.171)	**1 (70)**	**5.18 (226.76)**	**0.023 (<0.001)**
	Tmin	1 (42)	0.33 (75.06)	0.569 (0.001)	1 (23)	2.00 (26.95)	0.158 (0.258)	**1 (70)**	**8.85 (227.32)**	**0.003 (<0.001)**
	GSL	1 (42)	0.36 (73.26)	0.549 (0.002)	1 (23)	0.52 (29.51)	0.473 (0.164)	**1 (70)**	**7.08 (235.89)**	**0.008 (<0.001)**
	Rainy days	1 (42)	0.04 (77.87)	0.849 (<0.001)	1 (23)	0.05 (31.57)	0.830 (0.109)	1 (70)	0.35 (303.88)	0.552 (<0.001)
Edaphic	Soil pH	1 (42)	0.52 (74.49)	0.471 (0.002)	1 (23)	0.16 (31.13)	0.687 (0.120)	1 (70)	1.39 (291.24)	0.239 (<0.001)
	SOC	1 (42)	0.36 (76.79)	0.551 (<0.001)	1 (23)	0.03 (31.54)	0.863 (0.110)	1 (70)	0.00 (304.58)	0.948 (<0.001)
	$CaCO_3$	1 (42)	0.03 (77.55)	0.869 (<0.001)	1 (23)	0.05 (31.57)	0.830 (0.109)	1 (70)	0.20 (304.46)	0.659 (<0.001)
	Clay content	1 (42)	1.98 (68.68)	0.159 (0.006)	1 (23)	0.80 (29.85)	0.371 (0.154)	1 (70)	2.55 (280.57)	0.111 (<0.001)
City	Population density	1 (42)	0.65 (76.39)	0.420 (<0.001)	1 (23)	0.35 (31.13)	0.556 (0.120)	1 (70)	0.80 (297.42)	0.372 (<0.001)
	Age	1 (42)	0.20 (76.95)	0.656 (<0.001)	1 (23)	0.44 (30.69)	0.508 (0.131)	1 (70)	0.17 (304.51)	0.681 (<0.001)
	EVI	1 (42)	0.40 (76.76)	0.525 (<0.001)	1 (23)	0.28 (31.38)	0.597 (0.114)	1 (70)	0.16 (303.63)	0.689 (<0.001)
	ETa	1 (42)	0.26 (75.80)	0.609 (0.001)	1 (23)	0.06 (31.37)	0.803 (0.114)	1 (70)	2.50 (270.33)	0.114 (<0.001)
Study	Duration	2 (40)	1.49 (69.36)	0.475 (0.003)	2 (22)	0.25 (31.24)	0.884 (0.091)	2 (71)	0.32 (298.40)	0.854 (<0.001)
	Type of gradient	2 (39)	3.62 (61.64)	0.164 (0.012)	2 (22)	1.47 (29.11)	0.479 (0.142)	3 (70)	4.70 (254.33)	0.195 (<0.001)
	Sampling method	3 (38)	3.80 (65.37)	0.283 (0.004)	2 (20)	0.64 (29.46)	0.726 (0.079)	**3 (69)**	**8.06 (194.91)**	**0.045 (<0.001)**
	Type of replication	3 (40)	5.71 (65.25)	0.127 (0.007)	1 (22)	0.07 (28.33)	0.799 (0.165)	2 (66)	4.21 (268.70)	0.122 (<0.001)

sample sizes (for species richness, tau = 0.158 and $p = 0.141$; for Shannon diversity, tau = 0.044 and $p = 0.778$; for abundance, tau = -0.077 and $p = 0.340$), confirming the absence of publication bias.

4. Discussion

4.1. Urban effects on the studied macrodecomposer arthropod taxa

Urban land conversion and associated environmental changes (i.e. pollution, salinization, soil sealing, elevated temperature, habitat fragmentation) negatively impacts native soils and its resident soil biota (e.g., Mabelis, 2005; Niemelä, 1999). Our meta-analysis clearly reflects these adverse effects on the biodiversity of both macrodecomposer groups: fewer species are detected in cities compared to less disturbed habitats in the same region. In a recent meta-analysis on terrestrial arthropods, Fenoglio et al. (2020) reported biodiversity loss across several arthropod taxa with the exception of spiders (Araneae). The analysis focused on predominantly aboveground taxa, including butterflies and moths (Lepidoptera), beetles (Coleoptera), mosquitoes and flies (Diptera) and bees, wasps and ants (Hymenoptera). Functionally, pollinators and predators dominated the literature with less than a handful publication on decomposers. While some common factors, especially ones related to dispersal may exist across these different taxa, others, such as presence of host plants and availability of nectar, are clearly irrelevant. On the one hand, though certain types of detritus are preferred over others, macrodecomposers are food generalists; consequently, resource quantity is the important filter for the majority of species. On the other hand, abiotic environmental factors are also important, potentially limiting their distribution.

Urbanization dramatically alters both surface and groundwater hydrology. Surface streams disappear or move underground in engineered pipes, and storm drain systems remove large amounts of rainwater from impervious surfaces quickly and efficiently. This, together with reduced infiltration in upland areas results in lowering the water table causing 'hydrologic drought' (Groffman et al., 2003). Most natural riparian floodplains connecting the terrestrial and aquatic habitats have disappeared. These riparian zones are important both as corridors connecting urban green spaces and as refugia during drought. Urban soils are also more hydrophobic (White and McDonnell, 1988) and often drier partially due to the urban heat island effect (Shi et al., 2012).

Our two taxa are often lumped together due to their similar size ranges and ecological function (David and Handa, 2010), however, they are markedly different in their relation to humidity and soil moisture. Terrestrial isopods are a unique suborder of crustaceans, a primarily aquatic taxon (Richardson and Araujo, 2015). While completely independent of the aquatic medium, their exoskeleton is still permeable (Quinlan and Hadley, 1983), thus, as a group, they are much more sensitive to moisture than diplopods, which are fully adapted to terrestrial life, although they still prefer moist microhabitats. Diplopods cope with drought by becoming inactive, i.e. aestivate during summer (Hopkin and Read, 1992). Within both groups, there is a range of adaptation to physiological drought tolerance, and different ways of coping with dry conditions.

In regions where precipitation is not limiting, the drier urban conditions could act as a strong environmental filter, excluding sensitive species (e.g., in the isopod families Ligiidae and Trichoniscidae; millipede species *Cylindroiulus punctatus*, *Chordeume sylvestre*), which are restricted to wet microhabitats such as riparian buffer zones. Soil moisture monitoring would provide more details on local environmental conditions. Unfortunately, field studies rarely collect such data, and remotely collected global soil moisture data are not available for urban land cover. Community shift toward dry-tolerant species has been also observed in urban ants (Menke et al., 2011).

Edaphic parameters did not influence either species richness or abundance. Neither group is particularly sensitive to soil properties, as long as pH, heavy metal or other contaminant concentration, or other factors are not too extreme (Hopkin and Read, 1992; van Gestel, 2012; Warburg, 1987). In fact, many isopod species can survive in soil-less substrate, which is why they are often found in basements, garages and similar habitats (Vilisics and Hornung, 2009). One important element for both groups is calcium (Ca) which they need to build their exoskeleton. Calcium is readily available in cities from concrete (Pouyat et al., 2015). In regions with naturally acidic soil pH, yet grass cover is desired (e.g., residential yards and golf courses), soils are amended with $CaCO_3$ to achieve lush green lawn. Runoff form these areas, coupled with aerial deposition in the form of concrete dust (Lovett et al., 2000) reaches unmanaged urban green spaces, such as forest fragments, resulting in higher Ca soil concentrations compared to their rural counterparts (Pouyat et al., 2008).

In contrast to edaphic factors, climate appears to influence both the direction and the magnitude of urbanization effect on abundance. The two major limiting factors on large-scale isopods and millipede distribution are low temperature and low moisture. At the low end of both MAT and Tmin, urbanization positively affected abundance and the

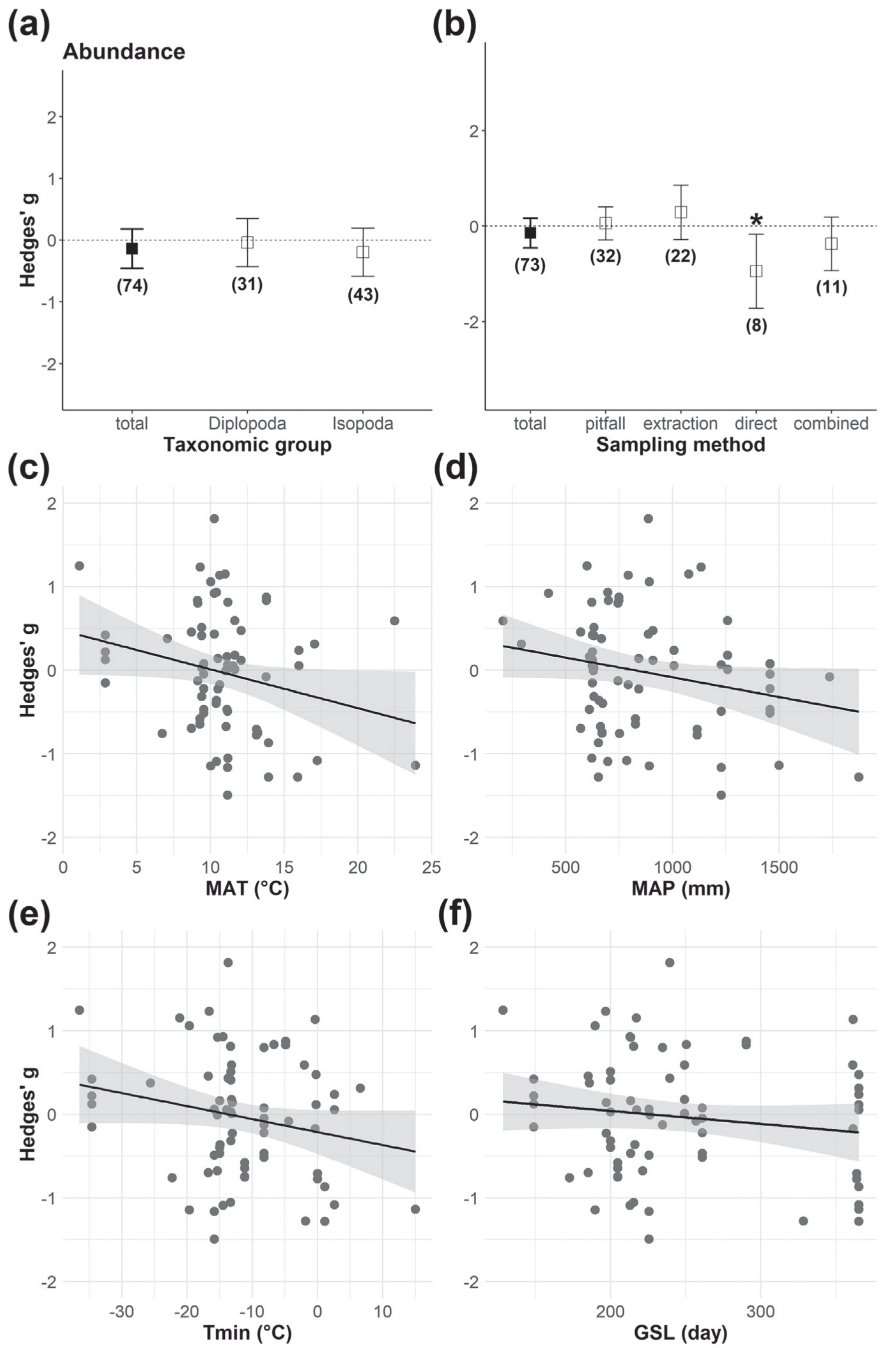

Fig. 3. Effects of urbanization on abundance of soil macrodecomposers (a), and the key properties significantly affecting the Hedges' g effect sizes (b-f). Horizontal grey dashed line indicates that urbanization has no effect. Error bars represent 95% confidence intervals (CIs). Urban effects were considered significant if the 95% CI did not cover zero. Sample sizes are given in parentheses. Asterisk denotes significant urban effect (* < 0.05). Regression lines are shown in black; grey shaded areas represent the 95% CI. Abbreviations: GSL-growing season length, MAT-mean annual temperature, MAP-mean annual precipitation, Tmin-mean annual absolute minimum temperature.

effect size decreased with increasing temperature. In cities, surface soil is warmer even in winter (Savva et al., 2010); moreover, building foundations, underground infrastructure and greenhouses can serve as winter refugia (Garthwaite et al., 1995; Wright, 1997). As a result, at high latitudes, despite being outside their natural ranges (Kuznetsova and Gongalsky, 2012), isopods are still present in cities (Vilisics and Terhivuo, 2009; Wright, 1997). These urban isopods and millipedes can be source populations to colonize natural habitats as the warming trend continues.

While the built infrastructure provides favorable conditions at extremely low temperatures, land management practices, for example irrigation, mulching, tree and ornamental shrub planting can overcome the other major limitation, low moisture conditions. In addition to altering the microclimate, these practices provide organic residue input, which are important resources for macrodecomposers. When urban land conversion happens in arid regions, excessive irrigation to keep the landscape green actually promotes establishment and survival of the arthropods (Cook and Faeth, 2006) resulting in a positive effect. Even in temperate regions, isopods are often the most abundant components in macroarthropod communities dominating pitfall trap samples (Szlavecz et al., 2018). The large variation in the middle ranges for both temperature and precipitation indicates that other factors might influence the isopod and millipede response to urbanization.

The significant negative correlation between effect size and climatic factors have been detected for abundance only, and do not reflect extinction and/or replacement of local native species, if existed at all. For instance, most of North America is devoid of endemic isopods, but very species rich in endemic diplopods (Golovatch and Kime, 2009; Jass and Klausmeier, 2000). To gain a deeper insight in how urbanization changes arthropod community assembly and persistence in general, we need to know species identities and relative abundances. For instance, to test the hypothesis of biotic homogenization of urban biota, we need information on the regional species pool, the degree of local extinction of native species and their replacement with non-native species. Most papers do not report this kind of detail, highlighting the 'taxonomic bottleneck' problem in biodiversity research (Kim and Byrne, 2006). Community structure has been reported where the local fauna is well known and either species identification is easy or taxonomic experts are involved (e.g., Bogyó et al., 2015; Nasu et al., 2018; Riedel et al., 2009). A more detailed examination of different dimensions of biodiversity, including regional biogeography, reveals both the commonalities and differences between the two arthropod taxa. For instance, detailed faunistic studies in Warsaw, Poland (Jedryczkowski, 1981, 1982) showed that millipede diversity was more negatively affected, with 60% loss of the regional species pool, while this number was 40% for the isopod fauna. However, including suburban areas in the survey improved detection level to above 80%, and the difference between the two groups disappeared (Szlavecz et al., 2020).

Another dimension, time is largely ignored in urbanization studies. Most reports reflect a snapshot of urban and wildland communities; only few studies focus on change over time (e.g., Rzeszowski and Sterzynska, 2016). Given the highly dynamic nature of urban ecosystems, long-term data are paramount for understanding the direction and scale of change, including adaptive changes over time. Unfortunately, in many regions of Asia, Africa and South America, where the native fauna is less explored, while extensive urban or agricultural land conversion is currently taking place, local extinction of native species may even go undetected.

4.2. Methodological considerations

Even though sampling methods did not have an effect on species richness and Shannon diversity, we feel it is important to evaluate these methods in the urban setting. Pitfall traps and direct observations are the preferred method for studying epigeic (surface-active) macrofauna. However, pitfall trap samples reflect 'activity-density', a combined measure of abundance and surface activity (Melbourne, 1999) creating a bias toward more mobile species or sex within a species (Dangerfield and Hassall, 1994; Hornung et al., 2015), and against small species and juveniles (Topping and Sunderland, 1992). Pitfall traps are easy to install, and can operate for extended periods of time which allows for larger number of individuals per sample. However, operating pitfall traps in a human dominated environment has some drawbacks: for safety reasons, the preservative used does not allow for long term collections and the traps could be vandalized or destroyed (Szlavecz et al., 2011).

The significant negative effect using direct sampling might be at least partially due to the method itself. Visual observations are made in daylight, and both groups exhibit negative phototaxis (Cloudsley-Thompson, 1960): mainly in open, grassy areas, even at high abundances, animals hide under cover objects, in soil cracks, and other dark places, coming out to forage only after sundown. In wooded areas covered with leaf litter, they are more evenly dispersed thus more easily found. Direct observations are also subjective and highly dependent of the skill and experience of the observer.

Like the majority of meta-analyses, the present study also has some uncertainties and limitations, which need to be considered when interpreting the results. The literature search was significantly hampered by the fact that many publications are not indexed in large databases. Although we tried to extend the search to non-English language literature (6 studies in German, 2 studies in Russian, 1 study in Portuguese and in Spanish, respectively), important information might have been missed, especially from continents other that Europe and North America. Many studies, reporting on species presence in urban environments could not be included, because they were mostly observational and not replicated, thus not suitable for quantitative comparisons. Another common issue is incomplete datasets. We recommend that authors share all relevant information on species abundances and background information including location, habitat characteristics and local environmental conditions. Our analysis revealed a strong geographical bias with 76% of studies confined to temperate climate. Globally the rate of urban land conversion has exceeded the rate of urban population growth (Seto et al., 2010), projecting direct negative impacts on many biodiversity hotspots worldwide (Seto et al., 2012). We strongly emphasize that more urban studies from tropical, subtropical or cold climatic zones are needed to better understand climatic effects on global patterns of soil arthropods-land use interactions in urban context.

5. Conclusion

As the first global meta-analysis focusing on saprophagous soil macroarthropods, our study provided quantitative evidence that diversity of both millipedes and terrestrial isopods is threatened by urbanization. Moreover, despite the heterogeneity of studies, we identified some, mainly climatic factors as key drivers, which influence the direction and strength of urban effects.

Elevated temperature, CO_2 and other air pollutants, altered hydrology and fragmented habitats are common conditions in cities (e.g., George et al., 2007; Grimm et al., 2008; Ziska et al., 2003). Because these factors are also components of our changing earth system, cities have been proposed to serve as analogs to understand ecological responses to global environmental change (Carreiro and Tripler, 2005; Grimm et al., 2008). The altered conditions inevitably lead to local extinction of some species, while favor survival of other, usually disturbance tolerant species, leading to a different community structure. Future climate change scenarios agree in further temperature increase, but greatly differ in projecting precipitation patterns and associated soil moisture levels. The diverse urban landscape provides an opportunity to a deeper understanding of how soil fauna responds to altered climate at multiple scales. Moreover, the decomposer community plays vital role in maintaining overall soil health and restoring degraded soils (Guilland et al., 2018). As such, soil biodiversity has to be an essential component of designing, conserving and restoring urban green spaces for sustainable cities.

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CRediT authorship contribution statement

Zsolt Tóth: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Elisabeth Hornung:** Investigation, Writing – original draft, Writing – review & editing. **Katalin Szlavecz:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Visualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.149182.

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