Science of the Total Environment 859 (2023) 160145

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Review

Urbanization decreases species richness, and increases abundance in dry climates whereas decreases in wet climates: A global meta-analysis

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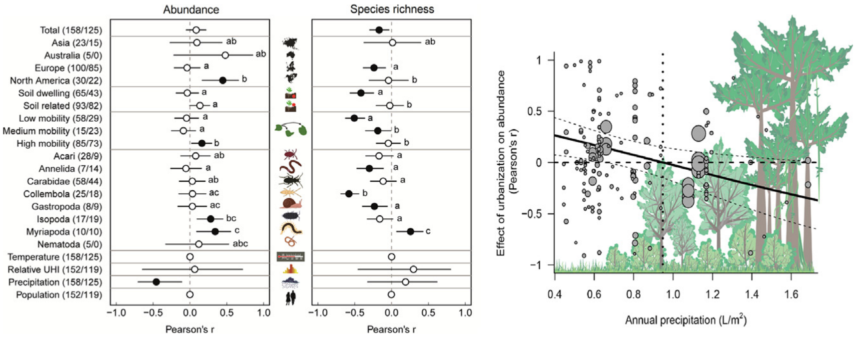
HIGHLIGHTS

- Soil invertebrates are threatened by urbanization but the data is inconsistent.
- We used a global meta-analysis with the climatic moderators to see general patterns.
- Species richness of annelids, springtails decreased with rise of urbanization.
- Abundance increased with urbanization in drier climates but decreased in wet ones.
- Making future cities more climate-neutral could better sustain soil biodiversity.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:
Carabid
Heat island effect
Irrigation
Mobility
Precipitation
Temperature

ABSTRACT

Soil invertebrates have an essential role in decomposition, nutrient turnover and soil structure formation, all of which are strongly threatened by urbanization. Sealing, compaction by trampling and pollution destroy and degrade city soils and potentially damage soil-living invertebrates. The existing literature on how urbanization affects soil invertebrates is inconsistent, presenting both negative and positive effects. Therefore, here we aimed to synthesize the effects of urbanization on soil invertebrates considering their taxonomic (Acari, Annelida, Carabidae, Collembola, Gastropoda, Isopoda, Myriapoda, Nematoda) and functional (soil living vs. soil-related; mobility) identities, as well as to examine how the overall effect is modulated by climatic conditions (total annual precipitation, annual mean ambient temperature), urban heat island effect (based on ambient temperature differences between urban and rural areas) and city population. In a systematic review using hierarchical and categorical meta-analyses, we extracted 158 effect sizes from 75 studies on abundance and 125 effect sizes from 84 studies on species richness. Invertebrate abundance showed an increase ($r = 0.085$), whereas species richness significantly decreased with increasing urbanization ($r = -0.168$). The reason behind this could be that a few generalist species can adapt well to the urban environment and achieve strongly elevated densities. The species richness of annelids ($r = -0.301$), springtails ($r = -0.579$), and snails ($r = -0.233$) decreased with advancing urbanization, most probably because these animals are sensitive to soil compaction and pollution, both of which are common consequences of urbanization. The temperature did not modify the effects of urbanization, but precipitation modified the effects on abundance ($r = -0.457$). Abundance increased with advancing urbanization in drier climates, probably because irrigation increased soil moisture, whereas it decreased in wet climates, as urban areas were drier than their surroundings. Making future cities more climate-neutral could better sustain soil biodiversity.

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http://dx.doi.org/10.1016/j.scitotenv.2022.160145
Received 29 July 2022; Received in revised form 17 October 2022; Accepted 8 November 2022
Available online 14 November 2022

Contents

1. Introduction

The ratio of the human population living in cities is constantly growing, resulting in bigger and bigger cities (Gu, 2019; United Nations, 2018). Urbanization profoundly modifies the environment during the process of building cities (Merckx et al., 2018). The primary problem caused by urbanization is the degradation and fragmentation of the original natural habitat, as well as its replacement with buildings and impermeable materials (asphalt, concrete, etc.), which is a major threat to biodiversity (Fenoglio et al., 2020; Ge et al., 2019). Additionally, urbanization causes increased noise, light, and chemical pollution (Johnson and Munshi-South, 2017; Pinho et al., 2021), as well as soil compaction (Fenoglio et al., 2020). Realizing this threat, more and more suggestions (bee pasture, insect hotels, green stepping stones, etc.) are made that aim to preserve or restore (semi-)natural habitats in urban areas.

These different "greening actions" are mostly based on the knowledge of the effects of urbanization on a few highly visible taxa, including plants, beetles, butterflies, bees, lizards, birds, and mammals. Despite its paramount importance, soil fauna is seriously underrepresented in urbanization research compared to aboveground fauna (Pinho et al., 2021). Soil is a complex system hosting immense biodiversity whose activity provides important ecosystem services, such as decomposition (Tresch et al., 2019), nutrient cycling, food production (Pulleman et al., 2012), and pest control (Korányi et al., 2022). Soil invertebrates provide several ecosystem services besides decomposition (Swift et al., 1979), such as increasing soil porosity, increasing water infiltration and bioturbation (Babu Ojha and Devkota, 2014), dispersing and regulating symbiotic mycorrhiza fungi (Hopkin, 1997), controlling dispersal of weeds and depredating pests (Kromp, 1999).

In the case of aboveground fauna, Saari et al.'s (2016) meta-analysis found that the abundance of arthropods decreased with increasing urbanization, especially in Europe, where cities are old and densely built, but their species richness did not change. Fenoglio et al. (2020) found an apparent negative effect of urbanization not only on the abundance and, but also on the species richness of aboveground arthropods, including Coleoptera, Lepidoptera, Diptera and Hymenoptera. There is no general consensus on how urbanization affects the below-ground fauna. One suggestion is that urbanization negatively affects both abundance and species richness (Holienkova and Krumpalova, 2016), especially in heavily urbanized areas. In such areas, impermeable, artificial surfaces dominate, with hardly any green area, and the remaining unsealed soil is often compacted, which is not suitable habitat for soil invertebrates. A second hypothesis claims that the abundance of soil invertebrates increases, while their species richness decreases with advancing urbanization because the urban environment is favourable to a few generalist species (Ge et al., 2019; Tresch et al., 2019). A third hypothesis suggests that urbanization can positively affect both abundance and species richness, at least in suburban areas that represent areas under intermediate disturbance (McKinney, 2008). All of the above hypotheses have some support in the scientific literature including a very wide range of taxonomic groups, but no general consensus has yet emerged.

Urbanization can differently affect the different layers of soil, and it is reasonable to consider their associated animals separately. The most common grouping is based on the soil layers most used by the given taxon. Euedaphic species (springtails, mites, earthworms) use the deeper soil, hemiedaphic ones (centipedes, springtails) the upper layer, and epedaphic species (isopods, carabids, millipedes) move on the soil surface and the litter layer (Bitzer et al., 2005). Different individual developmental stages of the same species may belong to different groups: carabid larvae live in the soil, while adults are primarily surface-active (Lövei and Sunderland, 1996). Additionally, residents of the soil can be permanent (live in the soil in every life stage), periodic (adults leave the soil but return regularly), temporary (only immature stages develop in the soil, but adults leave), or transient (the life-cycle is independent of the soil but the species spends some time in it) (Coleman et al., 2018). Although soil invertebrates are generally of lower mobility than aboveground ones (Croci et al., 2008), their mobility can still be very diverse. Winged animals are the most mobile ones (some carabids), but surface-active woodlice, millipedes, flightless carabids are also relatively mobile. Endogeic animals, like earthworms, have low mobility and smaller euedaphic animals (nematodes, mites, springtails) can even be considered residents with very little mobility (Zaitsev et al., 2014). Urbanization can affect these mobility groups differently, as mobile groups can move between separate but suitable habitat patches and utilize more resources (Piano et al., 2017), although a recent analysis (Fenoglio et al., 2020) found no difference between aboveground arthropods of different mobility. The effects of urbanization on soil invertebrates of different mobility are not sufficiently known.

Soil invertebrates are dependent on soil pH, moisture, and temperature, all of which are strongly determined by macro-climate. Consequently, ecosystem services (such as decomposition) depend on these parameters (Pinho et al., 2021). The effects of urbanization might be modified by climatic regimes (Chamberlain et al., 2020; Fenoglio et al., 2020). In areas with drier climates, urbanization makes the environment wetter through irrigation and by the creation of wetlands, ponds, and other anthropogenic sources of water (Nielsen and Ball, 2015). In wet climates, however, urbanization can make the environment drier than the surroundings because of increased runoff and evapotranspiration (Burian and Pomeroy, 2010). However, despite these general hypotheses, contradictory results can be found in the literature. For example, Do and Joo (2013) found similar carabid species richness in natural areas and urban forest fragments in the wet climate of Japan. Also, in the relatively wet climate of New Zealand, Parker and Minor (2015) found more isopods and myriapods in urban forest remnants than in natural forests. The abundance of mites decreased with advancing urbanization in the dry climate of Greece (Stamou and Argyropoulou, 1995).

Local climatic conditions and soil parameters can substantially differ along the urbanization gradient, which can influence soil invertebrates. One of the best-described phenomena is the urban heat island (UHI) effect, which shows that the more urbanized areas, usually closer to the city centre, are warmer than the neighbouring suburban or rural areas (Arnfield, 2003). Since urbanization also increases evapotranspiration and water runoff, urban areas are often also drier than the surrounding rural areas (Burian and Pomeroy, 2010; Pouyat et al., 2010). Urban areas, however, are often also irrigated, especially in drier climates, which causes higher soil moisture than the surrounding, more natural areas. This, in turn, increases the abundance of several soil invertebrate taxa (Ge et al., 2019).

In this study, we carried out a systematic review and a meta-analysis to test the overall effect of urbanization on soil invertebrate abundance and species richness. Although a few meta-analyses investigated the effects of urbanization on single groups of soil-related organisms (e.g. isopods and diplopods by Tóth et al. (2021), maturity index of nematodes by Pothula et al. (2016) or carabids by Martinson and Raupp (2013)), ours is the first comprehensive meta-analysis focusing on a broad range of soil invertebrates. We also aimed to test the effects of annual precipitation, annual mean temperature, relative UHI and city population size (number of inhabitants) on the responses to urbanization. Furthermore, we considered the soil stratum where organisms mainly live (soil-dwelling vs. soil-related), taxon identity (Acari, Annelida, Carabidae, Collembola, Gastropoda, Isopoda, Myriapoda, Nematoda) and their general mobility (low, medium, high).

We hypothesized that some generalist species could adapt very well to an urban environment, therefore, the overall abundance of soil invertebrates would increase with increasing urbanization. However, we expected that species richness decreases with advancing urbanization, because urban areas do not meet the habitat requirements of several specialists. Low-mobility species would also be negatively affected, because dispersal limitation between green patches, embedded in a hostile matrix makes them isolated and vulnerable to the negative effects of habitat fragmentation. However, the ambient temperature was not expected to affect soil invertebrates as the soil can buffer temperature changes (Fernández-Pascual et al., 2015). In contrast, increased precipitation was hypothesized to strongly modify the effect of urbanization, especially in dry climates, where irrigation in urban areas would increase abundance as well as species richness. We expected that the population size of the cities would not exert a strong influence on either variable as this factor can affect the generalists and specialists in opposite ways.

2. Methods

2.1. Literature search

We carried out a systematic review on the effect of urbanization on the abundance and species richness of soil invertebrates, which conforms to the standard review guidelines for a comprehensive literature review (Haddaway et al., 2018; Koricheva et al., 2013). For the searches, we used the Web of Science Core Collection (Science Citation Index Expanded) from 1975 to June 2021 and the Scopus database, all document types, from 1960 to June 2021 (for detailed PICO and search terms, see Supplementary material, Section 1). We performed the initial search on 3 March 2021, and we closed the database on 7 June 2021. We screened the titles and abstracts, and omitted irrelevant articles from the database. In addition, we applied a set of inclusion/exclusion criteria (Supplementary material, Section 2). We excluded non-English, population level, and review studies, studies not examining focal variables, not including focal taxa, examining groups that were not soil-living (e.g. aquatic snails or tree-dwelling mites), and free-living organisms (parasitic nematodes and mites), and studies with less than three spatial replications per urbanization category. We included studies only where the study area was well defined, so the definite city or cities were given. We also included a few additional studies conforming to our inclusion criteria from a recent meta-analysis (Tóth et al., 2021). Our initial search yielded 2008 studies, of which 213 were potentially relevant to test the effect of urbanization on soil invertebrates. In the end, 103 passed the exclusion/inclusion criteria (see the PRISMA diagram in Supplementary material, Section 2).

There was a substantial geographical bias in our dataset, as the majority (69.5 %) originated from Europe, 13.3 % from North America and 12.4 % from Asia. There were only three studies from Australia and one study each from South America and Africa (Fig. 1). Most of the studies investigated carabids (31.8 %), isopods (18.2 %), or springtails (12.9 %). The contribution of other taxa did not reach 10 % per taxon, so the studies were strongly biased towards carabids.

2.2. Data extraction

Urbanization in the primary studies was characterized in various ways: with the ratio of the sealed area (proportion of impervious surface such as buildings, roads, paved surfaces etc.), distance to the city centre, UHI effect, human population density, principal components analysis scores based on different variables describing urbanization (ratio of vegetation and sealed area, distance to the city centre). These measures highly correlate with each other, but the difference between studies can introduce some extra variability in the response variable.

We included studies on the following taxa: mites (Acari), earthworms (Annelida), ground beetles (Carabidae), springtails (Collembola), slugs and snails (Gastropoda), woodlice (Isopoda), myriapods (Myriapoda), and nematodes (Nematoda). The choice of these taxa was motivated by trying to include representatives of micro- (Nematoda), meso- (Acari, Collembola), and macrofauna. There is no consistency in the definition of soil macrofauna in soil science. Some researchers define macrofauna based on size (depends on life stage and age as well), others on taxonomy (Gongalsky, 2021); we used the taxonomic affiliation. We used abundance data expressed in various ways (activity density, density obtained by hand-sorting, extractions from soil sample or pitfall traps); for diversity, only species richness (species number at a sampling point), but no other diversity parameters were considered. Altogether, we found 103 relevant studies, and extracted 158 observations of 75 case studies for abundance, and 125 observations of 84 studies for species richness (Supplementary material, Section 3). Several studies provided data on more than one taxon or data from several locations or years, resulting in more observations (effect sizes) than the number of studies. A list of studies excluded during full-text filtering and reasons for exclusion is presented in Supplementary material, Section 4.

After screening each study, we extracted the relevant climatic data (total annual precipitation, annual mean ambient temperature at the study location) from the CHELSA (Climatologies at high resolution for the earth's land surface areas) database (Karger et al., 2017) using QGIS 3.18 (QGIS.org, 2021). The CHELSA database contains raster-based data about the Earth's land surface climatic conditions at 1 km resolution. CHELSA merges data from 1979 to 2013. We drew polygons around the study cities based on the OpenStreetMap layer and GADM database boundaries if available for the given city (GADM, 2018), and we extracted the mean of the total annual precipitation (L/m^2) and annual mean ambient temperature (°C). We used total annual precipitation and annual mean ambient temperature as continuous moderators. We also analyzed the UHI effect based on Magura et al. (2020). In short, we extracted daytime UHI from the database of the Center for International Earth Science Information Network - Columbia University (2016). UHI is expressed as the maximum daytime temperature difference between the urban area and its rural surroundings. We calculated relative UHI by dividing it by the annual mean ambient temperature. We used relative UHI in the analysis as this value corrects the UHI value for the different climatic zones.

We collected data on the human population size of the studied areas. If the study stated the exact size of the population, we used those data. Otherwise, we collected data from City Population (https://citypopulation.de/) or the United States Census Bureau (http://www.census.gov) within five years of the sampling time. In the analysis, we used the population in a unit of 100,000 people.

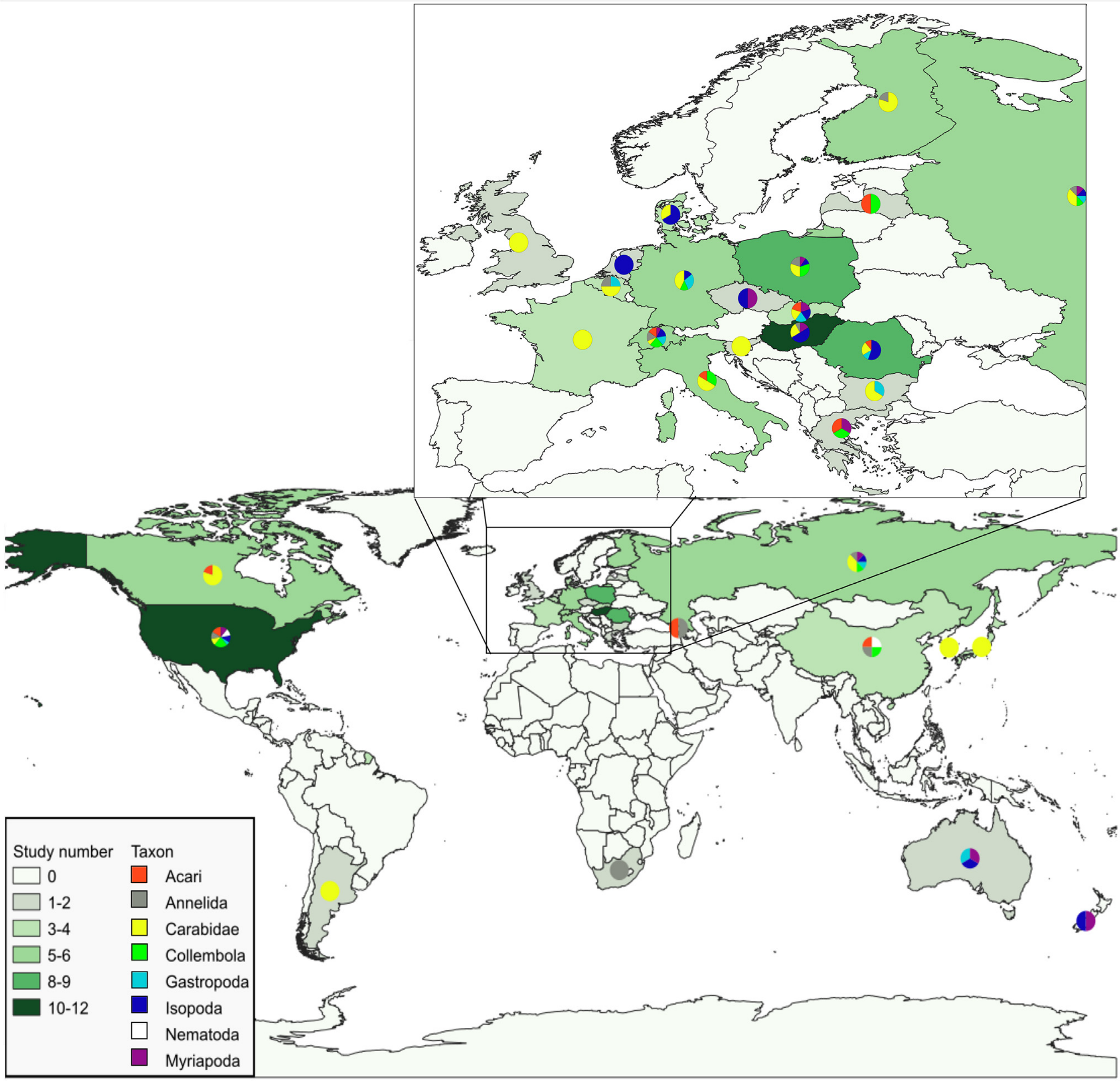

Fig. 1. Geographic distribution of studies in the meta-analysis ($n = 103$), two studies were performed in more than one country, eighteen studies examined two or more taxa. Green shades in the countries show the number of studies originating from the given countries.

2.3. Effect size calculation

We used the Pearson's correlation coefficient (Pearson's *r*) as an effect size. Pearson's *r* is an expression of linear association between two parameters, in our case, urbanization and abundance/species richness. Pearson's *r* can range from 1 (strong positive association) to -1 (strong negative association), whereas zero indicates no connection between the two parameters. Pearson's *r* is an effect size that can correct for differences in the metrics of the raw data (Borenstein et al., 2009). We converted data in different ways depending on the study's approach to urbanization. In cases where (1) raw abundance or species richness data were available but no test statistics were given, we calculated Pearson's *r* directly from the data. In cases where categorical data (rural/natural, suburban, urban) were available, we calculated Hedges' *g* from the means and standard deviations of abundance or species richness. Hedges' *g* is the unbiased standardized mean difference between groups, from which Person's *r* can be calculated to put all effect size data on the same scale (Borenstein et al., 2009). In the case of (2) two-level categorical data, we converted it directly to Pearson's *r*. In the case of (3) three or more level categorical data, we first calculated Hedges' *g* for the rural- suburban, and suburban-urban categories, then we calculated the combined effect size accounting for multiple comparisons before calculating Pearson's *r* following Batáry et al. (2018). In case of (4) continuous variables, they were converted to Pearson's *r* with the following methods. In the case of F-value, Chi-square value and *Z*-value, we converted these values to Pearson's *r* based on the equations of Koricheva et al. (2013). In the case of *p*-value, we used the calculator of Stangroom (2021) to calculate Z-value after *p*-value correction (*p*-value was converted from a two-sided hypothesis to a one-sided one), then used the equation of Koricheva et al. (2013). From R^2, we calculated Pearson's *r* with the equation of Nakagawa and Cuthill (2007). All of the equations can be found in Supplementary material, Section 5.

Several studies did not report any variance measures, which is necessary to calculate the initial effect size (Hedges' *g*) of categorical data. Because several taxa only had a few data, we did not want to discard these studies. Therefore, to make these studies analyzable, we simulated the standard deviation based on the rest of the collected data using the R *mice* package (van Buuren and Groothuis-Oudshoorn, 2011). Data with simulated variances are marked in the dataset (Supplementary material, Section 9.).

2.4. Meta-analysis

We used the R 4.1.0 statistical environment for all analyses (R Core Team, 2021). We converted Pearson's r values to Fisher's z to achieve normality (Borenstein et al., 2009). We used the Fisher's z-values in the meta-analysis models with the help of R *metafor* package (Viechtbauer, 2010). We transformed Fisher's z values and their 95 % confidence intervals back to Pearson's r for figures, as its interpretation is much easier than Fisher's z (Batáry et al., 2018). The back-transformed model estimates (Pearson's r) express the strength and direction of the effect of urbanization on soil invertebrates, which was considered significant if the confidence interval did not include the zero value.

We analyzed abundance and species richness in separate hierarchical mixed-effects meta-analysis models ('rma.mv' function) with the nesting factors of continent and study ID. As several studies originated from the same continent, the continent was the first nesting factor. The study ID was the second nesting factor, because of studies often contained more than one data point (e.g., the study had data for several cities, taxa, seasons, or years). When testing whether the continent moderated the effect of urbanization, we performed meta-analysis only with study ID as a random factor. Because of data deficiency from Australia, South America and Africa (<5 observations in case of species richness), we excluded them from the continent-level analysis.

First, we separately calculated the overall mean effect size for species richness and abundance. The output of each analysis contained the mean effect size with a 95 % confidence interval (CI), and total heterogeneity statistics (Q). The heterogeneity statistic is a weighted sum of squares tested against a χ^2 distribution (Borenstein et al., 2009). After the summary analysis, we used meta-analysis with moderators. The total heterogeneity in meta-analysis with moderators consisted of the variance explained by the moderator (between-group heterogeneity) and residual error variance (within-group heterogeneity) with χ^2 tests indicating their significance. A significant between-group heterogeneity indicates that the moderator significantly modifies the effects of urbanization (Borenstein et al., 2009).

In order to test the effect of urbanization on soil invertebrates, we tested several moderators. The first one was the stratum, where the taxon spends most of its lifetime. Hence, we classified them as follows:

i) soil-dwelling organisms (permanent and periodic residents) if they lived all of their life in the soil matrix (Acari, Annelida, Collembola, Nematoda), or
ii) soil-related organisms (temporary and transient residents) if they spent only some life-stages in the soil matrix (Carabidae, Isopoda, Myriapoda, Gastropoda).

We also classified them based on mobility:

- low mobility organisms having a very limited potential movement of one or a few metres (Acari, Collembola, Nematoda),
- medium mobility taxa having a potential movement range of ca. 100 m (Annelida, Gastropoda) and
- high mobility taxa with the potential movement of ≤1 km (Carabidae, Isopoda, Myriapoda) or over a kilometre in the case of some flying carabids.

We also tested the taxon itself as a moderator with the exception of Nematoda ($n = 2$) in the case of species richness. Finally, we performed models with total annual precipitation, annual mean ambient temperature, relative UHI and city population size as continuous moderators.

2.5. Publication bias

Publication bias arises when studies are prone to report one-directional effect more than the other (positive or negative) or when studies are prone to report significant effects but not non-significant ones. There are several ways to assess the potential publication bias of a dataset, but unfortunately, no single test is conclusive and using more tests simultaneously is recommended (Koricheva et al., 2013). To test for publication bias, we used funnel plots, Egger's test on the full data set and Kendall's rank correlation test on single models (Supplementary material, Section 6). Funnel plots are scatter plots of effect sizes against their variance (or sample size or standard error). If the identified literature is unbiased, the range of effect sizes decreases with the increase of sample size, which leads to a shape of an upturned funnel (Koricheva et al., 2013). Statistical tests, such as Egger's test or Kendall's rank correlation test can verify the symmetry of the funnel plot, indicating a most probably unbiased set of data. According to Egger's test, both species richness and abundance data were free from bias with sample size as a predictor. We found significant Kendall's rank correlation test in the case of species richness taxon-based models, relative UHI and population models (Supplementary material, Section 6: Table S1). However, we carried out sensitivity analysis with a single outlier point, and after leaving out this point, we found very similar results to the original one and the asymmetry of the funnel plot was not significant anymore. Consequently, the results were not sensitive to this outlier and it was not necessary to remove this outlier from the dataset.

3. Results

Overall, we found a non-significant effect of advancing urbanization on abundance ($r = 0.085$, 95 % CI = -0.051 to 0.217) and a significant negative effect on species richness ($r = -0.168$, 95 % CI = -0.296 to -0.035) (Table 1 and Fig. 2; see Supplementary material, Section 7). Continent was a significant moderator for both abundance and species richness. In the case of abundance, urbanization in North America had a significant positive effect ($r = 0.446$, 95 % CI = 0.166 to 0.660). In Europe, urbanization caused a significant negative effect on species richness ($r = -0.238$, 95 % CI = -0.383 to -0.082) (Table 1 and Fig. 2).

Effect sizes of the soil-dwelling groups were around zero for abundance ($r = -0.036$, 95 % CI = -0.187 to 0.116) and significantly negative for species richness ($r = -0.415$, 95 % CI = -0.562 to -0.243). In the case of the abundance of soil-related organisms, there was no significant moderation of the effects of urbanization ($r = 0.135$, 95 % CI = -0.003

Table 1

Summary table of meta-analysis models with an intercept on abundance and species richness showing total heterogeneity and heterogeneities explained by moderators (continent, soil stratum, mobility and taxon as factors, temperature, relative UHI, precipitation and population as continuous variables) with corresponding residual heterogeneities. UHI: Urban Heat Island.

		Abundance			Species richness		
Moderator		Q	df	*p*-Value	Q	df	*p*-Value
Total	Residual	899.5	157	<0.001	1729	124	<0.001
Continent	Moderator	10.82	3	0.013	3.220	2	0.200
	Residual	818.7	154	<0.001	1536	119	<0.001
Soil stratum	Moderator	11.33	1	0.001	117.3	1	<0.001
	Residual	894.7	156	<0.001	1695	123	<0.001
Mobility	Moderator	20.18	2	<0.001	144.3	2	<0.001
	Residual	887.0	155	<0.001	1673	122	<0.001
Taxon	Moderator	28.41	7	<0.001	278.2	6	<0.001
	Residual	848.4	150	<0.001	1654	116	<0.001
Temperature	Moderator	0.113	1	0.737	0.050	1	0.823
	Residual	899.4	156	<0.001	1727	123	<0.001
Relative UHI	Moderator	0.023	1	0.879	0.571	1	0.450
	Residual	888.3	150	<0.001	1724	117	<0.001
Precipitation	Moderator	6.406	1	0.011	0.509	1	0.476
	Residual	862.3	156	<0.001	1675	123	<0.001
Population	Moderator	0.064	1	0.800	0.974	1	0.324
	Residual	890.5	150	<0.001	1669	117	<0.001

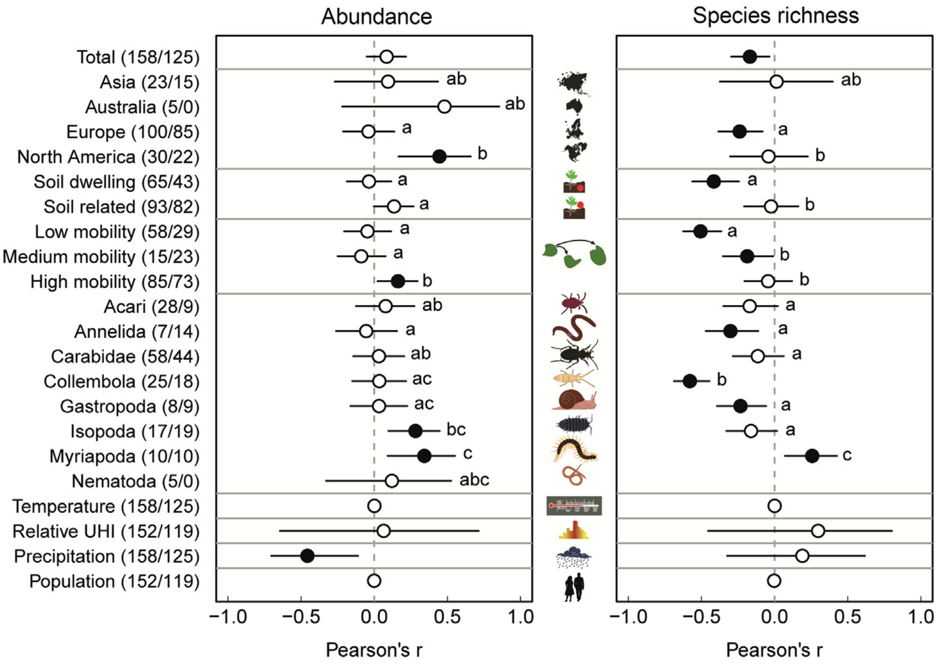

Fig. 2. The effects of urbanization on abundance and species richness of soil invertebrate fauna. Mean effect sizes (Pearson's *r*) with 95 % CIs are shown. Black dots represent significant ($p < 0.05$) differences from zero. Relative UHI means the urban heat island effect corrected for the mean annual temperature. The letters indicate significant differences between groups at $p < 0.05$. Numbers in parentheses indicate sample sizes (first number for abundance, second for species richness analyses). Note that temperature and population had very narrow, and thus invisible 95 % CIs.

to 0.269). Mobility was a significant moderator (Table 1 and Fig. 2). Organisms with high mobility had weakly increasing abundance under higher levels of urbanization ($r = 0.163$ 95 % CI = 0.023 to 0.296), whereas species richness in the low mobility group strongly decreased ($r = -0.506$, 95 % CI = −0.625 to −0.364), and that of the medium mobility group also decreased but only moderately ($r = -0.187$, 95 % CI = −0.353 to −0.009).

The abundance of Isopoda ($r = 0.282$, 95 % CI = 0.097 to 0.448) and Myriapoda ($r = 0.348$, 95 % CI = 0.092 to 0.553) showed a moderate increase with increasing urbanization. Species richness of the different taxa generally showed a decrease, moderate but significant decrease for Annelida ($r = -0.301$, 95 % CI = −0.470 to −0.112) and Gastropoda ($r = -0.233$, 95 % CI = −0.394 to −0.058), and a strong decrease for Collembola ($r = -0.579$, 95 % CI = −0.687 to −0.445). In contrast, the species richness of Myriapoda moderately increased ($r = 0.257$, 95 % CI = 0.070 to 0.427) with advancing urbanization (Table 1 and Fig. 2).

The annual mean temperature and the UHI did not modify the effect of urbanization on either abundance (mean temperature: $r = 0.001$, 95 % CI = −0.005 to 0.007, UHI: $r = 0.065$, 95 % CI = −0.645 to 0.714) or species richness (mean temperature: $r = 0.001$, 95 % CI = −0.006 to 0.007, UHI: $r = 0.298$, 95 % CI = 0.454 to 0.802) (Fig. 2). However, precipitation strongly modified the urbanization effect on abundance ($r = -0.457$, 95 % CI = −0.704 to −0.111) (Fig. 3). In drier environments, urbanization had a positive effect on soil invertebrate abundance, but this turned to a negative effect in wet environments with high precipitation. The population size of the cities (no. of inhabitants) did not affect the effect of urbanization either on abundance ($r = -0.001$, 95 % CI = −0.004 to 0.003) or on species richness ($r = -0.003$, 95 % CI = −0.008 to 0.003).

4. Discussion

The effects of urbanization on soil invertebrates caused a slight increase in abundance but a significant decrease in species richness. Living in the soil matrix (or not) and mobility were important moderators with negative effects on the richness of soil-dwelling and less mobile animals. The different taxa showed varying responses to urbanization from neutral to positive effects on abundance and neutral to negative effects on species richness (with the exception of Myriapoda). Most interestingly, the annual precipitation modified the effects of urbanization on abundance. In drier areas, urbanization increased, but in wet areas, urbanization decreased the abundance of soil-living invertebrates.

Despite the fact that we did not find a significant general effect of urbanization (analyzing it as a sole variable) on the total abundance of soil invertebrates, our results showed that urbanization could sustain soil

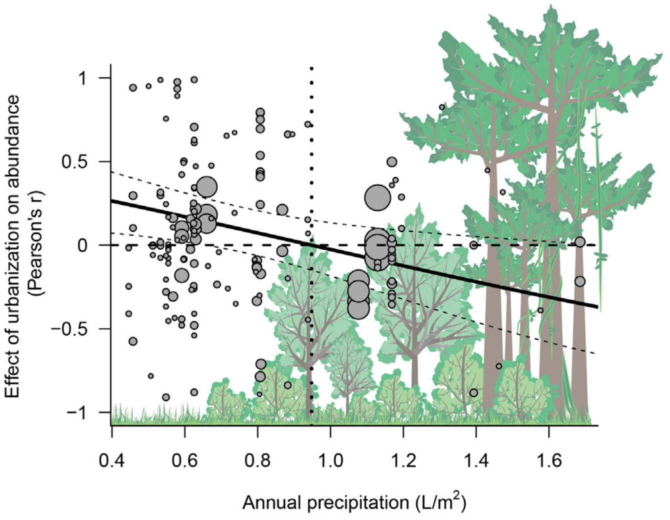

Fig. 3. Moderation effect of annual precipitation on urbanization on soil invertebrate abundance. Point size is proportional to the variance associated with the given effect size. The regression line was fitted with a meta-regression model with continent and study ID as a nesting factor. Dotted lines and grey areas indicate ±95 % confidence intervals. The horizontal dashed line indicates zero effect. The horizontal dashed line indicates zero effect, and the black vertical dotted line separates the data with a positive effect of urbanization on abundance (mainly in the dry climates) from the negative effects (in climates with high precipitation) at 0.95 L/m^2 precipitation. The sample size is 158, extracted from 75 studies.

invertebrate abundance while decreasing their species richness. This indirectly supported our hypothesis about the negative impact of urbanization on biodiversity (Ge et al., 2019; McKinney and Lockwood, 1999; Tresch et al., 2019). This pattern could be observed because urbanization causes habitat loss and creates a hostile matrix by sealing green infrastructure (network of natural and semi-natural areas like parks, lawns, natural remnants, alleys, private gardens, green roundabouts, etc.) (Blank et al., 2017).

The reason behind the increasing abundance with advancing urbanization can be high mobility, opportunistic feeding (isopods and myriapods, see below), a resource concentration effect or a short-long gradient bias. The resource concentration may emerge because of the unsuitability of the sealed area, and this may force the soil organisms to concentrate in the remaining green infrastructure. In addition, when the habitat is fragmented, the population of habitat specialists can be concentrated on the remaining patches (Tscharntke et al., 2012).

The significant moderation of continents on abundance, especially the strong positive effect of urbanization in North America compared to the negative effect in Europe could be caused by several reasons. The North American locations are not numerous in our study, thus any generalization should be cautiously made. The primary reason could be that the cities in North America are much younger than in Asia or Europe. Also, they are often less densely inhabited as well, which could be advantageous for a few generalist species (Saari et al., 2016). In addition, compared to Europe or Asia, the longitudinal differences in North America could cause the differences. The huge geographical bias in urbanization research is a problem because most of the existing and future megacities are located in less researched areas like South Asia, South America and Africa (United Nations, 2018). However, we have the fewest data from these areas.

When the different taxa are independently considered, urbanization seems to have taxon-dependent effects. The only significant effects were on the abundance of isopods and myriapods, two soil-related, highly mobile taxa. In the case of isopods, most probably only a few species are adapted to the urban environment, therefore the abundance of isopods, in general, could increase (Sfenthourakis and Hornung, 2018). For example, *Armadillidium vulgare* (Latreille, 1804), *Porcellio scaber* (Latreille, 1804), *Cylisticus convexus* (De Geer, 1778)*, Oniscus asellus* (Linnaeus, 1758)*, Philoscia muscorum* (Scopoli, 1763) are species with broad tolerance and abundant at urban sites (Hornung et al., 2007; Pop et al., 2019; Vilisics et al., 2007). Isopods are detritivores and food generalists, thus they can easily find food in the garbage, pet food or leaf litter (Szlavecz et al., 2018). In addition, isopods require moist environments, which irrigation, a current practice in cities may provide, and this can also contribute to their success (Cook and Faeth, 2006). Among diplopods, synanthropic species are typical of urban areas (Bogyó et al., 2015). Many isopods and myriapods can live in environments without soil substrate, e.g. in buildings, cellars, or other human constructions (Stoev, 2004; Szlavecz et al., 2018), which can contribute to their increased abundance. In another recent meta-analysis, Tóth et al. (2021) found a significant negative effect of urbanization on isopod species richness but not on abundance. We also found a negative effect on isopod species richness, although this was not significant. The unpredicted increase in myriapod species richness found in this analysis could be caused by the high heterogeneity of the urban environment, a high number of introduced species, and the existence of greenhouses which can increase species richness (Korsós et al., 2002). Botanical gardens and greenhouses are indeed mentioned at some of the study locations, e.g. Budapest (Hungary); these could influence the species richness through harbouring alien species.

The species richness was significantly and negatively affected in the following groups: annelids (soil-dwelling, medium mobility), snails (soil-related, medium mobility) and springtails (soil-dwelling, low-mobility). The effect size for springtails was significantly larger than the effect size for annelids or snails. All three groups are only weakly able to control water loss through their integument. Urbanization increases evapotranspiration and dries the soil (unless irrigated), so species sensitive to dry environments or fluctuations in water content (environment dries because of urbanization, or dries between irrigations) may disappear from cities. There are many springtail species of low mobility, which can increase the negative effect on the species richness of this group. Both annelids and springtails (both soil-dwelling) are sensitive to soil compaction, which is greatly increased with urbanization (Mody et al., 2020; Xie et al., 2018). Even though urbanization reduces the species richness of springtails, it can lead to a species-poor but more resistant community (Rzeszowski and Sterzyńska, 2016). Finally, gastropods are sensitive to disturbance and with increasing urbanization, the increasing disturbance could decrease their species richness (Hodges and McKinney, 2018).

We did not find a significant effect of urbanization on nematodes, carabids and mites. In the case of nematodes, we found only a few studies with sufficient spatial replication. Therefore, it is too early to draw conclusions about the effects of urbanization on nematodes. In the case of mites, the mean effect size on species richness was negative, comparable to the effect size on gastropods. However, the confidence intervals included zero, meaning a non-significant effect. This can be due to the few (nine) publications. Mites are difficult to identify, which could be the reason of fewer data on species richness than on abundance. The more mobile mites (phoretic mites, e.g. Binns (1982)) could survive in an urban environment as they can easily move between patches. The sedentary specialists are prone to local extinction because of vulnerability to changes in their patch of residence. In contrast, data about carabids are numerous, yet we found no significant effect. The explanation could be that carabids are the most researched group among the soil invertebrate taxa. Therefore, different climatic effects could act on them in different directions, resulting in a total effect size not different from zero. In addition, local effects are often more powerful than urbanization, preventing a homogenizing effect (Magura et al., 2010). On the other hand, different carabid sub-assemblages react differently to urbanization (Magura et al., 2020), which will also mask the summary effect size. For example, a strong increase in species richness and abundance is possible for open-habitat preferring species, while the abundance of forest species decreases (Gagné and Fahrig, 2011). It is also possible that there are some non-linear reactions in the case of carabids, which is hard to capture in a summary analysis. For example, in Sfântu Gheorghe (Romania), Tóthmérész et al. (2011) found the highest carabid species richness and abundance in the suburban areas. However, the dataset is not suitable for the study of gradient length and non-linearities, which needs further research.

In the case of climate parameters, temperature and UHI had no effect, most probably because soil can buffer temperature changes (Lal, 2002), and animals are adapted to the local climatic conditions. However, the amount of annual precipitation strongly modified the effect of urbanization. Dry regions showed a positive urbanization effect on soil invertebrate abundance, most probably because in drier regions, green infrastructure is regularly irrigated (Ge et al., 2019; Trammell et al., 2017). In these regions, abundance can increase in response to irrigation, even though these increases could be caused by non-native species, which in turn also contributes to biotic homogenization in urban areas (Ge et al., 2019; McKinney, 2006). Our results are in line with the findings of Chamberlain et al. (2020), who showed that a higher socioeconomic status of urban areas (where water is available) was associated with higher biodiversity, and this was especially pronounced in drier climates where water is a limited resource. In contrast, urbanization had a pronounced negative effect in areas with higher precipitation, where the biota is adapted to high soil water content. The mechanism behind the negative effect could be that extensive sealed areas also associated with the UHI effect, increased water runoff and reduced water infiltration due to soil compaction resulting in drier soils compared to the surrounding area (Burian and Pomeroy, 2010; Pouyat et al., 2010). However, we have to emphasize that soil invertebrates were rarely studied in wet areas (e.g. some parts of USA, South Korea, Japan, and China). Hence, we call for more studies from the tropics and other wet areas.

The human population size of the studied cities did not modify the effects of urbanization. The density of human population around the sampling sites can be important. This strongly correlates with traffic and building density but not necessarily with the overall size of the city, and it is used to describe the level of urbanization in some studies (Barbosa et al., 2010; Concepción et al., 2016). Barbosa et al. (2010) found that the population of the Italian provinces had an opposing effect on widespread vs. endemic species. The species richness of widespread species was higher in regions with higher populations while the species richness of endemic species decreased. Such an effect also could be the reason that we did not find a modifying effect of city size characterized by the number of inhabitants.

Decomposition is one of the main services provided by soil invertebrates that is driven by litter composition and the composition of the decomposer community (Meyer et al., 2020). Urbanization can transform invertebrate communities by increasing the abundance of some groups, decreasing the species richness of other groups or changing litter quality (Meyer et al., 2020; Nikula et al., 2010; Tresch et al., 2019). For fast and effective decomposition, not only the abundance but also the diversity and species richness of decomposers is important (Meyer et al., 2020; Tresch et al., 2019). Soil invertebrates also act as biological control agents (Kromp, 1999; Lal, 2002). Therefore, it is worth keeping the urban soil friendly by protecting it from compaction, pollution and overheating.

5. Conclusion

Our results supported the hypothesis that urbanization generally increases the abundance of some soil-living organisms but decreases their species richness. Low mobility and soil-dwelling invertebrates are disadvantaged by urbanization with substantial differences between taxonomic groups. However, to achieve a more holistic picture, more data are necessary on the effects of urbanization on less studied soil invertebrates such as springtails, mites, annelids, snails, myriapods and especially nematodes (Guilland et al., 2018). Moreover, most of the current data originate from Europe, and are virtually lacking from South America, Africa, and Australia.

We showed that climate strongly modified the effects of urbanization, therefore, it is important to consider the location and climate of the given study during the interpretation of research data. Climate change amplifies extreme weather conditions, like longer drought periods or very intense rainfalls. Therefore, making urban climates less divergent from their surroundings could be very important to maintain regional biodiversity, and abundance (van den Bosch and Nieuwenhuijsen, 2016). Finally, soil should also be protected from compaction and pollution to preserve soil biodiversity.

CRediT authorship contribution statement

Borbála Szabó: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing - Original draft preparation; **Dávid Korányi**: Validation, Writing - Reviewing and editing; **Róbert Gallé**: Validation, Writing - Reviewing and editing; **Gábor L. Lövei**: Validation, Writing - Reviewing and editing; **Gábor Bakonyi**: Validation, Writing - Reviewing and editing; **Péter Batáry**: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing - Reviewing and editing.

Data availability

The data is available at Zenodo Datarepository (https://zenodo.org/record/7322747#.Y3NbFJrMKUk).

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.

Acknowledgement

We thank Riho Marja for his valuable comments on statistics, Daisy Cárate for help with the plotting and Nikolett Gallé-Szpisjak for graphical enhancement of the figures. The authors acknowledge the support provided by the Hungarian National Research and Development and Innovation Office (NKFIH KKP 133839).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160145.

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