



Urban earthworm communities driven more by climate and elevation than urbanisation intensity

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Abstract

Soil biodiversity, particularly earthworms, plays a crucial role in ecosystem functions and services but remains largely understudied in urban environments. In this context, we conducted a synthesis analysis of 41 studies from urban environments (726 records, 1995–2024) to (1) describe patterns of earthworm communities, (2) identify the main drivers shaping urban earthworm communities, focusing on the effects of climate, degree of urbanization, soil properties, and local land use, with the expectation that climate would be the strongest driver, and (3) assess the occurrence of exotic earthworm species. Urban earthworm communities showed considerable variation in their abundance, biomass and species richness. Within our dataset, exotic species were detected in North America, South America, and Asia, but no records from European and African cities, despite their known presence there. However, there was a strong geographical bias, with 75% of records from Europe. Our results reveal that at the global scale, elevation, and annual variation in temperature and potential evapotranspiration are the most important predictors shaping total earthworm abundance. For total earthworm biomass, variation in potential evapotranspiration is the key predictor. At the plot scale, we found both positive and negative correlations between earthworm community metrics, soil properties, and specific land uses, namely urban forests and grasslands. We recommend additional standardised sampling, broader geographical and temporal coverage, and the investigation of urban-specific direct and indirect stressors, as crucial steps for understanding urban soil biodiversity and promoting beneficial management practices. Overall, this analysis indicates that urbanisation intensity showed no consistent effects on earthworm communities once climate and soil variables were accounted for. Given the importance of climate impacts, mitigation of climate change effects would be valuable for the maintenance of earthworm communities.

Keywords Oligochaeta · Urban ecology · Soil · Climate change · Bio-indicator · Occurrence · Diversity

Introduction

More than half of the world's population lives in cities, and the urban population is expected to double by 2050 (Angel et al. 2011), driving the expansion of urban environments often at the expense of rural areas. Here, we define 'urban environments' as ecosystems shaped by built infrastructure and high human population density occurring within an urbanisation intensity gradient, such as an urban-rural gradient. The increase in built infrastructure results in

fragmentation of the natural habitats and diversification of habitat types and land uses (Grimm et al. 2008). But there are also similar impacts belowground; native soil is often dramatically reduced, fragmented and compacted due to increasing impervious sealing compared to natural and agricultural areas (Botkin and Beveridge 1997; De Carvalho and Szlafsztein 2019; Gong et al. 2020). However, soil biodiversity plays a crucial role in supporting key ecosystem functions and sustaining Nature's Contributions to People (Schwarz et al. 2017; Weiskopf et al. 2024; Ziter 2016). Yet,

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the biodiversity of urban soils and the ecosystem services they provide remain largely understudied (Beninde et al. 2015; Guillard et al. 2018; Weiskopf et al. 2024), particularly for key organisms such as earthworms.

Studies on earthworm communities have reported positive, neutral, or negative effects of urban environments (Guillard et al. 2018; Schmidt 2024). For example, Pižl and Josens (1995a) observed decreasing earthworm biomass with increasing urbanisation intensity in Brussels, whereas Steinberg et al. (1997) reported higher earthworm abundance and biomass in urban areas than in rural forest stands in New York City. Pelosi et al. (2021) and Xie et al. (2022) found no significant effect of urbanisation intensity, near Paris and in Beijing respectively. While many studies have focused on abundance and biomass of earthworm communities, understanding the identity of the species within the local communities, as well as the species pool, (Aronson et al. 2016) is important to uncover shifts in community composition which can be hidden by aggregate metrics. Both the local earthworm community and regional species pool may include native and introduced species (Aronson et al. 2016; Francis and Chadwick 2015; Tóth et al. 2020). Given the poor dispersal capabilities of most earthworm species, urbanisation, and the associated impacts, may make native species particularly vulnerable to local extinction (Maréchal et al. 2021; Xie et al. 2018), whilst adaptations to harsh environments and human-aided dispersal mechanisms found in many wide-ranging exotic earthworm species (Baumann et al. 2024) may result in their dominance across urban habitats. There is a clear need for a synthesis of available data to ascertain generalities of the impacts on earthworm communities of increasing urbanisation across a range of soils, habitats, countries and climatic conditions.

Across the globe, urban environments are placed within different contexts and experience a variety of different drivers, some of which can have contrasting impact on earthworm communities. For example, the omnipresent concrete results in a higher soil pH which can benefit earthworms, but soil compaction from the construction machinery may increase bulk density reducing earthworm abundance and biomass (Smetak et al. 2007). The effect of other management practices found in urban environments, such as irrigation, fertilization and mowing, on earthworm communities are less well known. One recent study found that management practices (mowing, irrigation, mulching and weed removal) had minimal influence on the earthworm communities (Eydoux et al. 2024). However, in non-urban landscapes, management practices that increase soil carbon (e.g., mulching, organic fertilizers), increase water availability (e.g., irrigation) and avoid pesticides (e.g., manual weed removal) have positive effects on earthworms (Lee 1985; Torppa et al. 2024). Additionally, local socioeconomic and

cultural factors influence present and past human activities such as cultivation, recreation, and ornamental landscaping which, in turn, shape soil properties and earthworm species pool (Aronson et al. 2016; Guillard et al. 2018). The diverse soils and land uses, ranging from relatively undisturbed sites (e.g., old parks, remnant patches of semi-natural vegetation) to highly modified environments (e.g., compacted or more polluted areas), provides heterogeneous and diversified habitat conditions for earthworms, leading to contrasting patterns of population abundance and assemblage diversity (Schmidt 2024; Tóth et al. 2020; Xie et al. 2022). For instance, high abundance and diversity have been observed in small urban gardens and grass strips functioning as refuges (Maréchal et al. 2021; Pižl and Josens 1995a), whereas severe soil disturbance in residential areas may lead to lower earthworm populations despite the presence of green spaces (Li et al. 2020; Steinberg et al. 1997).

Previous large-scale studies have shown that climate is a prominent driver in shaping earthworm communities (Phillips et al. 2019; Rutgers et al. 2016). It is well established that urban areas, and the soil within them, experience shifts in climates, specifically higher temperatures and changes in precipitation regimes (Grimm et al. 2008; Shi et al. 2012). And while small increases in temperature may be beneficial to earthworm communities in regions with lower average temperatures and sufficient precipitation, it is unlikely to be beneficial if the temperature exceeds the species' thermal limits or if precipitation is reduced (Singh et al. 2019). Therefore, impacts of urbanisation on earthworm communities will likely also depend on the climatic environment.

Overall, there is a lack of clear, generalisable trends regarding urban earthworm communities. A comprehensive synthesis of urban earthworm studies worldwide is needed to identify common patterns and key environmental drivers. In this context, the systematic literature review presented here aims at synthesising cross-continental data on earthworm communities in urban environments, including their abundance, biomass, species richness, ecological categories and the dominance of native species. Quantifying, for the first time, the relative contribution of climate, topography, soil and urbanisation drivers to shaping earthworm communities. The main goal is to investigate the primary drivers structuring these communities, following the hypotheses that: (1) earthworm communities in cities are primarily influenced by the climate of where the city is located, and furthermore by soil and land use characteristics, and position along an urbanisation gradient and (2) earthworm communities in cities are dominated by exotic species as a result of introductions through human activities. These results will provide bases for effective management practices to maintain or promote beneficial earthworm communities.

Materials and methods

Literature search

A systematic literature review was conducted in December 2024 to find publications reporting original sampling data of earthworms in urban environments. This literature review was carried out querying ISI Web of Knowledge, using the “All Databases” option, applying the following search string: (*earthworm**) in the ‘topic’ field and (*urban* OR town* OR cities OR city OR agglomerat* OR conurbat* OR garden* OR park* OR avenue* OR allotment* OR road* OR highway* OR embankment* OR lawn* OR roof* OR wasteland* OR industr* OR technosol* OR anthrosol* OR brownfield* OR landfill* OR dump* OR metropolit* OR turf* OR golf* OR sward* OR greenspace* OR playing OR graveyard* OR cemetery**) in the ‘title’ field. This search returned 350 references, from which all the titles and abstracts were read to select papers potentially containing original field data on earthworms in urban environments. This screening of titles and abstracts resulted in 90 seemingly suitable articles (See PRISMA Diagram Fig. 1).

The full text of the resulting 90 articles was checked in more detail, and preselected for data extraction if they contained the following information:

1. Original data on at least one of the three earthworm community response variables (abundance, biomass, species richness) from multiple sites across an urban environment.
2. geographical coordinates or detailed info that allowed georeferencing of the study location.
3. the sampling protocol, including the sample area, land use and land cover information.

When the article appeared relevant for the review but some of the data was lacking, the authors were contacted by email and asked to send their original data (on earthworm abundance, biomass, species diversity, soil properties, coordinates, etc.) for each sampling site. Supplied data were incorporated into the database. Following screening of the full text and extraction of appropriate data (see Sect. ‘[Data from a set of selected papers](#)’), the full corpus for data extraction contained 41 studies (Fig. 1), including studies focused only on urban areas or incorporating an urban-rural gradient. In cases where multiple earthworm sampling time records were available on the same site, only the most suitable time record was retained, e.g., fall or spring in temperate regions, minimising temporal pseudo-replication. The full list of references for the 41 selected articles is given in Table S1.

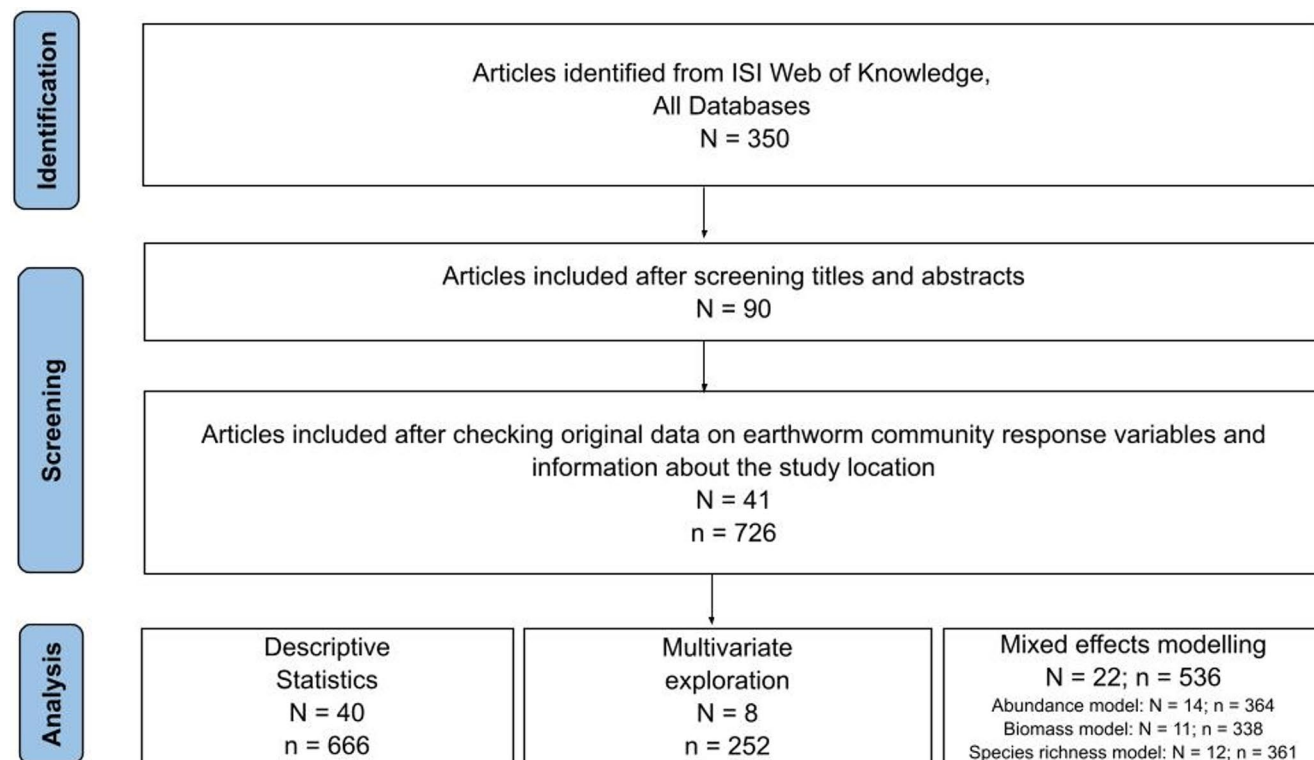


Fig. 1 PRISMA Flow Diagram for the literature search and the synthesis analysis on urban earthworms. N and n represent the number of articles and records, respectively

Data gathering

Data from a set of selected papers

From the 41 selected studies, the following information was gathered:

- Metadata: Author, year of publication, year of field sampling, sampling period, extraction method, and hierarchical level of aggregation (subplot, plot, site).
- Location: Coordinates in decimal degrees (latitude, longitude), quality of the georeferencing (3 classes: coordinates reported by the study, coordinates derived from maps based on toponyms provided by the authors or assigned to one of several aggregated sites within the studied urban area). Additionally, we included information on the site's classification as urban, peri-urban, or rural, either reported by the authors or inferred using the coordinates.
- Land use and land cover: Local land cover and use intensity from information provided by the authors (9 classes: arable high intensity, arable medium intensity, grass high intensity, grass medium intensity, grass low intensity, lawn, ruderal, trees managed, and trees unmanaged). Land-use intensity was classified based on reported management practices using the following criteria: Low=no biocide use, no artificial fertilizer, and no soil disturbance, and for grasslands a maximum of 1–2 mowing interventions per year; Medium=no biocide use, low fertilizer application, and no soil disturbance, or for grasslands frequent mowing; High=intensive and/or frequent physical interventions (e.g., soil work) and/or chemical interventions. Corine land cover class derived from geodata using the coordinates (3 aggregated classes: 100=urban fabric, 200=agricultural areas, 300=forests and semi-natural areas).
- Earthworm data: Total abundance (individuals per m²), biomass (grams per m²) and species richness (number, not corrected for sampling plot size). Where abundance and biomass were not provided per m², these values were converted based on the sampling area. Species richness was calculated when not directly reported, based on species presence. Where possible, abundance and biomass were also categorized by ecological category (anecic, endogeic, epigeic; explained below), based on species-level data from Bouché (1972) and the sWorm database (Phillips et al. 2021).
- Soil data: Soil texture (percentages of sand, silt, and clay), pH (in H₂O), and soil organic matter content (in %). When reported pH was measured in a different solution, values were converted to pH_{H₂O} (see Table S2).

Whilst other soil variables were also captured when present, data was rarely available.

Historically, earthworms have been divided into three main ecological categories (Bouché 1972): epigeics, endogeics and anecics. Epigeic earthworms live on the soil surface, ingest decaying organic matter and do not create deep or permanent burrows. Endogeic earthworms live mainly within the first 20 cm of the soil and feed on organic matter by ingesting the soil creating horizontal burrows. Finally, anecic earthworms create deep vertical burrows and ingest decaying organic matter at the soil surface. All three ecological categories contribute significantly to soil health and ecosystem services (Blouin et al. 2013; Le Bayon et al. 2021), even in urban landscapes and other ecosystems (Steinberg et al. 1997). However, according to their preferential habitats and behaviour, they may be differentially affected by disturbances occurring in urban environments, potentially because of their differing dispersal abilities (Caro et al. 2013).

Additional information on all variables and how they were derived from the selected articles are presented in Table S2. Following extraction of data, 726 records were obtained from the 41 studies, where a record is a single observation of the earthworm community (e.g., abundance, biomass, richness) at the sub-plot, plot or site level, depending on the sampling design of the original study. The extracted data are available in Table S1.

Data from other sources

The dataset was completed with the following geo-data from external sources based on the coordinates of the sampling sites:

- climate data: mean and standard deviation (SD) of annual temperature, annual precipitation, annual potential evapotranspiration ('PET'). Mean and standard deviations were calculated for the months within the year of sampling (Fig. S1). Additionally, the Global Aridity Index and Köppen climate classification were added (Table S3).
- topographic data: elevation (m above sea level), topographic index (the tendency for the soil to become saturated with water based on topographic position), and landform (a classification system based on the slope gradient, slope convexity and surface texture).
- urbanisation metrics: human population density ('HPD'; humans/km²), proportion of urban land use within one km² ('Urban 1km²'), road density (m/km²), distance to urban core (m), and size of the urban centre (km²). The impact of the urban core on surrounding ecosystems

is dependent on a variety of factors, including the size of the urban core (Alberti 2008). We expect that at the same distance, a larger urban core will result in larger negative impacts on biodiversity than smaller urban cores. Therefore, the ratio of these two variables was calculated ('Dist: Urban area ratio'), to maintain the interaction between these two variables. Where a ratio of < 1 indicates the site is outside the urban centre, and > 1 indicates it is within the urban core, with the highest ratios indicating a larger urban centre and/or less distance to the centre of the core.

Detailed information about the variables, data sources, how they were derived, and their units are presented in Table S4. Prior to all analysis, all continuous predictor variables (climate variables, urbanisation variables, topography variables and soil properties) were standardised to ensure comparability and improve model fit. Standardisation was performed by centring (subtracting the mean) and scaling (dividing by the standard deviation), which allows each variable to contribute equally to the analysis regardless of its unit or magnitude.

Data analysis

All data analysis was conducted in R version 4.4.0 (R Core Team 2024).

The completeness of the data varied across studies, particularly with regards to sampled soil properties, leading us to conduct analyses on different subsets of the database. In brief, first, a descriptive analysis of earthworm communities and related soil properties in urban environments was performed (described in 'Descriptive analysis'; Fig. 1). Second, a multivariate exploration was carried out using a co-inertia analysis to assess the co-structure between environmental variables (soil properties, land cover, land use intensity) and earthworm community metrics. This analysis was performed on a subset of records for which all these variables were simultaneously available from the original studies (described in 'Co-inertia analysis of environmental variables and earthworm community metrics'; Fig. 1). Finally, we developed regression models incorporating additional geospatial data on urbanisation, climate, soil pH and topography. For this, we used a subset of records containing earthworm community data, land cover, soil pH, and geographical coordinates (described in 'Mixed effects modelling'; Fig. 1).

Descriptive analysis

To characterise earthworm communities and soil properties in urban environments, we calculated mean, median,

standard deviation, and range for earthworm and soil variables. For earthworm communities, these variables were total abundance, abundance by ecological category, total biomass, biomass by ecological category, and total species richness. When available, we also gathered and analysed data on species' abundances. For soil properties, these included soil pH, soil texture (silt, clay and sand) and soil organic matter. We restricted our analysis to urban and peri-urban sites, excluding rural sites ($n=60$) for this descriptive analysis, which resulted in a dataset of 40 articles and 666 records (Fig. 1). Analyses were conducted for each variable based on data availability across all studies.

Co-inertia analysis of environmental variables and earthworm community metrics

A co-inertia analysis was performed to explore the co-structure between soil properties, land cover and land use intensity, and earthworm community metrics. To ensure a robust analysis, we kept variables whose combinations, after excluding missing values, allowed us to perform an analysis on a maximum number of records across the largest possible number of articles. Environmental variables included soil properties (pH, organic matter content, sand and clay), Corinne land cover, and land use intensity. Due to uneven representation, some land use intensity categories were merged (e.g., low and medium grass intensity; managed and unmanaged trees), resulting in five final categories out of the original nine (see Table S2). The community variables included total earthworm richness and total abundance, which were not highly correlated ($R^2=0.5$). This selection resulted in a total of 252 records across 8 articles (Amossé et al. 2016; Maréchal et al. 2021, 2024; Pelosi et al. 2021; Tiho and Josens 2000; Tresch et al. 2019; Vergnes et al. 2017; Xie et al. 2018) (Fig. 1). Including total biomass or ecological category abundances would have further reduced the dataset to only 3 articles and 192 records, which was not considered sufficiently representative. A co-inertia analysis was then conducted to assess the co-structure between these community and environmental variables. Statistical significance was tested using a Monte Carlo permutation test with 999 repetitions. All analyses were performed using the *ade4* package in R (Dray and Dufour 2007; Thioulouse et al. 2018).

Mixed effects modelling

To understand in more detail how urbanisation, climate, land cover and land use intensity, as well as the environment topography influenced earthworm communities, generalised linear mixed effects regression models were created. To be

suitable for the statistical model, the data had to meet the following criteria:

- Within each study, the sampling methodology needed to be uniform. There was one study where sampling methodology varied (as sites were located across multiple countries; Tóth et al. 2020), therefore this publication was considered as 4 studies, with each study including the records from one country.
- Studies needed to have coordinates at sampling site level, not aggregated at the study level. Studies with aggregated coordinates only were excluded from the analysis, unless the coordinates at the site level could be derived from mentioned toponyms or unless the authors provided them after email correspondence.
- Within each study, sites needed to span more than one km. Studies were excluded if all sites were clustered within less than one km of each other. This condition is due to geographically close sites having identical geodata (urbanisation, climate, and topographical data), preventing variation with nearly all predictor variables in the mixed effects model.
- For each model, all predictor variables were checked to ensure representativity. For categorical predictors, each category needed to have an adequate number of records. Underrepresented categories, and the associated records, were removed from the model's dataset. Where values were missing (NAs) from global data layers, these records were also removed.
- Sites that reported extreme values in urbanisation metrics (road density > 20,000 m/km², $n=4$; HPD > 40000 humans/km², $n=3$; dist: urban area ratio > 20, $n=5$), earthworm abundances (> 700 ind/m², $n=2$) or biomasses (> 300 g/m², $n=5$) were removed, as they were considered statistical outliers and decreased model robustness. These cut-offs were determined based on the distribution of the data.
- Sites needed to have measured soil pH. Sites with no information on soil pH were removed. While the dataset contained other soil property data (e.g., organic matter), these variables were not well represented across the sites and their inclusion would have resulted in too small datasets for modelling.
- For the species richness model, the number of replicates per site needed to be identical within each study (sampled area is already consistent within a study, due to consistent methodology) to help control for the non-linear relationship between species richness and sampling intensity.

Subsetting the database to ensure all data were suitable for the mixed effects modelling resulted in 536 records from 22

articles. As not all records included earthworm abundance, biomass and richness, the dataset was further split into subsets to build three separate models (Fig. 1). For each of the three community metrics (total abundance, total biomass, species richness), a mixed effects model was constructed. In the 'full model' for each community metric, the fixed effects included the four urbanisation metrics (dist: urban area ratio, road density, HPD and Urban 1 km), 8 climate variables (mean and SD of annual temperature, precipitation, and PET, as well as the aridity index and Köppen classification), two land cover and use intensity variables (CLC level 1 and local land use intensity), and four variables related to the physical soil environment (soil pH, topographic index, elevation, and landform) (Table S2). All continuous variables were in their scaled and centred form to aid model fitting. Due to the limited number of data points (Fig. 1) no interactions were considered within the model. To account for the heterogeneity across different studies (as different methodologies were used across all the studies), a random intercept was included for each study.

The abundance and biomass model used a 'tweedie' distribution (using the 'glmmTMB' function from the glmmTMB package; Brooks et al. 2017), and the species richness model was modelled with Poisson distribution (using the 'glmer' function from the lme4 package; Bates et al. 2015).

Multicollinearity between variables in the full model was checked based on variance inflation factors (VIFs), using the 'check_collinearity' function from the 'performance' package (Lüdtke et al. 2021). Variables were removed, starting with variables with the highest VIFs, until the remaining variables had VIFs < 10. However, in the biomass and species richness model, removing the variables with the highest VIFs resulted in the remaining variables having VIFs < 5. Following removal of the multicollinear variables, the residuals were checked to ensure all model assumptions were met using the DHARMA package (Hartig 2024).

All possible models were then constructed using the remaining predictor variables as described previously, using the 'dredge' function from the MuMIn package (Barton 2024). From all possible models only the top subset of models were used for the model averaging, those with deltaAICc of < 2. The importance of all predictor variables in the subset of models was calculated based on the cumulative AICs weights ('sw' function in the MuMIn package). Model estimates and predictions based on the average models were calculated based on the 'full' coefficients, also referred to as the zero method (Burnham and Anderson 2002), where, if a parameter is absent from a model in the subset, a zero is substituted before calculation of the parameter estimate is obtained by averaging over all models in the model subset. This results in a more conservative estimate of the coefficient

but is recommended when determining the strength of different predictors (Nakagawa and Freckleton 2011). Prediction abilities of the averaged model were evaluated using the root mean square errors (RMSE), using the models to predict the original dataset. RMSE are easily interpretable as they are on the same scale as the original data. Goodness of fit of the top subset of models was assessed using the conditional- R^2 (the variance explained by both the random and fixed effects) using the 'r.squaredGLMM' function in the MuMin package. For the species richness models, the trigamma method is reported (Nakagawa et al. 2017).

Results

Status of urban earthworm studies

The studied articles dated from the period 1995 to 2024, with most articles (54%) of our dataset published in the last 15 years (Table S1). Different methods were used to sample earthworm communities in urban areas, including chemical extraction (19% of the articles), hand-sorting combined with chemical extraction (22%), hand-sorting only (37%), and electrical extraction (22%). Most records are concentrated in Europe (542 records, with 52% in 11 articles from France and Switzerland), with fewer in North America (36 records; 5 articles) and Asia (58 records; 3 articles), while South America and Africa were underrepresented, with only 27 (in 3 articles) and 3 (in one article) records, respectively

(Fig. 2). Most articles focus exclusively on urban records (81%), although several explored a rural-urban gradient (Hubert et al. 2011; Pelosi et al. 2021; Steinberg et al. 1997), while others incorporated rural records as controls (Francini et al. 2018; Richardson 2019; Szlavecz et al. 2006; Tóth et al. 2020). Some articles contributed prominently to the dataset, in particular Tresch et al. (2019) accounting for 22%, with Francini et al. (2018) and Audusseau et al. (2020) each accounting for 12% of the total number of records. Among the 726 records, 47% (7 articles) are reported at the individual replicate level, 45% are aggregated at the site level (25 articles), and 8% represent averages across different sites but within the same land use or habitat type (9 articles; Table S1).

Earthworm occurrence and diversity metrics in urban environments

Total earthworm abundance in urban areas ranged from 0 to 1,177.8 ind/m², with an average of 148.6 ind/m² (SD=152.3) across 502 records (Table 1). When focusing on ecological categories, endogeic earthworms were the most abundant group, accounting for 66% of the total abundance, with an average of 56.5 ind/m² (SD=83.0), followed by anecics accounting for 23% of the abundance (mean=19.6, SD=27.2) and epigeics accounting for 11% of the abundance (mean=9.8, SD=23.1, Table 1). Total earthworm biomass in cities ranged from 0 to 608.9 g/m², with a mean of 575.6 g/m² (SD=81.9) over 427 records.

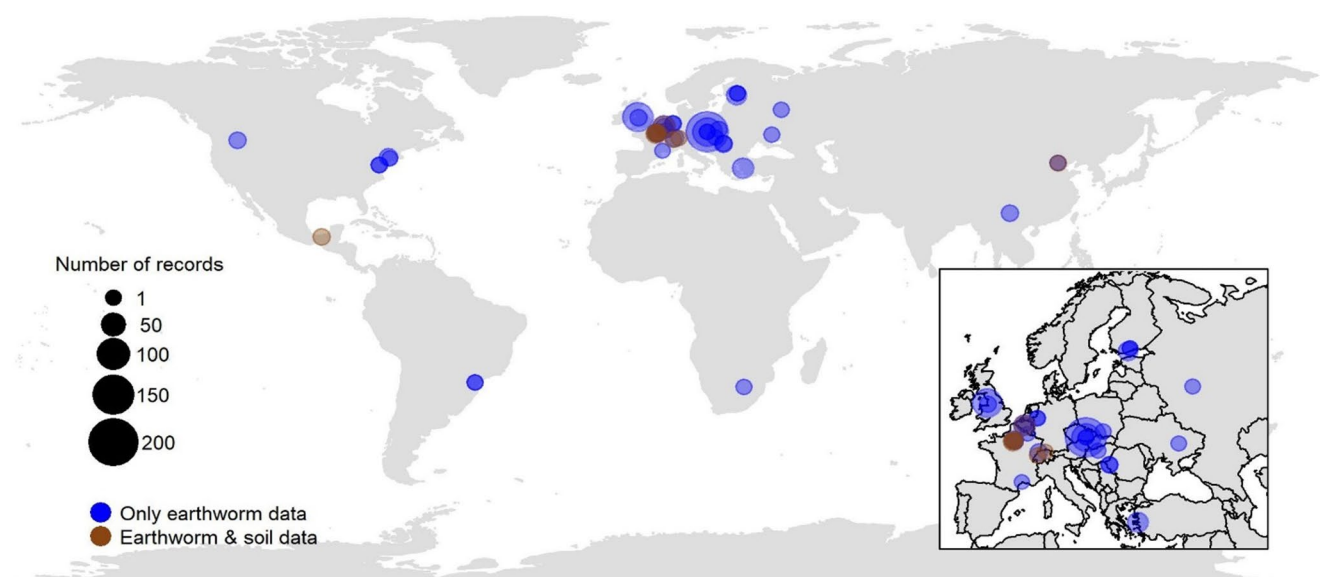


Fig. 2 Central locations of the selected studies reporting urban earthworm communities (with detailed European map inserted), dot size is continuous, and is proportional to the number of records in the study. Blue points indicate records with earthworm community data only

($N=37$ articles), while brown points represent sites with both earthworm and soil data [soil texture, soil pH and organic matter] ($N=28$ articles). Dot transparency is to aid in visibility, as some studies are closely-located

Table 1 Summary statistics of total earthworm abundance (ind/m²), biomass (g/m²), ecological categories (epigeic, anecic, endogeic), and species richness in urban environments. The table includes median (Median), mean (Mean), standard deviation (SD), minimum (Min), maximum (Max), the number of records (n), and the number of articles (N)

	Median	Mean	SD	Min	Max	n	N
Total abundance	103.7	148.6	152.3	0	1177.8	502	30
Epigeic abundance	0	9.8	23.1	0	173.8	377	17
Anecic abundance	11.1	19.5	27.2	0	188.9	377	17
Endogeic abundance	28.0	56.5	83.0	0	611.1	377	17
Total biomass	50.7	75.6	81.9	0	608.9	427	23
Epigeic biomass	0	1.5	5.9	0	53.1	258	5
Anecic biomass	56.1	68.5	66.4	0	533.3	258	5
Endogeic biomass	16.7	26.6	31.2	0	170.0	258	5
Species richness	3.0	3.4	2.1	0	12	500	26

Table 2 Summary statistics of soil pH, organic matter (%), silt (%), clay (%) and sand (%). The table includes median (Median), mean (Mean), standard deviation (SD), minimum (Min), maximum (Max), the number of records (n), and the number of articles (N)

	Median	Mean	SD	Min	Max	n	N
pH	7.2	7.0	1.1	3.1	8.8	504	26
Organic matter (%)	7.0	7.4	4.4	<0.1	34.9	447	22
Silt (%)	34.8	39.3	15.2	7.8	86.5	258	9
Clay (%)	21.1	19.9	9.6	1.1	49.5	258	9
Sand (%)	41.1	40.4	14.4	4.3	85.0	258	9

Anecic earthworms accounted for 70.9% of the biomass, with an average biomass of 68.5 g/m² (SD=66.4), followed by endogeics (mean=26.6 g/m², SD=31.2) and epigeics (mean=1.5 g/m², SD=5.9, Table 1). After removing 34 records that represented site averages, earthworm species richness at a site in urban environments ranged from 0 to 12 species, with a mean of 3.4 species (SD=2.1) across 500 records (Table 1).

Of the 423 records with information at the species level, a total of 50 earthworm species were recorded, along with 5 subspecies and 7 undetermined genera or species (Table S1). The species with the highest occurrence were *Aporrectodea rosea* (endogeic, 42%), *Allolobophora chlorotica* (endogeic, 40% of records), *Lumbricus terrestris* (anecic, 39%), *Aporrectodea caliginosa* (endogeic, 35%), and *Aporrectodea longa* (anecic, 33%). In North American cities, two exotic species were recorded in the United States (*Amyntas agrestis* and *Metaphire hilgendorfi*); at the sites where they were observed, they constituted the entire recorded earthworm community. In South American cities, 8 exotic species were found in Curitiba, Brazil, belonging to the genera *Amyntas*, *Aporrectodea*, *Dichogaster*, *Lumbricus*, *Metaphire* and *Pontoscolex* outnumbering the five native species recorded based on presence/absence data. In Asian cities, four exotic species were recorded: one in Beijing, China (*Bimastos parvus*), where it accounted for less than 15% of the earthworm community on average across 16 records, and three in Izmir, Turkey (*Allolobophora chlorotica*, *Aporrectodea caliginosa*, and *Dendrobaena veneta*) which together represented the entire earthworm communities where they were observed. No exotic species were recorded in African and European cities.

Soil properties derived from earthworm sampling showed that the mean soil pH 7.0 (SD=1.1, Table 2), although presence of some highly acidic sites resulted in a larger range of values (3.1 to 8.8). Soil texture variables exhibited substantial variation: sand content ranged from 4.3% to 85.0% (mean=40.4%, SD=14.4), silt from 7.8% to 86.5% (mean=39.3%, SD=15.2), and clay from 1.1% to 49.5% (mean=19.9%, SD=9.6, Table 2). Organic matter content varied from 0.005 to 34.9%, with a mean of 7.4% (SD=4.4, Table 2). A wide variety of soil types were present across the sites (Fig. S2).

Effect of environmental variables on earthworm communities

Soil properties and land use intensity

The co-inertia analysis revealed a significant relationship between the structure of environmental and earthworm community metric variables (p-value=0.001), with an RV coefficient of 0.13, indicating a loose co-structure between the two tables (Fig. 3). The first axis of the co-inertia analysis is driven by a gradient of organic matter content (0.43), clay (0.46), soil pH (−0.43), and high-intensity grassland (−0.47), with earthworm abundance (0.73) contributing most strongly to this axis particularly in relation to organic matter and clay content, and inversely with high-intensity grassland and pH (Fig. 3). The second captures a gradient mainly driven by forests cover (−0.69), with additional contributions from sand content (0.34) and low to medium intensity grassland (−0.34). Earthworm richness (−0.44) is

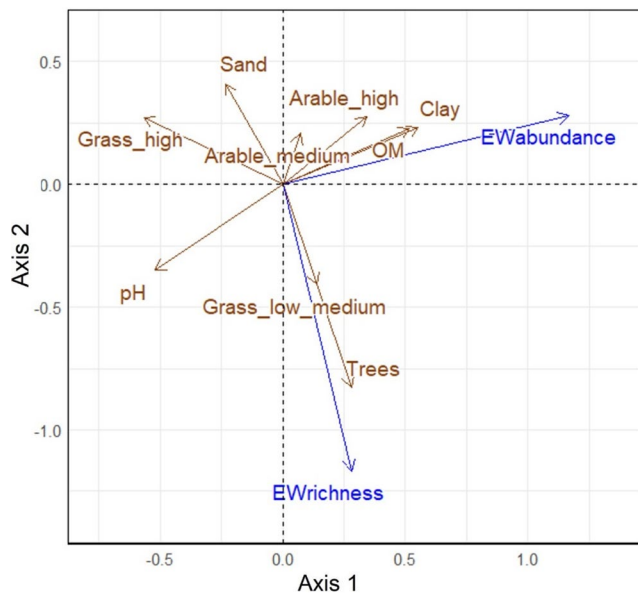


Fig. 3 Co-inertia analysis between environmental variables (brown) and earthworm variables (blue) on the first two principal axes

aligned with this axis, suggesting co-structure with sites characterized by forests and low to medium intensity grassland and an opposite trend to sandy soils (Fig. 3). In total, the two axes explained 98.7% of the variance.

Effects of environmental variables using measured variables and external geo-data

Across the 22 articles used in mixed effects modelling, the distance to a major urban core ranged from 0.10 to 112.5 km, with a mean of 18.8 km (SD=26.9). Human population density varied from 0 to 61,024 humans/km², with an average of 5,181 humans/km² (SD=7,921). Road density ranged from 0 to 131,050 m/km², with a mean of 7,596 m/km² (SD=8,859). The proportion of urban habitat within a 1-km grid ranged from 0 to 1, with a mean of 0.65 (SD=0.29). The majority of sites were within Europe (~79%), however this percentage varied within the subset of data used for the three different models.

Following the removal of collinear variables (Table 3), 65,536 models with total abundance as the response variable were created, out of which 13 with a deltaAICc < 2 (with weights varying from 0.51 to 0.06, and an average conditional-R² of 0.59; range: 0.57–0.61) were kept for the averaged model. The averaged model had a RMSE of 130.39; it contained 13 predictor variables, with the SD of the annual temperature, elevation and SD of the annual potential evapotranspiration (PET) jointly being the most important variables and with slopes significantly different from zero (Table 3; Fig. 4).

Table 3 Slope estimate, standard error (SE) and 95% confidence interval (95%CI) of the significant predictors resulting from the model averaging. Whilst the species richness model had the SD of the annual PET as the most important predictor, the slope was not significantly different from zero and therefore not presented here

	Estimate	SE	95%CI
Abundance Model			
Temperature (SD)	−0.51	0.14	−0.77; −0.24
Elevation	0.26	0.13	0.01; 0.51
PET (SD)	0.20	0.09	0.03; 0.38
Biomass Model			
PET (SD)	−0.32	0.13	−0.57; −0.07

Following removal of the collinear variables, 16,384 models were created to model earthworm biomass (Table 4). Thirty-five models of the full set had deltaAICc < 2, with weights ranging from 0.02 to 0.05 and an average conditional-R² of 0.64 (range: 0.55–0.73). The averaged model had 11 predictor variables, and a RMSE of 80.91, with SD of annual PET as the most important predictor variable with a slope significantly different from zero (Table 3; Fig. 5).

In total, 8,192 models were created to model changes in species richness, following removal of the collinear variables (Table 4). Among these 17 models with a deltaAICc lower than 2 were included in the subset of models, including 11 predictor variables with model weights ranging between 0.04 and 0.11 (and an average conditional-R² of 0.33 (range: 0.30–0.35)). The averaged model had an RMSE of 2.06. The most important variable was the SD of the annual temperature, but this did not have a slope that was significantly different from zero (estimate: −0.14; SE: 0.11; 95%CI: −0.36–0.07).

Discussion

Earthworm community patterns in urban environments are mainly shaped by climate and elevation

Mean urban earthworm abundance derived from this analysis (149 ind/m²) is within the range of 100 to 700 ind/m² reported for gardens in some major French cities (Guilland et al. 2018), and in UK urban areas (200 ind/m²; Burton et al. 2024). It also aligns with the predictions of Phillips et al. (2019), where global abundance values typically ranged from 5 to 150 ind/m². Our analysis revealed a mean species richness of 3.4 (range 0–12), which also falls within the range of 1 to 9.5 reported for urban environments by Guilland et al. (2018) and aligns with broader global trends of 1 to 4 species predicted by Phillips et al. (2019). Endogeic earthworms dominated urban communities, representing 66% of total abundance, followed by anecic (23%) and epigeic

Fig. 4 Prediction of how total abundance (ind/m²) varied with the (a) SD of the annual temperature, (b) elevation and (c) the SD of annual potential evapotranspiration PET (all three centred and scaled). Grey shading indicates the 95% Confidence Interval for the model prediction line. Predictions from the model are calculated when all other continuous variables are at their median value. Black dots are the data points ($n=356$ from 12 articles). All three variables were the most important within the model averaging framework, with slopes significantly different from zero, based on 95% CIs

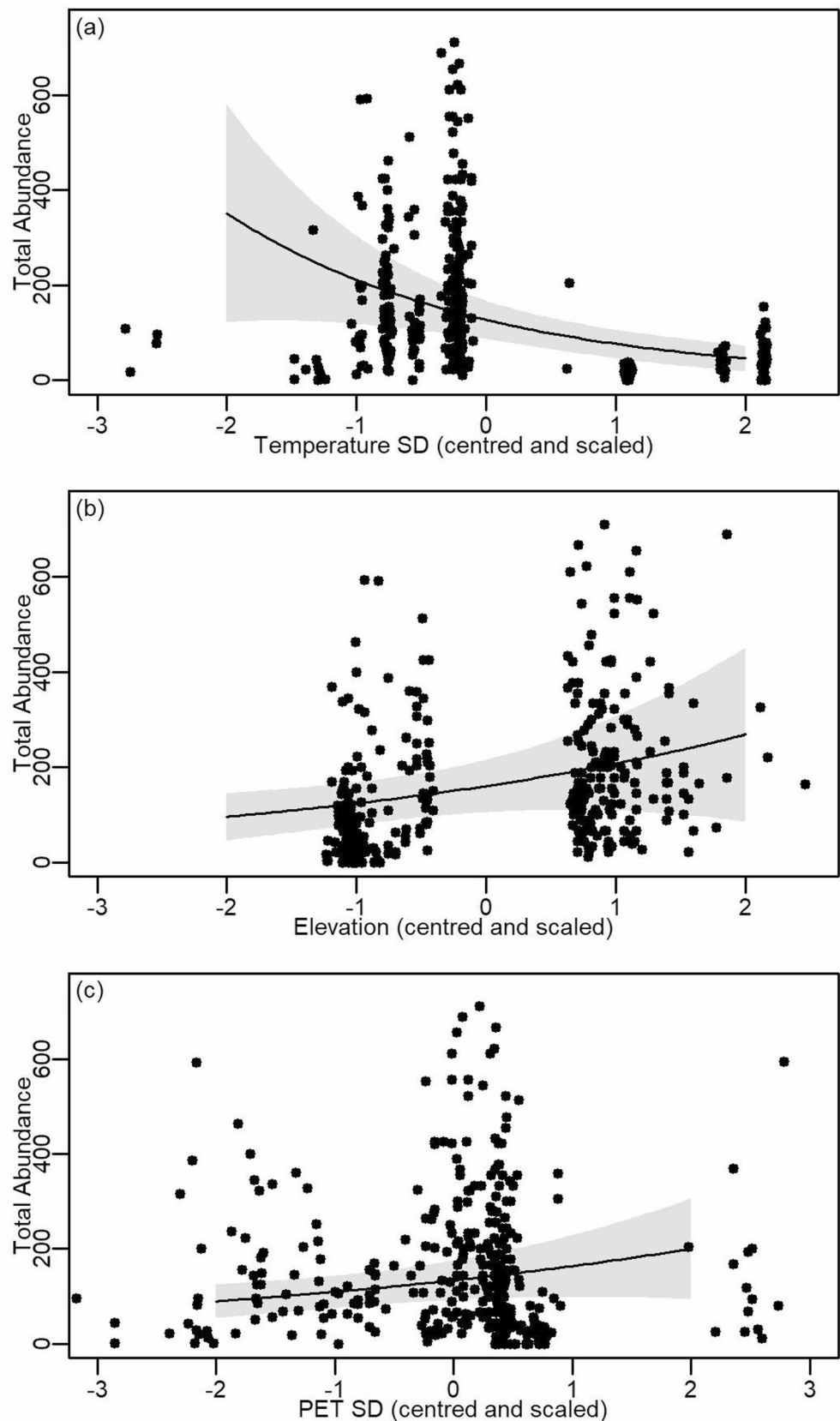


Table 4 Results from the model averaging approach. For each of the three models (abundance, biomass, and species richness), the status of each predictor variable is given. 'x' indicates that the variable was removed from the modelling process due to multicollinearity and '-' indicates that the variable was in the full suite of models, but was not included in the subset of models used for the averaged model. For the remaining variables, present in the averaged model, the ranked importance is given (1 = most important)

Model	URBANISATION					CLIMATE					USE OF LAND					SOIL/PHYSICAL PROPERTIES				
	Dist: Urban Area ratio	Road Density	HPD	Urban 1 km	PET (mean)	PET (SD)	Precipitation (mean)	Precipitation (SD)	Temperature (mean)	Temperature (SD)	Aridity	Köppen	CLC	Local Land	soil pH	Topographic Index	Elevation	Land form		
Abundance	9	11	13	12	4	1	5	7	8	1	x	x	-	-	10	6	1	-		
Biomass	11	9	-	-	6	1	4	5	x	7	10	x	3	x	2	-	8	x		
Richness	11	5	6	-	-	2	3	7	4	1	x	x	8	x	-	10	9	x		

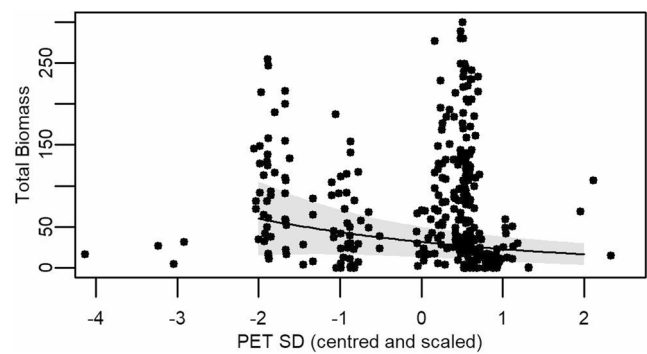


Fig. 5 Prediction of how total biomass (g/m^2) varies with the SD of the annual potential evapotranspiration (PET) (centred and scaled). Grey shading indicates the 95% Confidence Interval for the model prediction line. The prediction of the model is calculated when all other continuous variables are at their median value, and CLC is at "100" (artificial land covers). Black dots are the data points ($n=338$ from 11 articles). PET SD was the most important with the model averaging framework, with a slope significantly different from zero, based on 95% CIs

(11%). This functional composition, with a dominance of endogeic earthworms and smaller proportions of anecic and epigeic species, is similar to that observed in many agricultural and natural soils (Burton et al. 2024; Decaëns et al. 1998; Torppa and Taylor 2022). While this suggests a potentially comparable structure in terms of ecological strategies, one could have expected a higher proportion of anecic species, especially in grassy-like urban environments (Hoeffner et al. 2021). Given their key role in ecosystem services such as soil structure maintenance, nutrient regulation, and support of plant production, increasing the presence of anecic earthworms may represent a lever to further enhance soil functioning in urban environments (Capowiec et al. 2024; Huang et al. 2020; van Groenigen et al. 2014).

As we hypothesised, when we were able to account for soil pH, land cover and use intensity, measures of urbanisation, climate variables and the local physical environment within one modelling framework, we found that earthworm communities (abundance, biomass and species richness) in urban areas are mainly driven by topographic (elevation) and climatic variables (variability in annual temperature and PET). The relative importance of climate variables is in line with the global analysis of Phillips et al. (2019), which also highlighted that climatic variables might be more important in shaping earthworm communities compared with soil properties and habitat cover. However, analyses at sub-global scales (e.g., in Salako et al. 2023) have found variables such as habitat cover, soil moisture and clay content to be important alongside climatic variables.

Elevation was a strong predictor for total abundance of the earthworm communities, with higher elevations having higher number of individuals. This is in line with previous work outside of urban environments, where earthworm

densities have increased with increasing elevation, at least until similar altitudes as those represented within our study (González et al. 2007). Elevational studies of earthworms with longer gradients have found non-linear relationships, with peaks of diversity and density between 1000 and 2000 m (Ahmed et al. 2022; Fontana et al. 2020; Gabriac et al. 2023). These studies determined that the change in diversity with elevation was due to soil conditions, changing habitat (and therefore tree composition), environmental heterogeneity, as well as variations in climate (Gabriac et al. 2023; González et al. 2007). As far as we are aware, no study has previously investigated the role of elevation on earthworm communities within urban environments, and given the small elevational gradient (8 m to 840 m), and limited dataset preventing interactions between variables within the modelling framework, it is difficult to determine whether the effect of elevation on abundance is non-linear and whether the effect is as an indirect result of other drivers, such as climate. This would be an interesting avenue for further investigations in the future, with direct and indirect effects being specifically investigated using, for example, structural equation models (SEMs; Grace 2008).

We expected that the degree of urbanisation would have an impact on earthworm communities, but this was not the case based on the results of our mixed effects model. One possible explanation for this is the use of urbanisation metrics from global data layers. The need to rely on globally available data limits the possible variables that can be incorporated into the models. In addition, there could also be a mismatch in the spatial or temporal scale of the urbanisation and biodiversity metrics. Although the data layers were at a high resolution ($\sim 1\text{km}^2$), this is still considerably larger than the typical plot size of earthworm sampling. Similarly, some of the global data layers for the urbanisation metrics were not from the same year as the sampling for each site, despite reducing temporal mismatch as much as possible. Collecting standardised urbanisation metrics concurrently with earthworm sampling would provide the most useful information. Additionally, our analysis is focused on the gradients of urbanisation within urban contexts, and not the differences between urban and non-urban areas. This is an important distinction: some cities in our dataset may represent only medium to high levels of urbanisation. This limits our ability to detect any habitat filtering of the community as a result of a land use change from non-urban to urban (Aronson et al. 2016), potentially reducing the impact of urbanisation within our models. Beyond the degree of urbanisation itself, landscape-level features such as habitat heterogeneity and the configuration of green spaces may also play a critical role. Previous studies have found that these factors are strong predictors of earthworm diversity, abundance and biomass (Eydoux et al. 2024; Xie et al. 2018,

2024), as is often the case in non-urban landscapes as well (Frazão et al. 2017; Hoeffner et al. 2021).

Interacting effects of land use intensity and soil properties on urban earthworm communities

Although our mixed-effects models did not detect significant effects of land use types, land use intensity, or soil properties on earthworm communities, exploratory patterns from the multivariate analyses provide complementary insights into potential ecological drivers. These findings should be interpreted with caution due to the weak overall relationships (as indicated by a low RV coefficient), but they remain useful for identifying management levels in urban settings.

In terms of land use, urban grasslands with low to moderate management intensity tended to support high earthworm species richness, echoing trends observed in non-urban grasslands (Cluzeau et al. 2012; Decaëns et al. 2008; Rutgers et al. 2016). However, high-intensity urban grasslands in this dataset, which were typically subjected to frequent mowing, had reduced abundance, contrasting with the results of other non-urban grassland studies (Hoeffner et al. 2024). This difference may reflect not only direct effects of management but also indirect ones, such as repeated trampling and machinery use in public parks that is not present in non-urban grassland but can increase soil compaction and reduce habitat quality for earthworms (Cluzeau et al. 1992; Maréchal et al. 2024; Pižl and Schlaghamerský 2007; Smetak et al. 2007). In contrast, the sites with trees and shrubs, which were likely less disturbed and offering more complex microhabitats, were associated with higher species richness. These vegetated areas likely provide greater organic matter input, more stable soil conditions, and thermal and hydric refuges during extreme events, factors known to benefit earthworm populations (Cesarz et al. 2007; De Wandeler et al. 2018; Schwarz et al. 2015). However, the magnitude and direction of these effects may depend on specific vegetation characteristics, such as the C: N ratio of litter (De Wandeler et al. 2018), tree diversity (Cesarz et al. 2007), or tree identity (Schwarz et al. 2015). In contrast, urban arable land showed no consistent effects on earthworm communities. This may be due to the diverse management practices in urban cultivated areas, which vary in terms of tillage, fertilisation (both type and frequency), and other agronomic factors, leading to more variable effects on soil conditions and earthworm communities, both directly and indirectly.

Through the use of co-inertia analysis, soil characteristics also emerged as potentially influential in urban settings, echoing findings from other ecosystems (Decaëns et al. 2008; Joschko et al. 2006; Lee 1985; Rutgers et al. 2016), where factors such as pH, organic matter, and texture have been shown to shape earthworm communities.

Organic matter content was positively correlated with earthworm abundance, consistent with the idea that energy-rich substrates are a major driver of earthworm communities (Lee 1985; Rutgers et al. 2016). Textural effects were also apparent: higher sand content was associated with reduced total abundance, while lower clay content correlated with lower species richness. These patterns likely reflect the poor water-holding capacity and reduced structural stability of sandy soils, which are less favourable to earthworms (Hendrix et al. 1992; Lapiéd et al. 2009; Lee 1985). Finally, we observed a decline in species richness with increasing soil pH, contrary to most studies that report positive effects of pH on richness and abundance (Decaëns et al. 2008; Joschko et al. 2006; Ma et al. 1990). This discrepancy may relate to the relatively high average pH in our urban soils (mean pH=7.0), compared to the more acidic conditions commonly reported in the literature (Decaëns et al. 2008; Joschko et al. 2006). Elevated pH in urban contexts can result from the presence of alkaline construction materials such as cement, which may alter the availability of essential nutrients (Ca, P, Fe) and affect microbial processes critical for organic matter decomposition (Greinert 2015; Malik et al. 2018).

Urban areas as gateways for exotic earthworms?

Urbanisation is a strong driver towards biotic homogenisation (McKinney 2006), often resulting in the same set of species that are adapted to the adverse conditions found across cities around the world. Across our database, there was a very high degree of similarity of species across the different cities. Specifically, a high occurrence of *Aporrectodea rosea*, *Allolobophora chlorotica*, *Lumbricus terrestris*, *Aporrectodea caliginosa* and *Aporrectodea longa* within the communities sampled, which primarily reflects the dominance of data from European cities. However, other large-scale urban studies have also found low variation of species across different cities (Tóth et al. 2020). And while the majority of our cities are from countries within Europe, which often have similar species within their communities (Jupke et al. 2024), there is a clear dominance of peregrine/cosmopolitan species associated with urban areas. Indeed, other small-scale studies have found that within urban areas there is a dominance of cosmopolitan species, with endemic species typically lacking (Eydoux et al. 2024).

However, it is worth noting that despite the overrepresentation of studies from Europe in our dataset, no exotic species were observed in Europe, whereas such species were recorded in studies from America and Asia. This absence likely reflects the type of data available, as several studies based on qualitative or site-specific approaches have reported exotic species in European cities. For instance,

Microscolex dubuis was recently found in Montpellier (Mautuit et al. 2024), *Eukerria saltensis* and *Ocnerodrilus occidentalis* have been observed in England and Italy (Rota 2013), Sherlock and Carpenter (2009) reported 27 exotic species in the Royal Botanic Gardens, Kew. These observations, although not part of our quantitative dataset, confirm that urban areas, through activities such as horticulture and plant trade, can act as hotspots for the introduction of exotic earthworm species (Hendrix and Bohlen 2002; Padayachee et al. 2017). Moreover, exotic earthworm species found in urban environments in America and Asia are also present in other natural habitats on these continents, reflecting a broader invasion pattern beyond cities. In these regions, when exotic species were observed, they tended to dominate the earthworm communities in which they occurred, further highlighting their invasive potential (Brown et al. 2006; Chang et al. 2018; Huang et al. 2007; Szederjesi and Mısırlıoğlu 2017).

The ecological consequences of exotic earthworm species in urban environments remain poorly documented but may parallel those observed in natural or semi-natural ecosystems. All earthworms can alter soil structure, organic matter decomposition and nutrient cycling rates, however, when earthworm move into novel environments these actions can have negative impacts on the ecosystem, often leading to a decline in native soil fauna and flora (Frelich et al. 2006; Hale et al. 2006; Hendrix et al. 2008). For instance, in North American forests, invasive earthworms have been shown to reduce the litter layer by accelerating organic matter decomposition which leads to altered soil structure and nutrient cycling, subsequently affecting plant community composition. (Bohlen et al. 2004; Hendrix et al. 2008) and similar processes may occur in urban green spaces, especially when exotic species become dominant. Moreover, exotic earthworms can compete with native species, potentially reducing native diversity (Eisenhauer et al. 2007; Migge-Kleian et al. 2006). In urban contexts, where soils are already under multiple anthropogenic pressures, such invasions could further alter ecosystem functioning and compromise services such as carbon storage, soil water regulation, or plant–microbe interactions.

Recommendations for management practices

Overall, we found that climate is the main driver of earthworm communities. Thus, in the face of climate change (Lee et al. 2023), management practices need to focus on mitigating the local effects of this global change. As shown in our analyses, increasing variations in temperature and changes in PET can impact total abundance and biomass. As urban soils already have typically higher temperatures than the surrounding non-urban areas as a result of the heat

island effect (Shi et al. 2012), mitigating any increase in air temperature, as a result of strong seasonality, would also be beneficial to the earthworm communities. This can be done by increasing tree canopy cover (Ziter et al. 2019), but careful selection of plant species would be needed to ensure water use remains low (Schröder and Kiehl 2020).

While some earthworm species are particularly sensitive to changes in temperature (Phillips et al. 2025), changes in climate that affect soil moisture will likely have the largest impact on earthworm communities as a whole. Thus, maintaining appropriate soil moisture conditions should be a key management goal. Thankfully, many interventions for maintaining soil moisture occur through increased soil organic matter (Rawls et al. 2003) – which we also found to directly promote earthworm communities through resource provision (Lee 1985). Increasing soil organic matter through practices such as leaving mowing residues, applying compost, or using mulch will help maintain soil moisture at levels that support earthworm communities, as well as promoting activity of plant roots and microbes (Herrmann et al. 2023; Torppa et al. 2024). Addition of organic matter will also mitigate other anthropogenic impacts that we found to be detrimental to earthworm communities, such as the impact of soil compaction (Percival et al. 2025).

Recommendations for further studies

Given the current scarcity of studies on urban earthworm communities, with most studies concentrated in Europe, future research should prioritise expanding investigations to a wider range of cities across different regions of the world using standardised methods (such as ISO 23611-1:2018; ISO2018). Furthermore, the high spatial heterogeneity of urban environments, where metapopulation and metacommunity processes may play a key role (Andrade et al. 2021), suggests that current sampling efforts may underestimate true earthworm diversity. Species accumulation curves have rarely been applied in urban contexts, and adapted sampling designs are likely needed to better capture the local or regional species pool (Thompson et al. 2007). This is particularly important to detect rare native species or newly introduced exotics that may serve as early indicators of ongoing ecological change. There is also a need for long-term monitoring of urban earthworm communities. Since some existing data dates back to the 1990s, future studies have the possibility to investigate the impact of climate change on earthworm populations, as well as intra-annual variations linked to urban microclimates. To enhance comparability between studies, researchers should systematically document the characteristics of sampling sites (Xie et al. 2024), including both urbanisation factors and standardised soil property analyses. By increasing the comparability across

studies, it will increase our ability to identify key factors affecting earthworm communities in urban landscapes.

Future studies could explore how variations in the spatial organisation of cities, including differences in size, shape, and the proportion of built versus non-built areas, influence landscape structure, particularly in terms of habitat fragmentation and landscape homogenisation (Krauss et al. 2010; Maréchal et al. 2024; Püttker et al. 2020; Zhang et al. 2024). Investigating how fragmentation isolates earthworm populations and limits resource access, as well as how urban homogenisation modifies dispersal processes, ecological niches and species assembly, will provide important ecological insights. Additionally, examining the historical development of urban areas, including their expansion patterns and land-use transitions, to assess how these long-term changes have influenced soil and earthworm populations (Maréchal et al. 2021) would be an additional future avenue of research. The role of urban land management in shaping earthworm communities is also an area that could be focused on in future studies. The maintenance and use of non-built urban spaces, including mowing, irrigation, fertilisers and chemical applications, amendments and pedestrian activity, can either exclude certain earthworm species or introduce new ones (Baumann et al. 2024; Hoeffner et al. 2024; Pižl and Schlaghamerský 2007). Investigating how intensive management creates unfavourable conditions or how specific practices, such as tree and flower planting, promote earthworm diversity by providing suitable habitats and potentially introducing new species, would be valuable in understanding urban soil ecosystems. Indirect impacts from urbanisation should also be considered as they remain largely unexplored, such as the effects of transport-related vibrations (Caorsi et al. 2019) or artificial lighting at night (Nuutinen et al. 2014) on earthworm behaviour, movement, and survival. Soil pollution, another indirect but potentially significant factor, has been shown in a few studies to negatively affect earthworm abundance and species richness, mainly due to heavy metals and polycyclic aromatic hydrocarbons (PAHs), but overall, research remains scarce, and other pollutants are also likely to contribute to shaping urban soil fauna (Chatelain et al. 2024; Pižl and Josens 1995b; Steinberg et al. 1997). Future studies should aim to address these knowledge gaps to develop a more comprehensive understanding of earthworm ecology in urban environments.

Conclusion

Urban soils, and the biodiversity they contain, play a critical role in providing essential ecosystem services that contribute to the sustainability and resilience of cities, and are vital

for the health and well-being of urban populations. Therefore, understanding and managing urban soils is crucial for maximising these benefits. By conducting a global synthesis we provide a generalised overview of urban earthworm communities and highlight that cities can host diverse and abundant earthworm communities, as increasing urbanisation intensity does not directly impact the earthworm communities. Instead, our findings underline the importance of climatic, topographic, and local soil factors in shaping urban earthworm communities. We found that elevation, annual variation in temperature and potential evapotranspiration emerged as the main environmental drivers of earthworm abundance at the global scale, while biomass was primarily influenced by annual variation in evapotranspiration. At finer spatial scales, earthworm abundance was positively related to organic matter and clay content and negatively related to soil pH and urban high-intensity grasslands. Species richness was positively associated with forests and grasslands but negatively with sandy soils. While the dataset had a strong geographical bias towards European cities, with limited representation from other continents, exotic species were only represented in North America, South America and Asia, despite qualitative reports of exotic species in European and African cities. This lack of quantitative data emphasises the need to expand research, specifically beyond Europe, to improve our global understanding, and therefore maintenance of urban soil biodiversity. Utilising citizen science approaches would be one way to increase data generation. Additional further research into the long-term effects of urbanisation on soil biodiversity including nature-based approaches to soil restoration, the integration of green infrastructure that supports soil biodiversity and mitigates the impact of climate change, and the design of soil-friendly urban landscapes will be critical in ensuring the health and functionality of urban ecosystems for future generations.

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Data availability Data is provided as supplementary information files

Declarations

Competing interests The authors declare no competing interests.

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