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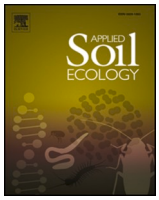

Research paper

Changes in remnant forest soils and earthworm communities over two decades

Ian Yesilonis [a,b,*], Sarah Placella [c], Csaba Csuzdi [d], Katalin Szlavecz [a]

[a] Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD, United States
[b] Northern Research Station, USDA Forest Service, Baltimore, MD, United States
[c] Root Applied Sciences, Oakland, CA, United States
[d] Department of Zoology, Eszterházy Károly Catholic University, Eger, Hungary

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ABSTRACT

Long-term urban soil studies provide details of how urban soils develop over time. Urban soils are affected by regional and local pressures related to air pollution and introduced species such as earthworms and vegetation, which can affect change within relatively short periods of time. In Baltimore, forest soils of an urban–rural gradient were re-sampled, and it was found that, over two decades, calcium (Ca) concentration and pH had increased. These forest soils are habitats for populations of earthworms, which feed on the leaf litter and, consequently, locally alter the forest floor. Given the profound impact that earthworms have on soil properties, changes in soil chemistry were examined to determine any relation to shifts in earthworm community composition and abundance, with a special focus on the invasive jumping worms. To answer this question, earthworm assemblages in urban, suburban, and rural forest patches were sampled in 2002 and 2020. Species biomass and density were determined and then compared to samples collected at the same locations. In 2020, mean biomass and density varied between 91 and 33 g m^{-2}, and 388 and 12 ind m^{-2}, respectively. The results indicate statistically significant correlations between soil properties (pH, Ca, leaf litter depth, and bulk density) and earthworm abundance within a given year. However, changes in soil properties were independent of changes in earthworm species or abundance. The dynamics of earthworm assemblages appear to be different in urban forests than rural ones, with rural forests containing more jumping worms than urban ones, which uniquely affects the forest ecosystems.

1. Introduction

Long-term data is important for observing trends in soil fauna communities and their relationship to soil properties in urban areas. Long-term soil studies are also critical to understanding the productivity and sustainability of forest and woodland ecosystem services (Knoepp et al., 2019). However, long-term studies of earthworms in forests with direct resampling (Hale et al., 2005a; Szlavecz et al., 2018), as opposed to chronosequences, are relatively rare. There are no long-term direct sampling studies that investigate earthworm community change and how it relates to soil chemical properties in urban areas.

Urban soils, like soils in any other ecosystems, are habitats for diverse macro- and microbiota (Szlavecz et al., 2017). Earthworms, a keystone group, fundamentally alter their physical environment, and in doing so, affect chemical properties (Ferlian et al., 2020) and soil structure (Lee, 1985). Earthworm activities such as consuming leaf litter (Satchell, 1967) and mixing of horizons (Edwards and Bohlen, 1996) affect soil conditions, which vary with soil parent material, land use history, and the assemblage of invading earthworm species (Frelich et al., 2006). In soils occupied by earthworms, surface soils have higher soil pH values (Desie et al., 2020; Lambkin et al., 2011) and higher Ca concentrations (Hobbie et al., 2006; Reich et al., 2005), as well as higher bulk density (Hale et al., 2005b; Lee, 1985; Szlavecz and Csuzdi, 2007), or, in some cases, lower bulk density (Fahey et al., 2013; Hale et al., 2005b). These litter soil habitat alterations affect soil ecosystem functions, organisms, and vegetation.

In urban ecosystems, a variety of filters shape species distribution, with human facilitation being particularly influential for earthworm communities. Studies examining urban-rural gradients offer further insights into how these filtering mechanisms vary between urban and rural

* Corresponding author at: Northern Research Station, USDA Forest Service, Baltimore, MD, United States
E-mail address: ian.yesilonis@usda.gov (I. Yesilonis).

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settings, thereby affecting earthworm community composition differently in each landscape. In urban areas, the filters that influence species distribution are (1) regional climatic and biogeographical factors, (2) human facilitation, (3) urban form and development history, (4) socio-economic and cultural factors, and (5) species interactions (Aronson et al., 2016). For earthworms, human facilitation is among the most important filters in urban areas. Dispersal, either by roads, fishing bait (Cameron et al., 2007), or yard waste bags are important vectors in urban environments (Chang et al., 2021; Dymond et al., 1997; Gundale et al., 2005). Additionally, habitat heterogeneity, dispersal barriers (Tiho and Josens, 2007) and habitat type affect earthworm community composition (Tóth et al., 2020). Urban–rural gradient studies (e.g., McDonnell and Pickett, 1990; Pouyat, 1991) provide an opportunity to examine the relative importance of filters influencing species distribution. For instance, the impact of filtering in urban forest patches is different from that in rural ones; therefore, earthworm community composition is expected to be different as well (Steinberg et al., 1997; Szlavecz et al., 2006).

In Baltimore, Maryland (MD), USA, urban forested areas are dominated by non-native earthworm species, especially European Lumbricidae and the rapidly spreading pheretimoids or jumping worms (Szlavecz et al., 2006; Tóth et al., 2020); moreover, the composition, density, and biomass of these earthworm communities can exhibit both short-term and long-term seasonal or annual variations. Even though European earthworms dominate in these forests, jumping worms are of special interest due to their fast spread in temperate deciduous forests and urban-suburban landscapes (Chang et al., 2021; Szlavecz et al., 2018). Jumping worms belong to 12 genera in the family Megascolecidae, which is native to East and Southeast Asia (Chang et al., 2009), and are found in all states of the mid-Atlantic and northeast USA (Moore et al., 2018). Earthworm community composition, biomass (Hale et al., 2005a) and density can vary seasonally or annually (Szlavecz et al., 2018). These variations may be short term, for instance, related to drought (Suarez et al., 2006), or long term, related to earthworm succession (Eisenhauer et al., 2007; Resner et al., 2011). No studies have been conducted to investigate population changes in earthworms within urban environments.

Previously, researchers had shown that along an urban–rural forest patch gradient in Baltimore, MD, soil Ca and pH increased and C:N ratios decreased over 17 years (Yesilonis et al., 2022). Factors influencing this change were possibly regional and local, such as air pollution and deposition, and biological, such as the presence of invasive species. The influence of earthworms on the chemical and physical properties of soil is known, but little information is available regarding how long-term changes in soil properties are affected by changes in earthworm population dynamics. Additionally, in these same sites, earthworms, mostly European lumbricids, were shown to have different abundances in urban and rural forests (Szlavecz et al., 2006).

Based on past research by Szlavecz et al. (2006), it was expected that earthworm biomass and density would vary along the urban-rural forest patch gradient. Additionally, it was anticipated that relationships between earthworms and soil characteristics would be evident, as indicated by prior research, e.g., Ferlian et al. (2020). However, the novelty of this study is related to two questions: 1) Does the composition of the earthworm community change over time along the urban-rural gradient after 18 years? Specifically, is there an increase in the biomass and density of jumping worms? This is of interest due to their expansion in temperate deciduous forests and urban areas. 2) Given the results of higher soil Ca and pH (Yesilonis et al., 2022), do changes in earthworm biomass, density, and community composition partially explain these trends in soil properties? To answer these questions, earthworms were collected and identified in the same plots whose soils (Pouyat et al., 2008; Yesilonis et al., 2022) and earthworms (Szlavecz et al., 2006) had previously been studied 18 years ago. The study addresses these knowledge gaps to inform urban forest managers about soil health.

2. Material and methods

2.1. Study area

The study area was in Baltimore City and County in Maryland, USA. The Baltimore metropolitan area has average annual air temperatures (from 2002 to 2020) of 13 °C and precipitation (from 2002 to 2020) of 1210 mm $year^{-1}$ (NOAA, 2022). Baltimore County and the northern half of Baltimore City lie within the Piedmont Plateau. The Piedmont Plateau is underlain by schist, gneiss, gabbro, and other highly metamorphosed sedimentary and igneous rocks.

Yesilonis et al. (2022) have provided the details of the site selection process. Briefly, forest patches along an urban–rural gradient were selected by the following criteria: 1) size ≥2 ha, 2) overstory dominated by white oak (*Quercus alba*) and tulip poplar (*Liriodendron tulipifera*), 3) slopes <25 %, and 4) age > 50 years with no visual signs of recent human disturbance and intensive management. The eight sites meeting these criteria were classified as urban, suburban, or rural based on their distance from the city center (Inner Harbor) and the type of development in the surrounding area (Fig. 1).

In each site, three 0.04 ha circular plots were randomly established for soil and earthworm sampling. Soil pH was determined using 1:2 soil-to-0.01 M $CaCl_2$ solution, organic matter content was determined by loss on ignition (470 °C for 24 h), and soil was digested with 7.7 N HNO_3 for 25 min for Ca concentration. For more in depth description of plot layout and soil methods please refer to Yesilonis et al. (2022). At each plot, the following samples were collected: 1) three 50 × 50 cm quadrats of leaf litter samples and 2) one undisturbed core for bulk density determination (0–10 cm) using the core method (Blake and Hartge, 1986). Leaf litter depth was measured at 9 points within a 50 × 50 cm grid; 3 grids were measured at each plot, for a total of 72 grids sampled. Additionally, in 2018, the leaf litter was collected from the grid, dried at room temperature, and weighed, to validate leaf litter depth (Supplementary Fig. S1). To eliminate any user bias, quadrats were randomized by throwing them behind the back of the field technician, and measurements were then taken. For 2001, a suburban (Pimlico) and an urban (Cylburn) forest did not have leaf litter depth data, and a rural forest (Loch Raven) only had one of the three plots sampled for leaf litter depth.

2.2. Earthworm sampling

The methods used to extract earthworms have been described by Szlavecz et al. (2006), but, to summarize, at each site, there were three plots, and in each plot, three earthworm quadrats were used for sampling, for a total of nine earthworm samples per site (Fig. 1; a total of 72 earthworm samples). Sampling took place from November 9 to 13 in 2002 and from October 19 to 23 in 2020. The sampling was done using a 25 cm × 25 cm quadrat using 0.2 % formaldehyde solution (Raw, 1959). The animals were euthanized in 50 % ethanol, fixed in 4 % formalin for two weeks, and preserved in 75 % ethanol. Adult earthworms were identified to species level; Csuzdi and Zicisi (2003) were used for Lumbricidae, Chang et al. (2016) for Megascolecidae, and Csuzdi and Szlavecz (2002) for *Diplocardia* sp. Biomass was considered the weight of the animal preserved in 75 % ethanol and patted dry with a paper towel just before weighing.

Initially, the soil was sampled in 2001, and earthworms were sampled a year later. Approximately two decades later, in 2018, the soil was re-sampled, and, in 2020, earthworms were re-sampled. For the remainder of the paper, “Year 1” will refer to the 2001 soil and 2002 earthworm data, and “Year 18” will refer to the 2018 soil and 2020 earthworm data.

2.3. Statistical analysis

The data analysis for this paper was generated using SAS software,

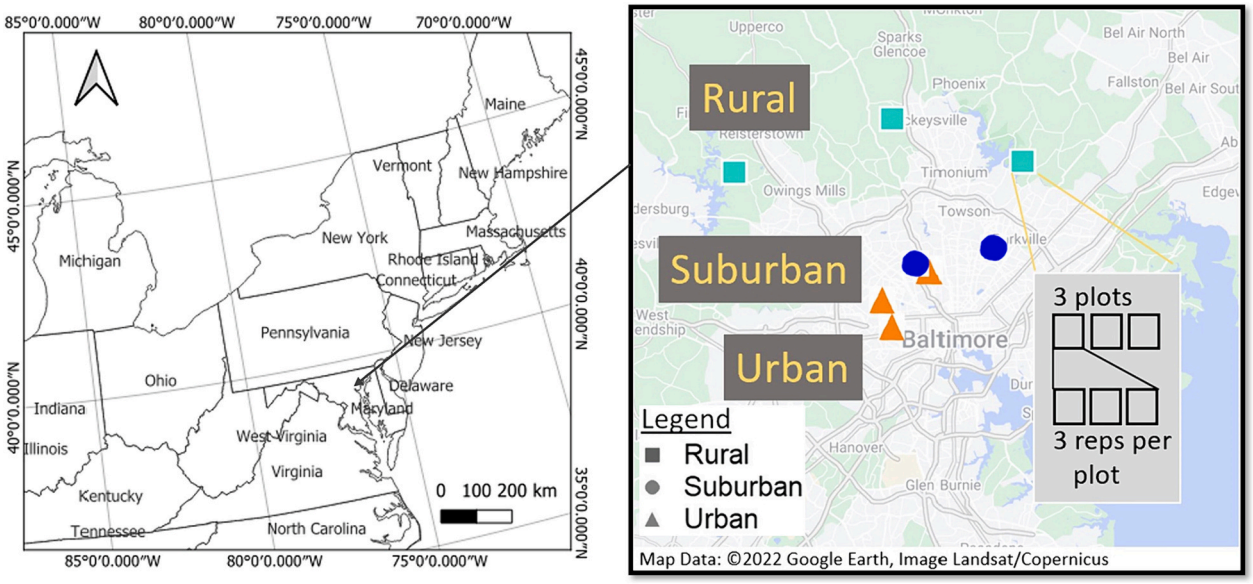

Fig. 1. Forest site locations ($n = 8$) along the urban-rural gradient. Sites were given a gradient designation of urban, suburban, or rural, determined by distance from city core and type of development in the surrounding area. Each site had 3 plots where soil variables were taken in 2001 and 2018. Within each plot, 3 quadrants (replications) were sampled for earthworms ($n = 72$), in 2002 and 2020.

version 9.4 (SAS, 2021); PC-Ord, version 7.09; and PAST (Paleontological Statistics), version 4.03. A repeated mixed model (SAS Proc GLIMMIX) was used to determine the statistical difference between Year 1 and Year 18, along the gradient, and the interaction of year and gradient. The year was used as the repeated measure or the random factor, the subject was plot nested within replication, the distribution was normal, the covariance matrix was unstructured, and degrees of freedom were determined according to Kenward and Roger method.

Cluster analysis and standardized principal component analysis (PCA) were performed to visualize the earthworm community differences along the gradient (PC-Ord). Succession vectors (Euclidean distances), which quantify how species composition changed over time, were determined using the Pythagorean theorem on PCA points (PC-Ord). Indicator species observed indicator value (IV) was performed to determine species influence by gradient and by year (PC-Ord).

3. Results

3.1. Earthworm assemblages along an urban–rural gradient

The two sampling campaigns recorded a total of 10 species of earthworms: the urban forests had 3 more species than the rural forest (5) and the suburban forest (5). The suburban forests contained five species, namely, *Aporrectodea caliginosa, Aporrectodea limicola, Lumbricus friendi, Lumbricus terrestris,* and *Octolasion lacteum,* while the five rural species were *Diplocardia patuxentis*, *L. terrestris, O. lacteum, Metaphire hilgendorfi,* and *Amynthas tokioensis*. The urban forests contained all but two of the species identified in rural and suburban forests, which were *D. patuxentis* and *M. hilgendorfi*. The density (individuals m^{-2}) of the adults was five times more in the urban forest than in the rural one—43 and 8 individuals m^{-2}, respectively (Supplementary Table S1).

Using adult density numbers in Year 1 and Year 18, both PCA and cluster analysis showed different community compositions at the urban and rural ends of the gradient. The PCA results showed a linear relationship in composition and abundance in earthworm species, which separated the urban forest from the rural forest in both Year 1 and Year 18 (Fig. 2). For Year 1, the urban forests with *Ap. caliginosa*, *O. lacteum, Ap. limicola*, and L. *terrestris* were separated from the rural forests with *D. patuxentis* and *M. hilgendorfi* (Fig. 2A). In Year 18, the rural forests were separated from the urban ones mainly because of pheretimoids, i.

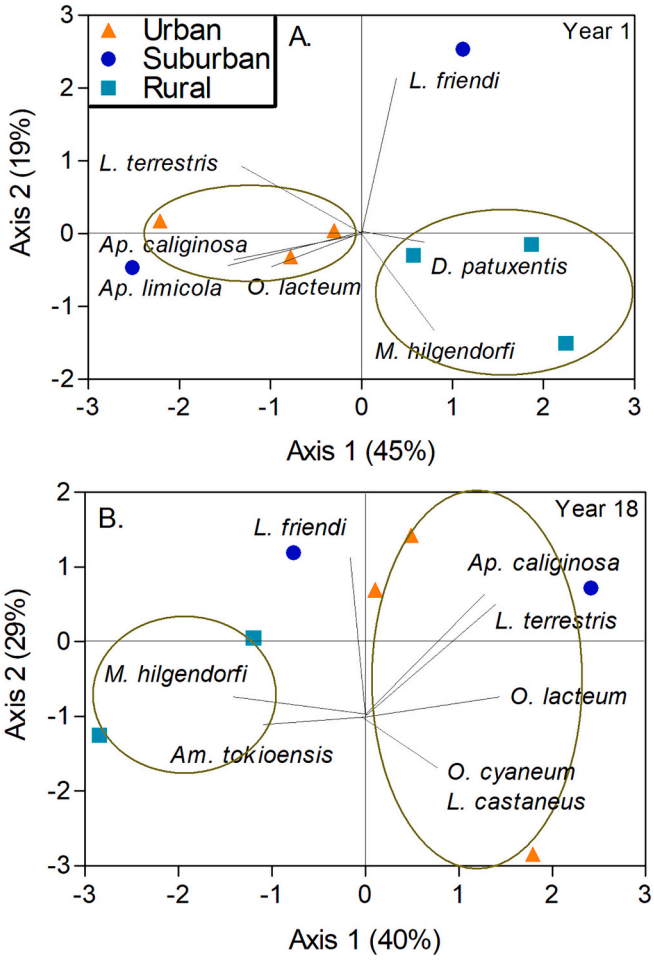

Fig. 2. Earthworm species were separated by urban and rural forest sites for both (A) Year 1 and (B) Year 18 using principal component analysis.

e., *M. hilgendorfi* and *Am. tokioensis* (Fig. 2B). At the site level, when both years were combined and run in one PCA, succession vectors from the PCA showed that Leakin Park forest (urban) Year 1 to Year 18 had the greatest community change at 5.3 (unitless) in the PCA ordination space, followed by Hillsdale Park forest (urban) and Liberty Reservoir forest (rural), both of which were at 2.5 (Supplementary Fig. S2).

Another method to explore community composition differences between sites is cluster analysis, which classifies earthworms from sites across the two different years into discrete groups. Cluster analysis separated Oregon Ridge Park (rural forest, Year 18) from all the other sites at the highest level of clustering, i.e., where all the information for the clustering has been accounted for, because no earthworms were found at this site in that year (Supplementary Fig. S3). The next highest division separated the rural forests of Liberty Reservoir (Year 1 and 18) and Loch Raven Reservoir (Year 18), both of which had pheretimoids (*M. hilgendorfi* and *Am. tokioensis*), from the other forests with no pheretimoids. The remaining clusters were separated by different species of Lumbricidae. The Loch Raven Reservoir forest in Year 1, unlike in Year 18, was grouped with the remaining clusters because of the presence of L. *terrestris* and lack of pheretimoids. However, the Loch Raven Reservoir forest (Year 1) was separated from the remaining others because of the presence of *D. patuxentis*. Next, *Lumbricus castaneus* and *Octolasion cyaneum* separated Leakin Park (Year 18) from the remaining cluster. As clusters became finer, a combination of *O. lacteum*, *L. friendi*, *Ap. caliginosa*, *Ap. limicola*, and L. *terrestris* were found to separate the sites.

Earthworm biomass and density for both adults and juveniles combined differed along the urban–rural gradient ($P = 0.0054$; SAS Proc Glimmix; Fig. 3). The density was the highest in suburban forests (257 ± 147 ind m^{-2}) and 93 % and 20 % lower in rural (18 ± 6) and urban (206 ± 32) forests, respectively (Fig. 3A). Rural forest earthworm biomass (25 ± 12 g m^{-2}) was four and three times lower than suburban forest (90 ± 29) and urban forest (81 ± 14) biomass, respectively (Fig. 3B). When present, *L. terrestris* dominated earthworm biomass, ranging from 66 % to 82 % of the total site biomass.

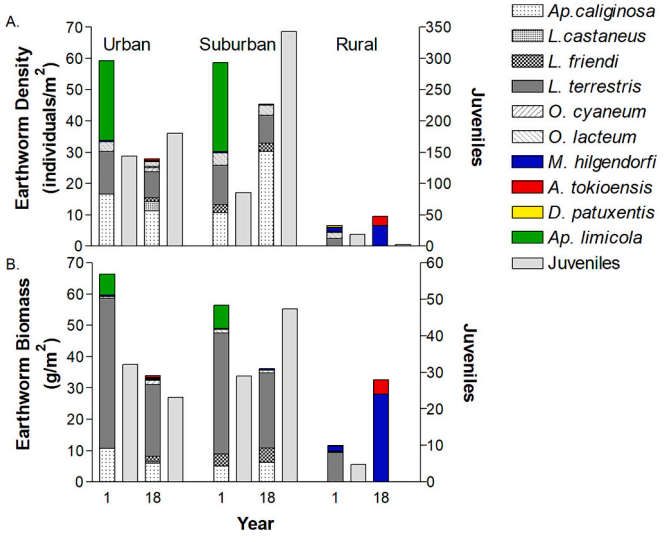

Fig. 3. Earthworm density and biomass along the gradient for each year. A.) There were significantly higher earthworm densities ($P \leq 0.05$) found at the urban and suburban end of the gradient compared to the rural end of the gradient. At the species level, *Aporrectodea caliginosa*, *Aporrectodea limicola* are higher at the urban end of the gradient while *Metaphire hilgendorfi* and *Amynthas tokioensis* are higher at the rural end of the gradient. B.) There were significantly higher earthworm biomasses ($P \leq 0.05$) found that the urban and suburban end of the gradient compared to the rural end of the gradient. *Lumbricus terrestris* is higher at the urban end of the gradient while *M. hilgendorfi* is higher at the rural end of the gradient.

An individual species may be influential in differentiating the community composition along the urban–rural gradient. The indicator species analysis for adults (individuals m^{-2}) indicates that a species is more abundant and constant in a section of the gradient than would be expected by chance using the observed indicator value (IV) (Dufrêne and Legendre, 1997). The higher the IV, the greater the influence a particular species has on the groups of the urban–rural gradient being analyzed. The highest IVs were for *Ap. caliginosa* (observed IV = 52, $P = 0.073$) and *M. hilgendorfi* (observed IV = 50, $P = 0.084$). *M. hilgendorfi* was found in the rural sites only, while *Ap. caliginosa* was found only in the urban and suburban sites (Fig. 3; Supplementary Table S1).

3.2. Earthworm abundance and soil properties

Strong relationships were found between biomass or density and the following soil chemical and physical properties: pH, Ca, bulk density, and leaf litter depth. Sites with higher pH had more earthworms. Approximately, a fourfold increase in earthworm biomass reflected an increase of one pH unit for both years (Fig. 4A). Following the same trend, Sites with higher Ca concentrations had more earthworms. In Year 18, a fourfold increase in earthworm biomass (from 50 to 200 g m^{-2}) reflected an approximately 2.5-fold increase in Ca (from 700 to 1700 mg kg^{-1}). However, in Year 1, a similar increase in earthworm biomass reflects a lower Ca response. (Fig. 4B). Sites with higher bulk density had more earthworms. This trend was more pronounced in Year 1 than in Year 18 (Fig. 4C). In Year 18, as earthworm biomass increased from 0 to 200 g m^{-2}, leaf litter depth decreased by 1.5 cm; for Year 1, no such relationship was found (Fig. 4D).

3.3. Earthworm assemblages in years 1 and 18

The number of adult individuals decreased by 47 % between the years: In Year 1, there were 125 individuals m^{-2} averaged by urban, suburban, or rural forest and then summed for the entire gradient, and in Year 18, there were 67 (Supplementary Table S2). Seven species were recorded in Year 1, and eight species were recorded in Year 18 (Supplementary Tables S1, S2). In addition to changes in numbers between the years, there were also differences in species. Two species, *Ap. limicola* and *D. patuxentis,* were recorded in Year 1 only, and three species, *L. castaneus*, *O. cyaneum*, and *Am. tokioensis*, were recorded in Year 18 only (Fig. 3, Supplementary Table S1). The indicator analysis for adults (individuals m^{-2}) by year showed *Ap. limicola* (observed IV = 50, $P = 0.081$) to be the most influential earthworm species to separate Year 1 and Year 18. *Ap. limicola* was abundant in Year 1 in all three urban forests and one suburban forest (Cylburn, Hillsdale Park, Leakin Park, and Pimlico) but was not found in Year 18 (Fig. 3, Supplementary Table S1). The variation in L. *castaneus* and *O. cyaneum* can be explained by one urban forest site, Leakin Park, which, in Year 18, did not have a population of *Ap. limicola* and in which the new populations of L. *castaneus*, *O. cyaneum*, and *Am. tokioensis* increased (Fig. 3, Supplementary Table S1). For a rural forest, Liberty Reservoir, there was an increase in the density of *M. hilgendorfi* and new populations of *Am. tokioensis*.

Biomass differences between the years exhibited the same trends as individual densities. However, as expected, the degree of change was highly influenced by species size. For instance, the contribution of the large *M. hilgendorfi* and *Am. tokioensis* to biomass changes was more significant than their contribution to density in rural forests, whereas the relationship was reversed for the smaller *Ap. limicola* in urban and suburban forests (Fig. 3).

3.4. Earthworm changes related to soil chemical and physical changes

As mentioned earlier, a relationship was present between earthworm biomass and pH, Ca, bulk density, and leaf litter depth for Years 1 and 18. Additionally, as previously reported, pH increased from 4.1 to 4.5 over time, and Ca increased by 35 % (Yesilonis et al., 2022).

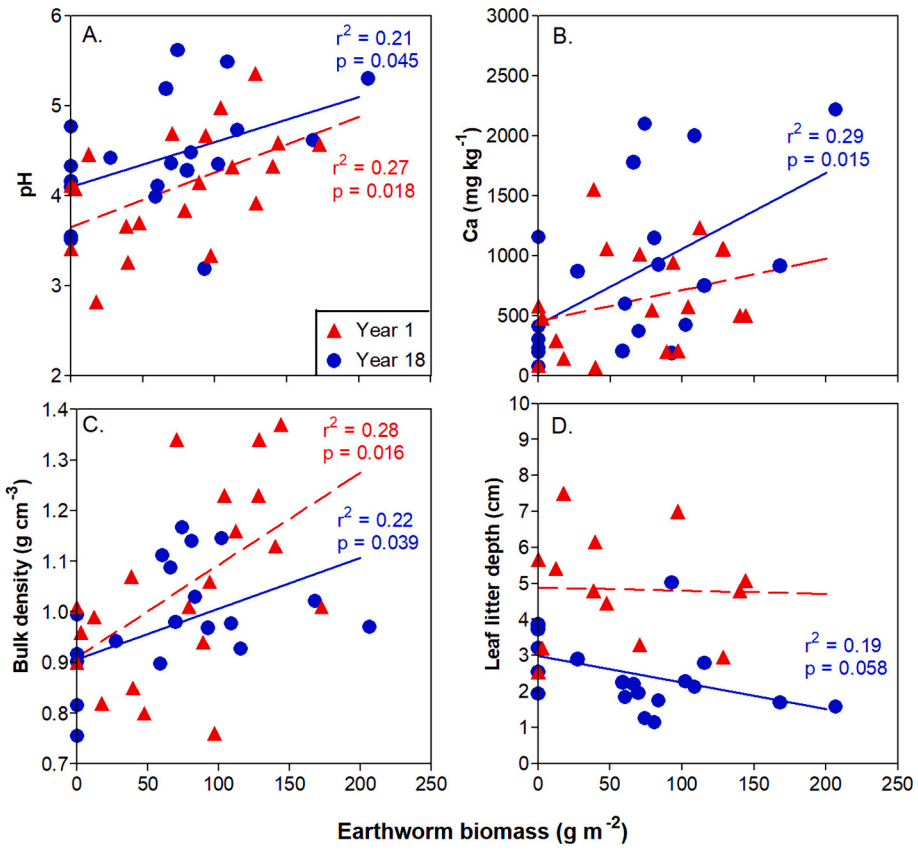

Fig. 4. Regression analysis of earthworm biomass (wet weight) and A.) the pH of the soil (soil pH was determined using a 1:2 soil-to-0.01 M $CaCl_2$ solution), B.) soil calcium (calcium was extracted using a 7.7 N HNO_3 acid solution), C.) bulk density (0–10 cm), and D.) summer leaf litter depth (cm). The dotted line is the Year 1 regression, and the solid line is the Year 18 regression.

Furthermore, bulk density and leaf litter depth changed between Year 1 and Year 18. A 10 % decrease in bulk density occurred, from 1.05 to 0.94 g cm^{-3} (Fig. 5A). The amount of leaf litter decreased by 44 % from Year 1 to Year 18 for all sampled plots along the gradient (Fig. 5B). However, there was no statistical change in earthworm biomass over time, but, even with these non-significant results, relationships between changes in earthworm biomass and changes in soil chemical/physical properties may exist. Therefore, to explore if earthworm biomass and density are related to changes in soil chemical and physical properties, the difference in biomass or density from Year 1 to Year 18 was regressed against the difference in soil chemical or physical properties (Ca, pH, bulk density, and leaf litter depth) from Year 1 to Year 18. However, no significant linear relationships were found.

4. Discussion

The general premise of the study was to examine changes in the earthworm communities of urban and rural forest patches and their influence on soil chemical and physical properties after 18 years. Differences in earthworm biomass and density along the urban–rural gradient were found, and, for the given years, earthworm biomass was strongly related to bulk density, leaf litter depth, Ca, and pH. Additionally, some changes were detected in earthworm community composition between the two sampling campaigns. Previous work focusing on forest soil properties along the urban-rural gradient in Baltimore found an increase in Ca concentrations and pH over approximately two decades (Yesilonis et al., 2022), while both bulk density and leaf litter volume (collected in Autumn) decreased over the same timeframe. However, the changes in soil properties and earthworm communities between the two years do not align in such a way that earthworm activity could be considered the sole driver of these soil changes. While earthworms are a key component affecting all physico-chemical and biological properties, in human-dominating systems, a multitude of interacting factors, including natural processes, human inputs, atmospheric deposition (nitrogen and pollutants), invasive plants, and deer browsing influence the trajectory of soil development.

4.1. Earthworm assemblages along an urban–rural gradient

All species detected in this study have been recorded either in Baltimore (Szlavecz et al., 2006; Tóth et al., 2020) or within the 60 km radius around the city (Szlavecz et al., 2018). Since the same species have been documented over the years, it may suggest stability in earthworm biodiversity. This consistency indicates that the habitat conditions remain suitable for these species and there haven't been drastic environmental changes over time that would influence populations. Contrary to expectations, jumping worms were caught only in the rural forests. However, numerous records of the presence of jumping worms (*Amynthas* spp. And *M. hilgendorfi*) in Baltimore City exist (Szlavecz unpublished; Chang et al., 2018), and the characteristic cast layer of these earthworms was also detected (Chang et al., 2021). The survey was conducted in the fall (October) and under relatively dry conditions. Dry conditions, coupled with the lack of leaf litter drives jumping worms to moist microhabitats (Snyder et al., 2011), such as dead logs (Chang et al., 2021) or riparian areas. The other reason they were not caught in the city is that their populations die back in the fall. In rural forests, the thick leaf litter layer provides food and shelter for these earthworms.

Earthworm biomass measured in this study was comparable to that in other studies of temperate hardwood (Edwards and Bohlen, 1996; Lee, 1985; Satchell, 1983), while density was higher. In general, both density and biomass were higher than in other urban forest studies

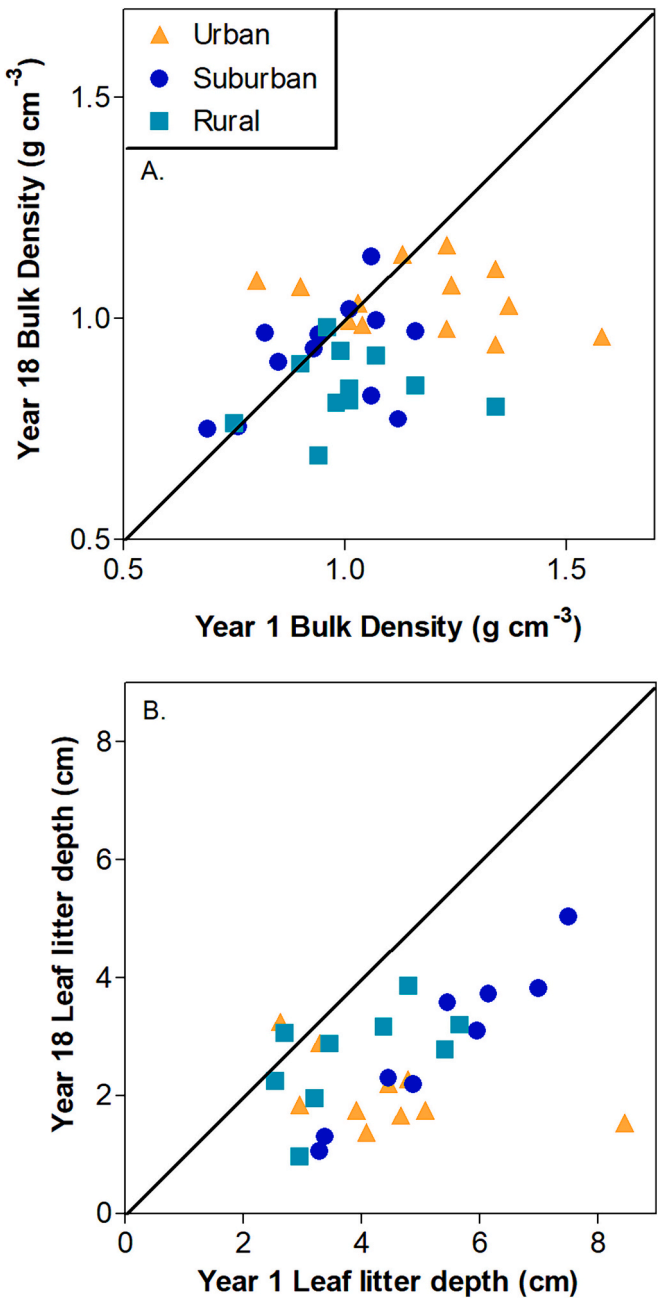

Fig. 5. Year 1 versus A) Year 18 bulk density (0–10 cm), and B.) Year 18 summer leaf litter depth (cm). The diagonal line represents the 1:1 line where there is no change between the years if the plots fall on this line.

(Heneghan et al., 2007; Tóth et al., 2020), although this may be due to differences in sampling methods or time of the year. The observed trends of higher biomass in urban areas and lower biomass in rural areas align well with findings from a study conducted along an urban-rural gradient in New York City (Steinberg et al., 1997) as well as a prior study in Baltimore (Szlavecz et al., 2006).

4.2. Earthworm abundance and soil properties

Earthworm activity, particularly invasive species, impacts soil structure by altering the composition and density of the uppermost layers. One of the most visible results of earthworm invasion is the disappearance of the loose, organic-rich upper horizon, often called the "duff layer" (Alban and Berry, 1994; Eisenhauer et al., 2007; Ma et al., 2014), as observed in the forest patches along the urban-rural gradient. Earthworms first consume the O layer and then incorporate organic material into the mineral layer, producing a "mull"soil. This process leads to higher bulk density of the surface soil and has been reported previously (Hale et al., 2005b; Yesilonis et al., 2016). Given these strong correlations between earthworm biomass and bulk density, and less so for earthworm biomass and leaf litter volume, the presence of a relationship between bulk density and leaf litter was suspected. The rationale is that bulk density is affected by the incorporation of the O horizon and leaf litter into the surface horizon by earthworms, but no strong correlation was found between bulk density and leaf litter.

While urban soils are generally considered to be compacted, higher bulk density in the urban forests was attributed to earthworm activity, especially as jumping worms dominate in the rural forests. These earthworms do not mix the litter layer in the surface horizon, and the loose cast they deposit on the soil surface keeps bulk density low. Given the modifications earthworms introduce to soil structure, it's important to understand the cascading effects on the ecosystem. The disappearance of the duff layer affects vegetation in these ecosystems. Plants often rely on the organic-rich duff layer for nutrients, water retention, and protection against soil erosion. Without this layer, certain native plants might struggle to thrive, potentially leading to a shift in plant community composition in North American hardwood forests invaded by non-native earthworms (Frelich et al., 2006; Hale et al., 2006).

As earthworm biomass increases, so does the pH of the soil. Desie et al. (2020) showed a below-ground feedback loop between earthworms, humus form, and soil pH that increased earthworm abundance in acidic European forests. Earthworms have been shown to increase pH for a couple of reasons: 1) earthworms incorporate organic humus into the surface horizon (Desie et al., 2020) and 2) some earthworm species produce Ca-rich casts (De Vleeschauwer and Lal, 1981; Lambkin et al., 2011) affecting pH values relative to surrounding soil. Similarly, there's a positive correlation between calcium and earthworm biomass. This relationship, though not as well-defined in Year 1, is evident in various studies. Earthworm abundance has been shown to correlate with Ca content in litter (Hobbie et al., 2006; Reich et al., 2005) and soil (Ponge et al., 1999). The relationship between earthworm activity, soil pH, and Ca concentration, is important to understand because of the broader ecological implications, for example, soil pH is a strong predictor of microbial community structure (Fierer and Jackson, 2006; Lauber et al., 2008; Rousk et al., 2010). Furthermore, with changes in pH and Ca levels, plant-soil feedbacks are affected (Wardle et al., 2004).

4.3. Earthworm assemblages in years 1 and 18

The two sampling efforts yielded 10 total species of earthworms with 5 species recorded in both years; two species were found only in Year 1 and three species only in Year 18 (Supplementary Table S1). In Year 1, *Ap. limicola* was abundant in all three urban forests and one suburban forest. As one of its common names, "European mudworm," indicates, this species is closely associated with wet conditions, such as riparian zones, forest vernal pools, and wetland ecotones. Its absence in 2018 may reflect drier conditions. Additionally, one of the forest sites, Cylburn Arboretum, experienced massive tree dieback, resulting in a more open patch and drier conditions. The other species found in Year 1 but not Year 18 was *D. patuxentis*, a small native earthworm in the family Acanthodrillidae. *Diplocardia* species in the region are endogeic and have low abundance.

The three species caught in Year 18 but not Year 1 were L. *castaneus*, *O. cyaneum*, and *Am. tokioensis*. One urban plot, Leakin Park, showed the largest change of earthworm species composition through the addition of all three species (Supplementary Fig. S2). Leakin Park is the largest of all the urban forests (176 ha compared to the other two urban plots of 14 and 47 ha), and the plots were widely distributed across the site. Its large size results in substantial variability in topography, soil moisture, vegetation, and many points of possible earthworm entry due to human

activity, which may explain the changes. Given that Leakin Park is the only forest that has been regularly monitored between the two sampling campaigns, this may reflect a real shift in the community composition.

In the past couple of decades, invasion by species in the family Megascolecidae, commonly referred to as jumping worms, has received considerable attention from different stakeholders. This "second wave" of earthworm invasion, which refers to invading jumping worms meeting resident communities (Chang et al., 2021), has been detected in the region (Szlavecz et al., 2018). While the European lumbricids are well established in many forested landscapes, including the urban forests in Baltimore, jumping worms represent a new, dynamic addition to the local earthworm assemblages. Furthermore, jumping worms create a granular cast layer, which has less structure than the existing soil, and may be more susceptible to soil erosion (Chang et al., 2021). Jumping worm (e.g., *Am. tokioensis*) biomass and density increased dramatically in one rural forest (Liberty Reservoir).

Human dispersal of earthworms has been shown to be more important to expanding populations than diffuse dispersal mechanisms such as road networks or earthworm mobility itself (Cameron et al., 2008). As Liberty Reservoir is a popular fishing spot, fishermen may dump earthworms as bait on the forest floor. Earthworms or their cocoons are transported by vehicles (Callaham et al., 2006; Cameron et al., 2007; Dymond et al., 1997; Gundale et al., 2005), which are important vectors within forested systems. Additionally, they spread as juveniles or cocoons through leaf piles and yard waste bags (Chang et al., 2021); evidence was found for this in Liberty Reservoir (Supplementary Fig. S4). Only jumping worms were caught at this site, and the soil profile was also characteristic of jumping worm activity with a loose cast layer on the surface and no evidence of mixing (Supplementary Fig. S5). This soil profile reflects real change rather than fluctuations over time.

4.4. Earthworm changes related to soil chemical and physical changes

Given the significant impact of earthworms on soil properties, it was expected that the forests showing the greatest change in soil properties would also exhibit the greatest difference in earthworm abundance and/or community composition. While in each year, earthworm biomass strongly correlated with bulk density, leaf litter depth, pH, and Ca, a correlation was not found between the rate of change of those soil properties and the rate of change in earthworm abundance. Possible reasons for the lack of this relationship are as follows: 1) Biomass and density did not change as much as anticipated, however even without measurable change, earthworm biomass and community composition could put steady and consistent cumulative pressure on soil change; 2) soils and earthworm communities change at different time scales; 3) assessing earthworm populations at two time points may reflect fluctuations as opposed to a trend, while changes in soil properties tend to be cumulative over time; and 4) in the heterogeneous urban landscape, differences in forest patch size, the impact of the surrounding landscape, site history, topography, and underlying parent material complicated the analysis.

As a key invertebrate group, earthworms can fundamentally alter the pathway of soil development (Ma et al., 2013; Yesilonis et al., 2016), but other factors influence this process. The amount of leaf litter, a dynamic resource component in seasonal forests, is known to correlate with the abundance of litter-feeding earthworms (e.g., Szlavecz et al., 2018). Again, there was a clear negative relationship within each year but not between years. Additional factors affecting leaf litter amount include variations in primary productivity, biotic activity, and decomposition rate, all of which are related to climatic fluctuations.

Changes in soil organic matter may affect bulk density, as higher organic matter concentrations result in lower bulk densities (Arvidsson, 1998; Honeysett and Ratkowsky, 1989; Soane, 1990; Zhang et al., 1997). However, soil organic matter slightly decreased over time (7.3 % in Year 1 and 6.9 % in Year 18), which should increase bulk density. This suggests soil organic matter may not provide a good explanation for the lower bulk density values found after 18 years. Additionally, earthworm assemblages consist of several ecologically different species occupying different niches in the physical and functional space (Bottinelli and Capowiez, 2021; Hsu et al., 2023). Different species assemblages impact the soil differently, as shown by Hale et al. (2005b) for bulk density, and the direction of the effect depends on initial conditions (Fahey et al., 2013). A more detailed analysis of earthworm ecological groups and their temporal dynamics will provide a better insight into their long-term effects on soil properties, including bulk density.

Long-term (decadal or longer) data on earthworm communities are rare (Beylich and Graefe, 2009; Butt et al., 2022; Szlavecz et al., 2018), and most focus on successional trends (Eisenhauer et al., 2007; Hale et al., 2005a; Resner et al., 2011; Tiunov et al., 2006). Results of two sampling campaigns 18 years apart should be interpreted differently for soil properties and earthworm assemblages. On the one hand, soil properties are more likely to reflect a real change due to the slower, gradual, and cumulative nature of soil development, especially in forest patches that are less exposed to major disturbances compared to other land uses in the urban landscape. On the other hand, earthworm assemblages can fluctuate seasonally, annually, or due to discreet disturbance events, therefore continuous monitoring is necessary to detect real trends. Furthermore, considering the site's historical data, certain distinctions, like the growing prevalence of jumping worms in rural areas, indicate real trends. These trends, therefore, justify the need for ongoing monitoring.

An examination of changes in soil properties related to changes in earthworm populations in areas where there exist stable populations may not yield causal relationships. However, changes in earthworm biomass and density may have a predominant influence on soil change in forest soils that have not previously contained earthworms. These forests, at least in the mid-Atlantic and northeast USA, are few and far between, but if baseline data could be collected before earthworms established themselves, differences in soil chemical and physical properties should strongly relate to changes in earthworm biomass and density.

5. Conclusion

This study is the first to resample an urban–rural forest patch gradient to investigate earthworm community changes and relate them to changes in soil characteristics. First, earthworm community assessment revealed different biomass and densities at the urban (and suburban) end of the gradient compared to the rural end of the gradient, suggesting different management approaches in urban and rural forest. Second, there were clear relationships between earthworm biomass and density and soil properties (leaf litter depth, bulk density, Ca, and pH) within a given year. Third, Asian pheretimoids or jumping worms are expanding zones in rural forests. Even though there are no proven methods to eradicate jumping worms on a large scale, it is still important to understand how they are advancing. Managers can implement public awareness campaigns in areas devoid of jumping worms to avoid infestations in these areas. Finally, while soil properties, such as leaf litter depth, bulk density, Ca, and pH changed in the past two decades, the earthworm community stayed relatively stable suggesting additional factors shaping soil development. These might include changes in tree composition, understory vegetation, deer browsing, nitrogen deposition, and, in urban landscapes, inputs from construction and other factors.

CRediT authorship contribution statement

Ian Yesilonis: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Sarah Placella:** Writing – review & editing, Methodology. **Csaba Csuzdi:** Writing – review & editing, Methodology. **Katalin Szlavecz:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2024.105534.

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