

REVIEW

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# Earthworm effects on soil biogeochemistry in temperate forests focusing on stable isotope tracing: a review

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## Abstract

Earthworms (Oligochaeta) are globally distributed soil-dwelling invertebrates that alter soil properties through feeding, casting, and burrowing behaviors. Soil physicochemical modification, which may directly influence the availability and dynamics of organic and inorganic nutrients in the soil, such as carbon and nitrogen, includes soil texture, porosity, and pH. Temperate forests produce year-round plant litter, the primary food source for earthworms, and litter processed by earthworms significantly contributes to soil organic material storage. In recent decades, studies on temperate forest ecosystems have attempted to elucidate and quantify the earthworm impact on soil organic material dynamics, mainly targeting carbon and nitrogen, using isotope analysis methods. This paper summarizes studies on the following topics: (1) effect of earthworm modification on soil property to understand these alterations' interaction with carbon and nitrogen dynamics, and (2) isotope tracing method, used to elucidate the earthworm effect on carbon and nitrogen transformation and movements in temperate forests. The particular emphasis on the isotope method is based on its capability of time-adjusted quantification of organic materials in the ecosystem compartments. Also, isotopic labeling in biomass has a broad range of applications, such as tracing assimilated food sources, identifying trophic interactions in soil food webs, and addressing material dynamics in complex linkages between earthworms and their environment. In addition, we provide perspectives on other methodologies, such as chronology and population ecology, as feasible options to further assist the isotope tracing of earthworms' impact on soil nutrient dynamics.

**Keywords:** Earthworm, Temperate forest, Soil organic material (SOM), Carbon and nitrogen, Nutrient cycling, Stable isotope tracing

## Introduction

Earthworms are universally distributed soil invertebrates found in natural and artificial ecosystems, including forests, grasslands, agricultural lands, orchards, and gardens [1]. Since earthworms are ectotherms and engage in cutaneous respiration in which gas exchange occurs through their moist, mucus-rich skin, they are abundant in warm and humid areas across temperate, subtropical, and tropical regions [2]. Amongst these habitats, earthworms

have preferences for soil with pH ranging between 5.96 and 8.65 and organic carbon contents over 1% [3]. Still, earthworm distribution varies because of their species-specific traits and food preferences [4].

Earthworms feed on mineral soil and associated soil organic material (SOM), such as litter from fine roots, fallen leaves, and branches [5]. Hence, forests and grasslands that yield year-round litter possess abundant earthworm communities. In several temperate and tropical regions, earthworms account for 40–90% of the soil macrofauna [6–8] and play a vital role in nutrient recycling and reuse [9].

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There are diverse research disciplines involving earthworms, including biogeochemistry, ecotoxicology, biodiversity, taxonomy, and vermicomposting [10]. Especially in the ecological field, investigations on earthworm biodiversity have been undertaken globally [11]. According to Phillips et al. [11], who reviewed the earthworm biodiversity monitoring conducted in the post-2000s, studies targeting the broadleaf deciduous forests and forest–grassland areas accounted for over 60% of the total study sites, highlighting the significance of temperate forests as earthworm habitats.

Compared to biodiversity investigations, fewer studies on biogeochemistry were conducted, and in limited regions. Previous review studies that addressed earthworms' effects on soil biogeochemistry focused on (1) tracking elements' (carbon, nitrogen, and phosphorus) quantitative partitioning in their pools and SOM transformations, (2) pedologic processes of soil layers, and (3) interactions between soil fauna according to material reallocation. Most investigations were undertaken on arable lands and grasslands, while forests accounted for a small proportion. Forests, grasslands, and arable lands differ in organic material input pattern and litter quality, so litter decomposition and SOM storage also vary with land type [12]. In general, dissolved organic matter concentrations of soil follow the order forests > grasslands > arable lands, mainly because of vegetation compositions [13–15]. Also, among management practices in arable lands, mineral fertilization and tillage, decrease SOM levels in the long run [16] and earthworm populations of deep burrowing species, [17] respectively. The SOM dynamics of forests are expected to be significantly different from those of arable lands, so this paper focuses on mechanisms within the scope of forests.

Litters are dead plant biomass comprised of cellulose, hemicelluloses, lignin, proteins, hormones, and other substances [18]. Plants synthesize and store organic compounds made up of nutrients, such as carbon and nitrogen. Dead plant biomass on the ground, a food source for soil fauna constituting organic compounds, is mineralized and released into the atmosphere as carbon dioxide, but most of it is fragmented and stored as SOM [5]. SOM takes a longer time, from months to decades, to be mineralized [19]. It is reported that forest soil holds more than 40% of the organic carbon among terrestrial carbon reservoirs [20, 21]. Small labile organic compounds and mineralized inorganic nutrients are reabsorbed into soil fauna or plant roots and again stored as biomass [18].

Furthermore, they are delivered to herbivores and predators of the upper food chain throughout the ecosystem. Therefore, litters are significant nutrient sources that sustain soil biota and ecosystems [22]. Earthworms decompose litter three times quicker than other invertebrates,

such as springtails and enchytraeids, considering their biomass, density, and collaboration with gut microbiota possessing the ability to break down carbohydrate polymers [18, 23]. Sometimes, earthworms can consume the entire leaf-fall in deciduous temperate forests [24, 25].

Temperate forests are characterized by the massive seasonal production of litter during autumn [26] and are usually categorized into four stand types: broadleaf deciduous, needleleaf evergreen, needleleaf deciduous, and mixed [27]. Global analysis on annual litterfall ranged between 3 and 11 Mg ha<sup>-1</sup>, which varied significantly by the forest stand types [26]. In a meta-analysis study, root and leaf litter were reported to account for 48% and 41% of annual litters, respectively [28]. Also, more than 70% of the above-ground litter consists of leaf tissue; the rest are stems, twigs, and other components [29], but the proportion of wood material rises with increasing stand ages [30, 31]. Accordingly, the production and decomposition of plant biomass determine temperate forests as a substantial carbon source and sink [27, 32, 33]. Earthworm decomposition has been investigated mostly on leaves rather than root litter, despite the potential contribution of roots due to (1) massive leaf litter production during autumn and (2) difficulties in underground experimental observations.

The traditional approaches for soil property modification and material cycling by earthworms rely on direct observation of their feeding activities, microscopic examinations of gut contents, palatability test, estimation of ingestion, consumption, and growth rates [34]. However, each method consumes considerable time and provides limited information about the feeding strategy and the assimilated dietary components. Experimental designs include incubating earthworms within chambers placed in laboratories (microcosm) or outdoor fields (mesocosm). Mesocosm studies reflect natural climatic conditions such as temperature and humidity.

Isotope analysis emerged as a powerful research tool for animal ecology [35], and earthworm research could also benefit from its application [36]. For SOM tracing, ratios of stable isotope pairs, mostly <sup>13</sup>C/<sup>12</sup>C and <sup>15</sup>N/<sup>14</sup>N, are measured using isotope ratio mass spectrometry [37]. One advantage of the isotopic method is that isotopes can be employed as tracers in undisturbed soil of field settings. Environmental conditions vary significantly in scale and frequency between indoor and outdoor experiments; the application of isotope analysis provides a much simpler design, advantage, and accuracy to field experiment measurements. These methods also trace assimilated food materials, identify trophic interactions of earthworms in soil food webs, and address nutrient dynamics in complex linkages of earthworms and their environments [38]. Furthermore, labeling isotopes enable

evaluation of their mean residence time and the half-life time in compartments. The mean residence time corresponds to the stock-to-exchange rates, which is not an intrinsic property of a compartment [39].

In the present paper, we synthesize recent discoveries of earthworm-derived biogeochemical changes in temperate forest soil and potential carbon and nitrogen dynamics, followed by litter and SOM decomposition. We also examine the current and latest methodologies for material dynamics to suggest future directions that may add more precision and efficiency to related studies, with particular implications regarding isotope tracing methods.

Hence, we have adopted the scoping review methodology [40] for this paper to generate a comprehensive literature review about the contribution of earthworms to soil biogeochemistry and isotopic measurements. The reviewed literature was restricted to peer-reviewed publications and grey literature from approved international bodies. The published online research was collected from Google scholar, Scopus, Web of Science, and Science Direct databases. The online catalog gathered published articles, books, book chapters, and doctoral dissertations from various libraries. Especially for the latest isotopic research addressed in the “[Isotope techniques for studying soil nutrient cycling by earthworms](#)” section, we sorted publications between January 1st, 1999 and November 1st, 2022. The search was limited to the following keywords to clearly indicate the main focus of our paper: temperate forests, carbon and nitrogen isotopes, litter decomposition, and SOM. Even in references, we excluded results from non-temperate forest sites and indoor experiments that used agricultural soils.

## Earthworms, soil, and nutrient cycling

### *Earthworms and soil properties*

Earthworms are ecosystem engineers that have considerable physical, chemical, and biological alterations in their habitats [41, 42] through their burrowing, feeding, and casting activities. Earthworms' vertical and horizontal burrowing activity affects the soil structure, resulting in a distinctive soil layer known as the drilosphere [43]. Studies have reported other earthworm-derived modifications on increasing soil porosity [44] and aggregate stability [45]. Also, water and air penetrate deeper soil through the earthworm burrows and promote the activity of aerobic microorganisms [46–48].

Earthworms' feeding activity greatly influences soil chemical properties. Earthworm-derived chemical modifications include soil pH [49], cation exchange capacity (CEC) [50], carbon and nitrogen stock [51–53], and inorganic nutrient contents, such as potassium and magnesium [54]. Along the earthworm intestinal tract, organic

materials are fragmented, converted into readily available carbon compounds or minerals and mixed with mucus; some are assimilated into biomass and the rest are released into bulk soil [55–57]. Moreover, earthworms carry organic materials into deeper soil, causing a vertical redistribution of nutrients [58, 59].

Earthworm casts are rich in labile carbon and nitrogen compounds, calcium, potassium, and magnesium compared to bulk soil because of their selective feeding and digestion of litter [4, 38, 60, 61]. Such chemical modification of soil promotes the activity of the surrounding microbiome and nutrient uptake of plant roots [62]. The estimated production of earthworm casts ranges between 31 and 293 kg year<sup>-1</sup> per 100 g m<sup>-2</sup> of earthworms [63–65]. The value varies depending on physical environmental conditions and earthworm species [66].

Soil's physical and chemical properties constantly interact with each other. For instance, earthworm casts with high organic matter content easily bind the surrounding soil particles, which promotes soil aggregate formation [67]. Soil aggregate content and porosity are positively correlated and lead to soil aeration and substrate infiltration.

Earthworm mucus is another driver for soil aggregate formation and organic material dynamics [68]. It is a water-soluble mixture of diverse saccharides, such as glucose, galactose, glucosamine [68], aminoacid [69], and glycoproteins [70]. Microbes utilize mucus as an energy source, so they are abundant and active in earthworms' intestines and mucus [71]. Likewise, there is also a high microbial population on the inner wall of the earthworm burrows [72, 73]. According to Scheu [74], daily carbon loss due to mucus production accounted for 0.2–0.5% of the total animal carbon in the case of *Octolasion lacteum*, which is an abundant species in temperate forests [74]. Daily mucus excretion of 1 g of earthworms is approximately 5.6 mg in dry weight [75, 76].

### *Soil properties and nutrient cycling*

As briefly addressed in the previous section, soil properties directly influence the availability and dynamics of soil nutrients. Among them, soil pH is the primary regulating factor of litter decomposition, primarily dependent on the soil fauna activities [77]. It is known that soil microbial biomass carbon and nitrogen, and the microbial community (e.g., nitrifiers) in soil positively correlate with soil pH [77]; soil acidity is often a limiting factor for bacterial activities [68].

In addition, organic carbon mineralization tends to represent higher rates in finely textured soils with low C:N ratios [78]. Soil containing more than about 15% clay can form aggregates, which can longer retain organic compounds [79]. Soil aggregates act as a reservoir for

labile organic compounds, offering protection from microbial degradation [80]. Moreover, clay minerals have a large specific surface area and surface charges, stimulating interactions with SOM and other minerals [81]. One study examined SOM storage in silt loam and sandy loam soils and reported that the latter had lower total carbon and nitrogen contents and minor concentrations of available nitrogen [80]. Also, low soil porosity often forms anaerobic microclimates in soil, with increased activities of anaerobic bacteria communities, including nitrogen fixers [82].

### Isotope techniques for studying soil nutrient cycling by earthworms

As we indicated in the previous section, isotope tracing is a promising method for material cycling in ecosystems. There are two general strategies in isotope analysis: natural abundance measurement and isotope labeling. The former method measures the naturally occurring isotope ratios. Since earthworms feed on mineral soil and SOM, it depends on the known isotopic ratio differences between food sources instead of the ratio linked to the original trophic hierarchy [83].

The isotope labeling method usually uses biomass (e.g., plant materials with artificially enriched isotope content) cultured in an airtight plant growth chamber provided with  $^{13}\text{CO}_2$  for photosynthesis and water-soluble  $^{15}\text{N}$ -inoculated substrates as nutrients. Isotope labeling is used to observe maximized changes by increasing the quantity of the isotopes, as the proportions of the isotopes are naturally very small ( $^{13}\text{C}\approx 1\%$ ,  $^{15}\text{N}\approx 0.4\%$ ).

This section addresses the latest studies on earthworm contribution to SOM dynamics using  $^{13}\text{C}$ ,  $^{14}\text{C}$ , and  $^{15}\text{N}$  analyses conducted in temperate forests globally. Table 1 represents studies in this scope with related methodology and major findings. These studies measured isotopes in soil, leachate, plant and mycorrhizal tissue, earthworm tissue, mucus, and casts to examine the earthworm-induced partitioning of nutrients in ecosystem compartments. The earthworm's species-specific preference for food sources and contribution to soil respiration were also investigated with isotopes. Earthworms' interaction with other organisms was studied by quantifying earthworm-derived carbon movement within the soil food web. Lastly, several cases have examined the soil structural alteration related to nutrient storage.

### The feeding ecology of earthworms

The feeding ecology of earthworms has been effectively investigated in several studies using the natural abundance of isotope ratio. In Northeast Asia, Uchida et al. [84] measured the natural masses of  $^{13}\text{C}$  and  $^{15}\text{N}$  in earthworm tissue, gut contents, and soil layers to examine the

feeding behaviors of several earthworm species. This study identified the vertical spatial niches and available food sources that vary according to earthworms' functional groups (epigeic, endogeic, or anecic group). Values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  typically increased from litter to deeper soil, and  $\delta^{15}\text{N}$  from earthworm tissue indicated that epigeic earthworms exploited resources in the early stages of decomposition of fresh litter, whereas endogeic earthworms consumed more degraded substances [84].

On the other hand, Bohlen et al. [51] reported earthworms' food preference and selection of leaf litter rather than stem and twig litters, based on different  $\delta^{13}\text{C}$  values among the forest floor materials. In shallower mineral soil,  $\delta^{13}\text{C}$  directly reflected that of remaining litter types that have neglected by earthworms [85].

Schmidt et al. [86] examined the carbon turnover within an earthworm using  $\delta^{13}\text{C}$ . They reported that when the earthworm food source switched from clover ( $\text{C}_3$  plant) to maize ( $\text{C}_4$  plant), the dietary  $\delta^{13}\text{C}$  signature was altered more rapidly in the mucus (4‰) than in the tissue (1‰) [86]. They also revealed that starvation does not cause  $^{13}\text{C}$  and  $^{15}\text{N}$  isotope ratio shifts in earthworms, but causes decreased mucus and tissue C:N ratio [86].

In addition, the soil food web was more enriched by the  $^{13}\text{C}$  from fine roots than from above-ground litter, with rapid fine root decay ( $k=0.9\text{ year}^{-1}$ ) [87]. This implies the potential significance of fine roots as a source of SOM processed by earthworms, as well as leaf litter.

### Species-specific traits of earthworms

Earthworms have interspecific variations in food preferences and ecological functions. Fahey et al. [57] investigated earthworm-induced sugar maple litter decomposition with different functional groups of earthworms [*Lumbricus terrestris* (anecic) and *Lumbricus rubellus* (epi-endogeic)]. Of  $^{13}\text{C}$  labeled litter, 37% was decomposed because of the elimination of forest floor, and loss of SOM and decrease in C:N ratio were observed; recovery of  $^{15}\text{N}$  was higher than  $^{13}\text{C}$ , with lower values for *L. terrestris* than *L. rubellus*, because higher overwinter activity of *L. terrestris* consumed more soil nitrogen [57].

Chang et al. [88] categorized earthworm species by origin, from exotics of Europe and Asia to natives of North America, to assess the species-specific and interspecific effect on litter decomposition and soil respiration (efflux of  $^{13}\text{CO}_2$ ). The interaction between the European species—*Octolasion lacteum* and *Lumbricus rubellus*—had a significant adverse impact on soil respiration, presumably by increasing anaerobic soil microsites. Moreover, litter-derived soil respiration was reduced by the Asian *Amyntas hilgendorfi* and *L. rubellus*, and by the North American *Eisenoides lonnbergi*, but not by *O. lacteum*

**Table 1** Studies on earthworm impact of nutrient dynamics using isotope methods conducted in temperate regions

Country Ecosystem	Tree species	Earthworm species	Study period	Isotope types	Major findings	References
Japan Evergreen broad-leaved forests	<i>Quercus crispula</i> , <i>Cinnamomum camphora</i> , <i>Castanopsis cuspidate</i> var. <i>sieboldii</i>	<i>Metaphire soubensis</i> , <i>Amyntas</i> spp.	1 time measure	<sup>13</sup> C, <sup>15</sup> N	Values of δ <sup>15</sup> N increased from litter to humus, to deeper soil; and the value of body tissue was higher in endogeic than in epigeic earthworms. Such <sup>15</sup> N enrichments indicate that the niches of earthworm species were affected from available food sources	Uchida et al. [84]
Ireland Artificial substrate	–	<i>Lumbricus festivus</i>	14 days	<sup>13</sup> C, <sup>15</sup> N	Earthworm diet switched from clover (C <sub>3</sub> ) to maize (C <sub>4</sub> ); the dietary δ <sup>13</sup> C signature altered more rapidly in the mucus (4‰) than in the tissue (1‰)	Schmidt et al. [86]
Germany	<i>Fagus sylvatica</i> , <i>Fraxinus excelsior</i>	<i>Octolasion tyrtaeum</i>	100 days	<sup>14</sup> C	Earthworms' mineralization on <sup>14</sup> C labeled lignin was more pronounced in treatments without (+ 14.1%) than in those with (+ 8.6%) mineral soil (Bw-horizon) because of earthworm's mixing of soil layers	Marhan & Scheu [97]
Deciduous broad-leaved forests	–	<i>Aporrectodea caliginosa</i> , <i>Lumbricus terrestris</i>	3 years	<sup>15</sup> N	6–14% of <sup>15</sup> N released from leaf-litter was recovered in plants. Earthworms increased plant acquisition of nitrogen from <sup>15</sup> N enriched leaf-litter; and higher degradability of litter resulted in the higher acquisition of nitrogen	Yang et al. [90]
Germany Artificial substrate	–	<i>Lumbricus terrestris</i>	7 days	<sup>13</sup> C, <sup>15</sup> N	<sup>15</sup> N-labeled earthworms can transfer <sup>15</sup> N through food web, into soil, plants, and aphids. <sup>15</sup> N incorporation was highest in earthworm casts (11,751‰) followed by earthworm tissue (454‰), plant roots (62‰), leaves (50‰), and aphids (37‰)	Grabmaier et al. [89]

**Table 1** (continued)

Country	Tree species	Earthworm species	Study period	Isotope types	Major findings	References
United States of America	<i>Acer saccharum</i> , <i>A. rubrum</i> , etc	<i>Lumbricus terrestris</i>	1 time measure	<sup>13</sup> C, <sup>15</sup> N	Earthworm presence decreases δ <sup>13</sup> C of forest floor materials and mineral soil because they prefer leaves as food sources which have higher δ <sup>13</sup> C than stem and twigs	Bohlen et al. [51]
	<i>Acer saccharum</i>	<i>Lumbricus terrestris</i> , <i>Lumbricus rubellus</i>	2 years	<sup>13</sup> C, <sup>15</sup> N	<sup>13</sup> C-labeled litters had higher recovery without (61–68%) than with (20–29%) earthworms. Recovery of <sup>15</sup> N was higher than <sup>13</sup> C, with lower values for <i>L. terrestris</i> than <i>L. rubellus</i>	Fahey et al. [57]
	No data	<i>Amyntas hilgendorfi</i> , <i>Lumbricus rubellus</i> , etc	21 days	<sup>13</sup> C	Litter carbon-derived soil respiration was reduced by <i>A. hilgendorfi</i> , <i>L. rubellus</i> , and <i>Eisenoides lonnbergi</i> , but not by <i>Octolasion lacteum</i>	Chang et al. [88]
	<i>Acer saccharum</i>	<i>Lumbricus terrestris</i> , <i>Lumbricus rubellus</i>	6 years	<sup>13</sup> C	Earthworms stimulated carbon storage into soil aggregates. Soil food web was more enriched by <sup>13</sup> C from roots than above-ground plant-litter	Fahey et al. [87]



**Table 1** (continued)

Country Ecosystem	Tree species	Earthworm species	Study period	Isotope types	Major findings	References
Deciduous broad-leaved forests	<i>Acer saccharum</i>	<i>Lumbricus terrestris</i> , <i>Lumbricus rubellus</i>	7 months	$^{13}\text{C}$ , $^{15}\text{N}$	$^{15}\text{NO}_3^-$ added to the soil was rapidly depleted in the presence of earthworms due to less retention of nitrogen in litter and upper soil layers, but not due to the acceleration of water penetration	Ewing et al. [96]
	<i>Acer saccharum</i>	Community dominated by <i>Lumbricus rubellus</i>	3 years	$^{13}\text{C}$ , $^{15}\text{N}$	$^{13}\text{C}$ - and $^{15}\text{N}$ -labeled litter input in earthworm-invaded plots resulted in greater $^{13}\text{C}$ and $^{15}\text{N}$ of microbial biomass than the inorganic nitrogen pool; depletion of carbon and maintenance of soil nitrogen pool are caused by earthworm stimulation of microbial biomass and activity	Groffman et al. [91]
	<i>Populus grandidentata</i> , <i>Quercus rubra</i> , <i>Acer rubrum</i> , etc	Community dominated by <i>Dendrobaena octaedra</i> , <i>Aporrectodea</i> spp., etc	150 days	$^{13}\text{C}$ , $^{15}\text{N}$	Recovery of litter $^{15}\text{N}$ depends on soil texture; it was greater in sandy loam (98.2%) than in sandy soil (66.2%) after earthworm additions. Earthworm tissue was a minor sink for $^{13}\text{C}$ (0.56%) and $^{15}\text{N}$ (2.26%), which was delivered from surface litter	Crumsey et al. [98]

[88]. The decrease in soil respiration may be due to earthworm-induced aggregate formation and ensuing reduction in microbial decomposition of labile carbon [88].

#### **Nutrient recycling between organisms, including earthworms**

Isotopes labeling in earthworm biomass can assist in investigating below- and above-ground interactions through the food web [89]. Grabmaier et al. [89] used  $^{15}\text{N}$ -labeled earthworms by culturing them with leguminous herbs and aphids. They observed earthworm-derived  $^{15}\text{N}$  incorporation into plant leaves (50%), root and mycorrhizal fungi (62%), and aphids (37%) [89]. The results quantitatively revealed the course of plants' utilization of nitrogen-containing nutrients to start from earthworm casts into plant compartments followed by delivery to associated organisms, such as symbiotic fungi and sap-sucking herbivore aphids.

Similarly, two studies were conducted in the European temperate forests by Yang et al. [90] and Marhan & Scheu [97]. Concerning litter quality, Yang et al. [90] used  $^{15}\text{N}$ -labeled ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) leaf-litter and measured the  $^{15}\text{N}$  reuptake of each tree species from earthworm casts [90]. Earthworms and mycorrhizal fungi participated in 2–7% nitrogen recycling from leaf litter and uniformly increased plant acquisition of leaf-derived nitrogen.

Earthworms' effects on soil materials and structures ultimately result in soil microbiome abundance and activities. Groffman et al. (2015) witnessed that the  $^{13}\text{C}$ - and  $^{15}\text{N}$ -labeled litter input in earthworm-invaded plots resulted in greater  $^{13}\text{C}$  and  $^{15}\text{N}$  microbial biomass than in the mineral nitrogen pool. The depletion of soil carbon and soil nitrogen maintenance was observed, presumably caused by earthworm stimulation of microbial biomass and activity [91]. This may be a mechanism for nitrogen retention in carbon-rich soil in response to the earthworm invasion [91]. This result is opposite to several pieces of research, conducted in agricultural or mixed soils, reporting a reduction in microbial biomass and increase in nitrogen turnover by earthworms [92, 93]. This could have reflected the difference in soil quality (e.g., SOM contents) and earthworm mixing of soil horizon [94]. Due to the tight coupling of soil carbon and nitrogen dynamics, earthworm impact on nitrogen cycling in forest soils is inseparable from litter quantity and qualities [51].

#### **Earthworm-induced soil nutrient storage**

Temperate deciduous forests in North America are characterized by exotic earthworm invasions from Europe and Asia, majorly due to human settlement and agriculture [95]. Earthworm invasion has caught the interest of scientists since the early twentieth century, when an

earthworm-induced modification to soil was observed. For instance, Ewing et al. [96] examined the physical reconstruction of soil layers by earthworms in terms of hydrology. It was found that  $^{15}\text{NO}_3^-$  added to the soil was more rapidly utilized in the earthworm-invaded plots than in uninvaded plots due to less nitrogen retention in litter and upper soil layers, but not due to the acceleration of the water infiltration stimulated by earthworm burrows [96].

Likewise, earthworms' effect on soil physical structure can be attributed to carbon retention. Marhan & Scheu [97] combined  $^{14}\text{C}$ -labeled lignocellulose decomposition with earthworm mixing of mineral soil layers. Earthworms' mineralization of lignocellulose was greater in treatments without (+14.1%) than in those with (+8.6%) mineral soil of Bw-horizon [97]. This may be because earthworm mixing of carbon-devoid mineral soil with earthworm casts containing  $^{14}\text{C}$  organic materials decreased microbial activities.

Soil texture is another factor that controls earthworms' effects on soil nutrient storage. Crumsey et al. [98] found that nitrogen retention was higher in sandy loam than in sandy soil [98]. Besides, Fahey et al. [87] exploited carbon storage inside soil aggregates amongst silt and clay [87]. Carbon inoculated in silt and clay remained roughly constant through time;  $^{13}\text{C}$  recovery declined only by 0.8% after 5 years.

#### **Future directions and suggested methodologies**

Most studies conducted in temperate forests or laboratories using soil from the temperate forests targeted *Lumbricus* spp. from limited functional groups. However, various earthworm species coexist as communities in forests, occupying distinct niches utilizing soil environmental heterogeneity [99]. Thus, monitoring an isolated species may not reflect intraspecies interactions and their full impact on SOM. In addition, when assessing the earthworm communities in quantitative studies, it is crucial to specify earthworm species composition and temporal fluctuations of earthworm density ( $\text{n m}^{-2}$ ) and biomass ( $\text{g m}^{-2}$ ) for the same reason. Such information may support the meta-analysis to synthesize and generalize earthworm effects in various ecosystems. Disciplinary integration of population ecology and ecosystem ecology to elucidate the impact of forest earthworm populations on nutrient cycling is one method for considering earthworms' life cycle and their changing density and biomass.

Extending our knowledge of forest-dwelling earthworms' lifecycles and seasonal population dynamics may support investigation of their apparent species-specific capabilities. However, monitoring in a timescale ranging from months to years can be an alternative to assessing earthworm influence without precise prior knowledge,



since very few cases have revealed earthworms' lifecycles. Developing such a method is especially in demand since hand sorting and mustard powder methods, mainly used in fields to sample earthworm individuals and assess their distributions, remain controversial in terms of their accuracy.

Forests invaded by exotic earthworms provide the best conditions for observing the changes induced by earthworm activity. North American temperate forests are attracting attention as new research destinations because of earthworm invasion in recent decades due to farming and climate change [51, 100]. Some studies utilize chrono-sequential analysis based on regional invasion time and following soil modification. The chrono-sequential analysis has the advantage of field measurement on a broader area compared to that of the mesocosm study, which cultures earthworms in a chamber installed in fields. Also, earthworm invasion is expected to become more frequent in higher latitude regions because of climate change and other anthropological factors. As such, chronosequence methodologies may be powerful tools that provide insight into earthworm-induced SOM dynamics. In addition, phylogenetic studies can further strengthen earthworms' impact on material cycling by analyzing their genetic correspondence of morphological, physiological, and ecological characteristics.

Leaf litter is a widely used material in experimental studies related to earthworm feeding. However, other parts of plants, such as fine roots and twig residues, are also essential sources of SOM for earthworms. Still, little is known about the earthworm's attribution to their decomposition [38, 101, 102]. Rhizotron is a practical tool for related research as it can visualize below-ground soil profiles and monitor root development in real time. Vidal et al. [103] investigated the decomposition stages of the  $^{13}\text{C}$ -enriched shoot and root litters in earthworm casts [103]. The different chemical compositions between shoot and root tissues appeared as a driving factor for their distinct decomposition processes. NanoSIMS (nanometre-scale secondary ion mass spectrometry) was used in that study to obtain microscale spatial images and monitor the changes in the structure and distribution of target organic materials, such as tissue walls.

We must verify correlations between environmental conditions of study sites and earthworm activities during material cycle studies to calibrate measurements. For instance, air temperature increases soil respiration and reduces soil carbon stocks, and soil texture is one factor that affects organic material stabilization by effectively binding SOM. Investigations in a broader region of different temperatures, humidity, and soil characteristics with a unified method are recommended to assess interactions between abiotic factors and earthworms.

## Conclusions

This paper addressed the earthworm influences on soil physicochemical properties and on carbon and nitrogen dynamics in temperate forest ecosystems. Since soil properties directly regulate the decomposition of litter, a major food resource for earthworms and SOM sources in forests, elucidating relevant mechanisms of nutrient cycling in forest ecosystems is essential. Among other methods to investigate SOM dynamics and partitioning in forest soil, carbon and nitrogen isotope analysis has been adopted by soil ecologists based on its efficiency and accuracy. Several studies have quantified trophic interactions of earthworms in soil food webs, palatability, assimilation of SOM into earthworm biomass, carbon and nitrogen turnover, and earthworm impact on soil carbon and nitrogen contents using this method in temperate forests. Other methodologies, including chrono-sequential measuring and population assessments, are recommended for further elaboration and verification of soil nutrient circulation, especially for carbon and nitrogen.

## Abbreviations

CEC: Cation exchange capacity; NanoSIMS: Nanometre-scale secondary ion mass spectrometry; SOM: Soil organic material.

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## Author contributions

GK performed and supported the collection and analysis of publications. MK supported material analysis. GK, HJ, H-SK, MK, and YS contributed in writing and formatting the manuscript. YS mainly supervised the current study as corresponding author. All authors read and approved the final manuscript.

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## Availability of data and materials

All data generated or analyzed during this study are included in this published article and its supplementary information files. References are included for each and every data gathered from the published articles.

## Declarations

### Competing interests

The authors declare that they have no competing interests.

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