

The potential of earthworms in soil carbon storage: a review

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Abstract

Earthworms are known to modify the soil structure and alter the physico-chemical as well as biological regimes of the inhabiting soil. Numerous studies focussing on the role earthworms play in soil carbon (C) mineralization and stabilization have been conducted, with recent reviews portraying earthworms as greenhouse-gas emitters. The present work aims (i) to assess all possible earthworm mediated C dynamics by compiling results of the past several years of research, and (ii) to identify gaps in knowledge and evaluate the need for further research. The review noted the role of earthworms in soil C sequestration to be site-specific; i.e., dependent on the ecosystem. It also noted that although the presence of earthworms may not increase the soil organic C stocks, over the long term they are capable of improving the resilience of C in mineral soils. The aggregates formed as a result of earthworms feeding and casting behavior serves as a mechanism for the physical stabilization of C trapped within. The calcite granule formation by certain Lumbricid species, possibly in an attempt to regulate CO₂ levels, is one of the many ways earthworms promote the chemical stabilization of C. Humification of organic matter by earthworms renders a biochemical stabilization mechanism for soil C. Nevertheless, we also address the ways by which earthworms emit CO₂, even though we found much of this emission to be indispensable, it being a living organism. The lack of long-term studies in the area is a drawback that leaves room for debate. Earthworms occurring globally in almost every ecosystem are in fact biochemical reactors that transform the labile C components into more stable forms. The review then sheds light on the so-called “soil carbon-earthworm dilemma” and finally concludes by stating that earthworms, while facilitating C input to the soil, simultaneously also support soil biological activities and the corresponding CO₂ emission, all of which may be seen as an integral part of the natural C cycle.

Key words: carbon dynamics, carbon dioxide, earthworms, mineralization, soil carbon, sequestration.

Abbreviations: C, carbon; OC, organic carbon; OM, organic matter; PhytOC, phytolith-occluded carbon; SOC, soil organic carbon; SOM, soil organic matter.

Introduction

Earthworms, being ecosystem engineers, play a crucial role in soil carbon (C) sequestration. Several studies highlighted the presence of earthworms to have a positive impact on the soil organic carbon (SOC) content (Gilot 1997; Bossuyt et al. 2005). The last decade has seen a surge in research on the impacts of earthworms on soil C dynamics. However, there are also varied results on the extent of the influence of earthworms on SOC content (Desjardins et al. 2003). A recent meta-analysis of 237 observations from 57 published studies (Lubbers et al. 2013) reported that earthworms caused a 33% increase in soil CO₂ emissions. A response study in Nature Communications conducted on the effect of two widespread invasive earthworm species on soil C sequestration potential showed that earthworms generated a ‘carbon trap’ and facilitated C sequestration (Zhang et al. 2013). The present paper reviews the important findings of the past several years of research, with the notion to address

the ways in which earthworms regulate the soil C dynamics.

Earthworm mediated soil carbon stabilization

Earthworms greatly influence soil structural characteristics, like creating soil aggregates (Lavelle et al. 1997). It drastically changes the microbial diversity as well as the activity of the inhabiting soil through its feeding and burrowing activities. They were found capable of improving soil organic matter (SOM) sequestration in both the temperate (Caravaca, Roldán 2003; Bossuyt et al. 2005; 2006; Zhang et al. 2013) as well as tropical ecosystems (Blanchart et al. 1993; Fragoso et al. 1997; Blanchart et al. 1999; Jouquet et al. 2007; Wu et al. 2017a; Sruthi, Ramasamy 2018). The three main mechanisms for SOM stabilization and thus the consequent SOC storage, as proposed by Stevenson (1994) and Christensen (1996), are (i) physical protection, (ii) chemical stabilization and (iii) biochemical stabilization of organic matter (OM).

Earthworm activity mediated physical protection of carbon: protection of carbon via aggregation

The underlying mechanism for greater sequestration of SOC in earthworm treatments was found to be likely due to the physical protection of OM within aggregates formed by earthworms (Angst et al. 2017). Flocculation of negatively charged soil particles with polyvalent cations is known to increase aggregation in soils (da Silva et al. 2016). In the intestine of earthworm, flocculation results in the formation of OM-enriched aggregates (Arthur 1963; Shipitalo, Protz 1989). The casts of earthworm resemble spherical aggregates in contrast to the prismatic aggregates formed as a result of plant roots and other physical processes. These spherical aggregates have a greater percentage of C and nitrogen (N) when compared to the prismatic aggregates (Frouz et al. 2011). Aggregates of diameter greater than 250 μm are called macroaggregates and those less than that are called microaggregates (Tisdall, Oades 1982). Due to their greater stability and lower turnover rates, microaggregates (53 to 25 μm) play an important role in SOM dynamics. The average turnover time of C within free microaggregates and macroaggregates, when present in the surface 10 cm, was calculated to be 420 and 140 years, respectively (Jastrow et al. 1996). During the transit of soil and OM through the gut of the earthworm, the existing microstructure of soil gets broken down. However, new micro-aggregates are formed within the gut and are excreted as macroaggregates of the cast (Bossuyt et al. 2004). OM resistant to degradation becomes the foci of aggregate formation (Shipitalo, Protz 1989). Aggregates alter soil food web interactions and consequent microbial turnover by acting as physical barriers between SOM and microbes. They also affect the capability of the enzymes to degrade SOM, thereby protecting them (Elliot, Coleman 1988). The high carbohydrate content and calcium humates formed as a result of flocculation within the folds of the gut act as cementing agents helping bind mineral particles together, thereby conferring the high bulk density casts with greater stability (Blanchart et al. 1993; Scullion, Malik 2000). The strong compaction that the casts undergo at the tail muscles of earthworms before being excreted also adds to its stability (McKenzie, Dexter 1987).

A recent meta-analysis on the fertility of earthworm casts found it to have on an average 40 to 48% more organic carbon (OC) than the bulk soil (Van Groenigen et al. 2019). The casts age and stabilize via the physical process termed as thixotropic hardening, whereby a rearrangement of particles and water films occurs resulting in the re-establishment of the edge-to-edge contact of clay particles without water loss. The further aging and drying of aggregates cause it to shrink, promoting closeness and also facilitating the formation of strong bonds between plants and microbial polysaccharides (found within the OM) with the clay fractions (Shipitalo, Protz 1989; Bossuyt et al. 2005). Thin sectional analysis of the casts revealed a cortex region, a 25 μm thick dense layer of fine particles,

which probably impedes air and water movement, creating an anaerobic condition unfavorable for microbes, thereby protecting the OM within from decay (Elliott, Coleman 1988; Blanchart et al. 1993).

The long-term efficiency of protection of OM within aggregates depends mainly on two factors (i) the maximum amount of aggregates possible at a given site and (ii) the life span of these aggregates (Lavelle et al. 2004). The properties of casts are different for different species of earthworms and based on several studies it is found to depend on many factors, which include the feeding behavior of the species, the digestion pattern of the earthworm and associated microbes within its gut, besides the nature of the ingested food as well as soils (Gilot 1997; Liu, Zou 2002; Fonte et al. 2007; Ekschmitt et al. 2008; Zhang et al. 2009; Bottinelli et al. 2010; Shan et al. 2010; Bernard et al. 2012; Gómez-Brandón et al. 2012; Aira, Domínguez 2014; Clause et al. 2014; Kernecker et al. 2014; Amossé et al. 2015; Chang et al. 2016; Abail et al. 2017). Even though Zhang et al. (2013) stated that over the short term, the biological traits of earthworms did not influence the magnitude of C mineralization, he highlighted the fact that over the long term, these traits were the determining factors with respect to reducing the availability of C and hence regulating soil C stabilization.

The role of epigeic earthworm species in aggregate formation is mainly dependent on the contact of detritus with minerals (Bossuyt et al. 2005; Seeber et al. 2006). Intriguingly, epigeic ones feeding on litter are capable of transferring the C from the litter into the soil, where it is stored in a more stabilized form via the aggregation process (Zhang et al. 2013; Wu et al. 2017a). Epigeic species incorporated the C derived from the litter as well as soil, into all measured aggregate fractions of the soil (Sánchez-de León et al. 2014; Wu et al. 2017a). Even though earthworms initially accelerate C mineralization, their total soil C mineralization was found not to surpass the C mineralization mediated by soil microbiota alone because of the limited availability of only a small pool of potentially mineralizable carbon (PMC) (Fig. 1). Another noteworthy finding was that the C remaining in the earthworm worked soil was found to be more stable than the C of the control soil without earthworms (Zhang et al. 2013; Angst et al. 2019). They, in fact, transformed the labile C into nonlabile forms (Wu et al. 2017a).

The endogeic species stabilize the OC already present in the soil through the formation of large macroaggregates and transformation of the labile C into recalcitrant forms (Sánchez-de León et al. 2014; Wu et al. 2017a). Lavelle and Spain (2001) thereby termed endogeic earthworms as “major agents of soil aggregation and SOM stabilization”. The same observation was made by Sánchez-de León et al. (2014). The endogeic species *Aporrectodea caliginosa* worked soil was found to have a greater proportion of newly formed large (> 2000 μm) as well as small macro-aggregates (> 250 μm to 2000 μm), with more C in it when compared

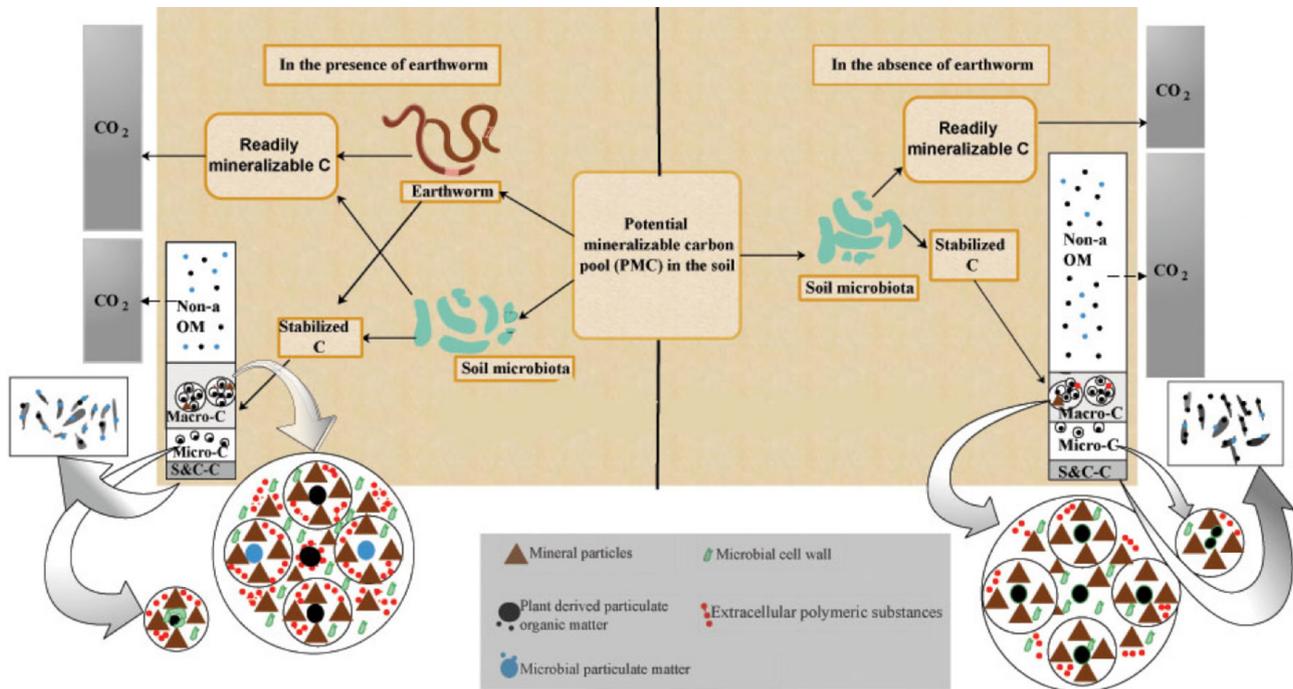


Fig. 1. Conceptual model of C dynamics both in the presence and absence of earthworms. Macro-C, C slowly stabilized in macroaggregate; micro-C, C slowly stabilized in microaggregate; S & C-C, C slowly stabilized in silt and clay fractions; non-a OM, non-aggregate associated organic matter fraction; solid arrows, confirmed response; dashed arrows, probable outcome. Modified and adapted from Zhang et al. 2013; Lubbers et al. 2017; Angst et al. 2019.

to the bulk soil (Martin 1991; Bossuyt et al. 2004, 2005). A large proportion of microaggregates were formed rapidly (within 12 days incubation) inside the macroaggregates in the presence of this species. These microaggregates were found to be water stable and contained C derived from fresh residues (Ketterings et al. 1997). The C mineralization rate was seen to be four times lower in the casts (3% year⁻¹) of *Millsonia anomala* when compared to the control soil (11% year⁻¹).

Anecic species are known for their permanent or semi-permanent burrows, which extend deep into the soil; they feed on surface decaying organic residues, which they drag into their burrows (Shipitalo, Le Bayon 2004). A few days of deposition by *Amyntas khami* (anecic species) created casts with simple organization and high water-stability which reached up to 20 cm in height. The casts were found to be a buildup of low sized aggregates (< 500 µm) with a suggested life span of several months to years (Blanchart et al. 1999). The time required for a water drop to penetrate into aggregates was found to be significantly greater for casts when compared to control soils (Jouquet et al. 2008). These casts were also found to contain a greater proportion of OC and N in the 50 to 250 µm class (Hong et al. 2011). The absence of voids and large pores in the casts might be the possible reason for the physical protection of OM against mineralization within the casts (Jouquet et al. 2008; 2011). CO₂ emissions were found to be significantly lower from cast aggregates less than 250 µm in size when compared to aggregates greater than 500 µm (Jouquet et al. 2011). When

compared to the casts of endogeic species (*A. caliginosa*), anecic species (*Lumbricus terrestris*) casts contained higher OC content (Schrader, Zhang 1997).

It is of great importance to understand the complex interactions between the biotic and abiotic factors in the system studied. A 21-day-long incubation study using a combination of plants, compost, and earthworms, was carried out to assess their relative importance in aggregate formation and structural stability of soil (Deeb et al. 2017). The management practice of the site also influenced the distribution of aggregates. It was found that the deployment of a combination of species (*L. terrestris*, *Lumbricus rubellus*, and *A. caliginosa*) promoted the formation of small macroaggregates (Frazão et al. 2019). Earthworms were found to have a positive influence on the soil aggregation only in the presence of plants or C input in the form of roots (Fonte et al. 2012) or plant litter input (Fonte, Six 2010). The effect of earthworms on aggregate stability also varied based on differences in the residue added (Coq et al. 2007).

Earthworm activity mediated chemical stabilization of carbon: formation of organo-mineral complexes – sorption
Although the maceration by earthworms makes the otherwise inaccessible cellulose in lignocelluloses available to gut microorganisms (Hammel 1997), the mixing of ingested material with stabilizing agents in the anterior gut (Lavelle 1997) followed by further biochemical processes along with re-absorption of water in its hindgut results in

the formation of stable organo-mineral complexes (Wolters 2000; Vidal et al. 2019). Clay associated OM is known for its stability and slow formation. However, earthworms help accelerate the formation of these slow pools by its feeding activity (Marhan et al. 2007a). The occurrence of comparatively higher pH, divalent cations (Ca^{2+} and Mg^{2+}) and cation exchange capacity in the casts when compared to the surrounding soil, contributes to the increase in the electrostatic binding between particles in the casts, consequently conferring greater stability to it (Six et al. 2004; Oyedele et al. 2006; Jouquet et al. 2008). Interactions between minerals and OM are partly controlled by mineral properties (Baldock, Skjemstad 2000) and partly by stabilizing agents such as polysaccharides produced by living microorganisms during the decomposition process. This favors the adsorption of minerals and increases inter-particle cohesion (Chenu, Stotzky 2002) leading to the strengthening of organo-mineral bonds in casts.

When moist, the linkages between organo-mineral complexes were found to be limited to mainly water and cation bridges. The aggregate stability of the casts was enhanced by the clay-polyvalent cations-OM bonds (C-P-OM). In most cases, Ca^{2+} and to a lesser extent Mg^{2+} was part of the C-P-OM bond. In dry casts, a significant portion of it was composed of coordination complexes, which are found to be quite strong (Shipitalo, Protz 1989). The amorphous Fe, sesquioxides associated with organic complexes and polysaccharides attached to heavy fraction were found to be higher in casts when compared to the surrounding uningested soil. The macroaggregate stability of casts was found to be mainly associated with the amorphous Fe and Al and the light fraction OM, while the microaggregate stability of casts was found to be due to the heavy fraction (Oyedele et al. 2006). The presence of reactive minerals like Fe and Al has been found to be correlated with increased SOC content (Kaiser, Zech 1999; Baldock, Skjemstad 2000). The analysis of the composition of casts of 60 earthworms (Bernier 1998) revealed that it is composed of organic and mineral particles, thus further confirming the formation of organo-mineral complexes. The mineral sorption of OM is often considered as the primary means of SOC protection (Lehmann, Kleber 2015).

Earthworm activity mediated chemical stabilization of carbon: calcite granule formation

Many earthworm species, especially those belonging to the family Lumbricidae, are true biomineralizers in that they have specialized calciferous glands that produce CaCO_3 granules (Darwin 1882). These granules are mainly composed of calcite, with small amounts of amorphous CaCO_3 , vaterite, and aragonite (Gago-Duport et al. 2008; Brinza et al. 2013). Granule calcite is produced in the calciferous glands by the dissolution of CO_2 into bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}), which then transforms into amorphous CaCO_3 before finally stabilizing

into calcite via a dissolution-reprecipitation mechanism (Briones et al. 2008a). The calcite granules formed in the calciferous glands are then transferred into the earthworm oesophagus, from where they move into the intestine before finally being expelled into the soil (Hodson et al. 2015). Several reasons have been attributed for the granule secretion and C sequestration potential is one among them. It was found that at a higher temperature and elevated CO_2 levels, earthworms increased the production of granules. As the life span of these granules is greater than 300 000 years, they can serve as long-term reservoirs of C in the form of CaCO_3 (Versteegh et al. 2014).

The anecic *L. terrestris* is a typical example of a CaCO_3 producing species with a production rate ranging between 0.8 to 2.9 mg per earthworm per day (Versteegh et al. 2013). With a field population density in the range of 1.9 to 61.8 individuals m^{-2} , the calculated precipitation of 2 to 261 kg C ha^{-1} year $^{-1}$ is quite a significant contribution to the soil C pool (Versteegh et al. 2014). The calciferous glands of earthworms thus provide a mechanism for regulating the CO_2 level in tissues as well as help fix the environmental and metabolic CO_2 (Briones et al. 2008b; Lambkin et al. 2011). CaCO_3 was also found to act as a cementing agent for the OM that passes through the gut, thus positively affecting the soil structure and SOC stabilization (Rowley et al. 2018). This capacity of certain earthworm species to fix environmental CO_2 holds immense potential as a C sequestration strategy.

Earthworm activity mediated chemical stabilization of carbon: protection of carbon via hydrophobicity and resistance to water desegregation

The OM incorporated in the casts of earthworms confers hydrophobicity to the casts, thereby further promoting its stability (Jouquet et al. 2008). The lowest wettability of casts was found to correspond with the largest concentration of OC and microbial biomass C (Lipiec et al. 2014). This reduced wettability of the casts, in turn, restricted microbial activity due to the absence of water, thereby decreasing the accessibility of microorganisms to OM (Lutzow et al. 2006). The cast of compacting species (e.g. *Pontoscolex corethrurus*, *Amyntas khami*, and *Millsonia omodeoi*), which is characterized by cortex and a low porosity peripheral part, confers stability to aggregates against water desegregation and thus consequently protects the SOM. The low porosity of casts keeps a check on the water infiltration rate into it and thus prevents slaking (Blanchart et al. 1999). Upon the incorporation of maize residues, *Metaphire guillelmi* was found to increase the hydrophobicity of humic acid (Zhang et al. 2011). Another study on earthworm activity and cast composition illustrated the accumulation of biologically stable polymethylenic compounds, which included hydrophobic by-products of decomposition (Vidal et al. 2019).

Earthworm activity mediated chemical stabilization of carbon: indirect role in the formation and transportation of phytolith-occluded carbon

When compared with the bulk soil, earthworm casts were found to contain a greater amount of water-extractable Si and monosilicic acid $[\text{Si}(\text{OH})_4]$ irrespective of the soil type and management history due to the presence of silicate solubilizing bacteria in its gut (Hu et al. 2018). Bioturbation of the soil by earthworm was found to increase the xylem transport of Si in cucumber and maize crops (Bityutskii et al. 2016). When monosilic acid is taken up by plant roots, it is deposited in the form of non-crystalline Si minerals within the cell wall, lumen and the intercellular space of plants forming Si phytoliths. These then during plant growth occlude within them a part of OC (1 to 6%), which is extracted from the atmospheric CO_2 during photosynthesis (Parr, Sullivan 2005). Upon decomposition of plant OM, the phytolith-occluded C (PhytOC) is deposited in the topsoil and is found to be very resistant to degradation, thereby acting as a potential carbon sink. Due to its high resistance to degradation, PhytOC could account for about 82% of the total C in well-drained soil, even after 1000 years of OM decomposition (Parr, Sullivan 2005; Li et al. 2015). Bioturbation by earthworms also results in massive horizontal and vertical translocation of preserved phytolith (Fishkis et al. 2010; Pearsall 2005; Zangerlé et al. 2016). Research on the role of earthworms in the formation of PhytOC and consequent C sequestration holds great potential.

Earthworm mediated biochemical stabilization of carbon

In terrestrial ecosystems, a major portion of OC of litter enters the fast turn over pool of OM. This contributes only to short-term C sequestration. One of the main challenges is the development of more stable, slow turn over pools of OC, such as the refractory humus (non-hydrolyzable during drastic chemical treatment) with turnover times above 1000 years (Sanderman, Amundson 2003; Seneviratne 2003). Vermicomposting, the process by which earthworms are used to convert OM to humus-like material vermicompost (Muralikrishna, Manickam 2017), is known to speed up humification of OM by 40 to 60% when compared to natural composting process (Sharma, Garg 2018). Vermicompost, due to its slow decomposition rates and low CO_2 emissions, qualify as a climate-smart soil management practice (Hossain et al. 2017). Even though initially there occurs a release of CO_2 from the OM to the atmosphere, once the OM gets encapsulated in humus form as a result of ingestion by earthworms, a major proportion of OM is transformed to the slow pool (Seneviratne 2003). The fragmentation, aeration as well as the turnover of OM through earthworm feeding and burrowing activities, along with intense microbial activity occurring inside its gut, accelerates the humification process (Zhang et al. 2011; Lemtiri et al. 2014). The high level of peroxidase

and cellulase activity in earthworm gut also indicates the important role earthworms play in the decomposition and condensation stage of the humification process (Hartenstein 1982; Zhang et al. 2000). This cellulase activity, in turn, enhances the degradation of cellulose present in the composted residue, resulting in an increase in the concentration of water-soluble C as well as carbohydrate in the soil (Caravaca, Roldán 2003). Studies have demonstrated not only the capacity of earthworms to form humic substances from non-humified substrates (Businelli et al. 1984), but also revealed high values for the C ratio of humic acid to fulvic acid for all earthworm treated soils, pointing to the humifying capacity of earthworm (Businelli et al. 1984; Zhang et al. 2011). Bernier (1998) found that the majority of earthworm species enriched the humus profile of mountain spruce forest by incorporating the OM within the mineral matrix. The development of a humus profile by earthworms was of great importance, as the regeneration of the forest was very much found dependent on the mull (humus) recovery. Thus earthworms not only played an important role in the formation of recalcitrant humus, but also indirectly helped in the regeneration of forest, thus promoting phytosequestration of C. The presence of earthworms significantly altered the lignin signature of the SOM. The increased lignin content (coumaryl, syringyl, and vanillyl phenols) in the presence of earthworms indicated the possible protection of OM in aggregates. The casts were enriched in less-oxidized lignin compounds (Zhang et al. 2003; Ngo et al. 2012). Lignin, due to its recalcitrance to enzymatic degradation, serves as a structural barrier protecting the labile C compounds from microbial attack (Swift et al. 1979).

Earthworms are known to influence soil microbial communities as well as activities of other soil-inhabiting invertebrates, and hence alter the SOM dynamics. Even though the majority (about 85 to 90%) of C turnover in the soil is microbially mediated (Wolters 2000), the microbes, due to their limited motility (Parales, Harwood 2002; Lueders et al. 2006), are very much dependent on large organisms (such as earthworms) and roots for access to new substrates (Bernard et al. 2012; Gómez-Brandón et al. 2012). This phenomenon of stimulating the dormant microbial community using soil invertebrates and root activities was termed as 'the sleeping beauty paradox' (Lavelle et al. 1995). Bioturbation by earthworms causes the biological reworking of soils (Meysman et al. 2006) and results in the introduction of organic components into it, thereby increasing microbial activity in the soil (Sheehan et al. 2008). Vidal et al. (2019) reported that, along with the decay of the litter-derived OM, there was a parallel buildup of microbial dominated OM, both as living microbial biomass and dead microbial residues. The addition of large quantities of labile C in the form of mucus by earthworms during the ingestion of OM also boosts the build-up of microbial biomass in mineral soil. The increase of microbial

necromass in the mineral associated OM and small occluded particulate OM, at the expense of plant compounds in the less stable fractions, promotes the sequestration of OC (Fig. 1; Angst et al. 2019). Thus, high microbial activity, in turn, is known to support C sequestration with microbial necromass, forming a major source of OM in soil (Ludwig et al. 2015). Bacteria, being large sources of carbohydrate, result in the increased stabilization of aggregates, as the carbohydrate contents act as stabilizing agents. Due to the greater structural stability and larger availability of nutrients in casts, earthworm casts are home to large populations of fungi, bacteria, and actinomycetes, as well as associated enzyme activities (Edwards 2004). The stability of casts and resultant protection of OC is attributed to the intimate mixing of decomposed OM with soil particles and further binding of OM by microbial mucilage and fungal hyphae (Haynes, Fraser 2003). As the casts age, although the microbial biomass of the casts remains the same, the microbial activity decreases and thereby the C mineralization also decreases (Aira et al. 2010). The exotic endogeic species *P. corethrurus* was found to transiently triple rhizodeposit C retention by immobilizing it in the biomass of root-associated bacteria/fungi, thus facilitating the rhizodeposit C sequestration (Huang et al. 2015). In another scenario, where the earthworms utilized the microorganisms as their secondary food source (Zhang et al. 2000; Edwards, Bohlen 2020), worm digestion resulted in a bottleneck effect on the microbial population (Gómez-Brandón et al. 2010; 2012). The reduction in the microbial population would in a way diminish CO₂ emission due to microbial respiration. In non-flooded paddy fields supplemented with N fertilizers, earthworm bioturbation and occlusion of C and N in macroaggregates were found to play important roles in offsetting CO₂ emissions (John et al. 2015). The effect of earthworms on microorganisms depends mainly on the earthworm species and its dietary pattern (Egert et al. 2004; Hättenschwiler et al. 2005) and is itself a topic of extensive review.

Earthworm mediated carbon turnover and mineralization

Lubbers et al. (2017) proposed that earthworm stimulates mineralization of freshly added residues via accelerating decomposition to a greater extent than the stabilization of the residue-derived C within the biogenic structures. They put forward three main simultaneous mechanisms that cause earthworms to promote C mineralization (i) earthworms accelerate the decomposition of freshly added residue, (ii) earthworms cause mobilization of older SOC pools and associated mineralization, and (iii) earthworms via turnover of aggregates cause the release of stored C. Besides these, we include other mechanisms that possibly result in earthworm mediated C loss: (iv) earthworm activity mediated soil erosion, (v) fresh casts harboring

microbes resulting in microbial respiration, and (vi) earthworm respiration, and (vii) C loss via mucus excretion.

Acceleration of decomposition of freshly added residue

The potential of earthworms to accelerate decomposition through its feeding activity is one of the reasons why earthworms are held accountable for the depletion of the soil C pool and the resultant emission of CO₂ (Knollenberg et al. 1985; Fahey et al. 2013). In a 750-day-long mesocosm experiment, where loess type soil was surface-applied with maize residues every six months, the presence of earthworms resulted in a 25% increase in CO₂ emission. Even though the study reported a decrease in the total C content of the soil, both epigeic and endogeic species showed a trend to increase C associated with the macroaggregate fraction (Lubbers et al. 2017). This result does suggest that earthworms simultaneously enhance decomposition as well as incorporate C into the aggregate fraction. However, the introduction and invasion of earthworms to areas previously uninhabited by them may negatively affect soil C sequestration. It may be noted that the observation can be a habitat-specific phenomenon, which in the short term can result in rapid decomposition of SOM followed by the release of CO₂ (Hendrix et al. 2008).

Exotic earthworm invasion of habitats previously uninhabited by earthworms. Case Study I: Invasion of forests in North America by exotic earthworms. Introduction of European and Asian earthworm species by Europeans resulted in the colonization of these species over wide areas of North American forests previously devoid of earthworms (Alban, Berry 1994; Scheu, Parkinson 1994; Dymond et al. 1997). Disruption of soil C sinks upon the invasion of exotic earthworms in these forests was due to the feeding activity of earthworm, which resulted in a rapid decline of the litter layer (10 to 0 cm) at a pace at which the forest could not regenerate (Mortensen, Mortensen 1998; Hale et al. 2005; Bilbrey 2013). Although increased inputs of C into the soil was taking place, this was counterbalanced by the offset due to loss as CO₂ (10 g m⁻² year⁻¹ C loss) emission and dissolved OC leaching from soil (Crumsey et al. 2013; Cameron et al. 2015) as a result of increased porosity caused by earthworm burrows. The invasion of earthworms in North American forests also caused a decline in the plant diversity of the forest (Craven et al. 2017) and resulted in a forest decline syndrome, which further declined C sequestration via phytosequestration (Frelich et al. 2006).

Exotic earthworm invasion of habitats previously uninhabited by earthworms. Case Study II: Earthworm invasion of peatland soil. The Zoige Peatland on the Eastern Tibet Plateau, which houses 1% of the total SOC of the earth, is a typical example where earthworm invasion via water table declination caused a dramatic decrease in the SOC level. The decomposition activities of the earthworm along with increased microbial activity in the OM rich soils probably contributed to the decline in SOC. In earthworm

invaded sites, a 16 and 31% decrease in SOC content was observed in the upper and lower soil layers respectively (Wu et al. 2017b). It may, however, be noted that water table declination in peatland itself can result in significant CO₂ emission (Cao et al. 2017), which was then further augmented by earthworm invasion. The overall observation was a result of temporal and spatial changes in the peatland condition, which may be reversible in due course of time.

Mobilization of decade-old soil organic carbon by endogeic earthworms

It has been shown that endogeic earthworms, when compared to anecic and epigeic earthworms, have the highest radiocarbon concentrations, which indicated that these species depended on a diet comprised of comparatively older (5 to 8 years) (Fox et al. 2006; Marhan et al. 2007; Hyodo et al. 2008) and more mineralized OM (Briones et al. 2005; Ferlian et al. 2014). However, the observation that earthworms augmented the C pools associated with the insoluble silt/clay size classes (Fox et al. 2006) should not be overlooked. SOC is strongly sorbed to the silt and clay fraction via strong ligand exchange and polyvalent cation bridges, while only weak linkages exist between SOC and sand particles (Sposito et al. 1999). Endogeics were further found to assimilate C associated with small particle size fractions attached to clay-humus complexes (Ferlian et al. 2014). However, a similar study conducted in France found that although endogeic earthworms ingested large amounts of humified OM, the recalcitrant pool of OM was not assimilated by them (Martin et al. 1992). In spite of the mobilization of older SOC by endogeic earthworms, in studies exceeding 100 days it was found that they caused a reduction in mineralization by 15 to 39% (Scheu, Wolters 1991; Scheu 1997).

Although endogeics feed on 5- to 8-year-old OM, it must be noted that the soil below ~ 20 cm is abundant with SOC with radiocarbon ages ranging between 1000 to 10 000 years. With the advent and extensive use of radiocarbon isotope and modeling studies, the ultimate fate of so-called 'earthworm mobilized old C' can be easily predicted in the near future.

Aggregate turnover and the release of carbon stored within

Earthworm activities such as feeding and casting influence both aggregate turnover and SOM dynamics (Pulleman et al. 2005). Turnover rates of soil via earthworm casting activity in temperate grasslands ranges from 40 to 70 t ha⁻¹ year⁻¹ (Bouché 1983), in tropical savannas it ranges from 500 to 1000 t ha⁻¹ year⁻¹ (Lavelle et al. 2004). In an extreme case, this turnover of soil by earthworms was seen to be responsible for the development of an entire ecosystem in the Llanos of Colombia and Venezuela, the "surales" (Zangerlé et al. 2016). The formation of microaggregates by endogeic earthworms involves the disruption of pre-existing microaggregates during its passage through the

earthworms gut, resulting in the incorporation of organic debris and microbial material, which then becomes encrusted with plasma and thus serves as nuclei for the new microaggregate formation within macroaggregate (Barois et al. 1993; Shipitalo, Protz 1989; Pulleman et al. 2005). Eudrilid earthworms were found to feed partly on large compact casts egested by large earthworms, and then egest small, fragile aggregates (Blanchart et al. 1999), thereby releasing the C stored within. Experimental studies using endogeic earthworms found that the incorporation of radish residues in the soil caused an increase in the turnover of macroaggregates. However, this did not cause a significant increase in cumulative CO₂ fluxes (Giannopoulos et al. 2010). The fresh casts of earthworms house a large number of microorganisms which possibly would utilize the stabilizing agents (plant and microbial polysaccharides) in the casts as their energy source, thus slowly breaking down the aggregates (Oades 1993). Though earthworms do sometimes directly or indirectly cause the breakdown of macroaggregates, it must be noted that the C incorporated in microaggregates by them has a slower turnover rate than C in macroaggregates, thereby facilitating C sequestration (Jastrow et al. 1996).

Carbon loss via earthworm activity mediated soil erosion

Earthworm activity in steep slope ecosystems was found to influence the soil erosion rate, thereby leading to a C loss ranging between 3.34 and 15.85 kg of C ha⁻¹ year⁻¹ depending on the vegetation type (Jouquet et al. 2010). Though earthworm casting activity is capable of resisting soil erosion, it is the labile fresh casts that are sensitive to erosion in places with intense rainfall. Fresh casts of *M. anomala* were observed to disappear under a rain of 18 mm. However, when protected by vegetation cover it was found to persist for months. The casts of Eudrilidae species were observed to contribute to the formation of a surface crust, which impeded water infiltration and thereby increased surface soil erosion (Blanchart et al. 1999). However, Blanchart et al. (2004) in another study reported that the dry casts of earthworms formed a layer of free macroaggregates, which was found to be more stable than the surrounding soils. During rainfall, this layer was said to protect the soil from particle detachment by absorbing the kinetic energy of the raindrops and thereby preventing erosion. Thus, the net effect of earthworm activity on soil erosion and consequent C losses depends on a number of interacting factors and not on earthworm activity alone.

High mineralization rate via microbial activity in the presence of earthworms

Fresh casts are considered as the hub of intense microbial activity where accelerated decomposition, as well as mineralization of C, takes place (Aira et al. 2009; Abail et al. 2017). The accelerated decomposition in the fresh casts may be attributed to the priming effect developed as a

result of the addition of water and intestinal mucus to the mixture of soil and OM (Lavelle, Martin 1992; Don et al. 2008). The short-term change in SOM turnover as a result of labile C addition is called the priming effect (Kuzyakov, Domanski 2000). Such a supply of fresh plant-derived carbon to subsoils (0.6 to 0.8 m) was found to act as an energy source for soil microorganisms, thereby catalyzing the mineralization of 2567 ± 226 -year-old carbon (Barot et al. 2007). With anecic species dragging fresh litter from the surface into their burrows in the subsoil, the role they play indirectly in the mineralization of old C via microbial activity is questionable. The priming effect in biopores formed by *L. terrestris* was found to be 2.5 times greater than the bulk soil as a result of the favorable conditions provided by earthworms (Hoang et al. 2017). C metabolism enzymes β -glucosidase and cellulase were found to be higher in the casts when compared to the surrounding uningested soil (Zhang et al. 2000; Aira et al. 2003). The enhanced production of β -glucosidase enzymes facilitates the greater potential for C turnover (Hoang et al. 2016; Lipiec et al. 2016). It must, however, be noted that accelerated enzyme activity and functional diversity make the soil less vulnerable to degradation, thereby increasing the stability of the ecosystem (Chen et al. 2015). The total microbial biomass, microbial groups (bacteria and fungi) and microbial activity were found to be higher in fresh casts when compared to the surrounding soils (Tiunov, Scheu 2000; Aira et al. 2003; 2005). Subsequent to earthworm invasion, the increased mean CO_2 flux in earthworm microcosms could be probably due to earthworm respiration as well as earthworm induced microbial respiration (Speratti, Whalen 2008; Crumsey et al. 2013). Another significant change upon exotic earthworm invasion is the shift from a slow-cycling soil system dominated by fungus to a faster cycling bacteria-dominated or less fungi-dominated system, which causes net C loss (Wardle 2002; Chang et al. 2017).

Aging of casts clearly decreases the microbial activity due to limitations in the availability of labile C needed for microbial metabolism (Aira et al. 2005; Gómez-Brandón et al. 2011). The substrates within microaggregates in aged casts starts to become less decomposable (i.e., increase in lignin-derived compounds) and more stabilized, thus progressively starving the microorganisms (Vidal et al. 2019).

Earthworm respiration

Respiration is a key component of the global C cycle. Earthworms breathe by diffusion of O_2 and CO_2 through their moist skin. Different species of earthworms have different respiration rates (Šustr, Pižl 2009). Litter-dwelling species *L. castaneus* and *Dendrobaena rubida* have a relatively high respiration rate compared to the organic-mineral soil dwellers *Allolobophora rosea* and *Octolasion cyaneum* (Phillipson, Bolton 1976). A possible explanation suggested for the variation in the respiration rates is the

fixation of metabolic CO_2 by the calciferous glands present in certain species. The gross C mineralization with respect to earthworm respiration, in the moist savannas of Lamto, was found to be equivalent to 5 to 6% of C incorporated annually via primary production. Despite the numerous studies conducted in relation to earthworm respiration (Pomerat, Zarrow 1936; Phillipson, Bolton 1976; Uvarov 1998; Šustr, Pižl 2009; Nieminen et al. 2015; Yonemure et al. 2019), limited studies have reported ways in which earthworm respiration affected the SOC content.

C loss via mucus egestion

Earthworm mucus is a notable source of C for soil microbial activity, which in turn controls nutrient cycling (Lavelle et al. 1989). Earthworms excrete a large amount of mucus through their body surface onto burrow walls and also through their intestinal tract into the casts. The daily C loss via mucus excretion through the body surface of adult specimens of *Octolasion lacteum* was found to be 0.2% while C loss via mucus excretion through the cast was found to be 0.5% of the total animal C. It may be noted that only a small proportion of the intestinal mucus enters into the casts, since the majority becomes reabsorbed in the posterior intestine of the earthworm. ^{14}C labeling studies reported that the C for mucus excretion was procured from the labile pools of SOM (Scheu 1991). During copulation, earthworms secrete greater quantities of mucus, but the C loss associated with this mode of mucus excretion has not yet been quantified. Although mucus egested is of low recalcitrance and acts as a priming agent, it also interacts with mineral particles and thereby may play a significant role in the stabilization of OM (Wolters 2000).

'Soil carbon-earthworm dilemma'

In an attempt to conclude, we would like to shed light on the 'soil carbon dilemma' (Janzen 2006) in line with the 'earthworm dilemma' (Lubbers et al. 2013). Our endless need to burn fossil C and the urgency to abate the consequent rising CO_2 levels have made us obsessed with the idea of turning soils as C sinks. Without increasing the C input to the soil, presuming the soil to build the SOC content, we are in fact anticipating to stifle all forms of biological activity including earthworm activity in the soil. Although soils can act as C sinks, it must not be forgotten that it also derives benefits from the decay of OM that provides life to the soil (Hopkins 1910). Earthworms, while facilitating C input to the soil, also simultaneously support soil biological activities and the corresponding CO_2 emissions, all of which are an integral part of the natural C cycle. This has brought forth the 'earthworm dilemma', where we are made to see earthworms as net greenhouse gas emitters that accelerate OM decomposition, but also increase soil fertility via aggregation and C stabilization (Lubbers et al. 2013). The CENTURY model simulation study indicated

Table 1. Role of earthworms in soil C dynamics

Mechanism	C storage	C mineralization	Uncertain
Aggregation	•	–	–
Hydrophobicity	•	–	–
Organo-mineral complexes	•	–	–
Calcite granule formation	•	–	–
Flocculation	•	–	–
Phytolith occluded C	•	–	–
Humification	•	–	–
Accelerated decomposition	–	•	–
Mobilization of older SOC	–	–	•
Aggregate turnover	–	–	•
Soil erosion	–	–	•
Priming effect	–	–	•
Earthworm respiration	–	•	–
Mucus egestion	–	–	•

that the SOM content decreased by 10% within 30 years as a result of earthworm removal (Lavelle et al. 2004). This indicates the relevance of earthworms in the ecosystem.

Conclusions: Current status and future prospective

The various mechanisms by which earthworms regulate soil C dynamics have been summarized in this paper (Table 1). In view of the collected data, it can be concluded that the effect of earthworms on soil C dynamics is quite complex and depends mainly on several factors viz. (i) the incubation period (ii) the quantity, as well as the quality of OM, amended (iii) the earthworm species present and (iv) the physicochemical and biological properties of the parent soil. We summarize here the key findings of the study. It is noted that over the short term, earthworms cause an increase

in C mineralization, while over the long term they induce the stabilization of C within macroaggregates formed as a result of its feeding and casting activities. Flocculation and mixing of OM with soil in the gut of earthworms promotes organo-mineral complex formation within aggregates, which are excreted out as casts. The hydrophobic nature of the cast further confers stability to the entrapped C. Earthworm mediated bioturbation increases the xylem transport of silica and thus indirectly plays a role in the formation of PhytOC. In addition, the calcium carbonate granule secretion by certain earthworm species, in an attempt possibly to regulate the elevated CO₂ levels, and the humification capacity of earthworms have both contributed to the long-term stable pool of C. Earthworm influenced soil C mineralization primarily involves its respiration as well as the respiration of the microorganisms it hosts in its fresh

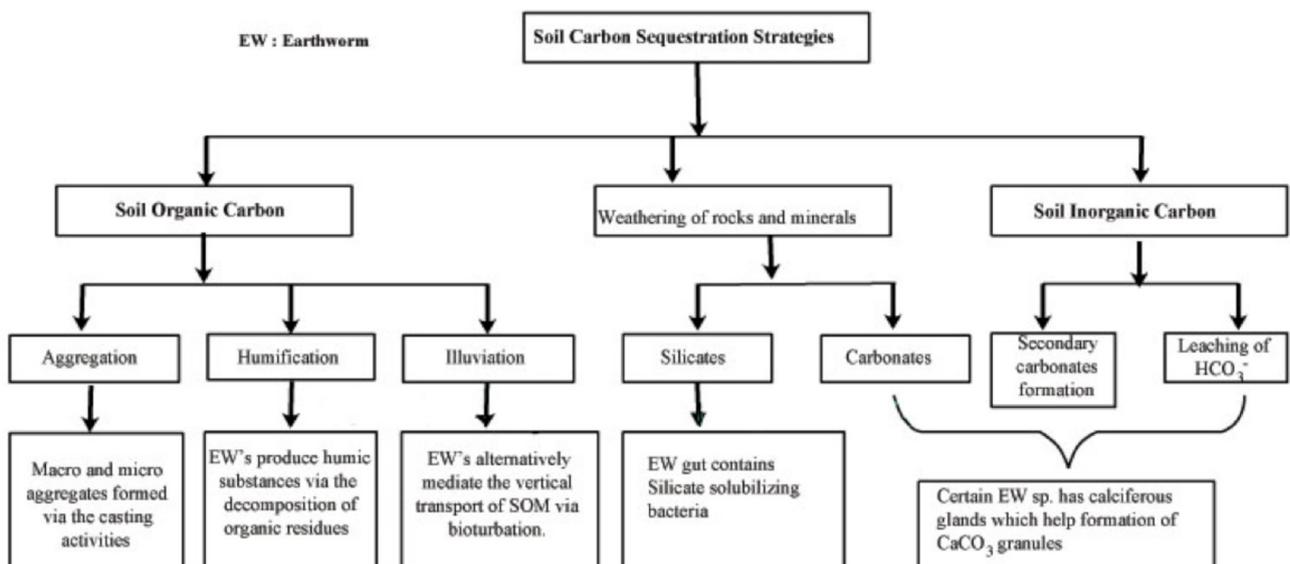


Fig. 2. The soil carbon sequestration strategies found to be influenced by earthworms. Modified and prepared from the scheme presented by Lal 2010.

cast. During the short term, earthworm invasion into areas previously devoid of them accelerates the decomposition of freshly added residues, but the long term impacts remain a topic of interest. In soils where earthworms were found for a long time, the C mineralization process was observed to slowly decrease, promoting the stabilization of OM and thus C sequestration. Most of the processes governing soil C sequestration (Lal 2010) are influenced by earthworms in one way or the other (Fig. 2). Except for the introduction of invasive species, all earthworm activities are found beneficial for the soil.

Recent studies portraying earthworms as CO₂ emitters are caught up in this 'carbon - earthworm dilemma', which signifies the role earthworms play in enriching the soil C stocks and at the same time emitting CO₂. This outlook draws our attention to the statement of Janzen (2006) that C gain need not always be good and C loss not always bad. In fact, it is not just a question of C gain or C loss; but what counts, is whether the balance between amount stored and amount used is tuned for the 'services' expected of the ecosystem in question. Therefore, a fruitful research objective would be to maintain the healthy balance between OC sequestered and that which is used by soil biota for their activity. The lack of long-term field studies is one of the reasons for the ambiguity in relation to earthworms' role in soil C dynamics. Most of the long-term studies conducted are mesocosm experiments in the absence of plants or other soil organisms.

The synergistic interaction between the earthworms and other soil organisms in the presence of a plant might be entirely different. Earthworm presence has been found to increase the shoot biomass of plants (Scheu 2003), which in turn promotes phytosequestration of C. This boosting of above-ground biomass and C stock by earthworms often is underestimated. The earthworm-developed Surales landscape unique to South America is an apt field site to study earthworm mediated C dynamics.

Another area of study is the site-specificity of earthworms' role in soil C dynamics, i.e., what may appear beneficial in a certain area need not be the same elsewhere. Future studies also need to be focused on estimating the degree of stability conferred upon SOM by soil organisms, rather than simply estimating soil C stock at a given time. The dynamic nature of SOC and biological activity urges the need to find the optimum conditions through management practices that balance C sequestration and C emission without hindering life and associated ecosystem processes in the soil. We conclude by stating that earthworms, while facilitating C input to the soil, simultaneously also support soil biological activities and the corresponding CO₂ emissions, all of which may be seen as an integral part of the natural C cycle.

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