Earthworms as catalysts in the formation and stabilization of soil microbial necromass

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Abstract
Microbial necromass is a central component of soil organic matter (SOM), whose management may be essential in mitigating atmospheric CO$_2$ concentrations and climate change. Current consensus regards the magnitude of microbial necromass production to be heavily dependent on the carbon use efficiency of microorganisms, which is strongly influenced by the quality of the organic matter inputs these organisms feed on. However, recent concepts neglect agents relevant in many soils: earthworms. We argue that the activity of earthworms accelerates the formation of microbial necromass stabilized in aggregates and organo-mineral associations and reduces the relevance of the quality of pre-existing organic matter in this process. Earthworms achieve this through the creation of transient hotspots (casts) characterized by elevated contents of bioavailable substrate and the efficient build-up and quick turnover of microbial biomass, thus converting SOM not mineralized in this process into a state more resistant against external disturbances, such as climate change. Promoting the abundance of earthworms may, therefore, be considered a central component of management strategies that aim to accelerate the formation of stabilized microbial necromass in wide locations of the soil commonly not considered hotspots of microbial SOM formation.

KEYWORDS
aggregates, carbon sequestration, casts, concept, hotspot, organo-mineral associations, substrate quality
INTRODUCTION

Management of soil organic carbon (SOC) via modifications to carbon inputs (Amelung et al., 2020; Janzen et al., 2022) has the potential to aid in offsetting carbon dioxide emissions and contribute to the climate targets put forward in the Paris Climate Change Agreement (Paustian et al., 2016). To be effective, it is imperative for such management to follow recent conceptual advances in soil organic matter (SOM) formation and stability. Recent concepts (Cotrufo et al., 2013; Kögel-Knabner, 2002; Liang et al., 2017) and empirical evidence (Kallenbach et al., 2015; Ludwig et al., 2015; Ma et al., 2018) recognize microbial necromass as an essential pool of SOC (specifically in grassland and arable soil; Angst et al., 2021; Liang et al., 2019). The manipulation of this pool via plant input-driven modifications to microbial physiology and traits (Kallenbach et al., 2015; Sokol et al., 2022) is thought to be critical in efforts to mitigate climate change. Central to recent concepts and the formation rate of microbial necromass is the efficiency of microbial growth on organic matter compounds (i.e., microbial carbon use efficiency (CUE)—the amount of carbon used for growth related to the carbon heterotrophically respired as CO2, which is directly linked to the quality of these organic compounds (e.g., low C/N and/or lignin/N ratios). The persistence of microbial necromass, in turn, is dependent on stabilization in aggregates and organo-mineral complexes (Castellano et al., 2015; Cotrufo et al., 2013; Schmidt et al., 2011). While evidence for the validity of recent concepts is steadily increasing (Angst et al., 2021; Ding & Han, 2014; Gillespie et al., 2014; Griepentrog et al., 2014; Liang et al., 2019), they neglect organisms relevant in many soils: earthworms. Earthworms belong to the main soil-forming agents in multiple soil orders (Kögel-Knabner & Amelung, 2021), and with a mean biomass of up to 39.2 g/m2 and mean abundances of up to 83 ± 2.0 ind./m2 globally (Figure 1a), they are the most important contributor to invertebrate biomass in many soils (which is ~2% of that of soil microorganisms; Bar-On et al., 2018; Curry, 2004; Fierer et al., 2009). The high abundance and burrowing activity of mineral soil-dwelling earthworms (endogeic and anecic species) result in the biophysicochemical alteration of their soil environment (Brown et al., 2000) and the displacement of large amounts of soil, which is estimated to be up to 35 Mg/ha/year in temperate ecosystems (Taylor et al., 2019). Referring to the extent to which earthworms "engineer" their environment (Capowiez, Sammartino, & Michel, 2014; Darwin, 1892; Frouz et al., 2009; Humphreys & Field, 1998; Scheu, 1987; Wilkinson et al., 2009), it is surprising that they have not found their way into recent concepts on SOM dynamics. Here, we argue that earthworms are key to the formation of microbial SOM resistant against external disturbances in wide regions of the mineral soil. Earthworms achieve this by concurrently alleviating constraints on microbial growth in space and time and fostering the formation of aggregates and organo-mineral associations. Embracing this central role of earthworms in SOM dynamics beyond their bioturbation activity enables a novel view on soil carbon sequestration and provides opportunities for integrated management strategies in the face of climate change.

2 | EARTHWORMS CATALYZE THE FORMATION AND STABILIZATION OF MICROBIAL NECROMASS—CONCEPT AND IMPLICATIONS

During their burrowing activity, earthworms ingest and mix organic matter with mineral soil, add easily decomposable compounds consisting of amino acids, sugars, and glycoproteins (Zhang et al., 2016), and egest this mixture as casts (Scheu, 1991). These casts may account for a major proportion of the whole soil profile, with soil ingestion rates by earthworms of up to 2000 and 500 Mg dry soil/ha/year in tropical and temperate ecosystems, respectively (Lavelle, 1988). Moreover, casts contain >50% higher amounts of water-soluble compounds and >84% higher contents of available nitrogen and phosphorus as compared to non-ingested soil (Brown et al., 2000; Van Groenigen et al., 2018). Significant increases in microbial biomass and activity in earthworm casts are well documented (Groffman et al., 2015; Hoeffner et al., 2018; Jouquet et al., 2013). Similarly well documented is the temporary nature of this effect, i.e., microbial biomass and activity in casts approach those in control soil several days after reworking (Brown et al., 2000).

We argue that via the creation of such transient microbial hotspots in casts, earthworms considerably accelerate the formation of microbial necromass (Angst, Mueller, Prater, et al., 2019; Mora et al., 2003; Vidal et al., 2019) by alleviating two factors commonly constraining microbial growth: first, addition of bioavailable compounds and provisioning of nutrients alleviate potential substrate limitations and increase microbial CUE (Barthod et al., 2021; Bohlen et al., 2002), and second, the intimate mixture of mineral soil and organic matter in casts (Scullion & Malik, 2000) co-locates microorganisms and substrates previously separated (Sokol et al., 2019). This results in the efficient built-up of microbial biomass and the concurrent and accelerated formation of microbial necromass due to a rapid microbial turnover in casts (Thu Hoang et al., 2020).

This process has important implications for SOM dynamics: first, due to the transient nature of microbial hotspots, microbial activity and, thus, SOM mineralization in casts are increased in the short term, which might result in the loss of bulk SOC (Lubbers et al., 2017). By contrast, the generated microbial necromass becomes stabilized on longer time scales via tight binding to mineral surfaces (Buckeridge, La Rosa, et al., 2020) and occlusion within cast aggregates (Bossuyt et al., 2005), processes that are favored by earthworms (Al-Mallik & Scullion, 2013; Gühr et al., 2020) and which render the remaining SOC more resistant against disturbances. Second, the abundance of bioavailable substrates in casts enables microbes to grow more efficiently on "recalcitrant" compounds via cometabolism (Marschner et al., 2008), such that microbial necromass formation would be partially independent of the quality of the pre-existing SOM. This is in contrast to the assumptions of recent concepts that plant input quality is a major driver of the formation rate of microbial necromass (Cotrufo et al., 2013). These concepts may not be unconditionally applicable in soils inhabited by earthworms.

Based on the considerations above, we propose an alternative concept embracing the central role of earthworms in how rapid and how much microbial necromass is generated in mineral soils.
This concept aligns recent ideas on the formation of stabilized SOM with the activity of earthworms and provides a novel perspective on the mechanisms underlying microbial necromass formation and stabilization in mineral soil. We specifically emphasize the relevance of this concept in extensive soil regions remote from "classical" hotspots of microbial SOM formation, such as the rhizosphere, detritusphere, or preferential flow paths of dissolved organic matter (Bundt et al., 2001; Kuzyakov & Blagodatskaya, 2015), due to the earthworm’s wide sphere of influence (from 0 to more than 100 cm depth, depending on the species). Management strategies that aim to increase soil microbial necromass and SOC sequestration may thus not only want to employ measures aimed at “directly” influencing microbial physiology (Kallenbach et al., 2015), but take a broader approach to also maintain or establish earthworm populations in mineral soils. This could be achieved by implementing various actions at the plot (to landscape) scale that additionally entail benefits for soil health and help adapt to and mitigate climate change (Lehmann et al., 2020; Pörtner et al., 2021). For example, increasing crop diversity, reducing tillage for certain soils, such as those affected by heat or erosion, and applying organic amendments

(Figure 2)
In regions with low crop yields, are expected to foster carbon sequestration, have positive effects on plant production, water quality, and human health, and reportedly increase earthworm biomass and abundance (Amelung et al., 2020; Lehmann et al., 2020; Wittwer et al., 2021). Diversification of plant species and planting of legumes in grassland soils, specifically in low-productivity pastures and savannas (Tilman et al., 2006), are expected to increase soil carbon sequestration and earthworm biomass and abundance (Eisenhauer et al., 2009; O’Mara, 2012; Singh et al., 2020; Wittwer et al., 2021). Similarly, an increase in tree functional diversity (De Wandeler et al., 2016) and establishment of species with well palatable tissues (e.g., broadleaf vs. coniferous trees; Curry, 2004) and positive influence on the soil’s base saturation (such as trees with high tissue Ca concentrations; Angst, Mueller, Eissenstat, et al., 2019; Reich et al., 2005) increase earthworm biomass and abundance in forest soils and can be considered in re- or afforestation efforts (Mayer et al., 2020).

While the central role of earthworms in the formation of microbial SOM is supported by recent experimental evidence (increases in microbial-derived amino sugars between 37% and 145% have been reported; Angst, Mueller, Prater, et al., 2019; Mora et al., 2003; Nguyen Tu et al., 2020; Vidal et al., 2019), the relevance of our concept to bulk SOC stability and stocks in various environments, for example, different soil groups, land uses, or covers (see also Figure 1), and in the context of a changing climate remains unclear (Phillips et al., 2019; Singh et al., 2019). The potential of earthworms to increase N₂O emissions (Drake & Horn, 2007; Lubbers et al., 2013) and the fact that invasive species may initially reduce overall soil carbon stocks (forest floor + mineral soil; Bohlen et al., 2004, but see also Ferlian et al., 2020) have to further be reconciled with the favorable effect of earthworm activity on microbial necromass formation reported here. To solve these unanswered questions, we encourage soil fauna-related studies to break new ground by combining biomarkers, isotopes, physical fractionations, and a spatially resolved sampling design in integrated field studies, with variations in land use/cover and climate change-related variables (such as temperature and precipitation) as central elements. Monitoring of carbon and nitrogen fluxes within this context will be of specific importance to disentangle the quantitative role of earthworms with respect to the soil’s greenhouse-gas balance and the whole SOC budget. Finally,
we emphasize the necessity to also untwine the role of other, widespread saprophagous invertebrates such as mites, colembolans, and nematodes (van den Hoogen et al., 2019) in the formation of microbial necromass and SOM, which will open up new opportunities for the management of soils as a carbon sink.

**AUTHOR CONTRIBUTIONS**

Gerrit Angst conceived of the concept and drafted the first version of the manuscript. Ingrid Kögel-Knabner and Nico Eisenhauer provided specific input on the presented concept and, together with Jan Frouz, Jan Willem van Groenigen, and Stefan Scheu, helped to improve all subsequent versions of the manuscript.

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**CONFLICTS OF INTEREST**

All authors declare no competing interests.

**DATA AVAILABILITY STATEMENT**

The data used to compile Figure 1 and the supplementary figures can be freely accessed at https://doi.org/10.25829/idiiv.1880-17-3189.

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**REFERENCES**

Al-Maliki, S., & Scullion, J. (2013). Interactions between earthworms and residues of differing quality affecting aggregate stability and microbial dynamics. *Applied Soil Ecology, 64*, 56–62. https://doi.org/10.1016/j.apsoil.2012.10.008

Amelung, W., Bossio, D., deVries, W., Kögel-Knabner, I., Lehmann, J., Amundson, R., Bol, R., Collins, C., Lal, R., Leifeld, J., Minasny, B., Pan, G., Paustian, K., Rumpel, C., Sanderman, J., vanGroenigen, J. W., Mooney, S., vanWesemael, B., Wander, M., & Chabbi, A. (2020). Towards a global-scale soil climate mitigation strategy. *Nature Communications, 11*(1), 1–10. https://doi.org/10.1038/s41467-020-18887-7

Angst, G., Mueller, C. W., Prater, I., Angst, S., Peterse, F., & Nierop, K. G. J. (2019). Earthworms act as biochemical reactors to convert labile plant compounds into stabilized soil microbial necromass. *Communications Biology, 2*(441), 1–7. https://doi.org/10.1038/s42003-019-0684-z

Angst, G., Mueller, K. E., Eissenstat, D. M., Trumbore, S., Freeman, K. H., Hobbie, S. E., Chorover, J., Oleksyn, J., Reich, P. B., & Mueller, C. W. (2019). Soil organic carbon stability in forests: Distinct effects of tree species identity and traits. *Global Change Biology, 14548*, 1529–1546. https://doi.org/10.1111/gcb.14548

Angst, G., Mueller, K. E., Nierop, K. G. J., & Simpson, M. J. (2021). Plant- or microbial-derived? A review on the molecular composition of stabilized SOM. *Soil Biology and Biochemistry, 156*, 108189.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on earth. *Proceedings of the National Academy of Sciences, 115*(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Barthod, J., Dignac, M. F., & Rumpel, C. (2021). Effect of decomposition products produced in the presence or absence of epigeic earthworms and minerals on soil carbon stabilization. *Soil Biology and Biochemistry, 160*, 108308. https://doi.org/10.1016/j.soilbio.2021.108308

Bohlen, P. J., Edwards, C. A., Zhang, Q., Parmelee, R. W., & Allen, M. (2002). Direct effects of earthworms on microbial assimilation of labile carbon. *Applied Soil Ecology, 20*(3), 255–261. https://doi.org/10.1016/S0929-1393(02)00027-6

Bohlen, P. J., Scheu, S., Hale, C. M., McLean, M. A., Magge, S., Groffman, P. M., & Parkinson, D. (2004). Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment, 2*(8), 427–435. https://doi.org/10.1890/1540-9295(2004)002[0427:NIEAAO]2.0.CO;2

Bossuyt, H., Six, J., & Hendrix, P. F. (2005). Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology and Biochemistry, 37*(2), 251–258. https://doi.org/10.1016/j.soilbio.2004.07.035

Brown, G. G., Barois, I., & Lavelle, P. (2000). Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains (Paper presented at the 16th world congress of soil science, 20–26 August 1998, Montpellier, France). *European Journal of Soil Biology, 36*(3), 177–198. https://doi.org/10.1016/S1164-5563(00)01062-1

Buckeridge, K. M., La Rosa, A. F., Mason, K. E., Whitaker, J., McNamara, N. P., Grant, H. K., & Ostle, N. J. (2020). Sticky dead microbes: Rapid abiotic retention of microbial necromass in soil. *Soil Biology and Biochemistry, 149*, 107929. https://doi.org/10.1016/j.soilbio.2020.107929

Buckeridge, K. M., Mason, K. E., McNamara, N. P., Ostle, N., Puissant, J., Goodall, T., Griffiths, R. I., Stott, A. W., & Whitaker, J. (2020). Environmental and microbial controls on microbial necromass recycling, an important precursor for soil carbon stabilization. *Communications Earth & Environment, 1*(1), 36. https://doi.org/10.1038/s43247-020-00031-4

Bundt, M., Widmer, F., Pesaro, M., Zeyer, J., & Blaser, P. (2001). Preferential flow paths: Biological “hot spots” in soils. *Soil Biology and Biochemistry, 33*(6), 729–738. https://doi.org/10.1016/S0038-911X(01)00218-2

Capowiez, Y., Bottinelli, N., & Jouquet, P. (2014). Quantitative estimates of burrow construction and destruction, by anecic and endogeic earthworms in repacked soil cores. *Applied Soil Ecology, 74*, 46–50. https://doi.org/10.1016/j.apsoil.2013.09.009

Capowiez, Y., Sammartino, S., & Michel, E. (2014). Burrow systems of endogeic earthworms: Effects of earthworm abundance and consequences for soil water infiltration. *Pedobiologia, 57*(4), 303–309. https://doi.org/10.1016/j.pedobi.2014.04.001
Phillips, H. R. P., Guerra, C. A., Bartz, M. L. C., Briones, M. J. I., Brown, G., Crowther, T. W., Ferlian, O., Gongalsky, K. B., van denHoogen, J., Krebs, J., Orgiazzi, A., Routh, D., Schwarz, B., Bach, E. M., Bennett, J., Brose, U., Decaëns, T., König-Ries, B., Loreau, M., ... Eisenhauer, N. (2019). Global distribution of earthworm diversity. Science, 366(6446), 480–485. https://doi.org/10.1126/science.aax4851

Pörntrig, H.-O., Scholes, R. J., Agard, J., Archer, E., Arnhet, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L. (William), Diamond, D., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., ... Nigo, H. (2021). Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change. IPBES Secretariat, Bonn, Germany. https://doi.org/10.5281/ZENODO.5101125

Potvin, L. R., & Lilleskov, E. A. (2017). Introduced earthworm species exhibited unique patterns of seasonal activity and vertical distribution, and Lumbricia terrestris burrows remained usable for at least 7 years in hardwood and pine stands. Biology and Fertility of Soils, 53(2), 187–198. https://doi.org/10.1007/s00374-016-1173-x

Reich, P. B., Oleksyn, J., Modrýn, J., Mrożinski, P., Hobbie, S. E., Eissenstat, D. M., Chorover, J., Chadwick, O. A., Hale, C. M., & Tjoelker, M. G. (2005). Linking litter calcium, earthworms and soil properties: A common garden test with 14 tree species. Ecology Letters, 8(8), 811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x

Scheu, S. (1987). The role of substrate feeding earthworms (Lumbricidae) for bioturbation in a beechwood soil. Oecologia, 72(2), 192–196. https://doi.org/10.1007/BF00379266

Scheu, S. (1991). Mucus excretion and carbon turnover of endogeic earthworms. Biology and Fertility of Soils, 12(3), 217–220. https://doi.org/10.1007/BF00337206

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Seiler, C., & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. Nature, 478(7367), 49–56. https://doi.org/10.1038/nature10386

Scullion, J., & Malik, A. (2000). Earthworm activity affecting organic matter and microbial activity in soils restored after open-cast mining for coal. Soil Biology and Biochemistry, 32(1), 119–126. https://doi.org/10.1016/S0038-0717(99)00142-X

Singh, J., Cameron, E., Reitz, T., Schädling, M., & Eisenhauer, N. (2020). Grassland management effects on earthworm communities under ambient and future climatic conditions. European Journal of Soil Science, 72(1), 343–355. https://doi.org/10.1111/ejss.12942

Singh, J., Schädling, M., Demetrio, W., Brown, G. G., & Eisenhauer, N. (2019). Climate change effects on earthworms - a review. Soil Organisms, 9(3), 114–138. https://doi.org/10.25674/soi913pp114
drilosphere is depth dependent. *Soil Biology and Biochemistry*, 147, 107852. https://doi.org/10.1016/j.soilbio.2020.107852

Tilman, D., Hill, J., & Lehman, C. (2006). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314(5805), 1598–1600. https://doi.org/10.1126/science.1133306

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., deGoede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Carels, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., … Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, 572(7768), 194–198. https://doi.org/10.1038/s41586-019-1418-6

Van Groenigen, J. W., Van Groenigen, K. J., Koopmans, G. F., Stokkermans, L., Vos, H. M. J., & Lubbers, I. M. (2018). How fertile are earthworm casts? A meta-analysis. *Geoderma*, 338(October 2018), 525–535. https://doi.org/10.1016/j.geoderma.2018.11.001

Vidal, A., Watteau, F., Remusat, L., Mueller, C. W., Nguyen Tu, T. T., Buegger, F., Derenne, S., & Quenea, K. (2019). Earthworm cast formation and development: A shift from plant litter to mineral associated organic matter. *Frontiers in Environmental Science*, 7(April), 1–15. https://doi.org/10.3389/fenvs.2019.00055

Wilkinson, M. T., Richards, P. J., & Humphreys, G. S. (2009). Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews*, 97(1–4), 257–272. https://doi.org/10.1016/j.earscirev.2009.09.005

Wittwer, R. A., Bender, S. F., Hartman, K., Hydbom, S., Lima, R. A. A., Loaiza, V., Nemecek, T., Oehl, F., Olsson, P. A., Petchey, O., Prechl, U. E., Schlaeppi, K., Scholten, T., Seitz, S., Six, J., & Van Der Heijden, M. G. A. (2021). Organic and conservation agriculture promote ecosystem multifunctionality. *Science Advances*, 7(34), 1–13. https://doi.org/10.1126/sciadv.abg6995

Zhang, D., Chen, Y., Ma, Y., Guo, L., Sun, J., & Tong, J. (2016). Earthworm epidermal mucus: Rheological behavior reveals drag-reducing characteristics in soil. *Soil and Tillage Research*, 158, 57–66. https://doi.org/10.1016/j.still.2015.12.001

Zou, X., & Gonzalez, G. (1997). Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. *Soil Biology and Biochemistry*, 29(3–4), 627–629. https://doi.org/10.1016/S0038-0717(96)00188-5

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