

<https://doi.org/10.17221/461/2022-PSE>

Chemical composition of earthworm casts as a tool in understanding the earthworm contribution to ecosystem sustainability – a review

MADALINA IORDACHE*

Department of Sustainable Development and Environmental Engineering, Faculty of Agriculture, University of Life Sciences "King Michael I", Timișoara, Romania

**Corresponding author: mada_iordache@yahoo.com*

Citation: Iordache M. (2023): Chemical composition of earthworm casts as a tool in understanding the earthworm contribution to ecosystem sustainability – a review. *Plant Soil Environ.*, 69: 247–268.

Abstract: Earthworms dominate the soil biota, and different structural and functional features of their biology and ecology have been studied and exploited to evaluate their contributions as ecosystem services. Due to their feeding ecology, burrowing and casting activity, earthworms are involved in the nutrient cycles, and therefore it is opportune to be considered when the biogeochemical cycles of the terrestrial ecosystems are analysed. All structural, microbiological and biogeochemical impacts of earthworms in soil start with their feeding and digestive functions, which end in casting. The casting activity consisting of the excretion of the ingested soil and organic matter after digestion processes depends on earthworm feeding behaviours and ecology, even described in the current literature as a new ecological feature: the casting ecology. The complexity of the chemical relationships occurring inside earthworm casts between main nutrients (organic carbon, nitrogen, phosphorus, potassium, calcium) highlights the complexity of the biogeochemical cycles and the great earthworms' contribution to these cycles in the ecosystems towards a better understanding of the soil sustainability through the soil biodiversity contribution. Due to this great contribution, the earthworms' casts should be included as indicators in the integrative conservation management of the ecosystems, as a re-thinking of the concept of ecosystem sustainability.

Keywords: soil biota; bioturbation; Oligochaeta: Lumbricidae; bioindicator; soil services

Biodiversity was widely reported to be correlated to sustainability, not only in natural ecosystems but also in anthropic ecosystems. Earthworms (Oligochaeta: Lumbricidae) have been many times confirmed as soil bioengineers (Jones et al. 1994, Boyle et al. 2019) and as environmental, biological drivers (Lemtiri et al. 2014, Phillips et al. 2020), and different structural and functional features of their biology and ecology were researched. The feeding and burrowing behaviours of these organisms are the most important providers of benefits and services in terrestrial ecosystems: the epigeic earthworms feed with surface litter and generally organic matter (Hoeffner et al. 2018) and are litter-dwelling species contributing to its decomposition and mineral recycling (Dungait et al. 2008); the endogeic earthworms are geophagous species, soil-dwelling species, horizontally burrowers, with major impact in increasing the soil fertility and improving important physical properties of it, such drainage,

aeration, texture, structure, bulk density (Iordache 2012); the anecic earthworms vertically and deeply burrow into the soil and feed with soil and surface litter (Dungait et al. 2008) by pulling it into the burrows and contributing this way to the improvement of numerous properties of soils (Iordache 2012). The casting activity of earthworms consisting of excretion of the ingested soil and organic matter after digestion processes depends on these three types of feeding behaviours and ecology of the earthworms, being even described in the current literature in the field as a new ecological feature of earthworms: the casting ecology (Boyle et al. 2019).

When earthworm casts have been structurally analysed, the studies have focused on the microscale architecture (Pey et al. 2013, Vidal et al. 2016), micromorphology (Shipitalo and Protz 1989), organo-mineral stability (Haynes and Fraser 1998, Bottinelli et al. 2010, Chen et al. 2021). However, due to their

implications in the nutrient cycles, through casting activity (between 36 and 108 t/ha/year (Lavelle and Spain 2001) in temperate ecosystems), such as nutrient enhancing and availability shifting between the nutrient pools of the soil as result of the properties of the biogenic casts (the formation of earthworm casts determines changes in the microbiota spread, distribution and composition across soil layers, alteration of the resources accessibility to soil biota, increased microbial and enzyme activity against the adjacent soil, reasons for why the casts are considered microbial hotspots) and also do to their contribution in modifying the soil characteristics through bioturbation (layer arrangement, aggregates, porosity, bulk density, runoff and sediment loss, water retention and management) through the soil ingestion and mixing during the burrowing activity, modifying thus the microbiological accessibility to the organic and inorganic soil nutrients, earthworms worth to be considered when the biogeochemical cycles of the ecosystems are analysed. During the food consumption and cast excretion, the earthworms are mixing the mineral and organic substrates of the soil and thus alter the nutrient cycles at these levels (Frelich et al. 2006), shifting subsequently the microbial community of soil and rising through their casts soil conditions as media for selective microbial growth (Traore et al. 2022), all these aspects with implications in the global natural cycles of gas emissions, like CO₂ and N₂O through complex chemical interactions (Tecimen et al. 2021). Earthworms accomplish the major role of supplying organic matter (mostly present in the first 20–30 cm of topsoil) to the soil food webs, making it more available to other soil microorganisms (Lemtiri et al. 2014) and converting it in their body tissues with different ratio C:N than initial input (Schmidt et al. 1999), regulating thus the C and N cycles and creating models and pathways of retention and loss of C and N at soil level. The main drivers of these contributions are the mechanistic and microbiological transformations mediated by earthworm digestion and excretion (casting) characteristics. According to their ecological type, earthworms ingest soil organic matter with different localisation in the soil profile, accessing this way different pools of C and N from it and acting as detritivore organisms with various niches of C and N (total, labile) related to the soil profile. The epigeic and endogeic earthworms access during their feeding the total and labile C and N from plant litter and residues and the microbial biomass (both mainly contributors of the soil organic matter (Vidal

et al. 2019)), but the endogeic and anecic earthworms also ingest mineral soil and determine transformed microstructural architecture and distribution between organic and mineral fractions (Le Mer et al. 2022) within casts, which create conditions for C and N loss (CO₂ mineralisation, denitrification, leaching) or protection (C sequestration, nitrification) (Lemtiri et al. 2014). The biological feature of earthworms involved in assessing these benefits is the digestive function, finalised in excretion, as casts. All structural, microbiological and biogeochemical impacts of earthworms in soil start with their feeding and digestive functions, which end in casting. Earthworms are cast into their burrows or on the soil, depending on the species and their feeding and burrowing ecology (Boyle et al. 2019, Vidal et al. 2019). The properties of earthworm casts and their contributions to the natural and human terrestrial ecosystems have been studied in field conditions and laboratory experiments. Earthworm casts represent a nexus among three factors when their chemical features are analysed: plant residues (above and below ground) (Fisk et al. 2004), mineral particles of soil, and soil microbiota (Vidal et al. 2019), representing therefore complex biogenic-organo-mineral aggregates (Lee 1985, Six et al. 2004, Sheehy et al. 2019). The research in the field already revealed that earthworms' casts are richer in several main nutrients (like nitrogen, phosphorus, and potassium) than the adjacent soil (Table 1), and their chemical composition depends on species (Suarez et al. 2004, Sheehy et al. 2019, Aira et al. 2022b), diet (Shi et al. 2019), soil type (Abail et al. 2017), site type (Nowak 1995, Chen et al. 2021), seasonality and climatology (Wang et al. 2021a), tillage (Bottinelli et al. 2010, Andriucă et al. 2012) or other chemical factors of the adjacent soil or food, like carbon content (Nowak 1995), C:N ratio (Decaens et al. 1999), exchangeable cations (Basker et al. 1993, Nowak 1995), or microbiology (Aira et al. 2022a,b). However, studies regarding the intrinsic chemical composition of earthworm casts and their implications in the biogeochemical cycles of the main nutrients in terrestrial ecosystems are scarce.

The chemical parameters included in this analysis have been chosen due to their significant importance in soil quality and plant nutrition and because several studies (Rawlins et al. 2008, Jia et al. 2012) recommend these parameters as indicators in assessing the evolution of ecosystems: organic carbon (OC), nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca). It was chosen to include the Ca in the analysis of earthworm casts because earthworms pre-

<https://doi.org/10.17221/461/2022-PSE>

Table 1. Contents of earthworm cast nutrients (C, N, P, K, Ca) as compared to the bulk soil

No.	Nutrient form	The content increase compared to bulk soil (%)	Earthworm species/ ecological group	Ecosystem type	Source
1	Organic C	82–94	<i>Millsonia inermis</i> (Michaelson 1892) – endogeic	Sudano-Sahelian agroecological cropping system amended with woody residues, West Africa	Traore et al. (2022)
2		330	<i>Pontoscolex corethrurus</i> (Muller 1857) – endogeic	30-year-old subtropical monsoon plantation (<i>Schima wallichii</i> dominated), China	Wang et al. (2021b)
3		50	<i>Amyntas khami</i> (Thai 1984) – anecic	small watershed, tropical environment, Northern Vietnam	Bottinelli et al. (2021)
4		40–48	meta-analysis	meta-analysis	Van Groenigen et al. (2019)
5		60–90	<i>Amyntas adexilis</i> (Thai 1984) – anecic	tropical environment, Northern Vietnam	Puche et al. (2022)
6		20.50	<i>Eisenia fetida</i> (Savigny 1826) – epigeic	no tillage semi-humid temperate continental monsoon climate, Northern China	Chen et al. (2021)
7		14.40	<i>Eisenia fetida</i> (Savigny 1826) – epigeic	ridge tillage semi-humid temperate continental monsoon climate, Northern China	Chen et al. (2021)
8		114.15	<i>Drawida assamensis</i> (Gates 1945) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
9		99.19	<i>Eutyphoeus scutarius</i> (Michaelson 1907) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
10		13.59	<i>Metaphire posthuma</i> (Vaillant 1868) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
11		10–22.72	<i>Lumbricus terrestris</i> L. (1758) – anecic	mesocosm	Nowak (1995)
12		12.72	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic	mesocosm	Nowak (1995)
13		15–19	<i>Eisenia fetida</i> (Savigny 1826) – epigeic	mesocosm	Shi et al. (2019)
14		0.87–4.92	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic and <i>Lumbricus terrestris</i> L. (1758) – anecic (dominants)	wheat crop, France	Bottinelli et al. (2010)
15	Dissolved organic C	927.27	<i>Lumbricus rubellus</i> (Hoffmeister 1843) – epigeic	mesocosm	Vos et al. (2014)
16		410	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic	mesocosm	Vos et al. (2014)
17		910	<i>Lumbricus terrestris</i> L. (1758) – anecic	mesocosm	Vos et al. (2014)
18	Total N	11.50	<i>Metaphire tschiliensis tschiliensis</i> (Michaelson 1928) – endogeic	mesocosm	Teng (2012)
19		197	<i>Pontoscolex corethrurus</i> (Muller 1857) – endogeic	30-year-old subtropical monsoon plantation (<i>Schima wallichii</i> dominated), China	Wang et al. (2021b)

Continued Table 1. Contents of earthworm cast nutrients (C, N, P, K, Ca) as compared to the bulk soil

No.	Nutrient form	The content increase compared to bulk soil (%)	Earthworm species/ ecological group	Ecosystem type	Source
20	Total N	40–48	meta-analysis	meta-analysis	Van Groenigen et al. (2019)
21		75.12	<i>Drawida assamensis</i> (Gates 1945) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
22		116.60	<i>Eutyphoeus scutarius</i> (Michaelsen 1907) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
23		28.72	<i>Metaphire posthuma</i> (Vaillant 1868) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
24	Available N	42.63	<i>Drawida assamensis</i> (Gates 1945) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
25		198.41	<i>Eutyphoeus scutarius</i> (Michaelsen 1907) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
26		66.70	<i>Metaphire posthuma</i> (Vaillant 1868) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
27	Mineral N	241 (mean)	meta-analysis	meta-analysis	Van Groenigen et al. (2019)
28	Total P	14.51	<i>Metaphire tschiliensis tschiliensis</i> (Michaelsen 1928) – endogeic	mesocosm	Teng (2012)
29		57.69	<i>Pontoscolex corethrurus</i> (Muller 1857) – endogeic	30-year-old subtropical monsoon plantation (<i>Schima wallichii</i> dominated)	Wang et al. (2021b)
30		40–48	meta-analysis	meta-analysis	Van Groenigen et al. (2019)
31	Available P	73–130	<i>Millsonia inermis</i> (Michaelsen 1892) – endogeic	Sudano-Sahelian agroecological cropping system amended with woody residues, West Africa	Traore et al. (2022)
32		84 (mean)	meta-analysis	meta-analysis	Van Groenigen et al. (2019)
33		30.08	<i>Drawida assamensis</i> (Gates 1945) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
34		33.22	<i>Eutyphoeus scutarius</i> (Michaelsen 1907) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
35		68.65	<i>Metaphire posthuma</i> (Vaillant 1868) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
36	Total available P	300–450	<i>Eisenia fetida</i> (Savigny 1826) – epigeic	mesocosm	Shi et al. (2019)
37	Total K	2.41	<i>Metaphire tschiliensis tschiliensis</i> (Michaelsen 1928) – endogeic	mesocosm	Teng (2012)
38	Available K	52.19	<i>Drawida assamensis</i> (Gates 1945) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
39		109.54	<i>Eutyphoeus scutarius</i> (Michaelsen 1907) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)
40		65.15	<i>Metaphire posthuma</i> (Vaillant 1868) – endogeic	bamboo plantations, West India	Chakraborty et al. (2020)

<https://doi.org/10.17221/461/2022-PSE>

Continued Table 1. Contents of earthworm cast nutrients (C, N, P, K, Ca) as compared to the bulk soil

No.	Nutrient form	The content increase compared to bulk soil (%)	Earthworm species/ ecological group	Ecosystem type	Source
41		7–12.6	<i>Eisenia fetida</i> (Savigny 1826) – epigeic	mesocosm	Shi et al. (2019)
42	Available K	4.34–34.78	<i>Lumbricus terrestris</i> L. (1758) – anecic	mesocosm	Nowak (1995)
43		8.69	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic	mesocosm	Nowak (1995)
44	Total Ca	27.55	<i>Metaphire tschiliensis tschiliensis</i> (Michaelson 1928) – endogeic	mesocosm	Teng (2012)
45	Total CaCO ₃	66.19	<i>Proselodrilus</i> spp. – endogeic	mesocosm	Garcia-Montero et al. (2013)
46		10–17	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic and <i>Lumbricus rubellus</i> (Hoffmeister, 1843) – epigeic (dominants)	3-5-year-old meadow, Poland	Makulek and Kusińska (1997)
47	Exchangeable Ca ²⁺	204–252	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic and <i>Lumbricus rubellus</i> (Hoffmeister 1843) – epigeic (dominants)	6-8-year-old meadow, Poland	Makulek and Kusińska (1997)
48		219–300	<i>Apporectodea caliginosa</i> (Savigny 1826) – endogeic and <i>Lumbricus rubellus</i> (Hoffmeister 1843) – epigeic (dominants)	permanent meadow, Poland	Makulek and Kusińska (1997)

sent oesophageal calciferous glands (Hopfensperger et al. 2011) with an incompletely elucidated role.

Organic carbon in earthworm casts

The content of organic carbon in soils depends on several main factors like vegetation (Wei et al. 2022), local climate (Mao et al. 2022, Wang et al. 2022), mineralisation degree of organic matter (Ortner et al. 2022), microbiota (Mueller et al. 2015). The soil stock in the first meter of the soil profile is more organic carbon than the atmosphere and the above-ground vegetation combined (FAO 2017). It is estimated that 75% of the total organic carbon (TOC) stored in terrestrial ecosystems is contained in soil, a double

amount than in the atmosphere (Dixon et al. 1994). Through casting, earthworms stabilise the soil organic carbon (SOC) into soil aggregates depending on the distribution of aggregate fractions (Wu et al. 2017, Arai et al. 2018) and mediate the redistribution and the storage of the SOC and N in soil macroaggregates (> 250 µm) as indicated a study in a no-tilled boreal soil (Sheehy et al. 2019). The organic carbon in earthworm casts depends on total pore area, tensile strength, and water repellence, which are indicators of the physical and structural stability of earthworm casts to be maintained unaltered in order to enhance the long-term carbon sequestration (Chen et al. 2021), along with increased earthworm abundance. Several studies (Li et al. 2014) showed that C miner-

alisation is strongly coupled with N mineralisation, and a positive correlation exists between C and N mineralisation in soil. The C is a driver both for earthworm activity and for N mineralisation (Sierra et al. 2014) because both depend on its availability. Two sources for the interactions that occurred between C and N have been revealed until present to be implicated in the natural biogeochemical cycles of carbon and nitrogen: the microbiological activity of soil and the chemical transformations of plant litter in relation to earthworms feeding and locomotion activities. The soil microbiota which serves as food for earthworms has a low possibility to move into the soil across the soil layers to reach organic food resources in order to find assimilable C to feed up (Lavelle et al. 1995, Brown et al. 2000), so the earthworms serve as vectors and accomplish this role, as a mutualistic association, resulting a priming-enhancement of microbiota after passing through earthworm gut (Lavelle et al. 1995), and thus both parts (earthworms and microbiota) contributing to C and N mineralisation in soil (Bernard et al. 2012, Abail et al. 2017). These mechanisms should be regarded as a qualitative enhancement because not always the species richness of the microbial communities are positively affected after earthworms ingestion, being noted as neutral (de Menezes et al. 2018) and negative (Furlong et al. 2002, Koubová et al. 2015) effects. Other two mechanisms through which the cycles of C and N are deeply related to the earthworm feeding particularities are the enhancement of the enzymatic activity of the microbiota involved in the decomposition of organic matter and associated with earthworm digestion (Jouquet et al. 2007, Don et al. 2008, Lu et al. 2021) and respectively the direct influence of earthworms on the expression of the microbial genes (Medina-Sauza et al. 2019), especially on the functional genes of the bacteria involved in N cycle (Ribbons et al. 2018, Lv et al. 2019), expressed as increase or decrease of N release as a species-depending mechanism (Lv et al. 2019). Fahey et al. (2011) explained the transport of C and N between plant litter and soil organic matter in a forest ecosystem through the close interrelations between C and N, which appear in two processes regarding the plant litter decomposition and mineralisation, both with high importance in earthworm feeding and cast production: the leaching of organic matter from plant litter, and the mineralisation of litter through digestion-associated microbial processes. Not always a high rate of earthworm-associated C

mineralisation produces changes in the total carbon of soil (Price-Christenson et al. 2020). However, there are many more factors which affect the natural cycle C-N in earthworm presence, like plant roots presence (Suarez et al. 2004), the presence of mycorrhizae (Paudel et al. 2016, He et al. 2018), or type and quality of food substrate (Lavelle et al. 1992, Marhan and Scheu 2005), cast ageing (Decaens et al. 1999, Aira et al. 2010, Bottinelli et al. 2020), cast freshness (Lavelle et al. 1992, Decaens et al. 1999), reabsorption processes of C and N taking place in the earthworm gut (Lavelle et al. 1992), certain climatic conditions or soil physical parameters (McInerney and Bolger 2000), seasonality (Subler and Kirsch 1998, Wang et al. 2021a). Thus, the C content increased along cast ageing, probably due to certain processes like CO₂ fixation, organic matter with the dead-root origin, and macrofaunal activities in earthworm casts (Decaens et al. 1999). Don et al. (2008) found that the diameter of an earthworm burrow is a factor affecting the C input into the soil, serving as a transport path and showed that the burrow diameter is an indicator of burrow age, especially if the increase of the diameter is associated with the increase of the depth. Also, factors like the status of the burrow, abandoned or inhabited, or the filling of the burrow (Leue et al. 2018) with new casts in attempting to reduce the burrow diameter according to species necessities are suggested in the evaluation of the contribution of earthworm casts to C-N cycles.

The content and availability of N and the dynamic of C in soil are significantly impacted by the practices of land use and the history of earthworm casts (Jouquet et al. 2007) because these affect the microbiological activity both in casts and in soil, impacting thus the mineralisation and the availability of the labile organic substrates, influencing thereby the microbial immobilisation in the soil of C and N. Thus, there was found that higher activity of acid phosphatase in old earthworm casts is associated with fungal activity (Jouquet et al. 2007), probably because the soil organic matter becomes less bioavailable during cast ageing (Jouquet et al. 2007), unlike fresh casts where bacteria dominate the microbial activity as a response to the great availability and lability of organic matter (Wolters and Joergensen 1992). Aira et al. (2010) showed that, only through the casting process (producing and ageing), endogeic earthworms *A. caliginosa* form isolated hot spots of microbial activity and biomass in soil, activity decreasing with cast ageing while the biomass remains

<https://doi.org/10.17221/461/2022-PSE>

constant although with a superior value for fungi as compared to bacteria. Several studies do not support this tendency of the microbial activity dominated by fungi in earthworm casts over time during the ageing process (Tiunov and Scheu 2000), suggesting that this is a species-mediated and environmentally-mediated phenomenon. Changes in the mineralisation of soil organic carbon in earthworm casts have also been reported to be related to the volume of the particulate organic matter and the pore architecture of casts in the anecic earthworm *Amyntas exiles* in a tropical ecosystem from northern Vietnam, emphasising the role of earthworms as biophysical stabilisers, stockers and controllers of soil organic carbon (Puche et al. 2022). Also, other earthworm physiological particularities are associated with C labilisation in casts, such as the earthworm mucus, which is secreted during the burrowing activities and cast formation and is rich in labile C compounds (Eisenhauer 2010).

Earthworms can sequester SOM in temperate ecosystems (Zhang et al. 2013) through casting, and their impact on carbon mineralisation was estimated at to 20% increase in certain experimental conditions (Garnier et al. 2022). Thus, earthworms become important in understanding the C and N mineralisation/sequestration processes in soils, which are complex phenomena needing further information to be elucidated. Recent studies (Zhang et al. 2018, 2020) showed that the stocking ways of TOC and total N in soil represent a very important tool in the evaluation of ecosystem sustainability to mitigate climatic changes and to bring carbon back into the soil is indicated by more relevant recent studies (Lubbers et al. 2013, Nigussie et al. 2017, Sheehy et al. 2019, Puche et al. 2022) to be a main goal in fighting climate warm alongside the reducing of carbon emissions, as two parts of a single balance. The activities which disrupt the natural soil profile, like activities involving land degradation, like surface mining (Liu et al. 2017), disturb the cycles of TOC and total N by reducing their pool in soil (Shrestha and Lal 2010). However, the pool of TOC and N_t in the soil can increase in adequate situations of soil management, like revegetation (Zhang et al. 2020) or exploitation of the bio-ecological features of soil biota, such as earthworm presence in soil (Padmavathiamma et al. 2008), among others. Regarding this last aspect, an "earthworm dilemma" (Lubbers et al. 2013) requires to be more investigation in the future by the scientific community: are the earthworms greenhouse emitters

(Rizhiya et al. 2007, Namoi et al. 2019, Santos et al. 2021) or, on the contrary, these organisms are carbon stockers (Zhang et al. 2013)? An answer based on the achievements of the current research in the field indicates that this depends on site-specific conditions of the ecosystem (Knowles et al. 2016, Thomas et al. 2020, Puche et al. 2022) or on other indirect factors like food substrate (Namoi et al. 2019). Thomas et al. (2020) showed that earthworms are involved in C storage through the following mechanisms: soil-organic matter aggregation in casts, hydrophobicity of casts, and organo-mineral complexes of casts. The physical stabilisation of C in earthworm casts by physical sequestration remains one of the reliable earthworms' ways to stabilise the C in soil (Alekseeva et al. 2006, Thomas et al. 2020, Puche et al. 2022). Certain studies showed that soil organic C protection in fresh earthworm casts becomes evident after 72 days, and long-term physical protection through organic C sequestration in earthworm casts lasts more than 400 days (Puche et al. 2022). Some studies showed that earthworms' presence not always increases the stocks of C in soil, but in the long term, the earthworm castings contribute to increasing the resilience of C in soils (Thomas et al. 2020), physically but also chemically because earthworms may exhibit as well chemical ways to stabilise the C such as regulating CO_2 by producing calcite granules (ability specific to certain lumbricid species – Canti and Pearce 2003), or bio-chemical ways such as humification of the soil organic matter in the form of humus-carbon resistant to microorganism decomposition (United States Department of Agriculture 2009) as a form of aggregate stability (Marashi and Scullion 2003, Neto et al. 2010, Desie et al. 2020), or enhance the presence of cementing agents like polysaccharides and lignin (Ge et al. 2001, Alekseeva et al. 2006) in casts in attempting to stabilise labile forms of C into more stable forms (Stevenson 1994, Thomas et al. 2020).

A table presenting a synthesis of C transformations during the earthworm activity of casting (Table 2) is listed below.

Nitrogen in earthworm casts

Some studies estimate that approximately 10% of the total organic matter of the soil present in the first 15 cm of soil is annually passing through the earthworms, and also these organisms process a similar percent of mineral N of the annual plant N

Table 2. Carbon (C) transformations related to earthworm-casting processes

No.	Process	Mediator factors	Determinant factors	Source
1	C mineralisation	Earthworm digestive system and feeding ecology	Mechanical grinding and peristaltic movements of the gizzard and gut on food Earthworm gut microbiota from digestive mucus Digestive enzymes of earthworm gut Earthworm casts microbiota Earthworm gut transit has priming-enhancement effect on ingested microbiota Earthworm locomotion is vector of soil microbiota movement across soil layers	Abail et al. (2017) Bernard et al. (2012) Bertrand et al. (2015) Brown et al. (2000) Don et al. (2008) Gopal et al. (2017) Jouquet et al. (2007) Lavelle et al. (1995) Li et al. (2014) Lu et al. (2021) Needham et al. (2004) Price-Christenson et al. (2020) Sierra et al. (2014)
2	C stabilisation	Earthworm casts	Biophysical stabilisation: – earthworm casting stabilises the organic C into soil aggregates Biochemical stabilisation: – producing CaCO ₃ granules from CO ₂ in the oesophageal calciferous glands (certain <i>Lumbricidae</i> species) – humification of the soil organic matter as humus-carbon resistant to microorganism decomposition – cementing agents (polysaccharides, lignin) which stabilise the labile forms of C into more stable forms	Alekseeva et al. (2006) Arai et al. (2018) Bossuyt et al. (2002) Canti and Pearce (2003) Desie et al. (2020) Fonte and Six (2010) Ge et al. (2001) Marashi and Scullion (2003) Neto et al. (2010) Puche et al. (2022) Six et al. (2000) Stevenson (1994) Thomas et al. (2020) Wu et al. (2017)
3	C sequestration	Cast structural stability	Physical sequestration: the long-term carbon sequestration is enhanced by the physical structural stability of earthworm casts (soil – organic matter aggregation, organo-mineral complexes) Re-absorption processes of C in the earthworm gut Casts hydrophobicity	Alekseeva et al. (2006) Chen et al. (2021) Lavelle et al. (1992) Lubbers et al. (2013) Nigussie et al. (2017) Puche et al. (2022) Sheehy et al. (2019) Thomas et al. (2020) Zhang et al. (2013)
4	C immobilisation	Earthworm casts	Microbial biomass immobilisation of C in earthworm casts (microbial hot spots) after mineralisation of the labile organic substrates Cast age: soil organic matter (SOM) is less bio-available in the aged casts (fungi-dominated) unlike fresh casts (bacteria-dominated)	Aira et al. (2010) Jouquet et al. (2007) Wolters and Joergensen (1992)
5	C redistribution	Earthworm drillosphere Earthworm-bioturbation of soil	earthworm digestive, casting and locomotion behaviours redistribute the soil organic carbon (SOC)	Sheehy et al. (2019)

<https://doi.org/10.17221/461/2022-PSE>

Continued Table 2. Carbon (C) transformations related to earthworm-casting processes

No.	Process	Mediator factor	Determinant factors	Source
6	C augmentation	Cast ageing	C content increases along cast ageing due to CO ₂ fixation microbiologically mediated	Decaens et al. (1999)
7	C labilisation	Earthworm digestive physiology: gut mucus	Earthworm mucus rich in labile C compounds	Eisenhauer (2010)
8	C emission	Earthworm digestive physiology and ecology Earthworm burrowing and casting behaviour	CO ₂ emissions through SOM decomposition after gut transit Earthworm burrowing and casting facilitate the greenhouse gasses escape from soil into the atmosphere	Knowles et al. (2016) Lubbers et al. (2013) Namoi et al. (2019) Puche et al. (2022) Rizhiya et al. (2007) Santos et al. (2021) Thomas et al. (2020)

uptake and, respectively, 50% of the P annual plant uptake (James 1991), both with implications in the nutrient cycle and mineralisation depending on the ecosystem characteristics. In terrestrial ecosystems, the relations of earthworms with the N cycle *via* their casts should be investigated as a holistic approach in the broad sense of the biogeochemical cycles, and not only from a chemical viewpoint, because many other parameters, such as the physical ones, were identified to contribute in N cycle. For example, a coarse soil texture could accelerate the denitrification rate within anecic earthworm casts (Nieminen et al. 2015, Sheehy et al. 2019), thus masking the earthworm effect of N mineralisation. An interesting finding on N loss in the soil through mineralisation as earthworm activity was reported by Bohlen et al. (2004) in a north temperate forest from North America, where earthworms were responsible for forest floor loss and thus suspected for N loss, but surprisingly there was found the earthworm role in the conservation of N originated from the forest floor in the mineral soil and no change in the soil total N for a depth of 12 cm, as well as no effect on C:N ratio. An earthworm-related factor responsible for the total N increase in the soil through casting is the diet which determines the final metabolic excreta (Padmavathiamma et al. 2008) as urine and mucus containing glycoproteic molecules (Morris 1985, Padmavathiamma et al. 2008, Guhra et al. 2020) released in soil and casts, and which is closely related to the earthworm ecological group (Lemtiri et al. 2014). Also, stimulating agents of N fixation (like gut mucus) could be involved in Lee (1985).

The earthworm contribution to the N cycle is pH dependent. In nitrate formation from ammonium, the increase of pH becomes an important factor, especially if it is associated with the increase of soil macropores through earthworm activity, as precursor conditions of aerobiosis for the nitrifying bacteria, responsible for nitrate production, and this has great importance in the distribution of the different forms of N with different leachability, across soil layers, as earthworm influence, because the nitrate is more leachable than ammonium and because the distribution of the nitrate and ammonium in the mineral and organic fractions of the soil is earthworm mediated (Qiu and Turner 2017, Ferlian et al. 2020).

The direct relation between N and pH and also between Ca and pH in the soil in earthworm presence was found by Salmon (2001) and García-Montero et al. (2013), and it results in a pH increase of the acidic soils through earthworm secretions containing N and CaCO₃ substances. But before this secretion mechanism is manifested in this way at the soil level, the intestinal secretions of earthworms rich in N alongside CaCO₃ secretion of the lumbricid species, both pH modulators, accomplish an important another role in the digestive tract of earthworms firstly (Lu et al. 2021) and offer a selective environment for specific bacteria targeting thus certain species to reproduce and to be excreted in casts in the surrounding soil, creating thereby a microecological environment, and resulting thus the major cause of earthworms' contribution in the ecological cycle of the nutrients.

Table 3. Nitrogen (N) transformations of different substrates by earthworm casting activity

No.	Earthworm-mediated determinant factor	Substrate	N transformations	Earthworm species/ ecological group	Source
N mineralisation					
Nitrification					
1	Earthworm-microbial interactions: enzymatic enhance of urease which rapidly hydrolyses the NH_4^+ -N and then can undergo ammonia oxidation and nitrification to generate plant-available NH_4^+ -N and NO_3^- -N	^{15}N -labeled urea	^{15}N up taken by plant: 33.07% ^{15}N retained in soil: 60.65% ^{15}N losses to environment: N_2O emission, NH_3 volatilisation and NO_3^- leaching: 4.04%	<i>Metaphire guillelmi</i> (Michaelsen, 1895) – endogeic	Na et al. (2022)
N mineralisation throughout earthworm gut					
Cast-enhance of β -glucosidase and N-acetyl- β -glucosaminidase activity					
2	Casts act as selective microbial growth media transit with nutrient enrichments	Endogleyic Acrisol of Sudano-Sahelian agroecological cropping (<i>Sorghum bicolor</i> (L.) Moench var. kapèga) system amended with woody (<i>Piliostigma reticulatum</i>) residues	Increase of total N content	<i>Millsonia inermis</i> (Michaelsen, 1892) – endogeic	Traore et al. (2022)
N mineralisation					
Denitrification					
3	Anaerobic activity of nitrate-reducing microbes in earthworm casts Oxy-reduction processes microbially mediated in earthworm casts	Incubated earthworm casts	Increase of exchangeable NH_4 and release of N_2O	<i>Rhinodrilus alatus</i> (Righi, 1971) – endogeic	Santos et al. (2021)
N mineralisation					
4	NH_4^+ increase rather due to earthworm metabolism source than from microbial biomass activity	5 cm-topsoil amended with ^{15}N -labeled decomposing material (composted straw)	NH_4^+ increase	Whatever the ecological group (epigeic, endogeic, anecic), with differences between groups	Cortez et al. (2000)
N mineralisation					
5	Microbiological ammonification cast-enhanced	Substrate from 1:2 mixture of Haplic Chernozem and quartz sand, planted with 11 grassland species	Release of NH_4^+ -N and NO_3^- -N	<i>Lumbricus terrestris</i> L. (1758) – anecic and <i>Apporectodea caliginosa</i> (Savigny, 1826) – endogeic	Zaller et al. (2013)
N mineralisation					
Nitrification					
6	Open mesocosms in a Cambisol from a Northern Japan forest	Open mesocosms in a Cambisol from a Northern Japan forest	Mesocosm NH_4^+ -N production (ammonification) and NO_3^- -N production (nitrification) in casts	<i>Eisenia japonica</i> (Michaelsen, 1892) – endogeic	Makoto et al. (2019)

<https://doi.org/10.17221/461/2022-PSE>

Table 3. Nitrogen (N) transformations of different substrates by earthworm casting activity

No.	Earthworm-mediated determinant factor	Substrate	N transformations	Earthworm species/ecological group	Source
N₂ fixation					
7	Active N ₂ -fixing bacteria on the body surface and/or in the gut Nitrogenase activity increased by the burrowing and feeding activity of earthworms	Fresh casts from meadow ecosystem (<i>Arrhenatherion elatioris</i> W. Koch 1926) and woodlot park ecosystem	Increase in nitrogenase activity as indicator of N ₂ -fixing bacteria activity	<i>Apporectodea caliginosa</i> (Savigny, 1826) – endogeic <i>Lumbricus rubellus</i> (Hoffmeister, 1843) – epigeic	Simek and Pizl (1989)
8	Biological N-fixation Earthworms increased the N content of soil due to the enhancement of the aerobic nitrogen-fixing activity	Mesocosm (Gray Lowland soil, silty clay supplemented with 1% carboxymethyl cellulose)	Increase of total-N, NH ₄ -N, NO ₃ -N, and the population of aerobic nitrogen-fixing bacteria Enhanced incorporation of ¹⁵ N to soil from atmospheric ¹⁵ N ₂	<i>Amyntas vittatus</i> (Goto and Hatai, 1898) – epi-endogeic	Ozawa et al. (2005)
9	Nitrification Microbial earthworm-cast contribution	Powder of ¹⁵ NH ₄ ¹⁵ NO ₃ (99 atom % ¹⁵ N)	NH ₄ ⁺ was nitrified, provoking the release of NO ₃ ⁻	<i>Apporectodea caliginosa</i> (Savigny, 1826) – endogeic	Agapit et al. (2018)
10	Denitrification Interactions between the structural forms, aggregate dynamics, microbiota	Incubated earthworm casts	Release of N ₂ O emissions	<i>Amyntas</i> spp. (Kinberg, 1867) – epigeic	Law and Lai (2021)
11	Denitrification Priming of denitrifying organisms Earthworm feeding behaviour facilitate the access to fresh organic matter for denitrification	¹⁵ N-labeled maize in crop residues (<i>Zea mays</i> L.)	Release of N ₂ O emissions	<i>Apporectodea caliginosa</i> (Savigny, 1826) – endogeic <i>Lumbricus rubellus</i> (Hoffmeister, 1843) – epigeic	Parkin and Berry (1994) Nebert et al. (2011)
12	Denitrifying anaerobic bacteria and other nitrate-dissimilating bacteria present in soil and activated after ingestion in the substrate-rich earthworm gut lumen	Microcosm with garden topsoil (10 cm)	NO ₃ completely reduced to N ₂ (NO ₂ and N ₂ O are transient products) in earthworm gut	<i>Apporectodea caliginosa</i> (Savigny, 1826) – endogeic	Ihsen et al. (2003)
13	NO ₃ ⁻ leaching <i>M. posthuma</i> produced granular labile casts prone to water disintegration with detrimental effect on soil roughness, aggregate stability and detachment, and NO ₃ ⁻ leaching	Rainfall simulation microcosm	NO ₃ ⁻ leaching	<i>Metaphire posthuma</i> (Vaillant, 1868) – endogeic	Jouquet et al. (2013)

Table 3 presents the N transformations determined by the earthworm casting activity related to substrate type and earthworm species, and feeding ecology.

Phosphorus in earthworm casts

While the dynamic of soil N within ecosystems is regulated mainly through biological activities, the soil phosphorus is regulated mainly through physical processes (Li et al. 2019, Yang et al. 2019), such strong adsorption to the mineral phase of soil (Suarez et al. 2004, Vos et al. 2019), soil temperature (Yang et al. 2019), and in the smaller measure through biological mechanisms like protons release into the rhizosphere by plants and microorganisms with great potential to solubilise P and reduce P limitations, which is a pH-dependent mechanism, more efficient in the acid soils (Pingree et al. 2017, Zurovec et al. 2021). Indirectly, climatic warming through soil warming, which increases enzymatic microbiological activity and accelerate mineralisation, can affect the P dynamic in soil (Zucarrini et al. 2020). Available P and pH are key factors that influence the structure and diversity of bacterial communities (Lu et al. 2021).

Several studies indicated that earthworm casts have significantly higher pH than the bulk soil regardless of their feeding and burrowing ecology (epigeic, endogeic, anecic) (Vos et al. 2019), which determines the increase of the phytoavailable P in casts. The mineralisation of P is stimulated through the microbial community from the earthworm gut (Lopez-Hernandez et al. 1993) and occurs in casts. Other studies show no differences between species in earthworm casts for pH and total reversibly adsorbed P (Vos et al. 2019) but indicate significant differences within species for the plant available P (Bohlen et al. 2004, Vos et al. 2019), suggesting the composition and distribution of earthworm species as the main regulators of plant available P. Other factors, like the land use history and the phase of ecological succession, are the main determinants in the P cycle because of the changes induced in the earthworm functional ecological groups dominating an area (Suarez et al. 2004).

Other studies showed bio-mediated mechanisms to be involved in the P phytoavailability in soil: the microbiological (bacterial and fungal) releasing (Basilio et al. 2022) and earthworm releasing (Liu et al. 2021), with important contribution since the easily plant-available forms of P in soil (mainly orthophosphates – Hawkesford et al. 2012) are limited

(Morel et al. 2000, Vos et al. 2019). The bacteria and fungi directly mediate the increase of plant available P in soil by producing organic acids and phosphatases and indirectly by inducing phytohormones secretion (Basilio et al. 2022).

Several mechanisms involved in the P cycle are earthworm-related: release of the plant easily available P from inorganic sources through earthworm contribution to plant root development and mycorrhizas enhancement (Meng et al. 2022); enzymatic hydrolysis of organic P into labile forms as a result of the earthworm digestive processes and of the casting activity which enhances and diversify the associated microbiome involved in the enzymatic mechanisms (Kohler et al. 2018, Meeds et al. 2021); proton excretion through plant roots and microorganisms, which creates appropriate conditions to solubilise the inorganic forms of P (Pingree et al. 2017).

Earthworms increase the bioavailability of P in soil (Pingree et al. 2017) by increasing the functional diversity of soil biota (Shu et al. 2022) and improving and regulating the enzymatic activity of soil (Zucarrini et al. 2020, Li et al. 2022, Shu et al. 2022), and also by enhancing the plant growth-promoting rhizobacteria in soil (Wu et al. 2012). This last contribution of earthworms has been demonstrated in a laboratory experiment by studying the concentrations of bioavailable P in earthworm casts after single (earthworms) and dual (earthworms and phosphate-solubilising bacteria *Bacillus megaterium* HKP-1) inoculation in the experimental soil. The results showed that in the earthworm casts significantly increased the abundance of these bacteria after a short (0–34 h) period of incubation and the concentrations of bioavailable P, with significantly higher concentrations for dual inoculation than for the single, explained through the synergic effect determined by the increased abundance of the phosphate-solubilising bacteria and increased activity of acid phosphatase determined in earthworm casts after gut transition and also by the bacterial addition, which recommends the practice of dual inoculation of earthworms and phosphate-solubilising bacteria to reduce the agriculture dependence for P-mineral fertilisers due to the bio-availability of P obtained through this type of earthworm contribution (Wu et al. 2012). Earthworms can also transform P from inorganic to organic forms independently of amendment addition (Nahidan and Ghasemzadeh 2022), thus contributing to P turnover in soil. There was also found a reduction of the total P in topsoil (12 cm) in earthworm presence when

<https://doi.org/10.17221/461/2022-PSE>

these are invaders and when these are epi-endogeic (Suarez et al. 2004), but this fact is compensated by the increase of the readily exchangeable and available P (resin-P) which partially is fixed as unavailable P, namely as NaOH-Po (organic P stored in stable organic matter), and another reduced part is lost through water leaching. In this case, in the presence of epi-endogeic earthworms, the water-leaching of P appeared when the labile P was recycled between organic and inorganic forms. The P water-leaching due to epi-endogeic earthworms is compensated by the continuous input of litter from the upper soil layers and by the bioturbation of the soil organic matter (including that from plant-root source) caused by ingestion and cast excretion at the topsoil level, and also by the structural changes in the topsoil structure determined by their feeding and locomotion behaviours, putting this way the soil particles and the comminuted organic matter in closer contact to the soil microbiota involved in P cycle, which means that the P leaching in soil depends both on the ecological group of earthworms and microbial availability. The increase of plant-available P of soil in epi-endogeic earthworm presence could also be explained through the earthworm's capability to increase the amount of readily exchangeable P in soil by influencing the exchange complexes of soil colloids (Suarez et al. 2004). But, when the earthworms were invaders but anecic, the amount of total P, unavailable and occluded inorganic P in the topsoil increased because the anecic earthworms are deep vertical burrowers of the soil and thus mobilise unweathered particles of the soil from depth to surface, making them more microbiologically-available and increasing thus the amount of total P at this level. Still, the NaOH-Po decreased, probably because the NaOH-Po amount was found to be correlated to the amount of water-stable soil aggregates produced by earthworm casting, which is lower in the anecic earthworms than in the epi-endogeic species (Flegel et al. 1998). This shifting between P fractions in the soil in earthworm presence shows that the earthworm-recycling between the organic and inorganic forms of labile P depends on the ecological group of earthworm.

Earthworm activity increases and diversifies the bioavailability of inorganic P (Pingree et al. 2017) when associated with other interactive factors (like charcoal in andisols of northern sub-boreal forests) even in conditions known to be unfavourable for P availability, like a low pH and highly limited post-fire soil environment specific to volcanic ash soils

ecosystem. In earthworm presence, the P was found to be fixed in Fe and Al hydroxides in the mineral soil as inorganic P or found as P stored in the stable organic matter, such NaOH-Po fraction (Suarez et al. 2004).

The ecological group of the earthworms is a factor associated as well with another effect of earthworms on the P cycle: several studies found that the epi-endogeic species are more efficient in the stimulation and increase of the P cycle in soil because they produce casts richer in exchangeable P than the anecic species, especially when this species ability is associated with the capacity to form water-stable aggregates and with the burrowing activity which can favour the P mineralisation (Suarez et al. 2004). The anecic species, known for their deep burrowing, are susceptible to bringing in the top layers of the soil materials from the deeper layers rich in Al and Fe hydroxides responsible for the P fixation as an inorganic fraction, balancing thus the P forms in soil due to earthworm activity (Suarez et al. 2004). The leaching of P was rarely reported in epigeic species (like *Dendrobaena octaedra*) (Scheu and Parkinson 1994a,b), suggesting rather that this effect remains largely an effect of soil mixing and microbial activity earthworm-related and also of the earthworm increasing of preferential flow out through burrowing than the result of the feeding ecology of this group (Suarez et al. 2004).

A great contribution of earthworms in P cycling was found to be plant related and dependent on the ecological feeding group of earthworms by Bohlen et al. (2004) within an experiment indicating a higher root uptake of P by plants in the presence of epigeic earthworms and its accumulation in leaves and thus the linking role of earthworms in P cycle in the relation soil-plant. Also, the geophagous earthworms were found to indirectly influence the solubility of P through their casting, which increases the net nitrification rates (Vitousek et al. 2010, Kawakami and Makoto 2017).

In soil, the plant available P and the total P have been found to be significantly positively correlated to the organic C in other studies (Shah et al. 2019), the organic P and the inorganic P have been found to be dependent on N fixing (Aleixo et al. 2020). Also, the plant available N and P are C-cycle related because they regulate the C productivity and sequestration (Tang et al. 2018). The relation between N and P in soil was demonstrated by Li et al. (2021) and Standish et al. (2022) in studies about the influence of N avail-

ability on P acquisition in soil which revealed that the determining mechanisms of this relation are biologically mediated: by phosphatase activity (Li et al. 2021) and mycorrhizal fungal colonisation (Li et al. 2021, Standish et al. 2022), which is suspected by several authors (Png et al. 2017) to be a phylogenetically competitive adaption in balancing the N and P pools of soil.

Potassium in earthworm casts

Although potassium is present in the soil in available forms, it is also present in forms hardly available for plants, such as silicates (K-feldspar, quartz) (Suzuki et al. 2003, Liu et al. 2011, 2016) or in non-exchangeable pools (Basker et al. 1994), but earthworms can increase its release from these hardly available forms due to the microbiological processes enhanced in their gut after what these minerals passed through earthworm digestion and which are measurable both in the gut and casts as higher bacterial diversity and modified taxa distribution than in the surrounding substrate, that regulate the pH values and produce enzymes or organic ligands (Basker et al. 1994, Carpenter et al. 2007) determining a direct decomposition and thus a biochemical mineral weathering and an acceleration of the mineral degradation, in forms of, among other elements (Fe, Al, Ca), more water-soluble K and HNO_3 -extractable K in casts than in the surrounding substrate. The biochemical mineral weathering microbially mediated by earthworms is also supported by the mechanical grinding and peristaltic movements of the gizzard and gut on food (Needham et al. 2004). The mineral weathering determined by earthworms' gut microbiota has occurred even after one day after the mineral fed with K-feldspar or quartz, in the forms of finer and rounded mineral grains in earthworm casts as compared to the initial mineral food (Suzuki et al. 2003), which demonstrate that earthworms are able to breakdown mineral grains and not just be selective when they choose to ingest finer particles of minerals from those existing in the food substrate. Earthworms' implications in the potassium cycle were generally related to the same factors as in N or P cycles: the microbial community of soils, the physical and chemical characteristics of soil, the physiological and ecological characteristics of earthworms and the ecosystem type. The presence by addition of earthworms in soil showed that the ecological type of feeding matters and significantly increased the available potassium of the soil in the

rhizosphere zone and optimised the bacterial community as structure, diversity, and beneficial taxa, whose presence was positively correlated to the potassium content of the soil, contributing thus to increase the effectiveness of K in soil (Lu et al. 2021). Earthworms are able to K biotransformation, activating the mineral or organic K and transforming it into rapidly available K and effective K in casts after the feeding, digestion and absorption processes, which could be a solution for K release in the low-potassium substrates to be used by plants (Zhu et al. 2013). Thus, the importance of earthworms in K cycles in the soil becomes essential for plants as another biological way for this purpose alongside the already known contribution of soil microorganisms (Das et al. 2022) because the soil is the main source of potassium for plants, and this nutrient is scarce in many soils of the world (Rengel and Damon 2008), especially as plant-available form (Zorb et al. 2014). The main physiological characteristic of earthworms in K enrichment in soil is the digestive transit with all its associated processes, especially the modifications induced in the structure and functions of the bacterial community of cast releasing (Wang et al. 2021b), regulating this way the nutrients cycle in the terrestrial ecosystems. A great contribution of earthworms through their casts to the K cycle is the shifting made between K pools of the soil: the K release from the non-exchangeable pool into exchangeable K (Basker et al. 1994). Several factors were found to influence the K availability in earthworm casts: the content of exchangeable K of the adjacent soil (Basker et al. 1994) and the vegetal contribution of K – the lower K content of plant debris than the soil content and it is weak bound in plant material and generally in organic matter as compared to N and P (Basker et al. 1992). However, several studies reported that certain earthworm species could have biological regulation of K through their metabolism (Mohammed and Rida 1995, Wu et al. 2012, Zhu et al. 2013), and these species succeeded in avoiding limiting factors of K availability.

Calcium in earthworm casts

Several studies indicated the implications of Ca in earthworms' contribution to the biogeochemical cycles.

Generally, earthworm casts are rich in Ca^{2+} (Jouquet et al. 2008), and several studies indicated that the divalent Ca^{2+} present in the casts increases

<https://doi.org/10.17221/461/2022-PSE>

the electrostatic binding between casts particles (Six et al. 2004, Oyedele et al. 2006, Jouquet et al. 2008, Thomas et al. 2020) resulting thus their higher stability through particle cohesion, and also regulate the linkage of organic matter to phosphorous and carbon (Shipitalo and Protz 1989). Earthworms (lumbricid earthworms) are Ca contributors in soil due to their biological characteristics – the calciferous glands, located in the oesophagus, which produce from CO_2 after several chemical transformations (Gago-Duport et al. 2008), a final stabilised compound, the calcite (CaCO_3) (Robertson 1936, Briones et al. 2008), which, together with small amounts of amorphous calcium carbonate, vaterite and aragonite (Gago Duport et al. 2008, Beck and Andreassen 2010, Brinza et al. 2014), will form spherulites with long-term stability achieved by amino acids or protein incorporation (Versteegh et al. 2014, Hodson et al. 2015), eliminated in casts. Thus, it results that earthworm granules of calcite are real long-time carbon sinks, especially because of their biogenic formation, being known that the abiogenic CaCO_3 is highly unstable and rapidly, within minutes, reaches transformations (Faatz et al. 2004, Rodriguez-Blanco et al. 2011, Bots et al. 2012) and it has a short life span in the inorganic systems (Hodson et al. 2015). Several calculations showed a contribution of earthworm casts to the C pool of soils through CaCO_3 production in calciferous glands up to 261 kg C/ha/year in some species (Versteegh et al. 2014) noted as significant (Briones et al. 2008, Thomas et al. 2020) mechanism of inorganic C stocking in soils, by fixing the environmental and metabolic CO_2 , and therefore an important argument in characterising lumbricid earthworms as C sequesters on long-term through their casts, and not just organisms with an interesting way to physiologically regulate the CO_2 into their body. The contributions of CaCO_3 from earthworm casts in the soil ecosystem are even more consistent because it is involved in the cementation and stabilisation of the organic matter after digestion, as Rowley et al. (2018) found.

Other studies reported the contribution of earthworm granules of amorphous calcium carbonate in regulating the soil pH and the pH of earthworms' tissue fluid, acting as a buffer excretion because it precipitates when the ions of HCO_3^- are in excess (Hodson et al. 2015). The Ca content in earthworms was found to act as a neutraliser of body liquids (Nowak 1995), and its value depends on the soil pH: it increases in acid habitats. It remains unchanged or decreases in alkaline habitats. The soil pH is also

one of the main factors controlling the availability of other soil nutrients, such as N, P, and K (Desie et al. 2020, Xu and Zhang 2021, Zurovec et al. 2021). It is not yet clear if the secretion Ca-rich of calciferous glands depends on the earthworm diet or if it is an earthworm-intrinsic biomineralisation process (Gago-Duport et al. 2008).

The earthworm cast composition in main nutrients (organic carbon, nitrogen, phosphorus, potassium, calcium) with complexity of their chemical interactions shows that earthworms create through their casts new relations in the ecosystem and accomplish a very complex function of the ecosystem: the biogeochemical cycles, which recommend earthworms' casts to be included as an indicator in the integrative conservation management of the ecosystems, as a rethinking of the concept of ecosystem sustainability.

REFERENCES

- Abail Z., Sampedro L., Whalen J.K. (2017): Short-term carbon mineralisation from endogeic earthworm casts as influenced by properties of the ingested soil material. *Applied Soil Ecology*, 116: 79–86.
- Agapit C., Gigon A., Puga-Freitas R., Zeller B., Blouin M. (2018): Plant-earthworm interactions: influence of age and proportion of casts in the soil on plant growth, morphology and nitrogen uptake. *Plant and Soil*, 424: 49–61.
- Aira M., Lazcano C., Gomez-Brandon M., Dominguez J. (2010): Ageing effects of casts of *Aporrectodea caliginosa* on soil microbial community structure and activity. *Applied Soil Ecology*, 46: 143–146.
- Aira M., Perez-Losada M., Crandall K.A., Dominguez J. (2022a): Composition, structure and diversity of soil bacterial communities before, during and after transit through the gut of the earthworm *Aporrectodea caliginosa*. *Microorganisms*, 10: 1025.
- Aira M., Perez-Losada M., Crandall K.A., Dominguez J. (2022b): Host taxonomy determines the composition, structure, and diversity of the earthworm cast microbiome under homogenous feeding conditions. *FEMS Microbiology Ecology*, 98: fiac093.
- Aleixo S., Gama-Rodrigues A.C., Gama-Rodrigues E.F., Campello E.F.C., Silva E.C., Schripsema J. (2020): Can soil phosphorus availability in tropical forest systems be increased by nitrogen-fixing leguminous trees? *Science of the Total Environment*, 712: 136405.
- Alekseeva T., Besse P., Binet F., Delort A.M., Forano C., Josselin N., Sancelme C., Tixier C. (2006): Effect of earthworm activity (*Aporrectodea giardi*) on atrazine adsorption and biodegradation. *European Journal of Soil Science*, 57: 295–307.
- Andriucă V., Gîrlă D., Iordache M. (2012): Comparative earthworm research in various ecosystems with different anthropic impact. *Research Journal of Agricultural Science*, 44: 149–153.

<https://doi.org/10.17221/461/2022-PSE>

- Arai M., Miura T., Tsuzura H., Minamiya Y., Kaneko N. (2018): Two-year responses of earthworm abundance, soil aggregates, and soil carbon to no-tillage and fertilization. *Geoderma*, 332: 135–141.
- Basilio F., Dias T., Santana M.M., Melo J., Carvalho L., Correia P., Cruz C. (2022): Multiple modes of action are needed to unlock soil phosphorus fractions unavailable for plants: the example of bacteria- and fungi-based biofertilizers. *Applied Soil Ecology*, 178: 104550.
- Basker A., Kirkman J.H., Macgregor A.N. (1994): Changes in potassium availability and other soil properties due to soil ingestion by earthworms. *Biology and Fertility of Soils*, 17: 154–158.
- Basker A., Macgregor A.N., Kirkman J.H. (1992): Influence of soil ingestion by earthworms on the availability of potassium in soil – an incubation experiment. *Biology and Fertility of Soils*, 14: 300–303.
- Basker A., Macgregor A.N., Kirkman J.H. (1993): Exchangeable potassium and other cations in non-ingested soil and casts of two species of pasture earthworms. *Soil Biology and Biochemistry*, 25: 1673–1677.
- Beck R., Andreassen J.P. (2010): Spherulitic growth of calcium carbonate. *Crystal Growth and Design*, 10: 2934–2947.
- Bernard L., Chapuis-Lardy L., Razafimbelo T., Razafindrakoto M., Pablo A.L., Legname E., Poulain J., Brüls T., O'Donohue M., Brauman A., Chotte J.L., Blanchart E. (2012): Endogeic earthworms shape bacterial functional communities and affect organic matter mineralization in a tropical soil. *ISME Journal*, 6: 213–222.
- Bohlen P.J., Groffman P.M., Fahey T.J., Fisk M.C., Suarez E., Pelletier D.M., Fahey R.T. (2004): Ecosystem consequences of exotic earthworm invasion of north temperate forests. *Ecosystems*, 7: 1–12.
- Bots P., Benning L.G., Rodriguez-Blanco J.D., Roncal-Herrero T., Shaw S. (2012): Mechanistic insights into the crystallization of amorphous calcium carbonate (ACC). *Crystal Growth and Design*, 12: 3806–3814.
- Bottinelli N., Hallaire V., Menasseri-Aubry S., Le Guillou C., Cluzeau D. (2010): Abundance and stability of belowground earthworm casts influenced by tillage intensity and depth. *Soil and Tillage Research*, 106: 263–267.
- Bottinelli N., Kaupenjohann M., Marten M., Jouquet P., Soucemarianadin L., Baudin F., Tran T.M., Rumpel C. (2020): Age matters: fate of soil organic matter during ageing of earthworm casts produced by the anecic earthworm *Amyntas khami*. *Soil Biology and Biochemistry*, 148: 107906.
- Boyle P.E., Richardson M.D., Savin M.C., Karcher D.E., Potter D.A. (2019): Ecology and management of earthworm casting on sports turf. *Pest Management Science*, 75: 2071–2078.
- Brinza L., Schofield P.F., Hodson M.E., Weller S., Ignatyev K., Geraki K., Quinn P.D., Mosselmans J.F.W. (2014): Combining μ XANES and μ XRD mapping to analyse the heterogeneity in calcium carbonate granules excreted by the earthworm *Lumbricus terrestris*. *Journal of Synchrotron Radiation*, 21: 235–241.
- Briones M.J.I., Lopez E., Mendez J., Rodriguez J.B., Gago-Duport L. (2008): Biological control over the formation and storage of amorphous calcium carbonate by earthworms. *Mineralogical Magazine*, 72: 227–231.
- 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. *European Journal of Soil Biology*, 36: 177–198.
- Canti M.G., Pearce T.G. (2003): Morphology and dynamics of calcium carbonate granules produced by different earthworm species. *Pedobiologia*, 47: 511–521.
- Carpenter D., Hodson M.E., Eggleton P., Kirk C. (2007): Earthworm induced mineral weathering: preliminary results. *European Journal of Soil Biology*, 43: S176–S183.
- Chakraborty S., Paul N., Chaudhuri P.S. (2020): Earthworm casting activities under bamboo plantations of West Tripura, India and their impact on soil physicochemical properties. *Current Science*, 119: 1169–1177.
- Chen X., Liang A., Wu D., McLaughlin N.B., Jia S., Zhang S., Zhang Y., Huang D. (2021): Tillage-induced effects on organic carbon in earthworm casts through changes in their physical and structural stability parameters. *Ecological Indicators*, 125: 107521.
- Cortez J., Billes G., Bouché M.B. (2000): Effect of climate, soil type and earthworm activity on nitrogen transfer from a nitrogen-15-labelled decomposing material under field conditions. *Biology and Fertility of Soils*, 30: 318–327.
- Das P.P., Singh K.R., Nagpure G., Mansoori A., Singh R.P., Ghazi I.A., Kumar A., Singh J. (2022): Plant-soil-microbes: a tripartite interaction for nutrient acquisition and better plant growth for sustainable agricultural practices. *Environmental Research*, 214: 113821.
- De Menezes A.B., Prendergast-Miller M.T., Macdonald L.M., Toscas P., Baker G., Farrell M., Wark T., Richardson A.E., Thrall P.H. (2018): Earthworm-induced shifts in microbial diversity in soils with rare versus established invasive earthworm populations. *FEMS Microbiology Ecology*, 94: fty051.
- Decaens T., Rangel A.F., Asakawa N., Thomas R.J. (1999): Carbon and nitrogen dynamics in ageing earthworm casts in grasslands of the eastern plains of Colombia. *Biology and Fertility of Soils*, 30: 20–28.
- Desie E., Van Meerbeek K., De Wandeler H., Bruelheide H., Domisch T., Jaroszewicz B., Joly F.X., Vancampenhout K., Vesterdal L., Muys B. (2020): Positive feedback loop between earthworms, humus form and soil pH reinforces earthworm abundance in European forests. *Functional Ecology*, 34: 2598–2610.
- Dixon R.K., Brown S., Houghton R.A., Solomon A.M., Trexler M.C., Wisniewski J. (1994): Carbon pools and flux of global forest ecosystems. *Science*, 263: 185–190.
- Don A., Steinberg B., Schoening I., Pritsch K., Joschko M., Gleixner G., Schulze E.D. (2008): Organic carbon sequestration in earthworm burrows. *Soil Biology and Biochemistry*, 40: 1803–1812.

<https://doi.org/10.17221/461/2022-PSE>

- Dungait J.A.J., Briones M.J.I., Bol R., Evershed R.P. (2008): Enhancing the understanding of earthworm feeding behaviour *via* the use of fatty acid $\delta^{13}\text{C}$ values determined by gas chromatography-combustion-isotope ratio mass spectrometry. *Rapid Communications in Mass Spectrometry*, 22: 1643–1652.
- Eisenhauer N. (2010): The action of an animal ecosystem engineer: identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, 53: 343–352.
- Faatz M., Grohn F., Wegner G. (2004): Amorphous calcium carbonate: synthesis and potential intermediate in biomineralization. *Advanced Materials*, 16: 996–1000.
- Fahey T.J., Yavitt J.B., Sherman R.E., Groffman P.M., Fisk M.C., Maerz J.C. (2011): Transport of carbon and nitrogen between litter and soil organic matter in a northern hardwood forest. *Ecosystems*, 14: 326–340.
- FAO (2017): Soil organic carbon: the hidden potential. Rome, Food and Agriculture Organisation of the United Nations. Available at: <https://www.fao.org/3/i6937e/i6937e.pdf>
- Ferlian O., Thakur M.P., Gonzalez A.C., San Emeterio L.M., Marr S., Rocha B.D., Eisenhauer N. (2020): Soil chemistry turned upside down: a meta-analysis of invasive earthworm effects on soil chemical properties. *Ecology*, 101: e02936.
- Fisk M.C., Fahey T.J., Groffman P.M., Bohlen P.J. (2004): Earthworm invasion, fine-root distributions, and soil respiration in north temperate forests. *Ecosystems*, 7: 55–62.
- Flegel M., Schrader S., Zhang H. (1998): Influence of food quality on the physical and chemical properties of detritivorous earthworm casts. *Applied Soil Ecology*, 9: 263–269.
- Frelich L.E., Hale C.M., Scheu S., Holdsworth A.R., Heneghan L., Bohlen P.J., Reich P.B. (2006): Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, 8: 1235–1245.
- Furlong M.A., Singleton D.R., Coleman D.C., Whitman W.B. (2002): Molecular and culture-based analyses of prokaryotic communities from an agricultural soil and the burrows and casts of the earthworm *Lumbricus rubellus*. *Applied and Environmental Microbiology*, 68: 1265–1279.
- Gago-Duport L., Briones M.J.I., Rodriguez J.B., Covelo B. (2008): Amorphous calcium carbonate biomineralization in the earthworm's calciferous gland: pathways to the formation of crystalline phases. *Journal of Structural Biology*, 162: 422–435.
- Garcia-Montero L.G., Valverde-Asenjo I., Grande-Ortiz M.A., Menta C., Hernando I. (2013): Impact of earthworm casts on soil pH and calcium carbonate in black truffle burns. *Agroforestry Systems*, 87: 815–826.
- Garnier P., Makowski D., Hedde M., Bertrand M. (2022): Changes in soil carbon mineralization related to earthworm activity depend on the time since inoculation and their density in soil. *Scientific Reports*, 12: 13616.
- Ge F., Shuster W.D., Edwards C.A., Parmelee R.W., Subler S. (2001): Water stability of earthworm casts in manure- and inorganic-fertilizer amended agroecosystems influenced by age and depth. *Pedobiologia*, 45: 12–26.
- Guhra T., Stolze K., Schweizer S., Totsche K.U. (2020): Earthworm mucus contributes to the formation of organo-mineral associations in soil. *Soil Biology and Biochemistry*, 145: 07785.
- Hawkesford M., Horst W., Kichey T., Lambers H., Schjoerring J., Moller I.S., White P. (2012): Functions of macronutrients. Available at: <https://doi.org/10.1016/b978-0-12-384905-2.00006-6>
- Haynes R.J., Fraser P.M. (1998): A comparison of aggregate stability and biological activity in earthworm casts and uningested soil as affected by amendment with wheat or lucerne straw. *European Journal of Soil Science*, 49: 629–636.
- He X., Chen Y., Liu S., Gunina A., Wang X., Chen W., Shao Y., Shi L., Yao Q., Li J., Zou X., Schimel J.P., Zhang W., Fu S. (2018): Co-operation of earthworm and arbuscular mycorrhizae enhanced plant N uptake by balancing absorption and supply of ammonia. *Soil Biology and Biochemistry*, 116: 351–359.
- Hodson M.E., Benning L.G., Demarchi B., Penkman K.E.H., Rodriguez-Blanco J.D., Schofield P.F., Versteegh E.A.A. (2015): Biomineralisation by earthworms – an investigation into the stability and distribution of amorphous calcium carbonate. *Geochemical Transactions*, 16: 4.
- Hoeffner K., Monard C., Santonja M., Cluzeau D. (2018): Feeding behaviour of epi-anecic earthworm species and their impacts on soil microbial communities. *Soil Biology and Biochemistry*, 125: 1–9.
- Hopfensperger K.N., Leighton G.M., Fahey T.J. (2011): Influence of invasive earthworms on above and belowground vegetation in a northern hardwood forest. *American Midland Naturalist*, 166: 53–62.
- Ihssen J., Horn M.A., Matthies C., Gossner A., Schramm A., Drake H.L. (2003): N_2O -producing microorganisms in the gut of the earthworm *Aporrectodea caliginosa* are indicative of ingested soil bacteria. *Applied and Environmental Microbiology*, 69: 1655–1661.
- Iordache M. (2012): Abundance of earthworms under fertilization with organo-mineral fertilizers in a chernozem from west of Romania. *Journal of Food Agriculture and Environment*, 10: 1103–1105.
- James S.W. (1991): Soil, nitrogen, phosphorus, and organic matter processing by earthworms in tallgrass prairie. *Ecology*, 72: 2101–2109.
- Jia X., Wei X., Shao M., Li X. (2012): Distribution of soil carbon and nitrogen along a revegetational succession on the Loess Plateau of China. *Catena*, 95: 160–168.
- Jones C.G., Lawton J.H., Shachak M. (1994): Organisms as ecosystem engineers. *Oikos*, 69: 373–386.
- Jouquet P., Bernard-Reversat F., Bottinelli N., Orange D., Rouland-Lefevre C., Duc T.T., Podwojewski P. (2007): Influence of changes in land use and earthworm activities on carbon and nitrogen dynamics in a steep land ecosystem in Northern Vietnam. *Biology and Fertility of Soils*, 44: 69–77.

<https://doi.org/10.17221/461/2022-PSE>

- Jouquet P., Bottinelli N., Kernels G., Henry-des-Tureaux T., Doan T.T., Planchon O., Tran T.D. (2013): Surface casting of the tropical *Metaphire posthuma* increases soil erosion and nitrate leaching in a laboratory experiment. *Geoderma*, 204–205: 10–14.
- Jouquet P., Bottinelli N., Podwojewski P., Hallaire V., Duc T.T. (2008): Chemical and physical properties of earthworm casts as compared to bulk soil under a range of different land-use systems in Vietnam. *Geoderma*, 146: 231–238.
- Kawakami T., Makoto K. (2017): Does an earthworm species acclimatize and/or adapt to soil calcium conditions? The consequences of soil nitrogen mineralization in forest soil. *Ecological Research*, 32: 603–610.
- Knowles M.E., Ross D.S., Gorres J.H. (2016): Effect of the endogeic earthworm *Aporrectodea tuberculata* on aggregation and carbon redistribution in uninvaded forest soil columns. *Soil Biology and Biochemistry*, 100: 192–200.
- Kohler J., Yang N., Pena R., Raghavan V., Polle A., Meier I.C. (2018): Ectomycorrhizal fungal diversity increases phosphorus uptake efficiency of European beech. *New Phytologist*, 220: 1200–1210.
- Koubová A., Chronáková A., Pižl V., Sánchez-Monedero M.A., Elhottová D. (2015): The effects of earthworms *Eisenia* spp. on microbial community are habitat dependent. *European Journal of Soil Biology*, 68: 42–55.
- Lavelle P., Lattaud C., Trigo D., Barois I. (1995): Mutualism and biodiversity in soils. *Plant and Soil*, 170: 23–33.
- Lavelle P., Melendez G., Pashanasi B., Schaefer R. (1992): Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex-Corethrurus* (Glossoscolecidae). *Biology and Fertility of Soils*, 14: 49–53.
- Lavelle P., Spain A.V. (2001): *Soil Ecology*. New York, Kluwer Academic Publishers.
- Law M.M.S., Lai D.Y.F. (2021): Impacts of wetting-drying cycles on short-term carbon and nitrogen dynamics in *Amyntas* earthworm casts. *Pedosphere*, 31: 423–432.
- Le Mer G., Bottinelli N., Dignac M.F., Capowiez Y., Jouquet P., Mazurier A., Baudin F., Caner L., Rumpel C. (2022): Exploring the control of earthworm cast macro- and micro-scale features on soil organic carbon mineralization across species and ecological categories. *Geoderma*, 427: 116151.
- Lee K.E. (1985): *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Sydney, Academic Press Inc.
- Lemtiri A., Colinet G., Alabi T., Cluzeau D., Zirbes L., Haubruge E., Francis F. (2014): Impacts of earthworms on soil components and dynamics. A review. *Biotechnologie, Agronomie, Société Et Environnement*, 18: 121–133.
- Leue M., Wohld A., Gerke H.H. (2018): Two-dimensional distribution of soil organic carbon at intact macropore surfaces in BT-horizons. *Soil and Tillage Research*, 176: 1–9.
- Li H., Mollier A., Ziadi N., Messiga A.J., Shi Y., Pellerin S., Parent L.E., Morel C. (2019): Long-term modeling of phosphorus spatial distribution in the no-tilled soil profile. *Soil and Tillage Research*, 187: 119–134.
- Li Q., Denton M.D., Huang Y., Zhou D. (2021): Nitrogen enrichment intensifies legume reliance on root phosphatase activity but weakens inter-specific correlations between N₂ fixation and mycorrhizal colonization. *Plant and Soil*, 465: 503–514.
- Li Q., Sun Y., Zhang X., Xu X., Kuzyakov Y. (2014): Relation between carbon and nitrogen mineralization in a subtropical soil. *EGU General Assembly Conference Abstracts*, 13120.
- Li W., Zhang P., Qiu H., Van Gestel C.A.M., Peijnenburg W.J.G.M., Cao X., Zhao L., Xu X., He E. (2022): Commonwealth of soil health: how do earthworms modify the soil microbial responses to CeO₂ nanoparticles? *Environmental Science and Technology*, 56: 1138–1148.
- Liu D., Lian B., Wang B., Jiang G. (2011): Degradation of potassium rock by earthworms and responses of bacterial communities in its gut and surrounding substrates after being fed with mineral. *PlosOne*, 6: e28803.
- Liu J., Hu J., Cheng Z., Li M., Liu Z., Wang J., Lin X. (2021): Can phosphorus (P)-releasing bacteria and earthworm (*Eisenia fetida* L.) co-enhance soil P mobilization and mycorrhizal P uptake by maize (*Zea mays* L.)? *Journal of Soils and Sediments*, 21: 842–852.
- Liu W., Xu X., Wu X., Yang Q., Luo Y., Christie P. (2006): Decomposition of silicate minerals by *Bacillus mucilaginosus* in liquid culture. *Environmental Geochemistry and Health*, 28: 133–140.
- Liu X., Bai Z., Zhou W., Cao Y., Zhang G. (2017): Changes in soil properties in the soil profile after mining and reclamation in an opencast coal mine on the Loess Plateau, China. *Ecological Engineering*, 98: 228–239.
- Lopez-Hernandez D., Lavelle P., Fardeau J.C., Nino M. (1993): Phosphorus transformations in two P sorption contrasting tropical soils during transit through *Pontoscolex corethrurus* (Glossoscolecidae: Oligochaeta). *Soil Biology and Biochemistry*, 25: 789–792.
- Lu Y., Gao P., Wang Y., Li W., Cui X., Zhou J., Peng F., Dai L. (2021): Earthworm activity optimized the rhizosphere bacterial community structure and further alleviated the yield loss in continuous cropping lily (*Lilium lancifolium* Thunb.). *Scientific Reports*, 11: 20840.
- Lubbers I.M., van Groenigen K.J., Fonte S.J., Six J., Brussaard L., van Groenigen J.W. (2013): Greenhouse-gas emissions from soils increased by earthworms. *Nature Climate Change*, 3: 187–194.
- Lv B., Zhang D., Chen Q., Cui Y. (2019): Effects of earthworms on nitrogen transformation and the correspond genes (*amoA* and *nirS*) in vermicomposting of sewage sludge and rice straw. *Biore-source Technology*, 287: 121428.
- Makoto K., Bryanin S.V., Takagi K. (2019): The effect of snow reduction and *Eisenia japonica* earthworm traits on soil nitrogen dynamics in spring in a cool-temperate forest. *Applied Soil Ecology*, 144: 1–7.

<https://doi.org/10.17221/461/2022-PSE>

- Makulek G., Kusińska A. (1997): The role of earthworms (Lumbricidae) in transformations of organic matter and in the nutrient cycling in the soils of ley meadows and permanent meadows. *Ekologia Polska*, 45: 825–837.
- Mao X., Zheng J., Yu W., Guo X., Xu K., Zhao R., Xiao L., Wang M., Jiang Y., Zhang S., Luo L., Chang J., Shi Z., Luo Z. (2022): Climate-induced shifts in composition and protection regulate temperature sensitivity of carbon decomposition through soil profile. *Soil Biology and Biochemistry*, 172: 108743.
- Marashi A.R.A., Scullion J. (2003): Earthworm casts form stable aggregates in physically degraded soils. *Biology and Fertility of Soils*, 37: 375–380.
- Marhan S., Scheu S. (2005): Effects of sand and litter availability on organic matter decomposition in soil and in casts of *Lumbricus terrestris* L. *Geoderma*, 128: 155–166.
- McInerney M., Bolger T. (2000): Temperature, wetting cycles and soil texture effects on carbon and nitrogen dynamics in stabilized earthworm casts. *Soil Biology and Biochemistry*, 32: 335–349.
- Medina-Sauza R.M., Álvarez-Jiménez M., Delhal A., Reverchon F., Blouin M., Guerrero-Analco J.A., Cerdán C.R., Guevara R., Villain L., Barois I. (2019): Earthworms building up soil microbiota, a review. *Frontiers in Environmental Science*, 7: 81.
- Meeds J.A., Kranabetter J.M., Zigg I., Dunn D., Miros F., Shipley P., Jones M.D. (2021): Phosphorus deficiencies invoke optimal allocation of exoenzymes by ectomycorrhizas. *ISME Journal*, 15: 1478–1489.
- Meng L.L., Srivastava A.K., Kuca K., Wu Q.S. (2022): Earthworm (*Pheretima guillelmi*)-mycorrhizal fungi (*Funnelformis mosseae*) association mediates rhizosphere responses in white clover. *Applied Soil Ecology*, 172: 104371.
- Mohammed A.M., Rida A. (1995): Effect of soil contamination on the role earthworms play in the liberation of potassium. *Revue D'Ecologie – La Terre et La Vie*, 50: 141–152.
- Morel C., Tunney P., Plenet D., Pellerin S. (2000): Transfer of phosphate ions between soil and solution: perspectives in soil testing. *Journal of Environmental Quality*, 29: 50–59.
- Morris G.M. (1985): Secretory cells in the clitellar epithelium of *Eisenia fetida* (Annelida, Oligochaeta): a histochemical and ultrastructural study. *Journal of Morphology*, 185: 89–100.
- Mueller K.E., Hobbie S.E., Chorover J., Reich P.B., Eisenhauer N., Castellano M.J., Chadwick O.A., Dobies T., Hale C.M., Jagodzinski A.M., Kalucka I., Kieliszewska-Rokicka B., Modrzyński J., Rozen A., Skorupski M., Sobczyk L., Stasinska M., Trocha L.K., Weiner J., Wierzbicka A., Oleksyn J. (2015): Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species. *Biogeochemistry*, 123: 313–327.
- Na L., Hu C., Jiang Y., Hu R., Shaaban M., Younas A., Wu Y. (2022): Earthworms promote the transfer of ¹⁵N-urea to lettuce while limit appreciably increase ¹⁵N losing to environment. *Environmental Research*, 212: 113423.
- Nahidan S., Ghasemzadeh M. (2022): Biochemical phosphorus transformations in a calcareous soil as affected by earthworm, cow manure and its biochar additions. *Applied Soil Ecology*, 170: 104310.
- Namoi N., Pelster D., Rosenstock T.S., Mwangi L., Kamau S., Mutuo P., Barrios E. (2019): Earthworms regulate ability of biochar to mitigate CO₂ and N₂O emissions from a tropical soil. *Applied Soil Ecology*, 140: 57–67.
- Nebert L.D., Bloem J., Lubbers I.M., van Groenigen J.W. (2011): Association of earthworm-denitrifier interactions with increased emission of nitrous oxide from soil mesocosms amended with crop residue. *Applied and Environmental Microbiology*, 77: 4097–4104.
- Needham S.J., Worden R.H., McIlroy D. (2004): Animal-sediment interactions: the effect of ingestion and excretion by worms on mineralogy. *Biogeosciences*, 1: 113–121.
- Neto L.D.D., da Silva I.D., Inda A.V., do Nascimento P.C., Bortolon L. (2010): Physical and chemical attributes of pedogenic aggregates and earthworm casts in different soil classes of Paraíba. *Ciência e Agrotecnologia*, 34: 1365–1371.
- Nieminen M., Hurme T., Mikola J., Regina K., Nuutinen V. (2015): Impact of earthworm *Lumbricus terrestris* living sites on the greenhouse gas balance of no-till arable soil. *Biogeosciences*, 12: 5481–5493.
- Nigussie A., Bruun S., de Neergaard A., Kuyper T.W. (2017): Earthworms change the quantity and composition of dissolved organic carbon and reduce greenhouse gas emissions during composting. *Waste Management*, 62: 43–51.
- Nowak E. (1995): Chemical composition of earthworm casts in different habitats of Poland. *Polish Journal of Ecology*, 43: 205–215.
- Ortner M., Seidel M., Semella S., Udelhoven T., Vohland M., Thiele-Bruhn S. (2022): Content of soil organic carbon and labile fractions depend on local combinations of mineral-phase characteristics. *Soil*, 8: 113–131.
- Oyedele D.J., Schjonning P., Amusan A.A. (2006): Physicochemical properties of earthworm casts and uningested parent soil from selected sites in southwestern Nigeria. *Ecological Engineering*, 28: 106–113.
- Ozawa T., Risa C.P., Yanagimoto R. (2005): Increase in the nitrogen content of soil by the introduction of earthworms into soil. *Soil Science and Plant Nutrition*, 51: 917–920.
- Padmavathiamma P.K., Li L.Y., Kumari U.R. (2008): An experimental study of vermi-biowaste composting for agricultural soil improvement. *Bioresource Technology*, 99: 1672–1681.
- Parkin T.B., Berry E.C. (1994): Nitrogen transformations associated with earthworm casts. *Soil Biology and Biochemistry*, 26: 1233–1238.
- Paudel S., Longcore T., MacDonald B., McCormick M.K., Szlavecz K., Wilson G.W.T., Loss S.R. (2016): Belowground interactions with aboveground consequences: invasive earthworms and arbuscular mycorrhizal fungi. *Ecology*, 97: 605–614.

<https://doi.org/10.17221/461/2022-PSE>

- Pey B., Cortet J., Watteau F., Cheynier K., Schwartz C. (2013): Structure of earthworm burrows related to organic matter of a constructed Technosol. *Geoderma*, 202: 103–111.
- Phillips H.R.P., Guerra C.A., Bartz M.L.C. et al. (2020): Global distribution of earthworm diversity. *Science*, 369: eabd9834.
- Pingree M.R.A., Makoto K., DeLuca T.H. (2017): Interactive effects of charcoal and earthworm activity increase bioavailable phosphorus in sub-boreal forest soils. *Biology and Fertility of Soils*, 53: 873–884.
- Png G.K., Turner B.L., Albornoz F.E., Hayes P.E., Lambers H., Laliberte E. (2017): Greater root phosphatase activity in nitrogen-fixing rhizobial but not actinorhizal plants with declining phosphorus availability. *Journal of Ecology*, 105: 1246–1255.
- Price-Christenson G.J., Johnston M.R., Herrick B.M., Yannarell A.C. (2020): Influence of invasive earthworms (*Amyntas* spp.) on Wisconsin forest soil microbial communities and soil chemistry. *Soil Biology and Biochemistry*, 149: 107955.
- Puche N., Rumpel C., Le Mer G., Jouquet P., Mazurier A., Caner L., Garnier P., Tran T.M., Bottinelli N. (2022): Mechanisms and kinetics of (de-)protection of soil organic carbon in earthworm casts in a tropical environment. *Soil Biology and Biochemistry*, 170: 108686.
- Qiu J., Turner M.G. (2017): Effects of non-native Asian earthworm invasion on temperate forest and prairie soils in the Midwestern US. *Biological Invasions*, 19: 73–88.
- Rawlins B.G., Vane C.H., Kim A.W., Tye A.M., Kemp S.J., Bellamy P.H. (2008): Methods for estimating types of soil organic carbon and their application to surveys of UK urban areas. *Soil Use and Management*, 24: 47–59.
- Rengel Z., Damon P.M. (2008): Crops and genotypes differ in efficiency of potassium uptake and use. *Physiologia Plantarum*, 133: 624–636.
- Ribbons R.R., Kepfer-Rojas S., Kosawang C., Hansen O.K., Ambus P., McDonald M., Grayston S.J., Prescott C.E., Vesterdal L. (2018): Context-dependent tree species effects on soil nitrogen transformations and related microbial functional genes. *Biogeochemistry*, 140: 145–160.
- Rizhiya E., Bertora C., van Vliet P.C.J., Kuikman P.J., Faber J.H., van Groenigen J.W. (2007): Earthworm activity as a determinant for N₂O emission from crop residue. *Soil Biology and Biochemistry*, 39: 2058–2069.
- Robertson J.D. (1936): The function of the calciferous glands of earthworms. *Journal of Experimental Biology*, 13: 279–297.
- Rodriguez-Blanco J.D., Shaw S., Benning L.G. (2011): The kinetics and mechanisms of amorphous calcium carbonate (ACC) crystallization to calcite, *via* vaterite. *Nanoscale*, 3: 265–271.
- Rowley M.C., Grand S., Verrecchia E.P. (2018): Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry*, 137: 27–49.
- Salmon S. (2001): Earthworm excreta (mucus and urine) affect the distribution of springtails in forest soils. *Biology and Fertility of Soils*, 34: 304–310.
- Santos A., Cremonesi M.V., Zanatta J.A., Cunha L., Drake H.L., Brown G.G. (2021): Emission of greenhouse gases and soil changes in casts of a giant Brazilian earthworm. *Biology and Fertility of Soils*, 57: 617–628.
- Scheu S., Parkinson D. (1994a): Effects of earthworms on nutrient dynamics, carbon turnover and microorganisms in soils from cool temperate forests of the Canadian Rocky Mountains – laboratory studies. *Applied Soil Ecology*, 1: 113–125.
- Scheu S., Parkinson D. (1994b): Effects of an invasion of an Aspen woodland (Alberta, Canada) by *Dendrobaena octaedra* on plant growth. *Ecology*, 75: 2348–2361.
- Schmidt O., Scrimgeour C.M., Curry J.P. (1999): Carbon and nitrogen stable isotope ratios in body tissue and mucus of feeding and fasting earthworms (*Lumbricus festivus*). *Oecologia*, 118: 9–15.
- Shah T.I., Rai A.P., Aziz M. (2019): Relationship of phosphorus fractions with soil properties in mothbean growing acid soils of North Western Indian Himalayas. *Communications in Soil Science and Plant Analysis*, 50: 1192–1198.
- Sheehy J., Nuutinen V., Six J., Palojarvi A., Knuutila O., Kaseva J., Regina K. (2019): Earthworm *Lumbricus terrestris* mediated redistribution of C and N into large macroaggregate-occluded soil fractions in fine-textured no-till soils. *Applied Soil Ecology*, 140: 26–34.
- Shi Z., Tang Z., Wang C. (2019): Effect of phenanthrene on the physicochemical properties of earthworm casts in soil. *Ecotoxicology and Environmental Safety*, 168: 348–355.
- Shipitalo M.J., Protz R. (1989): Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma*, 45: 357–374.
- Shrestha R.K., Lal R. (2010): Carbon and nitrogen pools in reclaimed land under forest and pasture ecosystems in Ohio, USA. *Geoderma*, 157: 196–205.
- Shu W., Yang Z., Xu Z., Zhu T., Tian X., Yang Y. (2022): Effects of one-dimensional nanomaterial polyaniline nanorods on earthworm biomarkers and soil enzymes. *Environmental Science and Pollution Research*, 29: 35217–35229.
- Sierra J., Loranger-Merciris G., Desfontaines L., Boval M. (2014): Aerobic microbial activity in four tropical earthworm-soil systems. A mesocosm experiment. *Soil Research*, 52: 584–592.
- Simek M., Pizl V. (1989): The effect of earthworms (*Lumbricidae*) on nitrogenase activity in soil. *Biology and Fertility of Soils*, 7: 370–373.
- Six J., Bossuyt H., Degryze S., Denef K. (2004): A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research*, 79: 7–31.
- Standish R.J., Daws M.I., Morald T.K., Speijers J., Koch J.M., Hobbs R.J., Tibbett M. (2022): Phosphorus supply affects seedling growth of mycorrhizal but not cluster-root forming jarrah-forest species. *Plant and Soil*, 472: 577–594.
- Stevenson F.J. (1994): Biochemistry of the formation of humic substances. In: *Humus Chemistry: Genesis, composition, reactions*. 2nd Edition, New York, John Wiley & Sons, 188–211.

<https://doi.org/10.17221/461/2022-PSE>

- Suarez E.R., Pelletier D.M., Fahey T.J., Groffman P.M., Bohlen P.J., Fisk M.C. (2004): Effects of exotic earthworms on soil phosphorus cycling in two broadleaf temperate forests. *Ecosystems*, 7: 28–44.
- Subler S., Kirsch A.S. (1998): Spring dynamics of soil carbon, nitrogen, and microbial activity in earthworm middens in a no-till cornfield. *Biology and Fertility of Soils*, 26: 243–249.
- Suzuki Y., Matsubara T., Hoshino M. (2003): Breakdown of mineral grains by earthworms and beetle larvae. *Geoderma*, 112: 131–142.
- Tang Z., Xu W., Zhou G., Bai Y., Li J., Tang X., Chen D., Liu Q., Ma W., Xiong G., He H., He N., Guo Y., Guo Q., Zhu J., Han W., Hu H., Fang J., Xie Z. (2018): Patterns of plant carbon, nitrogen, and phosphorus concentration in relation to productivity in China's terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 115: 4033–4038.
- Teng S.K. (2012): Evaluation on physical, chemical and biological properties of casts of geophagous earthworm *Metaphire tschiliensis tschiliensis*. *Scientific Research Essays*, 7: 1169–1174.
- Tecimen H.B., Gorres J.H., Melnichuk R.D.S. (2021): Effect of *Lumbricus rubellus* and *Amyntas agrestis* earthworms on soil biogeochemistry at the aggregate scale in northern hardwood forests. *Journal of Sustainable Forestry*, 40: 83–98.
- Thomas E., Shanti Prabha V., Kurien V.T., Thomas A.P. (2020): The potential of earthworms in soil carbon storage: a review. *Environmental and Experimental Biology*, 18: 61–75.
- Tiunov A.V., Scheu S. (2000): Microbial biomass, biovolume and respiration in *Lumbricus terrestris* L. cast material of different age. *Soil Biology and Biochemistry*, 32: 265–275.
- Traore S., Guebre D., Hien E., Traore M., Lee N., Lorenz N., Dick R.P. (2022): Nutrient cycling and microbial responses to termite and earthworm activity in soils amended with woody residues in the Sudano-Sahel. *European Journal of Soil Biology*, 109: 103381.
- United States Department of Agriculture – Natural Resources Conservation Service (2009): Soil quality indicators: Total organic carbon. Available at: https://www.nrcs.usda.gov/sites/default/files/2022-10/total_organic_carbon.pdf
- Van Groenigen J.W., Van Groenigen K.J., Koopmans G.F., Stokkermans L., Vos H.M.J., Lubbers I.M. (2019): How fertile are earthworm casts? A meta-analysis. *Geoderma*, 338: 525–535.
- Versteegh E.A.A., Black S., Hodson M.E. (2014): Environmental controls on the production of calcium carbonate by earthworms. *Soil Biology and Biochemistry*, 70: 159–161.
- Vidal A., Remusat L., Watteau F., Derenne S., Quenea K. (2016): Incorporation of ^{13}C labelled shoot residues in *Lumbricus terrestris* casts: a combination of transmission electron microscopy and nanoscale secondary ion mass spectrometry. *Soil Biology and Biochemistry*, 93: 8–16.
- Vidal A., Watteau F., Remusat L., Mueller C.W., Tu T.T.N., 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: 55.
- Vitousek P.M., Porder S., Houlton B.Z., Chadwick O.A. (2010): Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20: 5–15.
- Vos H.M.J., Koopmans G.F., Beezemer L., de Goede R.G.M., Hiemstra T., van Groenigen J.W. (2019): Large variations in readily-available phosphorus in casts of eight earthworm species are linked to cast properties. *Soil Biology and Biochemistry*, 138: 107583.
- Vos H.M.J., Ros M.B.H., Koopmans G.F., van Groenigen J.W. (2014): Do earthworms affect phosphorus availability to grass? A pot experiment. *Soil Biology and Biochemistry*, 79: 34–42.
- Wang M., Guo X., Zhang S., Xiao L., Mishra U., Yang Y., Zhu B., Wang G., Mao X., Qian T., Jiang T., Shi Z., Luo Z. (2022): Global soil profiles indicate depth-dependent soil carbon losses under a warmer climate. *Nature Communications*, 13: 5514.
- Wang X., Fu S., Wang X., Li Z., Li J., Zhang W. (2021a): One-year monitoring of daily earthworm cast production: surface cast contribution to soil fertility in a subtropical forest. *Forests*, 12: 865.
- Wang N., Wang W., Jiang Y., Dai W., Li P., Yao D., Wang J., Shi Y., Cui Z., Cao H., Dong Y., Wang H. (2021b): Variations in bacterial taxonomic profiles and potential functions in response to the gut transit of earthworms (*Eisenia fetida*) feeding on cow manure. *Science of the Total Environment*, 787: 147392.
- Wei Y., Liu M., Wang J., Dang X., Han Y. (2022): The effects of vegetation communities on soil organic carbon stock in an enclosed desert-steppe region of northern China. *Soil Science and Plant Nutrition*, 68: 284–294.
- Wolters V., Joergensen R.G. (1992): Microbial carbon turnover in beech forest soils worked by *Aporrectodea caliginosa* (Savigny) (Oligochaeta, Lumbricidae). *Soil Biology and Biochemistry*, 24: 171–177.
- Wu F., Wan J.H.C., Wu S., Wong M. (2012): Effects of earthworms and plant growth-promoting rhizobacteria (PGPR) on availability of nitrogen, phosphorus, and potassium in soil. *Journal of Plant Nutrition and Soil Science*, 175: 423–433.
- Wu J., Li H., Zhang W., Li F., Huang J., Mo Q., Xia H. (2017): Contrasting impacts of two subtropical earthworm species on leaf litter carbon sequestration into soil aggregates. *Journal of Soils and Sediments*, 17: 1672–1681.
- Xu H., Zhang C. (2021): Investigating spatially varying relationships between total organic carbon contents and pH values in European agricultural soil using geographically weighted regression. *Science of the Total Environment*, 752: 141977.
- Yang L., Yang Z., Peng Y., Lin Y., Xiong D., Li Y., Yang Y. (2019): Evaluating P availability influenced by warming and N deposition in a subtropical forest soil: a bioassay mesocosm experiment. *Plant and Soil*, 444: 87–99.
- Zaller J.G., Wechselberger K.F., Gorfer M., Hann P., Frank T., Wanek W., Drapela T. (2013): Subsurface earthworm casts can

<https://doi.org/10.17221/461/2022-PSE>

- be important soil microsites specifically influencing the growth of grassland plants. *Biology and Fertility of Soils*, 49: 1097–1107.
- Zhang J., Sun C., Liu G., Xue S. (2018): Effects of long-term fertilisation on aggregates and dynamics of soil organic carbon in a semi-arid agro-ecosystem in China. *PeerJ*, 6: e4758.
- Zhang P.P., Zhang Y.L., Jia J.C., Cui Y.X., Wang X., Zhang X.C., Wang Y.Q. (2020): Revegetation pattern affecting accumulation of organic carbon and total nitrogen in reclaimed mine soils. *PeerJ*, 8: e8563.
- Zhang W., Hendrix P.F., Dame L.E., Burke R.A., Wu J., Neher D.A., Li J., Shao Y., Fu S. (2013): Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nature Communications*, 4: 2576.
- Zhu X., Lian B., Yang X., Liu C., Zhu L. (2013): Biotransformation of earthworm activity on potassium-bearing mineral powder. *Journal of Earth Science*, 24: 65–74.
- Zorb C., Senbayram M., Peiter E. (2014): Potassium in agriculture – status and perspectives. *Journal of Plant Physiology*, 171: 656–669.
- Zuccarini P., Asensio D., Ogaya R., Sardans J., Penuelas J. (2020): Effects of seasonal and decadal warming on soil enzymatic activity in a P-deficient Mediterranean shrubland. *Global Change Biology*, 26: 3698–3714.
- Zurovec O., Wall D.P., Brennan F.P., Krol D.J., Forrester P.J., Richards K.G. (2021): Increasing soil pH reduces fertiliser derived N₂O emissions in intensively managed temperate grassland. *Agriculture, Ecosystems and Environment*, 311: 107319.

Received: December 30, 2022

Accepted: June 6, 2023

Published online: June 28, 2023