Applied Soil Ecology 150 (2020) 103473

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global meta-analysis

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ARTICLE INFO

Keywords:
Anecic worms
Endogeic worms
Epigeic worms
Forest floor mass
Litter decomposition
Soil carbon

ABSTRACT

A previous review of earthworm impacts on greenhouse-gas emissions concluded that earthworms elevated soil CO_2 emissions with no apparent influence on soil organic carbon (SOC), especially in laboratory incubations and in agroecosystems. This conclusion suggests that the elevated soil CO_2 emissions may come from enhanced plant litter decomposition. Despite the known important role of earthworms on regulating ecosystem processes, a quantitative analysis of the relationship between earthworms and decomposition in global terrestrial ecosystems is still missing. Here, we present a quantitative synthesis of earthworm effects on plant litter decomposition and SOC based on 340 observations from 69 independent studies. We found a positive correlation between earthworm density and the rate of plant litter decay, and that the presence of earthworms doubled the amount of litter mass loss on average. The presence of all three (anecic, epigeic and endogeic) earthworm functional groups was associated with higher litter mass loss than when either one or two functional groups were present. Anecic earthworms caused the strongest effect on litter mass loss, followed by epigeic earthworms, and there was no apparent influence by endogeic worms. Although the effect of earthworms on SOC was not significant based on all observations, the presence of any two of the three functional groups alone or two (epigeic and endogeic, or anecic and endogeic) and three (anecic, epigeic and endogeic) functional groups together decreased SOC concentrations. Our results indicate that the effect of earthworms on litter and SOC decay depends strongly on earthworm functional groups and diversity, and that a high diversity of earthworm functional groups accelerates litter mass loss and SOC decay. We anticipate that changes in land management practices are likely to alter ecosystem carbon cycling through alteration of earthworm abundance and diversity.

1. Introduction

The decomposition of plant litter and soil organic carbon (SOC) is controlled by climate, substrate quality, and soil biota (Coûteaux et al., 1995; Swift et al., 1979). Soil fauna are shown to accelerate the decay of plant litter (González and Seastedt, 2001) and the magnitude of this acceleration depends on climatic conditions (Heneghan et al., 1999; Wall et al., 2008). Earthworms are one of the major contributors to soil faunal biomass (Lavelle and Spain, 2001; Odum and Pigeon, 1970). As early as 1837, Darwin observed a qualitative relationship between earthworm activities and plant litter disappearance. Much attention has been paid to the role of earthworms on ecosystem processes and functioning during the last few decades. For example, invasive earthworms have been found to reduce forest floor mass considerably in North America (Bohlen et al., 2004a; Hendrix, 2006). A timely topic is to define the quantitative relationship between earthworms and plant litter decay and SOC levels in global terrestrial ecosystems, and to evaluate whether the earthworm influence on plant litter decomposition depends on climate, substrate quality, and its functional diversity. A meta-analysis of earthworm influence on CO_2 emissions, mostly from laboratory incubations and agroecosystems, suggested that the presence of earthworms increases soil CO_2 emissions by 33% yet, does not affect SOC stocks (Lubbers et al., 2013), which raises the question of where the increased CO_2 emissions come from.

The increased soil CO_2 emissions induced by earthworms might come from accelerated plant litter decay, because plant litter was added to the soil in 60% of the studies for the analysis of earthworm influence on soil CO_2 emission (Lubbers et al., 2013). Earthworm effect on litter decay depends on the quality of the litters (Araujo et al., 2004; Jiang et al., 2018; Qiu and Turner, 2016), litterbag mesh size (Szlavecz et al.,

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https://doi.org/10.1016/j.apsoil.2019.103473
Received 28 June 2019; Received in revised form 13 December 2019; Accepted 16 December 2019
Available online 31 December 2019

2011) and vegetation types (Qiu and Turner, 2016). Litter C to N ratios < 20:1 favor mineralization while those > 30:1 usually result in nutrient immobilization (Berg and Mcclaugherty, 2013). Most of previous studies have assessed direct and indirect effects of earthworms on litter decay using litterbags with ≥4 mm mesh size allowing earthworms to move freely in and out of the bags (Heneghan et al., 2007; Rajapaksha et al., 2013; Szlavecz et al., 2011), although litterbags with 1 mm mesh size were also used by some researchers (Liu and Zou, 2002). Progress was made by recognizing the role of earthworms in plant litter decay varied with litter and soil properties, earthworm abundance and composition, and vegetation types (Qiu and Turner, 2016). This may explain the observed pattern that earthworms exert negative or positive effects on SOC in some studies (Bohlen et al., 2004b; Eisenhauer et al., 2007; Hale et al., 2005; Wironen and Moore, 2006). Earthworms can affect SOC through altering microbial activities (Zhang et al., 2010) and the formation of soil macroaggregates (Bossuyt et al., 2005). Microbial biomass C:N ratio typically varied between 8:1 and 12:1 (Griffiths, 1997; Wright and Coleman, 2000). The stoichiometric imbalance between resource and microbial biomass reflects a limitation of microbial activity by a particular nutrient (Zechmeister-Boltenstern et al., 2016). Thus soil C:N ratio > 13:1 is likely N limited for earthworm growth. Earthworms are known to stabilize and protect SOC inside the newly formed macroaggregates (> 250 μm) that are converted from microaggregates (53–250 μm) in soils (Bossuyt et al., 2005).

Earthworm communities are broadly categorized into three functional groups (Bouché, 1977; Lavelle, 1988). Anecic earthworms live mostly in mineral soil and feed primarily on soil surface litter, whereas endogeic earthworms feed and live in the mineral soil layer (soil dwellers) and epigeic earthworms live and feed in the litter layer (litter dwellers). The boundaries between functional categories do not always exist and intermediates are numerous (Bouché, 1977). Earthworm functional groups play substantially different roles on processes that influence organic carbon decomposition. All earthworm functional groups can accelerate the decomposition of organic carbon through enhancing microbial inoculation to fresh plant litter, microbial biomass turnover through in and out of earthworm guts, direct consumption of digestible organic materials and conditioning of recalcitrant organic materials inside their guts. But they differ in the roles of plant litter fragmentation, conditioning of plant litter in cast and tunnel environment, priming effect on SOC decomposition, and clay protection of SOC (Crumsey et al., 2013; Hale et al., 2005). Anecics can accelerate plant litter decomposition by conditioning plant materials in middens (a mixture of plant litter and earthworm casts) or in earthworm permanent tunnels and by fragmenting plant litter thus increasing surface area for microbial activity. They can also cause negative or positive priming effect through mixing fresh plant litter with old SOC and slow down the decomposition of SOC through clay mixing. Whereas endogeics can accelerate plant litter decomposition through conditioning plant litter with their surface casts and through priming effect by their body excretes, they can also stabilize SOC through mixing plant materials with mineral clay resulting in chemical and physical protection from microbial decomposition (Sollins et al., 1996). But endogeics do not fragment plant litter. Epigeics can accelerate plant litter decomposition through fragmenting plant litter and triggering priming effect on the decomposition of plant litter and SOC, but they do not perform a role in the stabilization of SOC through clay mixing or in the conditioning of plant litter because they do not produce mineral casts.

Land-use change has occurred extensively worldwide in the last century. About 6 million km^2 of forests/woodlands and 4.7 million km^2 of savannas, grasslands and steppes have been converted for agricultural use since 1850 (Lambin et al., 2001). Global net annual emissions of carbon from land-use change increased from ~0.6 Pg C yr^{-1} in 1850 to ~1.3 Pg C yr^{-1} in the period 1950–2005 (Houghton, 2017), largely from the tropics (Bonan, 2008). Many studies have shown that converting natural vegetation to pasture (Liu and Zou, 2002), cropland (Zou and Bashkin, 1998), and tree plantations (González et al., 1996; Zou, 1993) often alter earthworm abundance (Spurgeon et al., 2013) and functional diversity (Decaëns and Jiménez, 2002; Smith et al., 2008). Converting a tropical wet forest to pasture was reported to eliminate anecic earthworms and introduce an exotic endogeic earthworms *Pontoscolex corethrurus* with elevated earthworm density in Puerto Rico (Leon et al., 2003; Zou and Gonzalez, 1997). Converting natural vegetation to agroecosystem also led to reduction in earthworm functional diversity and a dominance of endogeics in Mexico, Peru and India (Fragoso et al., 1997).

In this study, we used curve estimation and meta-analysis to examine the effect of earthworms, specifically their abundance and functional diversity, on the decay of plant litter and levels of SOC, mostly in tree plantations and natural forests worldwide. We ask the questions: (1) can earthworm affect plant litter decomposition and levels of SOC at the global scale? (2) how do earthworm functional groups and diversity differ in their roles in regulating plant litter decay and SOC levels? (3) does the effect of earthworms on litter decomposition and SOC levels depend on climate, vegetation types, litter quality, litterbag mesh size, soil C/N, soil aggregate size, experiment types and length of experimental time?

2. Materials and methods

2.1. Data collection

A data set was compiled using literature search of peer-reviewed publications about the effects of earthworms on litter decomposition or SOC from the ISI-Web of Science and Google Scholar research database. We used three different combinations of keywords: earthworm and litter decomposition; earthworm and forest floor; earthworm and soil carbon. A total of 69 studies published between 1985 and 2018 were found (Fig. 1 and Supplementary material, Tables S1-S5). An Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, United States of America) was used to extract numerical values from figures in selected articles in which data were graphically presented.

2.2. Data analysis

Curve estimation (IBM SPSS 22, SPSS Inc., Chicago, Illinois, United States of America) was used to examine the relationship between earthworm density and litter decomposition rate/SOC concentration. The linear regression model was chosen to describe the relationship between earthworm density and litter decomposition rate, and the exponential regression model was chosen to describe the relationship between earthworm density and SOC concentration. Because linear and exponential regression models were the best fitted models for the relationship between earthworm density and litter decomposition rate or SOC concentration, respectively. For the relationship between earthworm density and plant litter decomposition rate in curve estimation, we included studies that reported earthworm density and litter decomposition/decay rate; 40 observations from 13 studies were found (Fig. 1 and Supplementary material, Table S1). For the relationship between earthworm density and forest floor in curve estimation, we included studies that reported earthworm density and forest floor thickness or carbon stock; 32 observations from 12 studies were found (Supplementary material, Table S3). For the relationship between earthworm density and SOC content in curve estimation, we included studies that reported earthworm density and soil carbon concentratione (%, g C/kg soil or mg C/g soil); 70 observations from 12 studies were found (Supplementary material, Table S4). For the curve estimation, we included studies that reflected earthworm density under field conditions (i.e. earthworms were not reduced or added), and plant litter from the vegetation currently under the study sites so that these observations can reflect the balance between earthworm density and turnover of plant litter, SOC under field conditions. To be included in

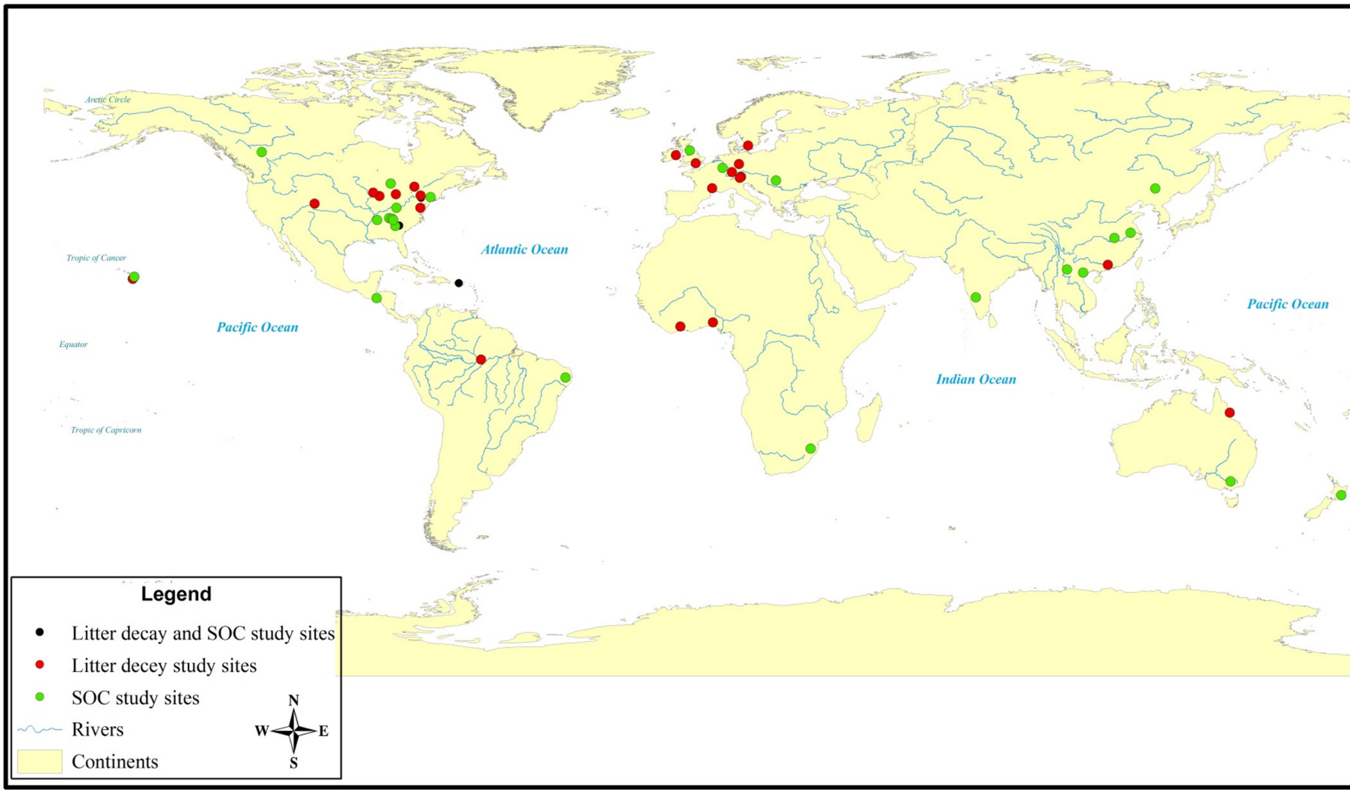

Fig. 1. Global distribution of study sites included in the curve estimation and meta-analysis. Red—litter decay study sites; green—SOC study sites; and black—sites for both studies. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the meta-analysis, the study had to report the means, standard deviation (SD) and replicate numbers of litter percent mass loss or SOC for the control treatment (C, with no earthworms or reduced earthworm number) and the experimental treatment (E, with earthworms or earthworm number do not reduce). For studies that did not report SD or standard error (SE), we conservatively estimated SD values as 150% of the average variance across the dataset (Lubbers et al., 2013). To evaluate the significance of the earthworm-induced effect on litter decomposition, 113 observations from 20 studies were found (Fig. 1 and Supplementary material, Table S2). For the magnitude of the earthworm-induced effect on SOC concentrationcentra, 120 observations from 22 studies were found (Fig. 1 and Supplementary material, Table S5). Because most of the studies do not report soil bulk density, we therefore converted SOC stocks with known bulk density (20 observations) to SOC concentrations. Besides earthworm functional groups, other details of experimental conditions were also specified in our analyses. We included studies that reported climate, vegetation types (naturally-grown forest, plantation, pastureland and crop), litter quality (litter C/N ratio and leaf versus root litter), litterbag mesh size, time length of experiment, soil depth, soil aggregate size, soil C/N ratio and experimental types (field versus laboratory). These parameters were the controlling factors that we considered for the earthworm effect on litter decay and SOC. We evaluated the influence of earthworms on litter decay and SOC concentration through these factors, but not on SOC stocks because of the limited SOC stock observations. Most studies comprised several treatments with and without the presence of earthworms, resulting in more than one observation per study. Not all studies provided information on each controlling factor and therefore the number of observations per controlling factor is not always identical to the total number of observations. As many of the meteorological data were not obtained directly from the published studies, we sorted them to different climatic conditions according to the Koppen climate classification. The magnitude of the earthworm-induced effect on litter decay and SOC were calculated as the response ratio (R), $R = E/C$, where E and C are the means of experimental and control treatments, respectively. Because the results of a meta-analysis may depend on how individual studies are weighted, we used the number of replications for weighting factor: $WR = ((NC * NE) / (NC + NE)) / S$, where NE and NC are the sample sizes for the experimental and control groups, respectively; and S is the total number of observations included in the study where the appointed observation came from. The summary grand-mean effect size for all observations or each categorical subdivision was calculated, and a bias-corrected 95% confidence interval (CI) was ascertained by applying the DerSimonian-Laird of random-effects method using OpenMee Win 10 (Higgins and Green, 2011; Liberati et al., 2009; Wallace et al., 2017). The effect of earthworm on litter decay or SOC concentration was considered significant at $P < 0.05$, if 95% CI did not overlap with response ratio value 1 (Liu and Greaver, 2010). Earthworm effects among treatments within each subgroup were considered to be significantly different from one another if their 95% confidence intervals did not overlap (Lubbers et al., 2013).

3. Results

We found that earthworm density correlated positively and linearly with litter decay rate across crop fields, tree plantations and natural forests (Fig. 2). Earthworm density also correlated negatively and exponentially with the thickness and carbon stock of forest floor mass (Fig. 3).

We found that the presence of earthworms increased litter mass loss by an average of 93.9%, ranging from 80.9 to 107.7% (Fig. 4). Earthworm functional groups differed substantially in their influence on litter mass loss, with an increase of 200.7% by the anecics, a 42.3% increase by the epigeics, and no effect on litter mass loss by the endogeics. Furthermore, the effect of earthworms on litter mass loss depended on earthworm functional diversity. The presence of three

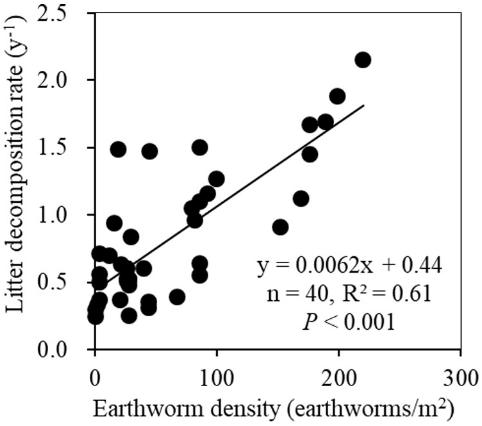

Fig. 2. Relationship between earthworm density and plant litter decay rate in crop fields, tree plantations and natural forests worldwide.

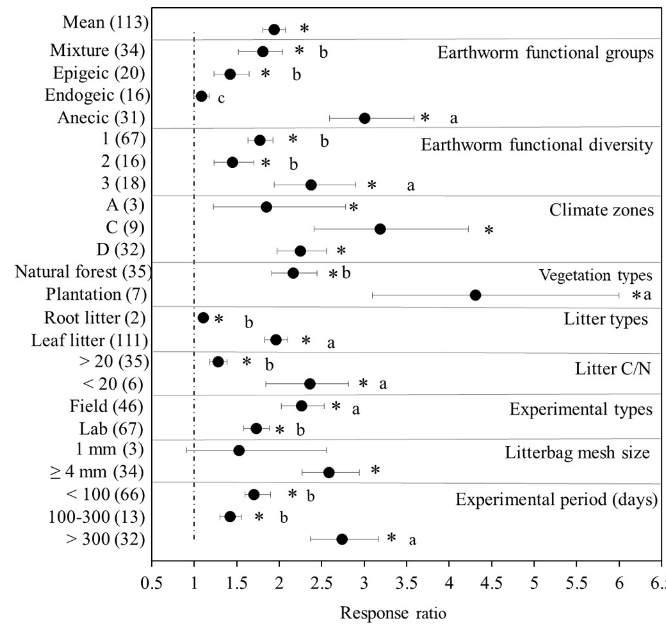

Fig. 4. Untransformed response ratios (sample size) pertaining to earthworm effects on litter decomposition. A: tropical; C: temperate; D: cold (continental); Mixture: two or three functional groups of earthworms together. Bars represent 95% confidence intervals, and numbers in parentheses indicate the number of experiments. * denotes significant earthworm effect at $P < 0.05$. Different letters denote significant difference between categories within each box; categories are considered to be significantly different when their 95% CI do not overlap.

(epigeic, anecic and endogeic) earthworm functional groups increased litter mass loss by 137.5% which was greater than those of one (77.5%) or two (45.6%) functional groups. The increase of litter mass loss by earthworms was greater in plantation forests (331.0%) than in natural forests (116.4%). Earthworm induced litter mass loss was more pronounced for leaf litter (96.2%) than for root litter (10.7%), for litter with C:N ratio $<$ 20 (136.1%) than litter with C:N ratio $>$ 20 (28.2%). The effect of earthworms on litter mass loss was significantly greater for litter incubated under field conditions (126.4%) than for litter incubated under laboratory incubations (72.8%). The presence of earthworms had no effect on litter mass loss when litterbag mesh size was 1 mm, but litter mass loss was increased by 158.57% when litterbag mesh size was $\geq$ 4 mm. We found that experimental period affected earthworm-induced litter mass loss differently. Percent litter mass loss by earthworms was greater for studies lasting longer than 300 days than studies lasting shorter than 300 days. Effects of earthworms on litter mass loss were invariant with climate.

Earthworm density did not correlate with mean SOC concentrations of mineral soil when functional diversity was not considered ($P = 0.743$, Fig. 5a), but values of worm density correlated negatively and exponentially with SOC ($P < 0.001$, Fig. 5b) when all three functional groups were present.

Our meta-analysis showed that the presence of earthworms had no effect on SOC stock or concentration when functional diversity was not considered (Fig. 6), but SOC concentration decreased by 12.8% and 19.7%, respectively, when two (epigeic and endogeic, or anecic and endogeic) and three (anecic, epigeic and endogeic) functional groups together or any two of the three functional groups alone were present; and there were no indications that anecics, epigeics or endogeics alone affected SOC concentrations. Earthworms decreased SOC concentration when soil C/N ratio was 8–12, whereas increased SOC concentration when soil C/N ratio was higher than 13. Concentrations of SOC were increased by 96.4% in soil aggregates $>$ 0.25 mm in size, and decreased by 13.3–16.4% in soil aggregates $<$ 0.25 mm in size under the presence of earthworms. Earthworms caused a decrease in SOC concentration only for experiments lasted longer than 365 days (12.7%). Earthworm effect on SOC concentration was invariant with climate, vegetation type, soil depth and experimental type (i.e. laboratory versus field experiment).

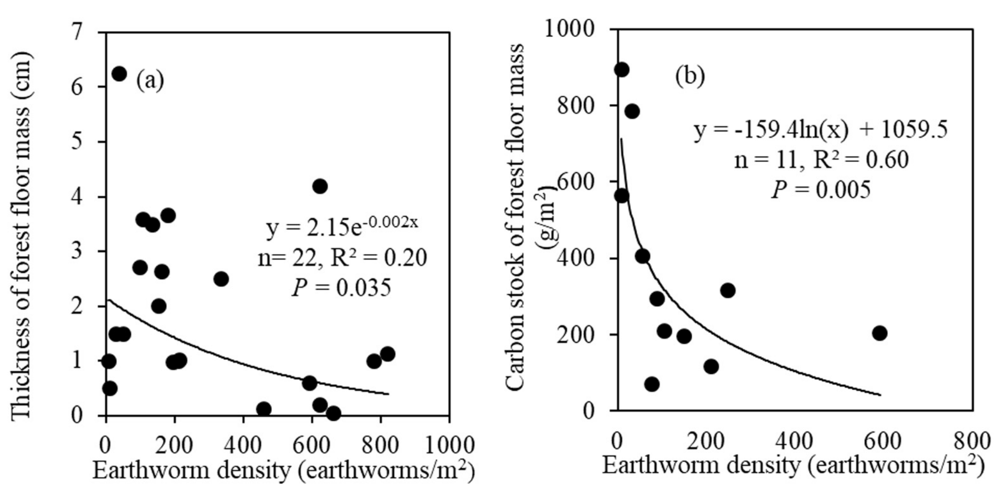

Fig. 3. Relationship between earthworm density and forest floor mass (a) thickness, (b) carbon stock worldwide.

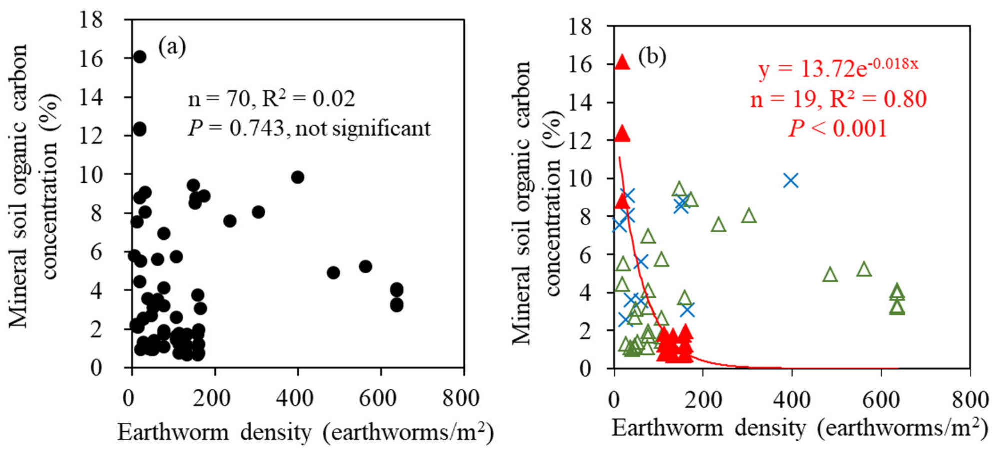

Fig. 5. Exponential relationship between earthworm density and SOC concentration across crop fields, pasture, and forests worldwide when (a) functional diversity was not considered and (b) categorized by earthworm functional group richness (× - - - one functional group of earthworms, △- - - two functional groups of earthworms, and ▲- - - three functional groups of earthworms).

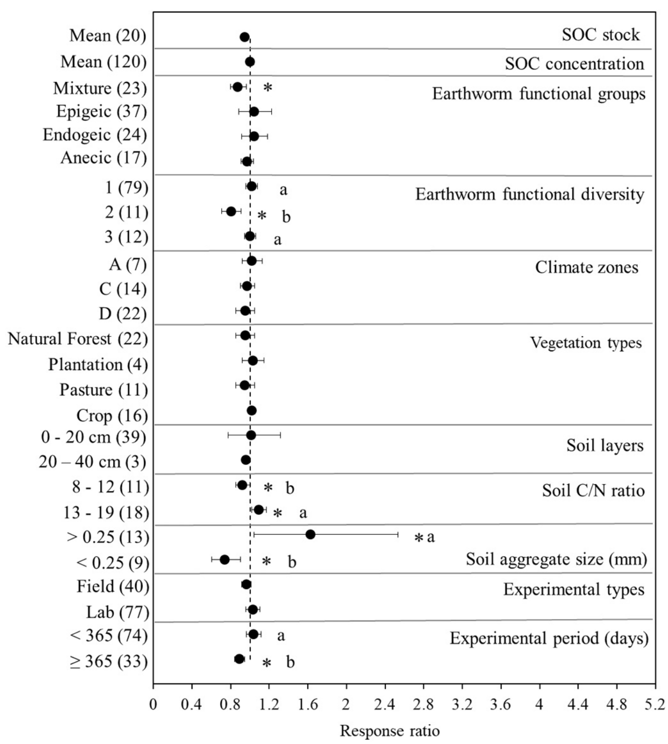

Fig. 6. Untransformed response ratios (sample size) pertaining to earthworm effects on SOC. All analyses were performed based on SOC concentrations except the first box on SOC stock per unit area. A: tropical; C: temperate; D: cold (continental); Mixture: two or three functional groups of earthworms together. Bars represent 95% confidence intervals, and numbers in parenthesis indicate the number of experiments. * denotes significant earthworm effect. Different letters denote significant differences between categories within the same box; categories are considered to be significantly different when their 95% CI do not overlap.

4. Discussion

4.1. The effect of earthworms on litter decay

At a global scale, we show that earthworms double the amount of litter mass loss but have no overall effect on SOC stock or concentration. The rate of plant litter decay increased linearly with earthworm density. This accelerated litter decay rate is strongest by anecic earthworms and when all three functional groups of earthworms are present.

Earthworm influence on litter decay through direct (feeding, fragmentation, and microbial inoculation) and indirect processes (altering microbial activity and composition). Anecic and epigeic earthworms can feed directly on plant litter (Curry and Schmidt, 2007). Anecic and epigeic worms can also directly fragment litter materials thus increasing surface area for microbial activity (Jiang et al., 2018). All three functional groups of earthworms play a direct role in accelerating the inoculation of microbes onto fresh litter materials through their movements and surface casting activities (Eisenhauer et al., 2007). The increased litter decay rate in mesh size 4 mm litterbags, compared with mesh size 1 mm litterbags, suggests that the increased litter decay rate by earthworms is largely attributed to their direct feeding and fragmentation activities rather than through inoculation role through casting activity.

We show that the decay of plant litter is strongly affected by earthworm functional groups and their diversity. Anecic earthworms feed directly on plant litter and produce casts that can accelerate the inoculation of microbes onto fresh and fragmented litter materials, imposing greater effect on litter decay than epigeic worms which cast less on a per area basis (Shipitalo et al., 1988). Endogeic earthworms rarely feed on surface litter and cast mostly belowground, consequently have no apparent effect on plant litter decay. The combination of all three functional groups enhances the joint effects of feeding, fragmentation, organic carbon conditioning, inoculation and organo-mineral mixing, and worms are most likely to survive when all three groups are present (Uvarov, 2010), likely resulting in the strongest effect on the decay of plant litter. However, as the habitats and food resources of these different ecological groups may overlap (Shuster et al., 2001; Uvarov, 2010), the outcome of inter-group interaction may be competition (Uvarov, 2010). For example, epi-/endo-geic species exert negative affect on anecic species. But anecic species often beneficially affects epi-/endo-geic species, through increasing food supply or provision of shelter in middens and the drilosphere. Therefore, litter mass loss under the presence of a mixture of earthworm functional groups can be lower than anecic worms alone, but higher than epigeic and endogeic worms.

We found that the responses of litter mass loss due to earthworm presence were different among vegetation types. Compared to natural forests, the higher increase of litter mass loss in plantations could be ascribed to the higher earthworm density in plantation than in natural forests. The mean earthworm density from the combined data was 234–298 individuals/m^2 in plantation, while 88.57% of earthworm density data was lower than 100 individuals/m^2 in natural forests. The higher density of earthworms in plantations than in natural forests have been well described in previous studies (Tondoh et al., 2007; Tsukamoto and Sabang, 2005). The positive relationship between earthworm density and litter decay rate of our collected data supports the notion that higher earthworm density led to quicker litter mass loss.

The more sensitive response of increase in leaf litter mass loss due to earthworms than in root litter mass loss can be explained by the higher palatability and lower C/N ratio of leaves than roots (Liu and Zou, 2002; Vidal et al., 2017). The increase in palatability of litter for earthworms with decreasing C/N of the litter (Jiang et al., 2018) can explain the higher litter loss by earthworms with decreasing C/N ratio of the litter.

Litter decomposition by earthworms has been divided into two stages (Cortez and Bouché, 1998). During the first stage (1st year), litter is ploughed and conditioned by earthworm casts and decayed because of microbial activities. The conditioned litter materials then become more palatable and are consumed by earthworms with an accelerated rate of litter mass loss during the second stage of litter decay (Cortez and Bouché, 1998). The latter explains the observed increase in litter mass loss by earthworms for experiments lasting longer than 300 days.

We found earthworms can increase litter mass loss significantly more in field than in laboratory experiments. First, it is because that field experiments lasted longer time than laboratory experiments. Nearly 85% of field experiments of the meta-analysis data set were longer than 300 days, while all laboratory experiments of our collected data were shorter than 300 days. Second, the abiotic and biotic conditions of laboratory experiments are different from field systems. For example, no diel or seasonal rhythm affects earthworm activity by an endocrinal regulation of the diapause (Cortez and Bouché, 1998). Last but not least, laboratory experiments are semi-closed systems as compared to field conditions, without floor mass or no external inputs such as litter fall, which provide more food resources for epigeic and anecic earthworms.

4.2. The effect of earthworms on SOC

Although earthworms overall do not show their effect on SOC stock or concentrations, the presence of two (epigeic and endogeic, or anecic and endogeic) and three (anecic, epigeic and endogeic) functional groups together or any two of the three functional groups reduces SOC concentrations.

Earthworms play direct and indirect roles in the decay of organic carbon (González et al., 2001; Lubbers et al., 2017). All three functional groups of earthworms feed on humified SOC to various degrees (Curry and Schmidt, 2007). Furthermore, earthworms can alter the microbial community (Dempsey et al., 2013; Scheu, 1987) through altering soil moisture and oxygen levels, through carbon conditioning in the earthworm gut (Daniel and Anderson, 1992), and through casting activities by endogeics and anecics that bring cations into the top soil and increase soil pH in some ecosystem (Cortez, 1998), thus indirectly influencing the decay of SOC. The earthworm gut has been described as a "mutualistic digestive system", in which the exoenzymes produced by ingested microorganisms enhance the degradation of complex organic matter during their passage through the gut (Jiang et al., 2018). Borrowing tunnels and cast materials are shown to have different nutrients and microbiota composition compared to the material prior to ingestion (González, 2002; Jiang et al., 2018).

We also show that the decay of plant litter and SOC is strongly affected by earthworm functional groups and their diversity. The combination of two functional groups, dominated here by the combination of epigeics and endogeics or anecics and endogeics, reflects joint effects of surface litter processing and soil organo-mineral complex processing by earthworms, resulting in apparent reduction of SOC concentration. Combination of at least two functional groups means inclusion of both litter processing by epigeic or anecic earthworms and soil mixing by anecic or endogeic earthworms, resulting in incorporation of surface plant materials into mineral soil layer that are likely to trigger priming effect on SOC decay (Hoang et al., 2017). An increase in earthworm functional diversity is shown to increase soil microbial biomass (Ferlian et al., 2018) and activities (Uvarov, 2010). Decomposition of SOC was largely driven by microbes (Lubbers et al., 2013), thus a low SOC concentration can be associated with high microbial biomass and activities under high earthworm functional diversity.

We expect to see that earthworm influence on decay of plant litter and SOC depends on substrate quality and climate (Wall et al., 2008), with an enhanced earthworm effect under conditions of low C/N ratio substrate and tropical climatic conditions. Earthworms are shown to feed preferentially on high quality organic materials with low C/N ratios (Jiang et al., 2018; Lubbers et al., 2013). However, we did not show climate dependency for the earthworm effect on litter and SOC decay as shown clearly for soil arthropods (Wall et al., 2008). Earthworm influence on litter and SOC decay is invariant with climate, vegetation, and soil depth, suggesting that earthworms play a similar role in decomposing plant litter and SOC across climate and vegetation types and soil depths.

Earthworms promote the transformation of soil structure from microaggregates and mesoaggregates to macroaggregates (Bossuyt et al., 2005), and the litter-derived carbon was sequestrated in macroaggregates through consumption and excretion activities of earthworms (Wu et al., 2017), this subsequently increases SOC levels in casts shown in macroaggregates ($>$ 0.25 mm in size) and decreased SOC levels in microaggregates and messoaggregates ($<$ 0.25 mm in size). Earthworm species from different functional groups differently affect soil aggregation and the accumulation of new C, and interactive effects occur when they are both present (Bossuyt et al., 2006). Endogeic earthworms living and feeding in the mineral soil are the primary group of earthworms that affect soil aggregation as they are geophagous (Bossuyt et al., 2006; Knowles et al., 2016). Epigeic species live mainly in the upper layers of soils and may have less effect on soil aggregation than endogeic species (Bossuyt et al., 2006). Interactive effects between the epigeic and the endogeic species occur mostly when the residue is placed on soil surface. While the epigeic species induced a larger incorporation of fresh residue into microaggregates within large macroaggregates, the combination of both species caused a much higher incorporation of fresh residue between microaggregates within macroaggregates (Bossuyt et al., 2006; Giannopoulos et al., 2010).

Our interpretation on the role of earthworms on SOC decay is likely weakened by the drawbacks of available data based on short experimental duration of often less than one year. Alteration of SOC concentration by earthworms within a short experimental duration can further be imbedded by the large existing SOC pool as shown in our analyses that SOC concentration is reduced by earthworms if the experiment lasts longer than 365 day but does not change if the duration is shorter than 365 days.

To sum up, anecic or epigeic species alone only accelerated litter decomposition, but were neutral to SOC level. Endogeic species alone had little effect on litter and SOC decay. The presence of two earthworm functional groups alone (epigeic and endogeic, or anecic and endogeic) or two and three (anecic, epigeic and endogeic) functional groups shows significant effect on litter and SOC decay. The mixture of three earthworm functional groups triggers greater effect on litter mass loss than one or two earthworm functional groups.

Increase in earthworm abundance can accelerate plant litter decay. Counteractively, reduction in earthworm functional groups may slowdown decay rate of plant litter and SOC, a plausible mechanism that explain the observed reduction in soil respiration under reduced plant diversity likely with reduced number of earthworm functional groups (Chen and Chen, 2019). Separately or jointly, alteration of earthworm abundance and functional groups following land-use change can exhibit a strong influence on ecosystem carbon cycling and thus cause an unrecognized effect on climate warming.

Declaration of competing interest

We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

Acknowledgments

This study was financially supported by a cooperative agreement between the USDA-Forest Service International Institute of Tropical Forestry and the University of Puerto Rico [14-JV-11120101-018, 2015]. Grizelle González was supported by the Luquillo Critical Zone Observatory [EAR-1331841] and the Luquillo Long-Term Ecological Research Site [DEB-1239764]. We thank N. Brokaw and A. E. Lugo for providing constructive comments. All authors declare there is no conflict of interest on this research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2019.103473.

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