

Plant leaf litter plays a more important role than roots in maintaining earthworm communities in subtropical plantations



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ABSTRACT

Despite the importance of earthworms to making soils productive, little is known regarding the relative importance of maintenance of the various types of earthworm populations. In this study, we assessed the impact of long-term removal of two potential sources of carbon input, viz. plant litter and roots, on earthworms of *Amynthas* sp. (epigeic) and *Pontoscolex corethrurus* (endogeic) that reside at and below the soil surface and primarily rely on litter and/or soil organic matter as a food source, in two different subtropical monoculture plantations. We found that *Amynthas* sp. disappeared and the density and biomass of *Pontoscolex corethrurus* was significantly reduced under litter removal treatment, whether roots were removed or not. In contrast, root removal had no significant impact on the density and biomass of both earthworm species. The results suggest that leaf litter, rather than roots, played key roles in maintaining the populations of both the epigeic *Amynthas* sp. and endogeic *Pontoscolex corethrurus* earthworms.

1. Introduction

Soil biota are highly dependent on above- and below-ground carbon (C) inputs, including those derived from litter and roots (Bais et al., 2006; Bradford et al., 2012; Pollierer et al., 2012). It has been well acknowledged that aboveground residue constitute the major C resources for soil biota (Moore et al., 2004; Schneider et al., 2012). However, some studies also showed that soil animals were instead strongly dependent on root-derived carbon in arable systems (Albers et al., 2006; Scheunemann et al., 2010, 2015), upland grasslands (Leake et al., 2006), and forests (Pollierer et al., 2007; Eissfeller et al., 2013).

It is well recognized that earthworms play an important role in mediating ecosystem processes and functioning (Edwards, 2004; Blouin et al., 2013) by acting as ecosystem engineers in soils (Jones et al., 1994). For example, earthworms can alter nutrient supply rates

(Edwards and Bohlen, 1996; Blair et al., 1997; Burtelow et al., 1998; Liu and Zou, 2002; Bohlen et al., 2004; Sabrina et al., 2013; He et al., 2018) and enhance plant growth (Lee, 1985; Brown et al., 1999; Scheu, 2003; van Groenigen et al., 2014; Xiao et al., 2018; Fonte et al., 2019). Accordingly, earthworms have been widely studied across different habitats from both ecological and ecotoxicological perspectives (Latif et al., 2013; Lubbers et al., 2013; Duarte et al., 2014; Da Silva et al., 2016; Pelosi et al., 2014; Buch et al., 2017; Wang et al., 2018; Zhang et al., 2018). Furthermore, earthworms can also serve as biological invaders and affect the properties and functioning of the invaded ecosystems (Eisenhauer et al., 2007; Hendrix et al., 2008; Fonte et al., 2012; Fisichelli et al., 2013; Dey and Chaudhuri, 2014; Teng et al., 2016).

Earthworms are generally categorized into three ecological groups: epigeic, endogeic, and anecic species. Epigeic earthworms live on the soil surface and feed on plant litter, endogeic earthworms live in

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horizontal burrows below the soil surface and feed on soil organic matter, and anecic earthworms live in vertical burrows below the soil surface, and travel between the mineral soils and soil surface, utilizing leaf litter as food (Bouché, 1977; Edwards and Bohlen, 1996). However, the manner by which the above- and below-ground C allocation affects the density and biomass of earthworm species in different functional groups remained poorly understood.

The majority of studies addressing how biotic and abiotic factors affect the feeding strategies of earthworms have been conducted in the laboratory, with few studies in the field. In addition, some studies based on a short-term litter removal protocol (1–2 years), revealed that the removal of aboveground litter did not significantly affect the biomass and density of endogeic earthworms (Gonzalez and Zou, 1999; Sánchez-de León and Zou, 2004; Dechaine et al., 2005). Therefore, it is necessary to assess the response of earthworms to changes in C inputs based on long-term experimental manipulations.

Both litter and roots comprise important sources of soil organic matter (SOM), however, root-derived C is usually more stable than litter-derived C in SOM (Rasse et al., 2005; Crow et al., 2009). In the present study, we aimed to investigate the long-term effects of litter and root removal on the density and biomass of earthworm species with different functional groups. We hypothesized that (1) the density and biomass of all earthworms would be reduced under litter removal treatment owing to lack of food resources and loss of habitat; (2) the density and biomass of endogeic earthworms would be reduced by root removal because they mainly utilize soil organic matter (Li et al., 2009) including rhizodeposits (Huang et al., 2015).

2. Materials and methods

2.1. Site description

The study was conducted in 10-year-old *Acacia crassicarpa* A. Cunn. ex Benth and *Eucalyptus urophylla* S. T. Blake monoculture plantations at the Heshan Hilly Land Interdisciplinary Experimental Station (60.7 m a.s.l., 112°50' E, 22°34' N) of the Chinese Academy of Sciences. The soil is an acrisol (FAO, 2006), and the climate is subtropical monsoon with a hot and humid summer and a cold dry winter. The mean annual temperature is 22.6 °C. The annual mean precipitation and evaporation are 1,700 mm and 1,600 mm, respectively. The plantations were established in 2005. Prescribed burning was performed prior to stand preparation. In 2014, the average height and diameter at breast height was 10.33 m and 11.20 cm for *A. crassicarpa* and 11.67 m and 11.40 cm for *E. urophylla*. Soil organic carbon (SOC), nitrogen (N), C/N, and pH in the 0–10 cm soil layer were 24 (g kg⁻¹), 1.4 (g kg⁻¹), 16, and 3.9 in the *A. crassicarpa* plantation and 21 (g kg⁻¹), 1.2 (g kg⁻¹), 17, and 3.9 for the *E. urophylla* plantation, respectively.

2.2. Experimental design

This experiment was initiated at *A. crassicarpa* and *E. urophylla* monoculture plantations in 2008 with three random replication stands for each plantation. In each replicated stand, one 12 m × 15 m plot was chosen randomly and divided into four 3 m × 15 m subplots with the following four treatments: (1) CK (control, both fallen litter and roots were kept intact); (2) LR (litter removal, aboveground litter was removed); (3) RR (root removal, roots were excluded); (4) LRR (both litter and roots were removed). In order to set a large net to avoid fallen litter moving into the subplots, the subplot with litter removal treatment (LR) was set randomly next to the subplot with treatment of both litter and roots removal (LRR); the rest two subplots were randomly allocated to CK and RR, respectively. Understory shrubs and herbs were removed in each plot prior to the experiment. In LR treatment plots, nylon mesh was installed at least 2 m above the plot to intercept newly fallen litter and the litter on the nylon mesh was removed every two weeks and visible litter on the soil surface was also removed from the LR subplots to

ensure the effect of litter removal, but plant roots were kept intact in LR subplots. In RR treatment plots, polyvinyl chloride (PVC) boards were inserted into the soil to 50 cm depth to prevent lateral root penetration into the plots from the exterior regions. This method was also reported to be sufficient to limit the lateral movement of earthworms (Liu and Zou, 2002). In LRR treatment plots, nylon mesh was installed at least 2 m above the plot and PVC boards were inserted into the soil as for the RR plots. Neither leaf litter nor roots were excluded from CK subplots (Zhang et al., 2016).

2.3. Sampling and chemical analysis of soil and litter

Soil and leaf litter were sampled from each subplot. The soil was taken from a depth of 0–20 cm in each subplot. The soils were sieved through a 2 mm sieve, air dried and stored at room temperature. The sampled soils were ground for the analysis of total C, total N, pH (soil: water = 1:2.5; Li et al., 2015). The fresh soils were used to measure microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN). MBC and MBN were measured using the chloroform fumigation-incubation method (Vance et al., 1987). The fresh soil (equal to 8 g dry soil) was used to measure phospholipid fatty acids (PLFAs). Procedures for the analysis of PLFAs were described in detail in Chen et al. (2015), and used to assess the soil microbial community. The PLFAs were classified as bacteria (i14:0, a15:0, i15:0, i16:0, a17:0, i17:0, 16:1ω7c, 17:1ω8, 18:1ω9, 18:1ω7c, cy17:0, and cy19:0), fungi (18:2ω6, 9), and actinobacteria (10Me16:0, 10Me17:0, and 10Me18:0) (Frostegård et al., 2011). The Gram-positive bacteria (G^+) was taken as the sum of PLFAs i14:0, i15:0, a15:0, i16:0, i17:0, and a17:0, and the Gram-negative bacteria (G^-) as the sum of 16:1ω9c, cy17:0, 18:1ω9c, and cy19:0 (Nie et al., 2013). Leaf litter was collected from the senescent leaves on the nylon mesh, dried at 70 °C for 48 h, and weighed for biomass estimation and then ground for testing the chemical composition (Zhu et al., 2016). The fine root mass was estimated using the method of in-growth cores (Vogt and Persson, 1991). In-growth cores were used to measure root growth in a defined volume of soil (Vogt and Persson, 1991). When preparing to install the in-growth cores, soil cores (16 cm in diameter) were taken next to trees at a distance of 140 cm from the trunk down to 20 cm. Soil material was sieved through a 5-mm mesh to remove root, large organic matter particles, and stones. Then, a nylon mesh bag (mesh size 2 mm) was inserted into the hole with the help of a plastic tube before the holes were refilled based on the original depth (Stober et al., 2000). The in-growth core experiment was set up in January 2014 in both plantations and harvested in January 2015. Soil moisture was measured using a TDR 300, a portable probe produced by Spectrum Technologies Inc. (Aurora, IL, USA). Soil temperature was recorded using the DS1922L temperature logger iButtons.

2.4. Collection and identification of earthworms

Earthworms were sampled by taking three 20 cm × 20 cm × 20 cm soil cubes in each subplot. The earthworms were hand sorted. Collected earthworms were weighed, counted, stored with 5% formaldehyde solution, and then identified to family, genus, and species level according to Xu and Xiao (2011).

2.5. Statistical analyses

Two-way analysis of variance was used to evaluate the main effects and interaction of litter and roots. Repeated measures analyses of variance were used to evaluate main effects of season, litter treatment, and root treatment, along with their interaction after the data of biomass and density for earthworms were transformed. Significance level was set at $P < 0.05$. All comparisons between treatments in the same year were performed using one-way ANOVA. All comparisons between each treatment in the same season in 2014 and 2015 were performed using an independent-samples T test. Forward stepwise multiple linear regression

was used to explore the relationships between the nine ecological factors and the biomass and density of *Amyntas* sp. and *P. corethrurus*. All data analyses were conducted using SPSS Version 16.0 for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Response of the earthworm community to litter removal

An epigeic earthworm of *Amyntas* sp. and an endogeic earthworm of *Pontoscolex corethrurus* were observed in this study. The *Amyntas* sp. disappeared and the density and biomass of *P. corethrurus* were reduced under both LR and LRR treatment in *A. crassicaarpa* and *E. urophylla* plantations regardless of the season (dry or wet) in 2014 and 2015 (Figs. 1–4). Both the density and biomass of the two earthworm species showed the same pattern of change (Figs. 1–4). The effects of season and litter treatment on both earthworm species were significant (Tables 1 and 2). The interaction between season and litter treatment on density and biomass of *Amyntas* sp. was also significant (Table 1). The *Amyntas* sp. disappeared with litter removal in both the *Acacia crassicaarpa* plantation and *Eucalyptus urophylla* plantation. Compared with the control, the density of *P. corethrurus* in the *Acacia crassicaarpa* plantation under LR and LRR treatments decreased by 48.65%–72.14% and 52.7%–73.69%, and the density of *P. corethrurus* in the *Eucalyptus urophylla* plantation decreased by 59.09%–63.32% and 60.61%–65.23%, respectively. Compared with the control, the biomass of *P. corethrurus* in the *Acacia crassicaarpa* plantation under LR and LRR treatments decreased by 65.1%–77.5% and 64.4%–81.8%, and the biomass of *P. corethrurus* in the *Eucalyptus urophylla* plantation decreased by 62.2%–72% and 67.8%–81.9%, respectively.

3.2. Response of the earthworm community to root removal

The density of *Amyntas* sp. under RR treatment decreased by 0–3% in the *Acacia crassicaarpa* plantation and 12%–21.45% in the *Eucalyptus urophylla* plantation compared with the control. The density of *P. corethrurus* under RR treatment decreased by 0–6.82% in the *Acacia crassicaarpa* plantation and 3.08%–9.1% in the *Eucalyptus urophylla* plantation. Similarly, the biomass of *Amyntas* sp. under RR treatment decreased by 0–7.69% in the *Acacia crassicaarpa* plantation and 6.56%–29.1% in the *Eucalyptus urophylla* plantation compared with the control. The biomass of *P. corethrurus* under RR treatment decreased by 0–7.8% in the *Acacia crassicaarpa* plantation and 2.9%–15.4% in the *Eucalyptus urophylla* plantation compared with the control. However, no significant differences were observed in the density and biomass of *Amyntas* sp. (Fig. 1; Fig. 3) or *P. corethrurus* (Fig. 2; Fig. 4) between control (CK) and RR treatments in either plantation, and no significant differences were observed between LR and LRR treatments, suggesting that root removal had no significant impact on earthworms (Figs. 1 and 3; Figs. 2 and 4).

The density of *Amyntas* sp. in the *E. urophylla* plantation was higher than that in the *A. crassicaarpa* plantation with this difference being significant in the wet season ($P < 0.05$) (Fig. 1). However, the biomass of *Amyntas* sp. did not significantly differ between the two plantations. For *P. corethrurus*, neither measure showed any difference between the two plantations (Fig. 2; Fig. 4).

3.3. Correlation between soil and litter properties and earthworms

In general, the patterns and variations of air temperature were similar in 2015 to those in 2014 from May to October, whereas the air temperature was higher in 2015 than that in 2014 in other months (Supplementary Fig. 1). Precipitation was lower in 2015 than that in 2014 from February until May but was markedly higher in October 2015

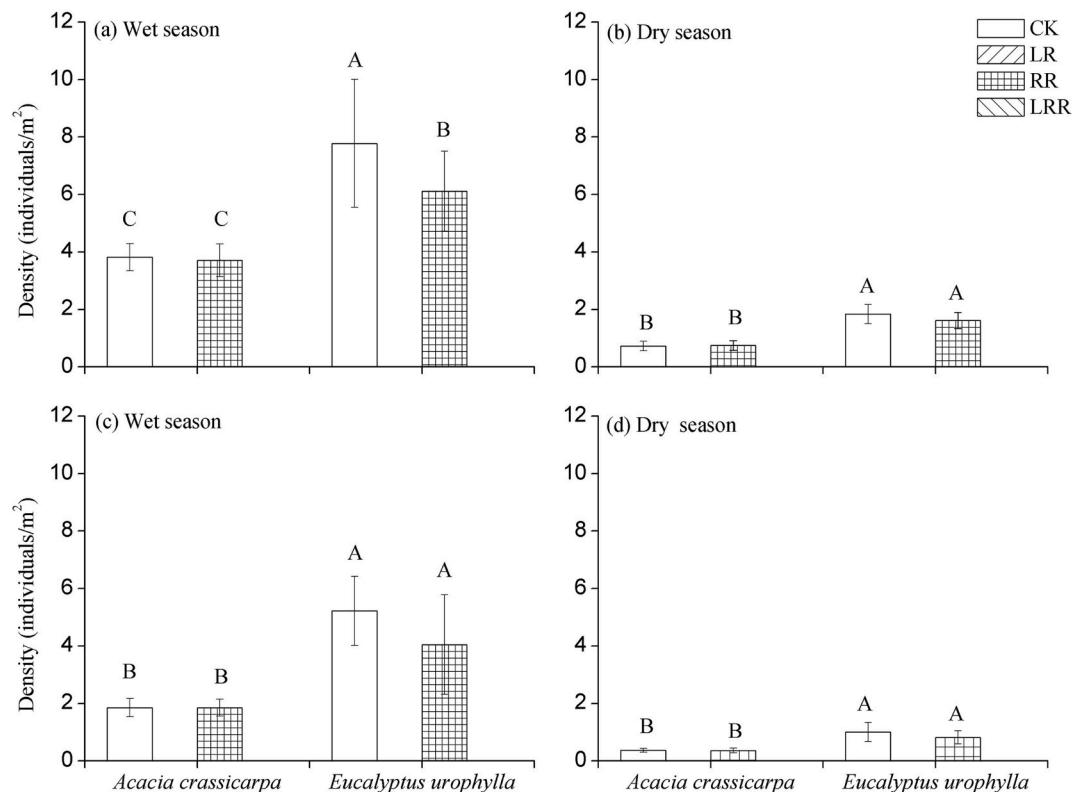


Fig. 1. Density (individuals/m²) of *Amyntas* sp. under four treatments in 2014 (a, b) and 2015 (c, d). The four treatments are as follows: (1) CK (control, both fallen litter and roots were kept intact); (2) LR (litter removal, aboveground litter was removed); (3) RR (root removal, roots were excluded); (4) LRR (both litter and roots were removed). Data represent the means \pm SD ($n = 3$). The same upper case letters indicate no difference between treatments in the same season of the same year, at $P < 0.05$; ANOVA results are shown in Supplementary Table S2.

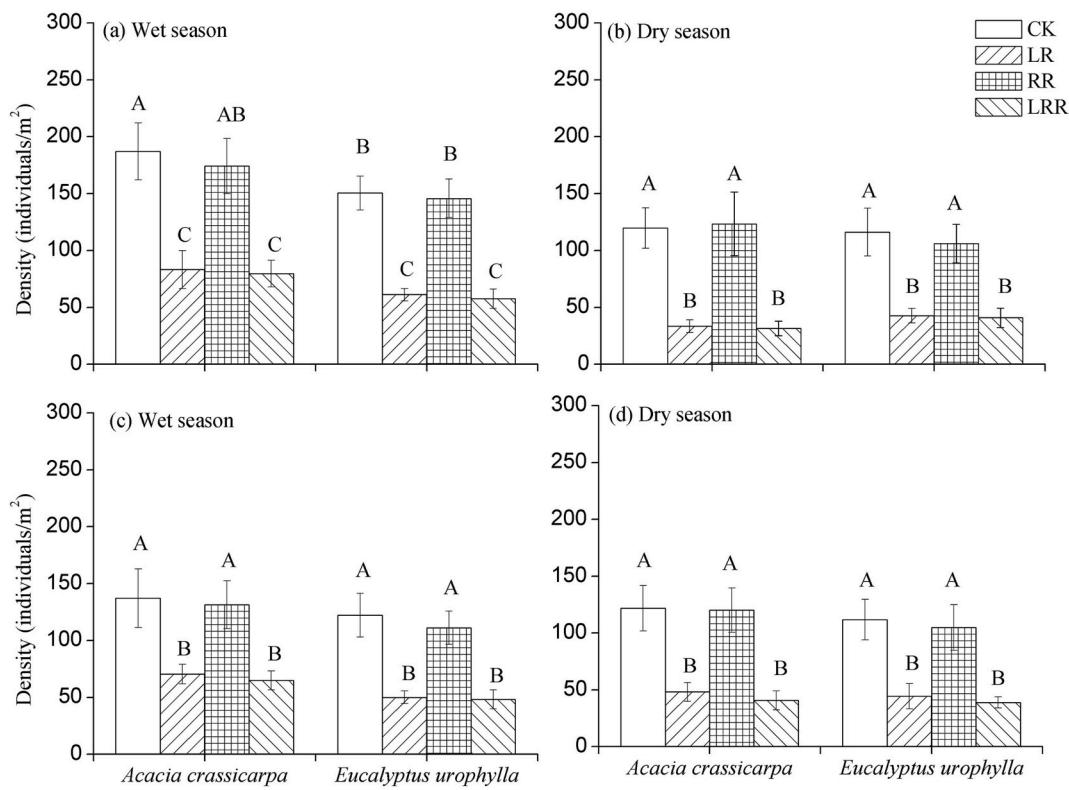


Fig. 2. Density (individuals/m²) of *Pontoscolex corethrurus* under four treatments in 2014 (a, b) and 2015 (c, d). The four treatments are as follows: (1) CK (control, both fallen litter and roots were kept intact); (2) LR (litter removal, aboveground litter was removed); (3) RR (root removal, roots were excluded); (4) LRR (both litter and roots were removed). Data represent the means \pm SD ($n = 3$). The same upper case letters indicate no difference between treatments in the same season of the same year, at $P < 0.05$; ANOVA results are shown in Supplementary Table S3.

(Supplementary Fig. 1). We used forward stepwise multiple linear regression to explore the relationships between the nine ecological factors and the biomass and density of *Amyntas* sp. and *P. corethrurus* earthworms. Results showed that the studied ecological factors were important for the biomass and density of *Amyntas* sp. and *P. corethrurus* earthworms (Table 4). Specifically, L_C ($P < 0.001$) and soil MBC ($P < 0.01$) were significant negative predictors for the density of *Amyntas* sp., while the relationship between soil MBC and the biomass of *Amyntas* sp. was negative ($P < 0.05$). L_C:P was a significant positive predictor for the density of *P. corethrurus* ($P < 0.001$). L_C:N was a significant positive predictor for the density and biomass of *Amyntas* sp. ($P < 0.001$), while L_Lignin:N was a significant positive predictor for the biomass of *P. corethrurus* ($P < 0.001$) and the density of *Amyntas* sp. ($P < 0.05$). Soil moisture was a positive predictor for the density of *Amyntas* sp. ($P < 0.05$). Soil temperature was a significant positive determinant for the biomass and density of *Amyntas* sp. ($P < 0.001$) and *P. corethrurus* ($P < 0.001$). Soil N was a positive predictor for the density ($P < 0.05$) and biomass of *P. corethrurus* ($P < 0.001$). Soil G⁺:G⁻ was a significant positive predictor for the density ($P < 0.01$) and biomass of *P. corethrurus* ($P < 0.05$).

4. Discussion

4.1. Effect of litter removal on the earthworm community

Generally, litter plays two major roles in forest ecosystems. First, it serves as an inherent resource input of organic matter containing C and nutrients (Arpin et al., 1995; Gonzalez and Zou, 1999; Jordan et al., 2003; Sayer, 2006). In addition, litter also forms a protective layer on the soil surface, which can regulate microclimatic conditions and serves as a suitable habitat for epigeic earthworm and some other litter-dwelling organisms (Arpin et al., 1995; Sayer, 2006). In the

present study, our results demonstrated that *Amyntas* sp. disappeared under both LR and LRR treatments, which supported our first hypothesis. This was most likely due to loss of habitat and food resources for *Amyntas* sp. when litter was removed. In addition, litter removal may also increase the possibility of high predation pressure on epigeic earthworm (e.g. *Amyntas* sp.), particularly from birds, mammals, and predatory arthropods.

SOM is determined largely by litter input from vegetation, which provides the food resources for soil communities. SOM often serves as a good predictor of the earthworm population (Hendrix et al., 1992; Edwards and Bohlen, 1996). It has been reported that earthworm populations could be markedly enhanced via organic amendments in disturbed habitats of low organic matter content (Edwards, 1983; Lof-s-Holmin, 1983; Lowe and Butt, 2002). In turn, endogeic earthworms are mostly geophagous, feeding on soil and deriving their nutrition primarily from SOM (Lavelle, 1988; Edwards, 2004; Curry and Schmidt, 2007; Abail et al., 2017). *P. corethrurus* was found to live on soil enriched with organic matter rather than on the fallen litter (Zhang et al., 2020). In this study, however, the density and biomass of endogeic earthworm *P. corethrurus* was reduced with litter removal. We considered that one of the main sources of SOM is from aboveground litter in the studied ecosystems, although dead roots and rhizodeposition can also serve as important sources (Curry, 2004). Ganihar (2003) suggested that partially decomposed leaf litter acts as a source of food for endogeic earthworms (e.g., *P. corethrurus*). Reduction of litter input to soil may decrease soil carbon content (Fontaine et al., 2004), resulting in the reduction of food resources for earthworms and decrease in the density and biomass of *P. corethrurus*. Notely, our results were in contrast to those of several studies that suggested that the removal of aboveground litter had little effect on endogeic earthworms, *P. corethrurus* (Gonzalez and Zou, 1999; Sanchez-de Leon and Zou, 2004; Dechaine et al., 2005). We considered that the duration of treatment might have caused this

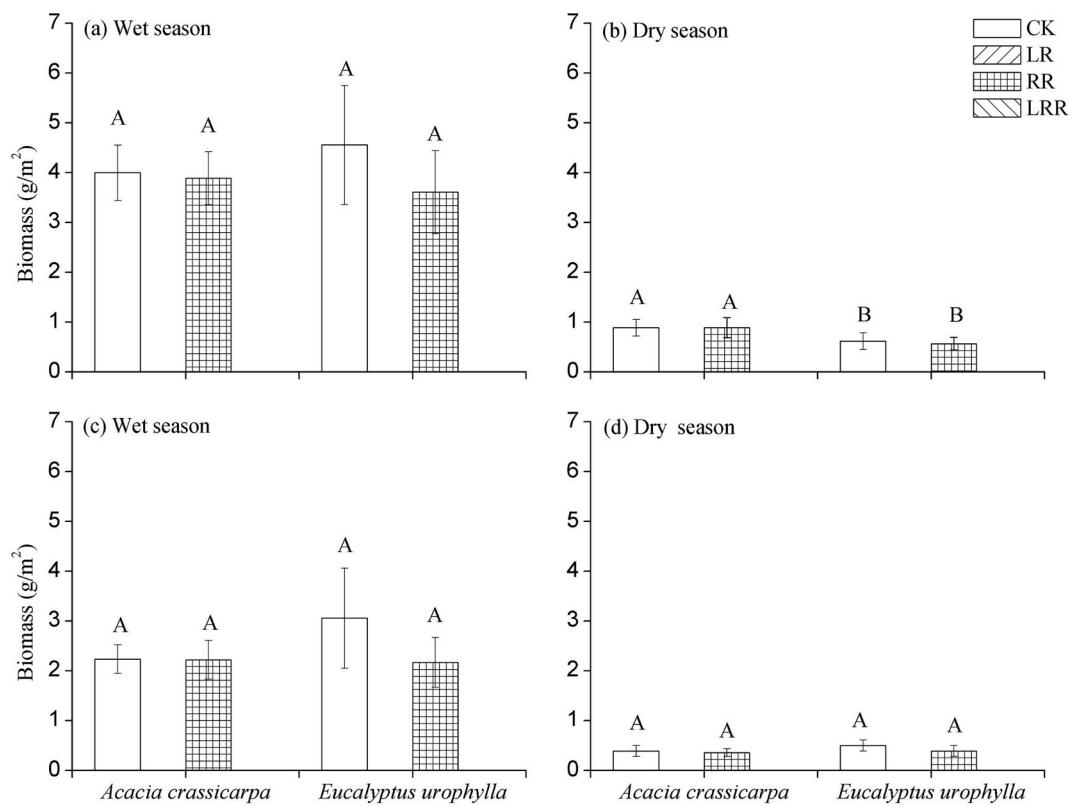


Fig. 3. Biomass (g/m^2) of *Amynthas* sp. under the four treatments in 2014 (a, b) and 2015 (c, d). The four treatments are as follows: (1) CK (control, both fallen litter and roots were kept intact); (2) LR (litter removal, aboveground litter was removed); (3) RR (root removal, roots were excluded); (4) LRR (both litter and roots were removed). Data represent the means \pm SD ($n = 3$). The same upper case letters indicate no difference between treatments in the same season of the same year, at $P < 0.05$; ANOVA results are shown in [Supplementary Table S4](#).

discrepancy, as the effects of long-term treatment (6 years) of litter removal on earthworms in our study might not have been disclosed in previous short-term studies (1–2 years).

Soil temperature and moisture comprise important factors influencing the earthworm community. In particular, it has been suggested that soil temperature determines the composition and structures of earthworm communities (Lavelle, 1983; Lavelle et al., 1989, 1999). In this study, soil temperature in LR and LRR subplots became higher in summer and lower in winter ([Supplementary Fig. 2](#)), which was unfavorable for the survival of earthworms. In this study, soil temperature was one of the most important factors affecting the density and biomass of *Amynthas* sp. and *P. corethrurus*, according to the forward stepwise multiple linear regression analysis ([Table 4](#)). In fact, changes in soil temperature reflected the change of seasons which had significant influence on earthworms ([Tables 1 and 2](#)). Moreover, soil temperature and moisture has been identified as the most potent regulators of earthworm distribution in a pineapple plantation (Dey and Chaudhuri, 2016). Additionally, soil moisture constitutes a key limiting factor for earthworm populations (Lavelle et al., 1987; Auerswald et al., 1996; Holmstrup, 2001; Eriksen-Hamel and Whalen, 2006; Pereault and Whalen, 2006; Eggleton et al., 2009; Schelfhout et al., 2017). For example, *P. corethrurus* may go into diapause under the condition that the soil moisture is too low (Guerra, 1994; Chuang et al., 2004). In a laboratory experiment, Zhang et al. (2008) also found that the primary factor limiting the reproduction of *P. corethrurus* was soil dryness. In this study, we found that soil moisture had a significant influence on the density of *Amynthas* sp. ($P < 0.05$).

4.2. Effect of root removal on earthworm species

Roots also serve as important sources of SOM; moreover, root-

derived C is usually more stable than litter-derived C in SOM (Rasse et al., 2005; Crow et al., 2009). It has been reported that root-derived C is an important resource for soil food webs in upland grassland and forest soils (Caner et al., 2004; Leake et al., 2006; Ruf et al., 2006; Pollierer et al., 2007; Eissfeller et al., 2013). Similarly, Pollierer et al. (2007) found that root-derived C was the dominant resource for forest soil decomposer communities. Scheunemann et al. (2015) suggested that soil arthropod communities are driven by roots rather than shoot residues of arable fields. Leake et al. (2006) reported that soil animals were strongly dependent on root-derived carbon in upland grasslands. Based on a ^{13}C -labelling experiment, Huang et al. (2015) observed that root-derived C was used by most earthworms especially for the exotic *P. corethrurus* in a subtropical soil. However, both *Amynthas* sp. and *P. corethrurus* did not show significant change under root removal treatment in the present study, which rejected our second hypothesis. Our results implied that root-derived resources are not as important as litter for *Amynthas* sp. and *P. corethrurus* in the present study, which differed from the findings of some previous studies (Caner et al., 2004; Leake et al., 2006; Pollierer et al., 2007; Eissfeller et al., 2013; Scheunemann et al., 2015). For *Amynthas* sp., we considered that this finding is reasonable because it would predominantly assimilate litter rather than SOM (Curry and Schmidt, 2007). However, it is difficult to understand why no change of *P. corethrurus* was observed under root removal treatment because they normally assimilate SOM (Curry and Schmidt, 2007).

One explanation may be that the in-growth method may have underestimated the fine root biomass, which might be responsible for the discrepancy between our study and previous studies. Litter removal caused a reduction of resource inputs for endogeic earthworms because leaf litter contributed to soil C to a much larger degree compared to roots in the studied systems. In other words, the non-measurable root-derived

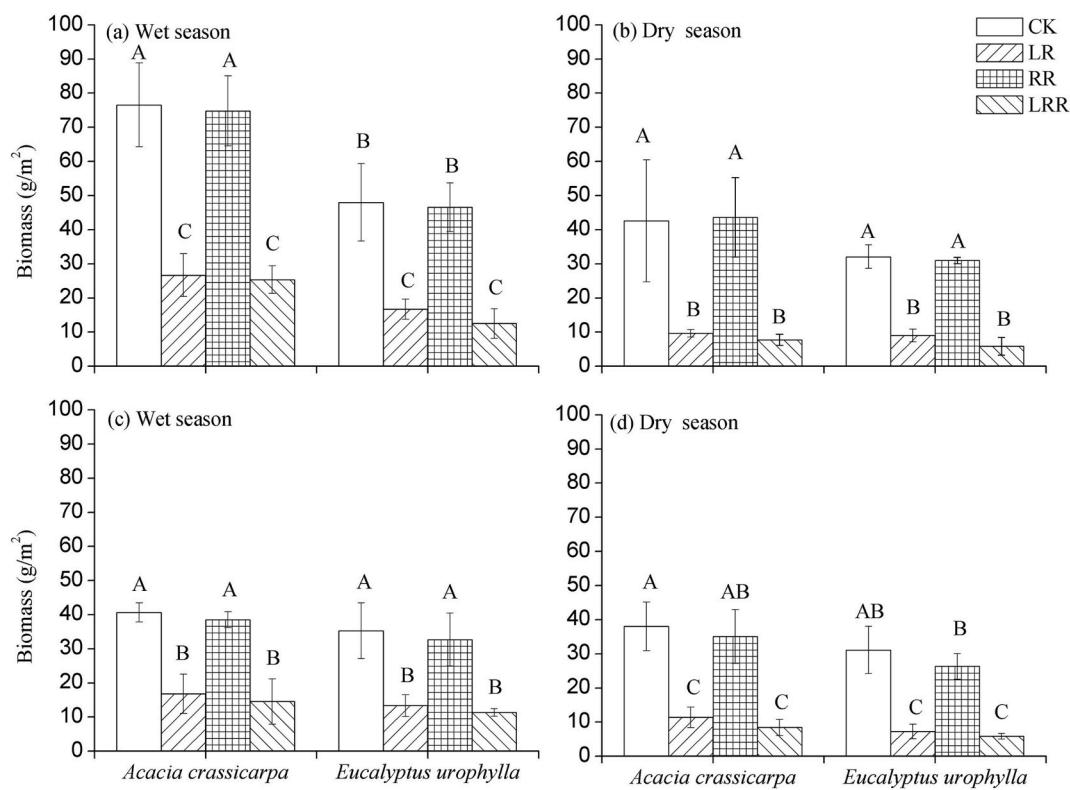


Fig. 4. Biomass (g/m²) of *Pontoscolex corethrurus* under four treatments in 2014 (a, b) and 2015 (c, d). The four treatments are as follows: (1) CK (control, both fallen litter and roots were kept intact); (2) LR (litter removal, aboveground litter was removed); (3) RR (root removal, roots were excluded); (4) LRR (both litter and roots were removed). Data represent the means \pm SD ($n = 3$). The same upper case letters indicate no difference between treatments in the same season of the same year, at $P < 0.05$; ANOVA results are shown in Supplementary Table S5.

Table 1

Results of repeated measures analyses of variance of the density and biomass of *Amyntas* sp. in the two plantations. Significance level was set at $P < 0.05$.

	Density			Biomass		
	F	df	P	F	df	P
Between subjects						
Season	46.24	1,40	<0.001	261.38	1,40	<0.001
Litter treatment	159.77	1,40	<0.001	702.59	1,40	<0.001
Root treatment	0.463	1,40	0.5	1.939	1,40	0.172
Season * Litter treatment	46.236	1,40	<0.001	261.38	1,40	<0.001
Season * Root treatment	0.19	1,40	0.665	0.971	1,40	0.33
Litter treatment * Root treatment	0.463	1,40	0.5	1.939	1,40	0.172
Season * Litter treatment * Root treatment	0.19	1,40	0.665	0.971	1,40	0.33
Within subjects						
Year	340.69	1,40	<0.001	215.93	1,40	<0.001
Year * Season	50.447	1,40	<0.001	53.55	1,40	<0.001
Year * Litter treatment	340.69	1,40	<0.001	215.93	1,40	<0.001
Year * Root treatment	0.085	1,40	0.772	0.093	1,40	0.762
Year * Season * Litter treatment	50.447	1,40	<0.001	53.551	1,40	<0.001
Year * Season * Root treatment	0.177	1,40	0.676	0.077	1,40	0.783
Year * Litter treatment * Root treatment	0.085	1,40	0.772	0.093	1,40	0.762
Year * Season * Litter treatment * Root treatment	0.177	1,40	0.676	0.077	1,40	0.783

Table 2

Results of repeated measures analyses of variance of the density and biomass of *Pontoscolex corethrurus* in the two plantations. Significance level was set at $P < 0.05$.

	Density			Biomass		
	F	df	P	F	df	P
Between subjects						
Season	52.407	1,40	<0.001	42.261	1,40	<0.001
Litter treatment	430.75	1,40	<0.001	280.99	1,40	<0.001
Root treatment	1.808	1,40	0.186	2.107	1,40	0.154
Season * Litter treatment	0.992	1,40	0.325	0.256	1,40	0.616
Season * Root treatment	0.009	1,40	0.926	0.022	1,40	0.882
Litter treatment * Root treatment	0	1,40	0.991	0.337	1,40	0.565
Season * Litter treatment * Root treatment	0.099	1,40	0.755	0.009	1,40	0.926
Within subjects						
Year	12.643	1,40	<0.001	36.316	1,40	<0.001
Year * Season	25.204	1,40	<0.001	20.181	1,40	<0.001
Year * Litter treatment	6.676	1,40	0.014	9.004	1,40	0.005
Year * Root treatment	0.148	1,40	0.702	0.115	1,40	0.736
Year * Season * Litter treatment	0.355	1,40	0.555	1.727	1,40	0.196
Year * Season * Root treatment	0.081	1,40	0.777	0.053	1,40	0.82
Year * Litter treatment * Root treatment	0.056	1,40	0.815	0.431	1,40	0.515
Year * Season * Litter treatment * Root treatment	0.067	1,40	0.797	0.106	1,40	0.747

Table 3The fine root biomass in the two plantations (mean \pm SE).

Treatment	Plantation type	
	<i>A. crassicarpa</i> (g/m ²)	<i>E. urophylla</i> (g/m ²)
CK	87.24 \pm 5.71Aa	65.02 \pm 8.91Aa
LR	66.97 \pm 3.55Ba	48.24 \pm 4.28Bb
RR	13.14 \pm 1.96Ca	10.91 \pm 1.59Ca
LRR	15.83 \pm 1.78Ca	13.44 \pm 1.49Ca

Note: For CK and LR treatments, the annual fine root includes live and dead fine roots. For RR and LRR treatments, no live root was found, so the annual fine root biomass is only dead fine roots. The dead fine roots were determined by hand-sorting from soil cores (20 cm \times 20 cm) in RR and LRR treatments. The live fine roots were measured by in-growth method. The different upper case letters indicate significant differences at $P < 0.05$ level between treatments in the same stand and the different lower case letters indicate significant differences at $P < 0.05$ level for the same treatment between the two plantations.

Table 4

Relationship between the biomass and density of *Amynthas* sp. and *Pontoscolex corethrurus* and selected environmental variables as determined by forward stepwise multiple linear regression analysis^a.

	Density of <i>Amynthas</i> sp.	Density of <i>P. corethrurus</i>	Biomass of <i>Amynthas</i> sp.	Biomass of <i>P. corethrurus</i>
L_C	-5.667***	Not entered ^b	Not entered ^b	Not entered ^b
L:C:N	5.05***	Not entered ^b	0.696***	Not entered ^b
L:C:P	Not entered ^b	0.858***	Not entered ^b	Not entered ^b
L_Lignin:N	1.322*	Not entered ^b	Not entered ^b	0.762***
S_Moisture	0.137*	Not entered ^b	Not entered ^b	Not entered ^b
S_Temperature	0.251***	0.315***	0.354***	0.352***
S_N	Not entered ^b	0.107*	Not entered ^b	0.207***
S_MBC	-0.181**	Not entered ^b	-0.141*	Not entered ^b
S_G ⁺ :G ⁻	Not entered ^b	0.122**	Not entered ^b	0.128*

^a Negative and positive relationships are indicated.

^b Not entered: the given variable was not entered into the regression model.

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$. L_C, L:C:N, L:C:P, L_Cellulose, L_N:P, S_N, S_Temperature, S_MBC, S_G⁺:G⁻ represent litter carbon, litter nitrogen, litter C: P, litter cellulose, litter N:P, soil nitrogen, soil temperature, soil microbial biomass carbon, soil G⁺:G⁻ (the ratio of soil gram-positive and gram-negative bacteria which were from PLFA analysis), respectively.

C input into soil, i.e., fine root litter and rhizodeposites, may not contribute significantly to the growth of *P. corethrurus*. Another explanation is that although root removal may prevent roots from entering the subplot from exterior soil, the original roots inside the subplot (Table 3) might still be undergoing decomposition and could provide soil C for *P. corethrurus* during the experiment. In addition, *P. corethrurus* can tolerate a wide range of climatic change and soil disturbance (Ortiz-Ceballos and Galindo-González, 2009; Taheri et al., 2018) because it exhibits a high efficiency for organic matter assimilation and lives in deeper soil layers (Brown et al., 2006; Buch et al., 2011). Some studies even suggested that endogeic earthworms are able to utilize stable C compounds in soil (Scheu, 1991; Martin et al., 1992; Briones and Schmidt, 2004; Fox et al., 2006; Fonte et al., 2007; Marhan et al., 2007; Pollierer et al., 2012; Ferlian et al., 2014). Endogeic earthworms may also utilize C associated with small soil particle size fractions (Martin et al., 1992; Marhan et al., 2007; Ferlian et al., 2014). In general, endogeic species are more resistant to disturbance (Fragoso et al., 1997; Briones and Schmidt, 2017; Gonzalez and Lodge, 2017). For example, endogeic *P. corethrurus* can be well adapted to and colonize a disturbed habitat (Hendrix et al., 2008; Darmawan et al., 2017). Consequently, *P. corethrurus* would not be readily affected by root removal.

4.3. Effects of environmental variables on the earthworm community

Climate also constitutes an important factor influencing the earthworm community (Coyle et al., 2017; Phillips et al., 2019; Singh et al., 2019). In the present study, both the density and biomass of the earthworms were higher in the wet season than those in the dry season for both years in the two plantations, with the total biomass of each earthworm being higher in 2014 than that in 2015 (Figs. 1–4). This may be due to the change of climatic parameters in 2014 and 2015. Climate can affect earthworms not only directly by influencing their biology and life processes but also indirectly through its effects on their habitat and food supply. In particular, Curry (2004) reported that temperature can play a major role in determining patterns of earthworm distribution and activity on a global scale, whereas moisture restriction often determines the patterns of earthworm distribution and activity on a local scale. Baker (1998) also found that precipitation can explain more of the variance in earthworm density than any other variables in southern Australia agricultural soils. Similarly, Blankinship et al. (2011) reported that precipitation limits all taxa and trophic groups of soil biota, particularly in forest ecosystems. In the present study, we found that the precipitation was lower from February to April in 2015 than that in 2014 (Supplementary Fig. 1). The extension of drought may impose severe constraint on earthworm activity, which is likely to reduce the reproductive rate of endogeic *P. corethrurus* because it enters diapause stage in response to drought. For example, although we found that the density and biomass of both earthworm species were higher in the wet season in 2014, this was even more pronounced for *Amynthas* sp. Additionally, our data revealed that the density and biomass of both species were higher even in the dry season of 2014 than those in the dry season of 2015 because the precipitation was higher in 2014 than in 2015.

Both litter quantity and quality could affect the earthworm community (Curry, 2004); moreover, it was reported that litter quality is more important than litter quantity in mediating earthworms (Swift et al., 1979; Boström and Lofs-Holmin, 1986; Zou, 1993; Ceszar et al., 2016). Muys et al. (1992) suggested that the effects of grassland afforestation on the earthworm community is dependent on the quality and quantity of the litter produced. In the present study, forward stepwise multiple linear regression analysis showed that litter quality was one of the most important factors affecting *Amynthas* sp. and *P. corethrurus* (Table 4). For example, litter C ($P < 0.001$), litter C:N ($P < 0.001$) and litter Lignin:N ($P < 0.05$) had significant impact on the density of *Amynthas* sp. These results were partially in agreement with previous studies (Gonzalez and Zou, 1999; Schelfhout et al., 2017). Gonzalez and Zou (1999) reported that the total biomass of endogeic and aceric earthworms was positively related to litter N and phosphorus (P) contents and negatively related to tannin content in a tropical forest.

In addition, we found that the density of epigeic earthworm *Amynthas* sp. was lower in the *A. crassicarpa* plantation than that in the *E. urophylla* plantation. This may have arisen because that the litter quality of *A. crassicarpa* was lower than that of *E. urophylla*, which was supported by the higher cellulose, lignin, and lignin:N of the *A. crassicarpa* litter compared to the *E. urophylla* litter in the present study (Supplementary Table S1). Nevertheless, some authors have demonstrated that earthworms prefer substrates with low concentrations of secondary compounds and polyphenols (Hendriksen, 1990; Rajapaksha et al., 2013; Liebeke et al., 2015). In contrast, the density and biomass of endogeic earthworms *P. corethrurus* were higher in the *A. crassicarpa* plantation. This might be due to a higher total SOC in the *A. crassicarpa* compared to the *E. urophylla* plantation, as it has been reported that the availability of SOC and soil N could improve earthworm development (Scheu and Schaefer, 1998; Tiunov and Scheu, 2004; Milcu et al., 2008). This research was carried out on subtropical plantations; therefore, its applicability to forests in the temperate and cold regions needs further investigation.

5. Conclusions

In the present study, litter input manipulation affected the earthworms of *Amynthas* sp. and *P. corethrurus*, primarily due to changes in resource supply. We found that leaf litter is more important than roots for both the *Amynthas* sp. and *P. corethrurus* in the two subtropical (*A. crassicaarpa* and *E. urophylla*) plantations. The relative contributions of the resource supply and litter-mediated habitat condition to earthworm community structure needs further studies.

Declaration of competing interest

The manuscript has not been published or presented elsewhere in entirety and is not under consideration by another journal. All the authors have approved the manuscript and agree with submission to your esteemed journal. We have read and understand your journal's policies, and we believe that neither the manuscript nor the study violates any of these. The authors have declared that no competing interests exist.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2020.107777>.

References

- Abail, Z., Sampedro, L., Whalen, J.K., 2017. Short-term carbon mineralization from endogeic earthworm casts as influenced by properties of the ingested soil material. *Applied Soil Ecology* 116, 79–86.
- Albers, D., Schaefer, M., Scheu, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. *Ecology* 87, 235–245.
- Arpin, P., Ponge, J.F., Vannier, G., 1995. Experimental modifications of litter supplies in a forest mull and reaction of the nematode fauna. *Fundamental and Applied Nematology* 18, 371–389.
- Auerswald, K., Weigand, S., Kainz, M., Philipp, C., 1996. Influence of soil properties on the population and activity of geophagous earthworms after five years of bare fallow. *Biology and Fertility of Soils* 23, 382–387.
- Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology* 57, 233–266.
- Baker, G.H., 1998. The ecology, management, and benefits of earthworms in agricultural soils, with particular reference to southern Australia. In: Edwards, C.A. (Ed.), *Earthworm Ecology*. CRC Press LLC, Boca Raton, pp. 229–257.
- Blair, J.M., Parmelee, R.W., Allen, M.F., McCartney, D.A., Stinner, B.R., 1997. Changes in soil N pools in response to earthworm population manipulations in agroecosystems with different N sources. *Soil Biology and Biochemistry* 29, 361–367.
- Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. *Oecologia* 165, 553–565.
- Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.J., 2013. A review of earthworm impact on soil function and ecosystem services. *European Journal of Soil Science* 64, 161–182.
- Bohlen, P.J., Pelletier, D.M., Groffman, P.M., Fahey, T.J., Fisk, M.C., 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. *Ecosystems* 7, 13–27.
- Boström, U., Lofs-Holmin, A., 1986. Growth of earthworms (*Allolobophora caliginosa*) fed shoots and roots of barley, meadow fescue and lucerne. Studies in relation to particle size, protein, crude fibre content and toxicity. *Pedobiologia* 29, 1–12.
- Bouché, M.B., 1977. Strategies lombriennes. *Ecological Bulletins* 25, 122–132.
- Bradford, M.A., Strickland, M.S., DeVore, J.L., Maerz, J.C., 2012. Root carbon flow from an invasive plant to belowground foodwebs. *Plant and Soil* 359, 233–244.
- Briones, M.J.I., Schmidt, O., 2004. Stable isotope techniques in studies of the ecological diversity and functions of earthworm communities in agricultural soils. *Recent Research Developments in Crop Science* 1, 11–26.
- Briones, M.J.I., Schmidt, O., 2017. Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis. *Global Change Biology* 23, 4396–4419.
- Brown, G.G., James, S.W., Pasini, A., Nunes, D.H., Benito, N.P., Martins, P.T., Sautter, K.D., 2006. Exotic, peregrine, and invasive earthworms in Brazil: diversity, distribution, and effects on soils and plants. *Caribbean Journal of Science* 42, 339–358.
- Brown, G.G., Pashanasi, B., Villenave, C., Patron, J.C., Senapati, B.K., Giri, S., Barois, I., Lavelle, P., Blanchart, E., Blakemore, R.J., Spain, A.V., Boyer, J., 1999. Effects of earthworms on plant production in the tropics. In: Lavelle, P., Brussard, L., Hendrix, P. (Eds.), *Earthworm Management in Tropical Agroecosystems*. CABI publishing, Wallingford, pp. 87–137.
- Buch, A.C., Brown, G.G., Correia, M.E.F., Lourençato, F.L., Silva-filho, E.V., 2017. Ecotoxicology of mercury in tropical forest soils: impact on earthworms. *The Science of the Total Environment* 589, 222–231.
- Buch, A.C., Brown, G.G., Niva, C.C., Sautter, K.D., Lourençato, L.F., 2011. Life cycle of *Pontoscolex corethrurus* (Müller, 1857) in tropical artificial soil. *Pedobiologia* 54S, S19–S25.
- Burtelow, A.E., Bohlen, P.J., Groffman, P.M., 1998. Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern United States. *Applied Soil Ecology* 9, 197–202.
- Canner, L., Zeller, B., Dambrine, E., Ponge, J.F., Chauvat, M., Llanque, C., 2004. Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. *Soil Biology and Biochemistry* 36, 1861–1872.
- Cesarz, S., Craven, D., Dietrich, C., Eisenhauer, N., 2016. Effects of soil and leaf litter quality on the biomass of two endogeic earthworm species. *European Journal of Soil Biology* 77, 9–16.
- Chen, D.M., Lan, Z.C., Hu, S.J., Bai, Y.F., 2015. Effects of nitrogen enrichment on belowground communities in grassland: relative role of soil nitrogen availability vs. soil acidification. *Soil Biology and Biochemistry* 89, 99–108.
- Chuang, S.C., Lee, H., Chen, J.H., 2004. Diurnal rhythm and effect of temperature on oxygen consumption in earthworms, *Amynthas gracilis* and *Pontoscolex corethrurus*. *Journal of Experimental Zoology. a, Comparative Experimental Biology* 301, 737–744.
- Coyle, D.R., Nagendra, U.J., Taylor, M.K., Campbell, J.H., Cunard, C.E., Joslin, A.H., Mundie, A., Phillips, C.A., Callahan Jr, M.A., 2017. Soil fauna responses to natural disturbances, invasives species, and global climate change: current state of the science and a call to action. *Soil Biology and Biochemistry* 110, 116–133.
- Crow, S.E., Lajtha, K., Filley, T.R., Swanston, C.W., Bowden, R.D., Caldwell, B.A., 2009. Sources of plant-derived carbon and stability of organic matter in soil: implications for global change. *Global Change Biology* 15, 2003–2019.
- Curry, J.P., 2004. Factors affecting the abundance of earthworms in soils. In: Edwards, C.A. (Ed.), *Earthworm Ecology*. CRC press, pp. 91–114.
- Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms—a review. *Pedobiologia* 50, 463–477.
- Da Silva, E., Nahmani, J., Lapiet, E., Alphonse, V., Garnier-Zarli, E., Bousserrhine, N., 2016. Toxicity of mercury to the earthworm *Pontoscolex corethrurus* in a tropical soil of French Guiana. *Applied Soil Ecology* 104, 79–84.
- Darmawan, A., Atmowidi, T., Manalu, W., Suryobroto, B., 2017. Land-use change on Mount Gede, Indonesia, reduced native earthworm populations and diversity. *Australian Journal of Zoology* 65, 217–225.
- Dechaine, J., Ruan, H.H., Sanchez-de Leon, Y., Zou, X.M., 2005. Correlation between earthworms and plant litter decomposition in a tropical wet forest of Puerto Rico. *Pedobiologia* 49, 601–607.
- Dey, A., Chaudhuri, P.S., 2014. Earthworm community structure of pineapple (*Ananas comosus*) plantations under monoculture and mixed culture in West Tripura, India. *Tropical Ecology* 55, 1–17.
- Dey, A., Chaudhuri, P.S., 2016. Species richness, community organization, and spatiotemporal distribution of earthworms in the pineapple agroecosystems of Tripura, India. *International Journal of Ecology* 2016, 1–19.
- Duarte, A.P., Melo, V.F., Brown, G.G., Pauletti, V., 2014. Earthworm (*Pontoscolex corethrurus*) survival and impacts on properties of soils from a lead mining site in Southern Brazil. *Biology and Fertility of Soils* 50, 851–860.
- Edwards, C.A., 1983. Earthworm ecology in cultivated soils. In: Satchel, J.E. (Ed.), *Earthworm Ecology—From Darwin to Vermiculture*. Chapman and Hall, London, pp. 123–137.
- Edwards, C.A., 2004. *Earthworm Ecology*, second ed. CRC Press, Boca Raton.
- Edwards, C.A., Bohlen, P.J., 1996. *Biology and Ecology of Earthworms*. Springer Science & Business Media.
- Eggleton, P., Inward, K., Smith, J., Jones, D.T., Sherlock, E., 2009. A six year study of earthworm (Lumbricidae) populations in pasture woodland in southern England

- shows their responses to soil temperature and soil moisture. *Soil Biology and Biochemistry* 41, 1857–1865.
- Eisenhauer, N., Partsch, S., Parkinson, D., Scheu, S., 2007. Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. *Soil Biology and Biochemistry* 39, 1099–1110.
- Eisseller, V., Beyer, F., Valtanen, K., Hertel, D., Maraun, M., Polle, A., Scheu, S., 2013. Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash. *Soil Biology and Biochemistry* 62, 76–81.
- Eriksen-Hamel, N.S., Whalen, J.K., 2006. Growth rates of *Aporrectodea caliginosa* (Oligochaetae: Lumbricidae) as influenced by soil temperature and moisture in disturbed and undisturbed soil columns. *Pedobiologia* 50, 207–215.
- FAO, 2006. World Reference Base for Soil Resources Report No. 103. FAO, Rome.
- Ferlian, O., Ceszar, S., Marhan, S., Scheu, S., 2014. Carbon food resources of earthworms of different ecological groups as indicated by ^{13}C compound-specific stable isotope analysis. *Soil Biology and Biochemistry* 77, 22–30.
- Fischell, N.A., Frelich, L.E., Reich, P.B., Eisenhauer, N., 2013. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. *Biological Invasions* 15, 1057–1066.
- Fontaine, S., Bardoux, G., Abbadie, L., Mariotti, A., 2004. Carbon input to soil may decrease soil carbon content. *Ecology Letters* 7, 314–320.
- Fonte, S.J., Botero, C., Quintero, D.C., Lavelle, P., van Kessel, C., 2019. Earthworms regulate plant productivity and the efficacy of soil fertility amendments in acid soils of the Colombian Llanos. *Soil Biology and Biochemistry* 129, 136–143.
- Fonte, S.J., Kong, A.Y.Y., van Kessel, C., Hendrix, P.F., Six, J., 2007. Influence of earthworm activity on aggregate-associated carbon and nitrogen dynamics differs with agroecosystem management. *Soil Biology and Biochemistry* 39, 1014–1022.
- Fonte, S.J., Quintero, D.C., Velásquez, E., Lavelle, P., 2012. Interactive effects of plants and earthworms on the physical stabilization of soil organic matter in aggregates. *Plant and Soil* 359, 205–214.
- Fox, O., Vetter, S., Ekschmitt, K., Wolters, V., 2006. Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. *Soil Biology and Biochemistry* 38, 1353–1363.
- Fragoso, C., Brown, G.G., Patrón, J.C., Blanchart, E., Lavelle, P., Pashanasi, B., Senapati, B., Kumar, T., 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. *Applied Soil Ecology* 6, 17–35.
- Frostegård, Å., Tunlid, A., Bååth, E., 2011. Use and misuse of PLFA measurements in soils. *Soil Biology and Biochemistry* 43, 1621–1625.
- Ganigar, S.R., 2003. Nutrient mineralization and leaf litter preference by the earthworm *Pontoscolex corethrurus* on iron ore mine wastes. *Restoration Ecology* 11, 475–482.
- Gonzalez, G., Lodge, D.J., 2017. Soil biology research across latitude, elevation and disturbance gradients: a review of forest studies from Puerto Rico during the past 25 years. *Forests* 8, 178.
- Gonzalez, G., Zou, X.M., 1999. Plant and litter influences on earthworm abundance and community structure in a tropical wet forest. *Biotropica* 31, 486–493.
- Guerra, R.T., 1994. Earthworm activity in forest and savanna soils near Boa Vista, Roraima, Brazil. *Acta Amazonica* 24, 303–308.
- He, X.X., Chen, Y.Q., Liu, S.J., Gunina, A., Wang, X.L., Chen, W.L., Shao, Y.H., Shi, L.L., Yao, Q., Li, J.X., Zou, X.M., Schimel, J.P., Zhang, W.X., Fu, S.L., 2018. Cooperation of earthworm and arbuscular mycorrhizae enhanced plant N uptake by balancing absorption and supply of ammonia. *Soil Biology and Biochemistry* 116, 351–359.
- Hendriksen, N.B., 1990. Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils* 10, 17–21.
- Hendrix, P.F., Callaham Jr, M.A., Drake, J.M., Huang, C.Y., James, S.W., Snyder, B.A., Zhang, W.X., 2008. Pandora's box contained bait: the global problem of introduced earthworms. *Annual Review of Ecology, Evolution and Systematics* 39, 593–613.
- Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W., Parmelee, R.W., 1992. Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont, U.S.A. *Soil Biology and Biochemistry* 24, 1357–1361.
- Holmstrup, M., 2001. Sensitivity of life history parameters in the earthworm *Aporrectodea caliginosa* to small changes in soil water potential. *Soil Biology and Biochemistry* 33, 1217–1223.
- Huang, J.H., Zhang, W.X., Liu, M.Y., Briones, M.J.I., Eisenhauer, N., Shao, Y.H., Cai, X., A., Fu, S.L., Xia, H.P., 2015. Different impacts of native and exotic earthworms on rhizodeposit carbon sequestration in a subtropical soil. *Soil Biology and Biochemistry* 90, 152–160.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jordan, D., Ponder Jr, F., Hubbard, V.C., 2003. Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. *Applied Soil Ecology* 23, 33–41.
- Latif, R., Malek, M., Mirmonsef, H., 2013. Cadmium and lead accumulation in three endogeic earthworm species. *Bulletin of Environmental Contamination and Toxicology* 90, 456–459.
- Lavelle, P., 1983. The structure of earthworm communities. In: Satchell, J.E. (Ed.), *Earthworm Ecology—From Darwin to Vermiculture*. Chapman & Hall, London, pp. 449–466.
- Lavelle, P., 1988. Earthworm activities and the soil system. *Biology and Fertility of Soils* 6, 237–251.
- Lavelle, P., Barois, I., Cruz, I., Fragoso, C., Hernandez, A., Pineda, A., Rangel, P., 1987. Adaptive strategies of *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta), a peregrine geophagous earthworm of the humid tropics. *Biology and Fertility of Soils* 5, 188–194.
- Lavelle, P., Barois, I., Martin, A., Zaidi, Z., Schaefer, R., 1989. Management of earthworm populations in agro-ecosystems: a possible way to maintain soil quality? In:
- Clarholm, M., Bergstrom, L. (Eds.), *Ecology of Arable Land. Perspectives and Challenges*. Springer, Dordrecht, pp. 109–122.
- Lavelle, P., Brussaard, L., Hendrix, P., 1999. *Earthworm Management in Tropical Agroecosystems*. CABI, New York.
- Leake, J.R., Ostle, N.J., Rangel-Castro, J.I., Johnson, D., 2006. Carbon fluxes from plants through soil organisms determined by field $^{13}\text{CO}_2$ pulse-labelling in an upland grassland. *Applied Soil Ecology* 33, 152–175.
- Lee, K.E., 1985. *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press, New York.
- Li, J., Li, Z.A., Wang, F.M., Zou, B., Chen, Y., Zhao, J., Mo, Q.F., Li, Y.W., Li, X.B., Xia, H.P., 2015. Effects of nitrogen and phosphorus addition on soil microbial community in a secondary tropical forest of China. *Biology and Fertility of Soils* 51, 207–215.
- Li, J.X., Zhang, W.X., Liao, C.H., Yang, Y.P., Fu, S.L., 2009. Responses of earthworms to organic matter at different stages of decomposition. *Pedosphere* 19, 382–388.
- Liebeke, M., Strittmatter, N., Fearn, S., Morgan, A.J., Kille, P., Fuchs, J., Wallis, D., Palchykov, V., Robertson, J., Lahive, E., Spurgeon, D.J., McPhail, D., Takáts, Z., Bundy, J.G., 2015. Unique metabolites protect earthworms against plant polyphenols. *Nature Communications* 6, 7869.
- Liu, Z.G., Zou, X.M., 2002. Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications* 12, 1406–1417.
- Lof-Holmin, A., 1983. Earthworm population dynamics in different agricultural rotations. In: Satchell, J.E. (Ed.), *Earthworm Ecology—From Darwin to Vermiculture*. Chapman and Hall, London, pp. 151–160.
- Lowe, C.N., Butt, K.R., 2002. Influence of organic matter on earthworm production and behavior: a laboratory-based approach with applications for soil restoration. *European Journal of Soil Biology* 38, 173–176.
- 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.
- Marhan, S., Langel, R., Kandeler, E., Scheu, S., 2007. Use of stable isotopes (^{13}C) for studying the mobilisation of old soil organic carbon by endogeic earthworms (Lumbricidae). *European Journal of Soil Biology* 43, S201–S208.
- Martin, A., Balesdent, J., Mariotti, A., 1992. Earthworm diet related to soil organic matter dynamics through ^{13}C measurements. *Oecologia* 91, 23–29.
- Milcu, A., Partsch, S., Scherber, C., Weisser, W.W., Scheu, S., 2008. Earthworms and legumes control litter decomposition in a plant diversity gradient. *Ecology* 89, 1872–1882.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and biodiversity. *Ecological Letters* 7, 584–600.
- Muys, B., Lust, N., Granval, P., 1992. Effects of grassland afforestation with different tree species on earthworm communities, litter decomposition and nutrient status. *Soil Biology and Biochemistry* 24, 1459–1466.
- Nie, M., Pendall, E., Bell, C., Gasch, C.K., Raut, S., Tamang, S., Wallenstein, M.D., 2013. Positive climate feedbacks of soil microbial communities in a semi-arid grassland. *Ecology Letters* 16, 234–241.
- Ortiz-Ceballos, A.I., Galindo-González, J., 2009. Influence of adult *Pontoscolex corethrurus* on development of cocoons and hatchlings. *Dynamic Soil, Dynamic Plant* 3, 119–121.
- Pelosi, C., Barot, S., Capowiez, Y., Hedde, M., Vandebulcke, F., 2014. Pesticides and earthworms. A review. *Agronomy for Sustainable Development* 34, 199–228.
- Perreault, J.M., Whalen, J.K., 2006. Earthworm burrowing in laboratory microcosms as influenced by soil temperature and moisture. *Pedobiologia* 50, 397–403.
- Phillips, H.R.P., Guerra, C.A., Bartz, M.L.C., Briones, M.J.I., Brown, G., Crowther, T.W., Ferlian, O., Gongalsky, K.B., van den Hoogen, J., Krebs, J., Orgiazzi, A., Routh, D., Schwarz, B., Bach, E.M., Bennett, J., Brose, U., Decaëns, T., König-Ries, B., Loreau, M., Mathieu, J., Mulder, C., van der Putten, W.H., Ramirez, K.S., Rillig, M.C., Russell, D., Rutgers, M., Thakur, M.P., de Vries, F.T., Wall, D.H., Wardle, D.A., Arai, M., Ayuke, F.O., Baker, G.H., Beauséjour, R., Bedano, J.C., Birkhofer, K., Blanchart, E., Blossey, B., Bolger, T., Bradley, R.L., Callaham, M.A., Capowiez, Y., Caulfield, M.E., Choi, A., Crotty, F.V., Dávalos, A., Cosin, D.J.D., Dominguez, A., Duhour, A.E., van Eekeren, N., Emmerling, C., Falco, L.B., Fernández, R., Fonte, S.J., Fragoso, C., Franco, A.L.C., Fugère, M., Fusilero, A.T., Gholami, S., Gundale, M.J., López, M.G., Hackenberger, D.K., Hernández, L.M., Hishi, T., Holdsworth, A.R., Holmstrup, M., Hopfensperger, K.N., Wang, E.H., Huhta, V., Hurrisso, T.T., Iannone III, B.V., Jordache, M., Joschko, M., Kaneko, N., Kanianska, R., Keith, A.M., Kelly, C.A., Kernecker, M.L., Klaminder, J., Koné, A.W., Kooch, Y., Kukkonen, S.T., Lalithanazara, H., Lammel, D.R., Lebedev, I.M., Li, Y.Q., Lidon, J.B.J., Lincoln, N.K., Loss, S.R., Marichal, R., Matula, R., Moos, J.H., Moreno, G., Morón-Ríos, A., Muys, B., Neirynck, J., Norgrove, L., Novo, M., Nuutinen, V., Nuzzo, V., Rahaman, P.M., Pansu, J., Paudel, S., Pérez, G., Pérez-Camacho, L., Piñeiro, R., Ponge, J.F., Rashid, M.I., Rebollo, S., Rodeiro-Iglesias, J., Rodríguez, M.Á., Roth, A.M., Rousseau, G.X., Rozen, A., Sayad, E., van Schaik, L., Scharenbroch, B.C., Schirrmann, M., Schmidt, O., Schröder, B., Seeber, J., Shashkov, M.P., Singh, J., Smith, S.M., Steinwandter, M., Talavera, J.A., Trigo, D., Tsukamoto, J., de Valença, A.W., Vanek, S.J., Virto, I., Wackett, A.A., Warren, M.W., Wehr, N.H., Whalen, J.K., Wironen, M.B., Wolters, V., Zenkova, I.V., Zhang, W.X., Cameron, E.K., Eisenhauer, N., 2019. Global distribution of earthworm diversity. *Science* 366, 480–485.
- Pollierer, M.M., Dyckmans, J., Scheu, S., Haubert, D., 2012. Carbon flux through fungi and bacteria into the forest soil animal food web as indicated by compound-specific ^{13}C fatty acid analysis. *Functional Ecology* 26, 978–990.
- Pollierer, M.M., Langel, R., Körner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters* 10, 729–736.

- Rajapaksha, N.S.S., Butt, K.R., Vanguelova, E.I., Moffat, A.J., 2013. Earthworm selection of Short Rotation Forestry leaf litter assessed through preference testing and direct observation. *Soil Biology and Biochemistry* 67, 12–19.
- Rasse, D.P., Rumpel, C., Dignac, M.F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* 269, 341–356.
- Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. *Soil Biology and Biochemistry* 38, 2390–2400.
- Sabrina, D.T., Hanafi, M.M., Gandahi, A.W., Mahmud, T.M.M., Aziz, N.A.A., 2013. Effect of mixed organic-inorganic fertilizer on growth and phosphorus uptake of setaria grass (*Setaria splendida*). *Australian Journal of Crop Science* 7, 75–83.
- Sánchez-de León, Y., Zou, X.M., 2004. Plant influences on native and exotic earthworms during secondary succession in old tropical pastures. *Pedobiologia* 48, 215–226.
- Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews* 81, 1–31.
- Schelfhout, S., Mertens, J., Verheyen, K., Vesterdal, L., Baeten, L., Muys, B., De Schrijver, A., 2017. Tree species identity shapes earthworm communities. *Forests* 8, 85.
- Scheu, S., 1991. Mucus excretion and carbon turnover of endogeic earthworms. *Biology and Fertility of Soils* 12, 217–220.
- Scheu, S., 2003. Effects of earthworms on plant growth: patterns and perspectives. *Pedobiologia* 47, 846–856.
- Scheu, S., Schaefer, M., 1998. Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. *Ecology* 79, 1573–1585.
- Scheunemann, N., Digel, C., Scheu, S., Butenschoen, O., 2015. Roots rather than shoot residues drive soil arthropod communities of arable fields. *Oecologia* 179, 1135–1145.
- Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. *Applied Soil Ecology* 46, 59–63.
- Schneider, T., Keiblanger, K.M., Schmid, E., Sterflinger-Gleixner, K., Ellersdorfer, G., Roschitzki, B., Richter, A., Eberl, L., Zechmeister-Boltenstern, S., Riedel, K., 2012. Who is who in litter decomposition? Metaproteomics reveals major microbial players and their biogeochemical functions. *The ISME Journal* 6, 1749–1762.
- Singh, J., Schädler, M., Demetrio, W., Brown, G.G., Eisenhauer, N., 2019. Climate change effects on earthworms—a review. *Soil Organisms* 91, 114–138.
- Stober, C., George, E., Persson, H., 2000. Root growth and response to nitrogen. *Ecological Studies* 142, 99–121.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. *Studies in Ecology* 5. Blackwell Scientific Publications, Oxford.
- Taheri, S., Pelosi, C., Dupont, L., 2018. Harmful or useful? A case study of the exotic peregrine earthworm morphospecies *Pontoscolex corethrurus*. *Soil Biology and Biochemistry* 116, 277–289.
- Teng, S.K., Aziz, N.A.A., Mustafa, M., Laboh, R., Ismail, I.S., Devi, S., 2016. Potential role of endogeic earthworm *Pontoscolex corethrurus* in remediating banana blood disease: a preliminary observation. *European Journal of Plant Pathology* 145, 321–330.
- Tianov, A.V., Scheu, S., 2004. Carbon availability controls the growth of detritivores (Lumbricidae) and their effect on nitrogen mineralization. *Oecologia* 138, 83–90.
- van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. *Scientific Reports* 4, 6365.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. Microbial biomass measurements in forest soils: the use of the chloroform fumigation-incubation method in strongly acid soils. *Soil Biology and Biochemistry* 19, 697–702.
- Vogt, K.A., Persson, H., 1991. Measuring growth and development of roots. In: Lassoie, J. P., Hinckley, T.M. (Eds.), *Techniques and Approaches in Forest Tree Ecophysiology*. CRC Press, Boca Raton, pp. 477–501.
- Wang, Y.L., Wu, Y.Z., Cavanagh, J., Yiming, A., Wang, X.H., Gao, W., Matthew, C., Qiu, J.P., Li, Y.S., 2018. Toxicity of arsenite to earthworms and subsequent effects on soil properties. *Soil Biology and Biochemistry* 117, 36–47.
- Xiao, Z.G., Wang, X., Koricheva, J., Kergunteuil, A., Le Bayon, R.C., Liu, M.Q., Hu, F., Rasmann, S., 2018. Earthworms affect plant growth and resistance against herbivores: a meta-analysis. *Functional Ecology* 32, 150–160.
- Xu, Q., Xiao, N.W., 2011. *Terrestrial Earthworms (Oligochaeta: Opisthopora)* of China. China Agricultural Press.
- Zhang, C.L., Li, X.W., Chen, Y.Q., Zhao, J., Wan, S.Z., Lin, Y.B., Fu, S.L., 2016. Effects of *Eucalyptus* litter and roots on the establishment of native tree species in *Eucalyptus* plantations in South China. *Forest Ecology and Management* 375, 76–83.
- Zhang, H., Yang, X.D., Du, J., Wu, Y.X., 2008. Influence of soil temperature and moisture on the cocoon production and hatching of the exotic earthworm *Pontoscolex corethrurus*. *Zoological Research* 29, 305–312 (in Chinese with English abstract).
- Zhang, L.H., He, N.N., Chang, D.L., Liu, X.Y., Zhang, X.H., Xu, Y.Z., Zhao, C.Y., Sun, J., Li, W.M., Li, H.X., Hu, F., Xu, L., 2018. Does ecotype matter? The influence of ecophysiology on benzo[a]pyrene and cadmium accumulation and distribution in earthworms. *Soil Biology and Biochemistry* 121, 24–34.
- Zhang, W.X., Li, J.X., Guo, M.F., Liao, C.H., He, X.X., Lin, Y.B., Fu, S.L., 2020. The presence of earthworm *Pontoscolex corethrurus* rather than organic matter sources indirectly controls N_2O flux in tropical plantation soils. *European Journal of Soil Biology* 96, 103150.
- Zhu, X.M., Chen, H., Zhang, W., Huang, J., Fu, S.L., Liu, Z.F., Mo, J.M., 2016. Effects of nitrogen addition on litter decomposition and nutrient release in two tropical plantations with N_2 -fixing vs. non- N_2 -fixing tree species. *Plant and Soil* 399, 61–774.
- Zou, X.M., 1993. Species effects on earthworm density in tropical tree plantations in Hawaii. *Biology and Fertility of Soils* 15, 35–38.