



## Different impacts of native and exotic earthworms on rhizodeposit carbon sequestration in a subtropical soil



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### ABSTRACT

Earthworms are known to regulate the sequestration of soil and leaf litter carbon (C). However, their impacts on the more accessible rhizospheric C, which represents a major energy source for soil food webs and an essential factor for C sequestration, are still unclear. Previous studies indicate that earthworms regulate the dynamics of SOC and leaf litter-C by increasing C accessibility to microbiota. However, in the case of labile rhizodeposit-C, microbiota might not require any pre-conditioning by earthworms and may rapidly metabolize most of this root-derived C. Consequently, potential pathways by which earthworms may affect the fate of rhizodeposit-C would be to regulate the biomass and/or activity of rhizosphere microbiota and, further, to mineralize/stabilize microbial products. A <sup>13</sup>C<sub>2</sub> labelling experiment was performed to determine the impacts of four different earthworm species on the fate of tree rhizodeposit-C in a subtropical soil. We hypothesized that endogeic earthworm species, representing primarily geophagous species, would closely interact with soil microbiota and sequester the microbially metabolized rhizodeposit-C more efficiently than epigeic and anecic earthworm species. We found that irrespective of ecological group affiliation, the three native earthworms did not affect rhizodeposit-C sequestration. In contrast, the exotic endogeic species stimulated the immobilization of rhizodeposit-C in the biomass of root-associated bacteria and/or arbuscular mycorrhizal fungi and, further, accessed the microbiota-metabolized rhizodeposit-C more efficiently. As a consequence, the exotic endogeic earthworm species transiently tripled rhizodeposit-C retention in soil. We propose that the weak linkages between native earthworms and rhizodeposit-related microbiota limit earthworm impacts on rhizodeposit-C sequestration. However, the exotic endogeic species *Pontoscolex corethrurus* may potentially alter rhizodeposit-C dynamics in invaded areas by shifting rhizosphere microbial community composition. This work highlights a distinct mechanism by which earthworms can regulate C dynamics and indicates a significant contribution of invasive earthworm species to belowground processes.

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### 1. Introduction

Rhizodeposition is the largest source of labile carbon (C) inputs to the soil, and rhizodeposits are primarily composed of easily decomposable compounds, e.g., sloughed off root caps, border cells

and root hairs, high molecular weight secretions (mucilages), and low molecular weight organic substances (root exudates) (Nguyen, 2003; Jones et al., 2009). Rhizodeposits account for 5–40% of the net photosynthesized C (Farrar et al., 2003; Nguyen, 2003; Condon et al., 2010) and fuel most processes occurring in the rhizosphere (Högberg et al., 2001; Hütsch et al., 2002; Bardgett et al., 2014). Root-derived C (including both root litter and rhizodeposits) is estimated to account for 50–70% of the C stored in soils of boreal forests (Clemmensen et al., 2013). Also, the contribution of rhizodeposition to soil ecological processes may be enhanced by current

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global environmental changes. For instance, although the rising atmospheric CO<sub>2</sub> concentration may simply increase throughput of C (Staddon et al., 2014), it has been suggested to increase the C allocation to root growth and the rhizosphere (Rogers and Runion, 1994; Phillips et al., 2012), which may in turn affect soil C sequestration positively (Wilson et al., 2009) or negatively (Cheng et al., 2012). Also, Boone et al. (1998) concluded that live roots and rhizodeposition are key factors in regulating C emission and C sequestration rates in a warmer world.

Soil biota play a determining role in regulating ecosystem functioning and the response of soils to global change (Bardgett and van der Putten, 2014). Earthworms that act as ecosystem engineers have a strong influence on belowground processes through feeding, burrowing, and casting activities (Lavelle et al., 1997; Brown et al., 2000; Scheu, 2003). Earthworms are known to regulate the sequestration of soil organic carbon (SOC) and leaf litter C (Fahey et al., 2013; Lubbers et al., 2013; Zhang et al., 2013). However, their impacts on the more accessible C released into the rhizosphere, which represents an important energy source for soil food webs (Pollierer et al., 2007; Bonkowski et al., 2009; Gilbert et al., 2014) and an essential factor in soil C sequestration (Miltner et al., 2012; Cotrufo et al., 2013), are still unclear. Therefore, a better understanding of the magnitude of earthworm impacts on the fate of rhizodeposit-C is needed.

There are five pathways by which earthworms may affect rhizodeposit-C sequestration in soil. Firstly, earthworms may enhance rhizodeposit-C sequestration by facilitating plant growth (Berova and Karanatsidis, 2009; van Groenigen et al., 2014) and the rhizodeposit-C input into soil. Secondly, earthworms may directly access and mineralize and/or stabilize rhizodeposit-C (Brown and Doube, 2004; Gilbert et al., 2014). Thirdly, earthworms may change the fate of rhizodeposit-C by enhancing its accessibility to microbiota as shown for SOC and leaf litter-C (Zhang et al., 2013). Fourthly, earthworms may affect rhizodeposit-C dynamics through regulating the biomass and/or activity of rhizodeposit-related microbiota (Brown and Doube, 2004). Finally, earthworms may indirectly access rhizodeposit-C from microbiota and their residues and, further, affect the retention of rhizodeposit-C through gut processes. Given that most of this root-derived C is readily accessible to rhizosphere microbiota (Todorovic et al., 2001; Kuzakov and Larionova, 2005; Balasooriya et al., 2014), we consider that the last mechanism is potentially of most relevance. Hence, we hypothesized that endogeic earthworm species, which represents primarily geophagous species, would closely interact with soil microbiota and access microbially metabolized rhizodeposit-C more efficiently, and consequently, have a greater contribution to rhizodeposit-C sequestration than anecic and epigeic earthworm species.

Given that the effect of invasive species on the composition and functioning of native ecosystems may be particularly strong when it is functionally dissimilar to the native community (Wardle et al., 2011; Frelich et al., 2012), we compared the effects of three native earthworm species belonging to different ecological groups (epigeic, endogeic, and anecic species) with that of the exotic endogeic species *Pontoscolex corethrus*, which is invasive in south subtropical China. This exotic endogeic species is resistant to stress/disturbance (e.g., drought and infertility) probably due to its behaviour of curled-up quiescence and the presence of well-developed calciferous glands (Fig. S1), which may have important roles in regulations of water and acid-base balances (Briones et al., 2008). In fact, *P. corethrus* is one of the most widespread pantropical species (Marichal et al., 2012) and the sole exotic earthworm species in the region south of the Nanling mountain ranges of China (Zhang et al., 2005; Hendrix et al., 2008). The proportion of the population density of this invasive species has

increased from less than 50% (Liao and Chen, 1990) to more than 95% in some non-natural forests in the last few decades in tropical regions of China, i.e., native earthworm species can only be occasionally sampled (data not shown). In addition, *P. corethrus* has been observed to be dominant in some primary forests of South America (Marichal et al., 2010). The presence of this peregrine earthworm species may profoundly alter soil structure, water infiltration, and soil fertility (Jouquet et al., 2006; Briones, 2014). Hence, it is essential to compare the functioning of native and exotic earthworm species to better understand the changes of earthworm contributions to C dynamics in response to the invasion of *P. corethrus*.

Therefore, a <sup>13</sup>CO<sub>2</sub> labelling experiment was performed to quantify the impacts of these earthworm species on the belowground sequestration of recently photosynthesized C by a common tree species *Schima superba* in the subtropical region of China. We determined the incorporation of rhizodeposit-C into bulk soil and different sized aggregates, and earthworm gut contents and tissues as well as the mineralization potential of soil retained rhizodeposit-C. The effects of different earthworm ecological groupings on soil microbial biomass and activity and their δ<sup>13</sup>C signatures were examined to explore the underlying mechanisms.

## 2. Materials and methods

### 2.1. Construction of the labelling chamber

In September 2011, a labelling chamber (2 m long × 1.6 m wide × 2 m high) was built to permit the injection and monitoring of CO<sub>2</sub>. The chamber was constructed using an aluminium frame, Plexiglas walls (5 mm thick) and roof (2 mm thick). A CO<sub>2</sub> probe (GMM220 Series CO<sub>2</sub> transmitter modules, Vaisala, Netherland), a quantum sensor (LI190SB, Campbell Scientific, Inc., USA), and a temperature and relative humidity probe (CS215, Campbell Scientific, Inc., USA) were fixed inside the chamber and connected to a control panel and a data logger outside. A <sup>13</sup>C-labelled and a non-labelled CO<sub>2</sub> gas cylinder were also connected to the control panel. If the concentration of CO<sub>2</sub> inside the chamber did not reach the desired concentration, the valve would automatically open to release more <sup>13</sup>CO<sub>2</sub> or non-labelled CO<sub>2</sub> into the chamber. An air-conditioning system was installed to maintain a constant temperature (20 °C) inside the chamber.

### 2.2. Establishment of the microcosms

The soil (C%: 6.22 ± 0.10%; N%: 0.41 ± 0.01%; clay%: 19.67 ± 0.88%; pH: 3.80 ± 0.01; δ<sup>13</sup>C: -27.48 ± 0.03‰; δ<sup>15</sup>N: -0.78 ± 0.07‰) used in the microcosm experiment was collected from the 0–15 cm layer of a 70-year old forest in Dinghushan Biosphere Reserve, Guangdong, China (23°12' N, 112°34' E). It is a lateritic red soil with *S. superba* as one of the dominant tree species. In June 2012, 3 kg of fresh sieved soil (≤2 mm; soil water content: 33.9 ± 0.2%) was used to fill 30 nylon-bags (20 cm wide × 40 cm long, mesh size ≤0.25 mm), with the bags preventing earthworms from escaping. Each of these soil-filled nylon-bags was introduced into a plastic pot (20 cm in diameter × 20 cm in height), and one seedling of *S. superba* (50–60 cm in height) was planted in each pot. All 30 pots were watered using a drip irrigation system every 3 days, and the watering stopped when excess water started to drain through the holes at the bottom.

### 2.3. Collection and inoculation of earthworms

In September 2012, earthworms belonging to three ecological groups were hand-sorted in the field from the same location as the

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