



## Differentiating between root- and leaf-litter controls on the structure and stability of soil micro-food webs



Xiaoli Fu <sup>a, \*</sup>, Dali Guo <sup>a, b</sup>, Huimin Wang <sup>a, b, c, \*\*</sup>, Xiaoqin Dai <sup>a</sup>, Meiling Li <sup>d</sup>, Fusheng Chen <sup>e</sup>

<sup>a</sup> Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

<sup>b</sup> College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100190, China

<sup>c</sup> Jiangxi Key Laboratory of Ecosystem Processes and Information, Ji'an 343725, China

<sup>d</sup> Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

<sup>e</sup> Collaborative Innovation Center of Jiangxi Typical Trees Cultivation and Utilization, College of Forestry, Jiangxi Agricultural University, Nanchang 330045, China

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### ABSTRACT

The dynamics of soil food webs play a key role in determining the ecological response of terrestrial ecosystems to current and future environmental change. Both root and leaf litter fuel the micro-food webs (microorganisms and nematodes) in soil, but whether the root and leaf litter would favor different components of the micro-food webs is not clear, especially the relative importance of these two litter sources on the stability of the micro-food web.

We compared micro-food webs in mineral soils without added litter, with added leaf litter and with added root litter and investigated the effect of the litter carbon source on the resistance of the micro-food webs to added nitrogen and added nitrogen and phosphorus.

The nematode community was more sensitive than the microbial community to the carbon source. Root litter was favored by bacteria, and leaf litter was preferred by fungi. Herbivorous nematodes were controlled more by the input of leaf litter than the input of root litter. Fertilization increased the effects of the root litter on the structure of the nematode community and thus moderated the effects of the litter source on the micro-food web. When both nitrogen and phosphorus were added, the root litter fueled the more resistant first trophic level (microorganisms), and the leaf litter fueled the more adaptable second trophic level (nematodes).

Our results suggest that the input of leaf litter would be more important than the input of root litter for promoting a conservative cycling of nutrients and more positive soil feedback effects on plant growth. Our results also indicate that leaf litter and root litter help micro-food webs to adapt to exogenous disturbance in different ways, which would aid our mechanistic understanding of how soil food webs and their associated ecosystem processes would respond to current and future environmental changes.

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## 1. Introduction

Climatic change is anticipated, and research into the effects of

\* Corresponding author.

\*\* Corresponding author. Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.

E-mail addresses: [fuxl@igsnr.ac.cn](mailto:fuxl@igsnr.ac.cn) (X. Fu), [wanghm@igsnr.ac.cn](mailto:wanghm@igsnr.ac.cn) (H. Wang).

the agents of global change on soil food webs is extensive, because the dynamics of the food webs can be linked to ecosystem processes and play a key role in determining the ecological response of terrestrial ecosystems to current and future environmental change (Bengtsson et al., 1995; Bardgett et al., 2013; Van der Putten et al., 2013). Soil biota are essentially fueled by the two carbon (C) inputs from leaf litter and root litter (Högberg et al., 2010; Eisenhauer and Reich, 2012). Shaw et al. (2002) found that the allocation of C to roots (which becomes root litter at the end of each year) decreased but aboveground biomass (which becomes leaf litter at the end of

each year) increased in response to elevated CO<sub>2</sub> in a moderately fertile California annual grassland. These findings indicated that the quantities of inputs of leaf and root litter may respond differently to global change. The quality of the C generally differs substantially between root and leaf litters (Ma et al., 2016), and soil food webs are influenced directly by the environmental changes (e.g. elevated CO<sub>2</sub>, warming and altered precipitation) during global change (Blankinship et al., 2011) and may also be influenced indirectly due to the variation in the inputs of root and leaf litter during global change. Determining how and to what extent global change influences soil food webs therefore requires an understanding of the relative importance of inputs from leaf and root litter to the food webs.

The relative effects of above- and belowground C on soil food webs can be inferred by using DIRT (detritus input, removal and trenching) plots and monitoring the relative contributions of root litter and leaf litter to heterotrophic soil respiration (produced by soil microbes and fauna). Belowground litter can have a higher (Sulzman et al., 2005) or lower (Bowden et al., 1993) influence on the activity of food webs than aboveground litter. These variable results are likely associated with the status of soil nutrients (Sulzman et al., 2005) and indicate that more investigations need to be conducted to establish a tentative general rule. Trenching can also lead to underestimates of a root's contribution, because the severed roots in a trenched plot are generally ignored, even though the measurement of soil respiration cannot separate the relative importance of the C sources for different levels of the food chain. Attempts to trace C matter flows through biological systems can be realized alternatively by analyzing the C stable isotope fractionation in food chains (Ruess et al., 2005; Tiunov, 2007; Crotty et al., 2011). The effects of leaf and root C inputs have been successfully differentiated for larger meso- and macrofauna (two or more levels higher than microbes in the food chain) by enriching a forest canopy with <sup>13</sup>C-depleted CO<sub>2</sub> and directly measuring appropriate amounts of the soil fauna tissue (Pollierer et al., 2007). The C from roots was the predominant C source for the majority of earthworms, chilopods, gastropods, diplurans, collembolans, mites and isopods (Pollierer et al., 2007). Few studies have explicitly compared the relative importance of leaf and root C sources for nematodes by using stable isotope analysis, because the direct content analysis of such small animals is quite difficult (Kudrin et al., 2015). However, a mesocosm experiment, including the leaf litter addition and root presence treatments, showed that root C inputs (root litter and exudation) have a stronger impact on soil nematode structure and complexity than leaf C inputs (Keith et al., 2009).

Direct anthropogenic disturbance can regulate the dynamics of soil food webs. Fertilization with nitrogen (N) and phosphorus (P) is a widespread direct anthropogenic disturbance, because N and P are generally the most common limiting elements in terrestrial ecosystems. The growth of food webs is dependent on the C:N:P stoichiometry of the organic substrate (Ferris et al., 1998; Manzoni et al., 2012), which can be readily changed by fertilization (Chen et al., 2015), indicating that N and P availability and the litter C source can have interactive impacts on the food webs. Most studies of the response of food webs to environmental variables, however, have addressed responses to a single factor (Chen et al., 2007; Eisenhauer and Reich, 2012; Liu et al., 2012; Nielsen et al., 2015) or a combination of two factors (Maraun et al., 2001; Sarathchandra et al., 2001; Meidute et al., 2008). Multifactor experimental manipulations of the litter C source, N availability and P availability are rare.

We conducted an experiment in a subtropical plantation in China. The soil was highly weathered and had little available P (Hall and Matson, 2003). We added large amounts of leaf or root litter to

the mineral soil to differentiate between the effects of these two litter C sources on the soil food web. The input of C was comparable to the C stock of the mineral soil. We compared the micro-food webs (microorganisms and nematodes) in soils without added litter, with leaf litter added to the soil surface and with root litter incorporated into the soil. We determined how N addition or a combination of N and P addition interacted with the litter C source to affect the micro-food web. We hypothesized that (1) leaf litter would mostly affect fungal-based (fungi and fungivorous nematodes) food webs, and root litter would mostly affect bacterial-based (bacteria and nematodes that feed on bacteria) food webs, because the average C:N ratio is higher for fungi than bacteria, so bacteria are more likely to use a lower C:N ratio than fungi (Wallenstein et al., 2006) and (2) the fungal-based food web fueled by leaf litter would be more resistant to fertilization than the bacterial-based food web fueled by root litter, because the slower growing fungi and fungivorous nematodes are more resistant than bacteria to disturbance (de Vries et al., 2012).

## 2. Methods

### 2.1. Study site and experimental design

This study was conducted at the Qianyanzhou Ecological Station (26°44'39"N, 115°03'33"E; 102 m a.s.l.) in Jiangxi Province in southeastern China. The station is approximately 204 hm<sup>2</sup> and has a typical subtropical climate. The mean annual temperature is 17.9 °C, with a minimum mean daily temperature of 6.4 °C in January and a maximum of 28.8 °C in July. The mean annual precipitation is 1489 mm, most of which falls between March and June. The main soil type is red earth of the orthic acrisol category in the FAO system (Li et al., 2017). The zonal vegetation was evergreen broadleaved forest, which has been nearly completely removed by human activities. *Cunninghamia lanceolata* has become the major forest component.

An experiment was conducted in the framework of the FunNP (Ecosystem functions, N deposition and P addition) experiments established in 2011 in *C. lanceolata* plantations. Understorey vegetation was removed before the FunNP experiment was established. The FunNP experiment had six treatments: a control with no fertilization, N addition at 50 kg ha<sup>-1</sup> y<sup>-1</sup>, N addition at 100 kg ha<sup>-1</sup> y<sup>-1</sup>, P addition at 50 kg ha<sup>-1</sup> y<sup>-1</sup>, NP addition at 50 kg N ha<sup>-1</sup> y<sup>-1</sup> and 50 kg P ha<sup>-1</sup> y<sup>-1</sup> and NP addition at 100 kg N ha<sup>-1</sup> y<sup>-1</sup> and 50 kg P ha<sup>-1</sup> y<sup>-1</sup>. The FunNP experiment had a randomized complete block design with five blocks arranged on five hilly slopes. The six treatments were assigned randomly to equal-sized plots (20 × 20 m) within each block. Detailed information of the FunNP experiment can be found in Chen et al. (2015).

We randomly chose three blocks and used nine plots of three of the FunNP treatments: the control (CK), N addition at 100 kg ha<sup>-1</sup> y<sup>-1</sup> (+N) and NP addition at 100 kg N ha<sup>-1</sup> y<sup>-1</sup> and 50 kg P ha<sup>-1</sup> y<sup>-1</sup> (+NP). The rate of N addition of 100 kg ha<sup>-1</sup> y<sup>-1</sup> tested the sensitivity of the system to N addition rather than simulating the effects of a more realistic increase in N supply in this area, which is approximately 50 kg ha<sup>-1</sup> y<sup>-1</sup>. Two 3 × 5 m subplots were delimited in each plot to establish the microcosms of the C-source treatments in PVC tubes (inner diameter, 30 cm; length, 40 cm). The two subplots were separated by approximately 14 m, on the upper and lower parts of the plot. Because the ranges of spatial dependence was around 1 m for the different nematode groups (Viketoft, 2013) and generally less than 10 m for the microbial community (Saetre and Bååth, 2000; Franklin and Mills, 2003), we assumed that the two subplots within each plot were independent. Each subplot had three treatments of litter decomposition, consisting of bare soil, soil with leaf litter and soil with root litter, except for the

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