



# Using structural equation modeling to test established theory and develop novel hypotheses for the structuring forces in soil food webs



Yuanhu Shao<sup>a</sup>, Weikai Bao<sup>b</sup>, Dima Chen<sup>c</sup>, Nico Eisenhauer<sup>d,e</sup>, Weixin Zhang<sup>a</sup>, Xueyong Pang<sup>b</sup>, Guoliang Xu<sup>f</sup>, Shenglei Fu<sup>a,\*</sup>

<sup>a</sup> Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

<sup>b</sup> Key Laboratory of Ecological Restoration, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China

<sup>c</sup> Institute of Botany, Chinese Academy of Sciences, State Key Laboratory of Vegetation and Environmental Change, Beijing 100093, China

<sup>d</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

<sup>e</sup> Institute of Biology, University of Leipzig, Johannisallee 21, 04103 Leipzig, Germany

<sup>f</sup> School of Geographical Sciences, Guangzhou University, Guangzhou 510006, China

## ARTICLE INFO

### Article history:

Received 14 April 2015

Received in revised form 19 June 2015

Accepted 19 June 2015

### Keywords:

Collembola

Mites

Nematodes

Predator–prey

Soil invertebrates

## ABSTRACT

Understanding the structuring elements of soil food webs is a major challenge for ecologists. Given the complex nature of soil food webs, common treatment-based experiments and bivariate data analyses can only capture part of that complexity. Structural equation model (SEM) is a promising multivariate technique that may help understand direct and indirect relationships in complex soil food webs. As bacterial and fungal energy channels, as well as bottom–up and top–down forces operate simultaneously, we used SEM to explore the complex interactions among multiple trophic levels in soil food webs. Further, SEM allowed us to test established theory and to refine and derive hypotheses regarding the structuring forces of soil food webs. We studied detritus-based soil food webs in a 55-year-old subtropical *Illicium verum* forest ecosystem by sampling different important soil food web components, including main soil microbial groups, soil nematodes, and soil microarthropods. The SEM results confirmed established theory by showing the central role of the fungal energy channel, and bottom–up effects were more important for the structure of the food web than top–down forces in the studied subtropical forest soil. In addition, we could derive some novel and refined hypotheses regarding important feeding links in soil food webs. For instance, we provide hypotheses on feeding preferences of different groups of soil biota and on the strength of bottom–up versus top–down effects in forest soil food webs. Overall, we highlight that SEM provides a framework to understand complex interactions and energy pathways in soil food webs in a multivariate context, test established theory, and propose novel experimental tests.

© 2015 Elsevier GmbH. All rights reserved.

## 1. Introduction

The soil harbors a huge fraction of the biodiversity on the planet, and multitrophic interactions in soil are extraordinarily complex (Bardgett and Wardle, 2010; Bardgett and van der Putten, 2014; Powell et al., 2014). Meanwhile, interactions within detritus-based food webs play a significant role in determining how ecosystems function (Wardle 2002; Bardgett and van der Putten, 2014; Ferris and Tuomisto, 2015). Soil microorganisms are the

basal components of detritus-based food webs and are essential to release the nutrients bound in detritus at the final stage of decomposition (Wardle et al., 2004). The primary consumers of detritus in soils are bacteria and fungi, and the associated decomposition pathways are described accordingly as bacterial or fungal channels (Moore et al., 1988; Wardle and Yeates, 1993). Generally, bacteria absorb soluble organic compounds, and fungi derive their carbon and energy by degrading more recalcitrant organic sources (Chapin et al., 2011). In addition to those bottom–up forces, soil microorganisms are strongly influenced by microbial feeders, such as soil nematodes and microarthropods (Scheu et al., 2005; Fu et al., 2005).

Soil nematodes are ubiquitous and cover all major trophic levels in the soil, also interacting intimately with soil microorganisms

\* Corresponding author at: Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, 723 Xingke Road, Tianhe District, Guangzhou, 510650, China. Fax: +86 20 37252831.

(Bongers and Ferris, 1999). Different nematode groups feed on a wide range of different resources, e.g., soil bacteria, soil fungi, roots and root hairs, as well as on other nematodes, enchytraeids, and rotifers (Yeates et al., 1993; Coleman et al., 2004). Soil microarthropods (mainly Collembola and mites) also play a crucial role in soil carbon dynamics (Seastedt, 1984), and they are found in most soil types. Generally, Collembola and oribatid mites are considered to be mainly fungivores, but they can partially feed on dead organic matter and other resources (Seastedt 1984; Coleman et al., 2004; Chahartaghi et al., 2005). Most prostigmatid and mesostigmatid mites are predators, and they can feed on nematodes, small arthropods or their eggs (Coleman et al., 2004; Klarner et al., 2013).

Energy transfer between the trophic levels may travel via either the bacterial or fungal-based channel in detritus-based soil food webs with important implications for turnover rates and nutrient cycles (Wardle, 2002). Generally, bacteria have lower carbon assimilation efficiencies and faster turnover rates than fungi (Adu and Oades, 1978), while fungi have a higher C:N ratio and a longer generation time than bacteria (Moore et al., 1988; Six et al., 2006). The interactions among soil microorganisms, soil nematodes, and microarthropods play a vital role in determining many soil characteristics. However, most of the critical ecological interactions in the complex detritus-based soil food web remain unknown (Bardgett and Wardle, 2010). A better understanding of the driving forces and the main energy pathways of soil food webs is crucial to shed more light into the soil black box. This will help, for instance, to predict soil food web dynamics and nutrient cycles in soils affected by anthropogenic environmental alterations.

Structural equation modeling (SEM) is often used for investigating complex networks of relationships and can reveal support for causal relationships that bivariate analysis cannot clarify (Grace et al., 2014). In recent years, studies from regular treatment-based experiments showed that SEM is a powerful alternative to other multivariate approaches in food web ecology (Scherber et al., 2010; De Vries et al., 2012; Eisenhauer et al., 2013, 2015). The complex structure of soil food webs requires the investigating of links between nodes in a multivariate context. Further, as bacterial and fungal energy channels as well as bottom-up and top-down forces operate simultaneously (Wardle 2002; Bardgett and Wardle, 2010), we expected SEM to represent a powerful tool in exploring the complex interactions among multiple trophic levels in soil food webs. In the present study, we investigated the relationships between major soil food web components (soil microorganisms, nematodes, microarthropods) and resources (fallen litter and soil) in a subtropical *Illicium verum* forest ecosystem. To explore the most important components and complex interactions in detritus-based soil food webs SEM was used, which was informed by simple regression analyses to infer the dominance of bottom-up versus top-down forces.

Our objectives were to (1) test the relative importance of top-down vs. bottom-up paths for different soil biota in a multivariate context in a subtropical forest ecosystem, (2) identify main energy pathways in the studied soil food web, and (3) allow SEM to inspire the development of novel hypotheses regarding the structuring forces in soil food webs.

## 2. Materials and methods

### 2.1. Site description

*I. verum* Hooker fil. (common name: star anise), native to southern China and northern Vietnam, is an important spice and medicinal plant in China (Chempakam and Balaji, 2008). China has the largest star anise planting areas in the world, and Guangxi is the largest star anise planting and producing area in China. The study

site is located in an *I. verum* plantation in Shanglin county of Guangxi, southern China (23°25'N, 108°32'E). The mean annual temperature is 20.9°C and the mean annual precipitation is 1789.2 mm. The *I. verum* plantations were established in 1956, saplings were planted with a spacing of 5 × 5 m. Sixty mature *I. verum* individuals were randomly chosen at a southward hillside with a slope of 20–50° in late August 2011, covering an area of approximately one hectare. The projected canopy area for each of the 60 *I. verum* individuals was regarded as a plot. Four subplots of 10 × 10 cm (0.01 m<sup>2</sup>) were set up (east, south, west, and north) under each selected mature *I. verum* individual canopy. Soil samples (10 × 10 cm) were taken at 0–10 cm depth from each subplot. Then the four samples were combined to form one composite sample. As a result, 60 composite samples were taken. Litter was collected from the soil surface before soil samples were taken.

### 2.2. Soil and litter analyses

Soil moisture was measured gravimetrically by drying fresh soil at 105°C to constant weight (Liu, 1996). Soil and litter organic C was determined by the dichromate oxidation method and total soil and litter N was measured with an ultraviolet spectrophotometer after Kjeldahl digestion (Liu, 1996).

Phospholipid Fatty Acids (PLFA) analysis was conducted using the method described by Bossio and Scow (1998) and measured by gas chromatography. The biomass of bacteria was determined using the sum of fatty acids iso 15:0, anteiso 15:0, 15:0, iso 16:0, 16:1ω9c, iso 17:0, 17:0, anteiso 17:0, 17:0cy, 18:1ω5c and 19:0cy. The biomass of fungi was determined as the sum of 18:1ω9c and 18:2ω6c. Protozoa were identified by the PLFA biomarkers: 20:2ω6c, 20:3ω6c, 20:4ω6c (Kowalchuk et al., 2004). Notably, Protozoa were not included in the statistical analyses of this study due to the relatively low biomass of Protozoa as indicated by PLFA biomarkers and the disagreement regarding the use of those markers (Ruess and Chamberlain, 2010).

Nematodes were extracted from 50 g of fresh soil using Baermann funnels for each composite soil sample (Barker, 1985). After fixation in 4% formalin solution, nematodes were counted under an inverted microscope, and the first 100 individuals encountered were identified to genus or family (Bongers, 1988) and classified into trophic groups: herbivores, bacterivores (Ba), fungivores (Fu), predators, and omnivores (Yeates et al., 1993). Density was expressed as ind. g<sup>-1</sup> dry soil. As genera designated as the predatory trophic group were found infrequently in our experiment, we combined omnivorous and predatory nematodes for statistical analyses.

Microarthropods were extracted from each core with Tullgren dry funnels for 48 h (Brady, 1969). Fresh soil was placed in the Tullgren funnel, which had a 0.425-mm mesh and which was irradiated with fluorescent lamps (5 W, 15 cm above the soil) for 48 h. Microarthropods that fell through the mesh were collected and stored in vials containing 75% ethanol. All specimens were sorted and counted with a dissecting microscope and examined with a LEICA S8APO research microscope. Microarthropods were identified as collembolans (Janssens, 2007), oribatid mites, predatory mites (mainly prostigmatid and mesostigmatid mites) (Johnston, 1982), and other microarthropods. Density was expressed as ind. m<sup>-2</sup>.

### 2.3. Data analysis

In order to inform the directions of the paths in SEMs, we performed correlations for the hypothesized trophic links. Given that bottom-up, top-down forces, and a multitude of non-trophic interactions operate simultaneously (Wardle 2002; Bardgett and Wardle, 2010), we considered a net bottom-up effect when correlations between the consumer (predator) and the resource (prey) were positive. On the contrary, we used net top-down paths

Download English Version:

<https://daneshyari.com/en/article/2060988>

Download Persian Version:

<https://daneshyari.com/article/2060988>

[Daneshyari.com](https://daneshyari.com)