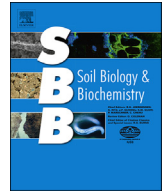




Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Understanding soil food web dynamics, how close do we get?

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ARTICLE INFO

Article history:

Received 31 January 2016

Received in revised form

20 June 2016

Accepted 21 June 2016

Available online 29 June 2016

Keywords:

Food web interactions

Stable isotopes

Networks

Gut content analysis

Soil community function

Biodiversity

ABSTRACT

Soil food webs are traditionally considered to have distinct energy channels through which resources flow belowground. Resources enter the soil food web either from roots or from detrital inputs. Compared to this traditional view we are now much more aware of the flow of carbon, nitrogen and other resources through the microbes in the soil food web. Currently, the function of some groups of bacteria and fungi is known. The lowering of the costs of high throughput sequencing methods enables us to acquire more data on who is around, when and where in the soil food web. For soil fauna, gut content analyses in combination with sequencing can reveal feeding preferences, which enables establishing real trophic links based on observations, which can then be visualised as networks of feeding interactions. The fate of carbon flow through the soil food web can be traced by using stable isotopes combined with sequence based techniques. This provides insight into trophic connections and interaction strength. As the sequencing costs decrease rapidly, the level of detail in soil food web knowledge will similarly increase rapidly and enhance the feasibility of combined techniques. Using these techniques to broaden our insight into soil subsystems and their soil food webs will lead to more targeted decisions on management practices.

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1. Essay text

In soil ecology, evaluations to estimate the effectiveness of land management practices, both in agriculture as in natural areas, have long been focussed on soil abiotic properties. Since the study of [Hunt et al. \(1987\)](#) awareness of soil food webs and their effect on nutrient dynamics has risen ([Berg and Bengtsson, 2007](#)). Available knowledge of micro- and mesofauna, was based on morphological identification and functional knowledge based on experiments. Modellers expanded the expert knowledge to a conceptual idea on how soil food webs function, which is still used to date ([Moore et al., 1988](#); [de Ruiter et al., 1993](#); [Holtkamp et al., 2008](#)). During the last decades, the knowledge on soil food web biodiversity and function is rapidly expanding due to the improved accessibility of next generation sequencing and stable isotope techniques. However, in most cases these techniques are used to address rather specific research questions revealing only bits and pieces of the soil

food web. Therefore, to date there has not been an update for the concept of the soil food web as it was proposed by [Hunt et al. \(1987\)](#) which makes use of the technological innovations.

Without a conceptual update it is not easy to get a full overview of soil microbes and fauna and all their connections. Yet, it is important to take biotic properties into consideration as microbes and soil fauna interfere through their feeding actions with nutrient availability to plants, and also alter plant community composition due to suppression or enhancement of specific plant species by pathogens and mutualists ([Maron et al., 2011](#); [Birkhofer et al., 2012](#)). Here, I propose the use of a combination of techniques to expand knowledge of soil biota in a food web context in order to enhance functional predictability of ecosystems. Better insight into the functionality of soil food webs might help to explain why dynamics of soil biota differ widely between soils.

During intensification as well as extensification of land use, shifts in plant community composition can influence the soil community via root exudates, other rhizodepositions, root morphology, and association with mycorrhizal fungi. During land use intensification, there is usually a tillage and fertilization regime. Tillage will set back the development of fungal hyphal networks including mycorrhizae and will damage other disturbance sensitive organisms such as nematodes ([Schalamuk and Cabello, 2010](#); [Ito](#)

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et al., 2015; Säle et al., 2015). Fertilization will diminish the needs of plants to form symbiotic interactions with mycorrhiza or rhizobia, increasing the chance that this symbiosis is turned into a parasitic lifestyle of the symbiont (Verbruggen et al., 2015). Also, as crops are usually planted in monocultures, this changes the dynamics of the soil food web completely as specific pathogens and mutualists start to accumulate in the root zone of these plants (see schematic representation in Fig. 1). As many crops are selected for their high biomass properties they are due to trade-off effects often poorly defended. This makes them prone to crop pests and diseases which are often treated by herbicides and pesticides which have a further detrimental effect on the soil food web community (Chelinho et al., 2012; Peijnenburg et al., 2012). On the other hand, after the abandonment of agricultural practices, early successional plants will establish in these fields which strongly influence the soil food web via root exudates and later litter build-up. Usually, in early successional systems net soil pathogen effects will build-up over time (Kardol et al., 2006), creating the opportunity for mid-successional plant species to colonize the system. These plant species influence and change the soil community in their root zone such that also later successional plants can enter the system. As late successional plant species enhance their own establishment by mutualist enhancement, they slowly outcompete the mid-successional species over time (Kardol et al., 2006).

Root exudates influence the composition of the bacterial and fungal community (Haichar et al., 2014; Kaiser et al., 2015). Changing microbial community composition will in turn influence bacterivores and fungivores, as well as their predators' community assemblage, and also plant community composition by feedbacks from mutualists (Weidner et al., 2015), pathogens (Kardol et al.,

2006), or nutrient immobilization (de Kroon et al., 2012). When the plant community changes due to soil community changes this is called the direct pathway. However, there is also an indirect pathway. Dead plant litter will form detritus. Fragmenters enlarge the surface of detritus, which allows bacteria and fungi to feed on the easily available substrates. In the end of the process, organic matter is formed. The consistency of the organic matter will determine, to a large extent, how the soil food web is formed, which in turn will influence the plant community. This is called the indirect pathway (Wardle et al., 2004). Moreover, the direct and indirect pathways might be linked due to priming events from fresh exudates (Shahzad et al., 2015). How these decomposition processes actually work is not always clear. Labelling the different sources of carbon enables studying the pathways separately (Kušlienė et al., 2014; Shahzad et al., 2015). For land use intensification the main factor of change is usually known (tillage, crop-species planted, or fertilizer regime), although it is not always straightforward. The factor of change is less obvious for land use extensification; this type of change allows for in-depth studies into whether plant or soil communities are the major drivers of ecosystem dynamics (Harris, 2009; Koller et al., 2013).

The use of networks in ecology enables visualization of multi-species interactions (Dunne, 2006). In case of aboveground networks, such as pollinator networks (Bascompte, 2010), these interactions are usually recorded in field or experimental set-ups and represent actual interactions. However, when displaying a network of soil microbes in the rhizosphere, the interactions between the species are often correlations based on co-occurrence or abundance data (Barberán et al., 2012). Although these correlations might reflect real interactions, these interactions are still very hard

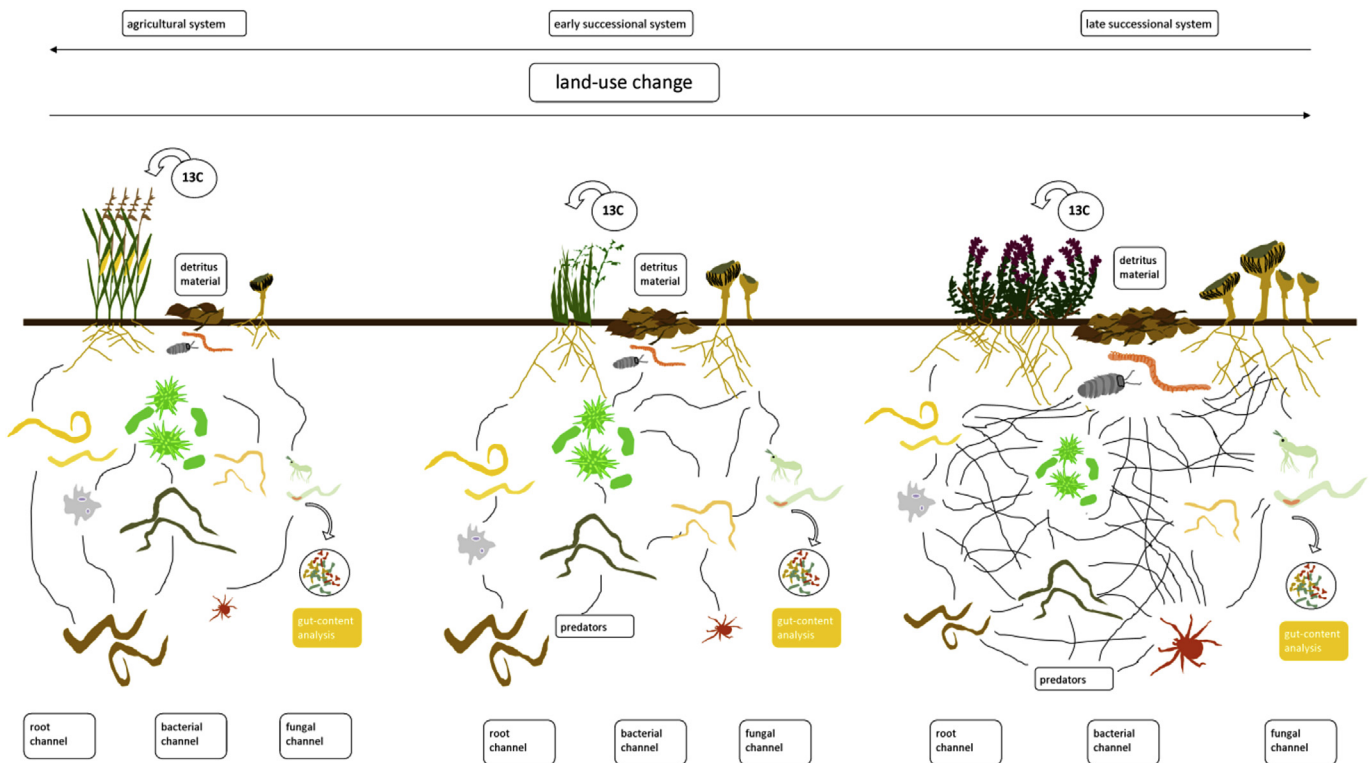


Fig. 1. Schematic representation of soil food web change during secondary succession Soil food web development during land use change from an agricultural system to a late-successional species-rich grassland. During this transition the soil food web gets more connected and C-flow shifts from a more bacterial dominated energy channel (bacteria, protists, bacterivorous nematodes and earthworms) to a more fungal dominated energy channel (fungi, fungivorous nematodes, collembola and fungivorous mites). Also shown is a direct feeding channel on the roots via root-feeding nematodes and omni-carnivorous nematodes into the higher trophic levels. Detritus is accumulating due to more recalcitrant matter in the system, stimulating the fragmenter community (earthworms, millipedes and woodlice) and the fungal community (from sugar-fungi towards wood degrading fungi) that are highly connected to the rest of the food web. $^{13}\text{C}_2$ -labelling techniques in combination with gut content analyses can reveal a change in species assemblage of the fungal community in the fungivores. The figure was mainly based on the data discussed in the main text in the context of the EcoFINDERS project.

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