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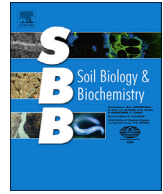
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Understanding soil food web dynamics, how close do we get?

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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

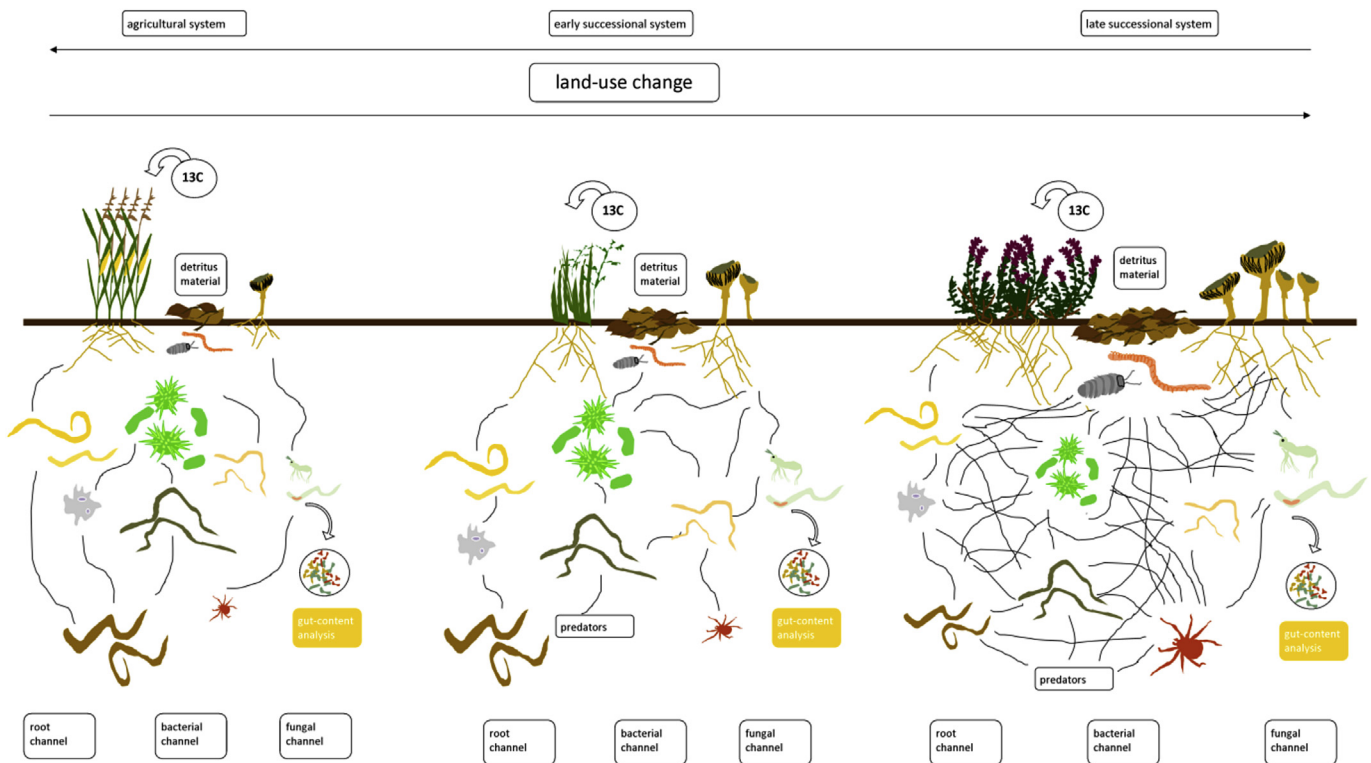


Fig. 1. Schematic representation of soil food web change during secondary succession Soil food web development during land use change from an agricultural system to a late-successional species-rich grassland. During this transition the soil food web gets more connected and C-flow shifts from a more bacterial 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.

to prove. This is because co-occurrence of microbes in the soil does not guarantee these organisms are able to interact with each other. The 3D structure of the soil might mean that although microbes are near to each other, they might not be able to interact due to spaces between soil aggregates that form an interaction barrier (Wolf et al., 2013, 2015). On the other hand, if these species do interact then it is very hard to determine the nature of this interaction. It might be a direct feeding relation, but can also be competition for a similar resource or facilitation when, for example, each other's waste products are used. Due to the large diversity of functionality in microbes, it might be very well possible that the many steps in the breakdown of complex organic molecules will be performed by a conglomerate of multiple microbes involved in different parts of the breakdown pathway. Therefore, combining sequencing data with functional measurements such as isotope tracing may result in a more informative representation of a soil network or food web because flows of nutrients become visible (see schematic representation in Fig. 1).

Labelling of plants with ^{13}C in the form of $^{13}\text{CO}_2$ can be done in air-tight chambers where net CO_2 can be monitored. To access the efficiency of label uptake, freeze-dried plant shoot, root and soil material can be ground and measured (Neufeld et al., 2007; Drigo et al., 2010; Crotty et al., 2011). The fate of the carbon through the soil food web can be studied by sampling the components of the food web at the relevant time points. As the label is exuded by the root as exudates during the first dark reaction after pulse labelling, microbes will receive the label first. Microbes can be studied to some detail by extracting Phospholipid Fatty Acid/Neutral Lipid Fatty Acid (PLFA/NLFA) fractions and by comparing the amount of labelled versus non-labelled microbes (Frostegård and Bååth, 1996; Boschker and Middelburg, 2002; Bååth, 2003; Drigo et al., 2010). This will provide information on how much label is incorporated into the microbial biomass. However, labelled versus non-labelled PLFA fractions do not separate the active biomass from the inactive part. Therefore you need DNA/RNA-Stable Isotope Probing (DNA/RNA-SIP) analysis whereby ^{13}C labelled DNA or RNA is separated from the non-labelled DNA by isopycnic centrifugation (Hannula et al., 2012). Both fractions can be sequenced separately which provides information about the community that actively takes up the label. These microbes are direct consumers of rhizo-depositions as they directly took up the label from the plants. Higher trophic levels are extracted with methods such as Oostenbrink elutriation for nematodes (Oostenbrink, 1960) and Tullgren extraction for macro-invertebrates. After collection, the individuals are sorted into feeding groups and measured (Bradford et al., 2007). Usually, these groups receive the label later and incorporate the label in their biomass one week after the pulse labelling event. They incorporate the label because they feed on plants or on the microbes. With this method ^{13}C can be traced through the soil food web, providing knowledge on the flow of carbon through the soil food web as is represented in Fig. 1.

Fungivores, bacterivores and their predators all have a gut in order to actively ingest food. Recently, several techniques have been developed to collect the gut contents of higher trophic levels in the food web to determine what these individuals have been eating (Read et al., 2006; Eitzinger and Traugott, 2011; Cabos et al., 2013; A'Bear et al., 2014; Eitzinger et al., 2014; Günther et al., 2014). These methods help to distinguish the trophic links from other direct or indirect links in the network of soil interactions and can, especially in combination with isotopic labelling, be very helpful in unravelling soil food web connections (Fig. 1). Additionally, modelling can help to provide a wider overview where evidence is still missing. For instance, total carbon and nitrogen budgets can be measured for some parts and estimated for the missing part. However, we usually lack information on assimilation efficiencies

as these are extremely hard to measure. Unfortunately, these assimilation efficiencies often turn out to be highly sensitive variables in the models. More information on how quickly ingested carbon can be transformed to biomass in the different groups of soil biota, for example, would be very valuable to improve the predictability of models. More collaboration between modellers and experimentalists can help solve these uncertainties in food web models.

In a European consortium of soil ecologists, a collection of areas under different intensities of human impact were studied using most of the above described methods resulting in a detailed overview of the soil community change during secondary succession. Archaea, bacteria, fungi and arbuscular mycorrhizal fungi (AMF) were sequenced whereas protists, nematodes, enchytraeids, mites, collembola, spiders and earthworms were morphologically identified (Plassart et al., 2012; Thomson et al., 2015; Creamer et al., 2016; Dirilgen et al., 2016; Griffiths et al., 2016; Lemanceau et al., 2016). In one of these human impact sites, an ex-arable land chronosequence in the Netherlands, soil cores were collected. These cores were labelled to follow the fate of the soil carbon through the system. A network was built with the use of sequencing data, but trophic links could not be separated from other links as no gut content analysis was performed. However, detailed information was obtained on the rate of carbon travelling through the food web using stable isotope analyses. The correlation strength in the network (based on sequencing) could then be related to the carbon flow from one trophic level to the other (based on stable isotopes). It showed the importance of fungi in this secondary succession system, which may provide valuable insight for further research on the role of fungi in such systems and how the community change of early successional fungi to late successional fungi could be stimulated by management practices.

Insight into soils and their food webs, additional to measures of soil physical and chemical properties, will give valuable insight into why soil communities function so differently. Moreover, it will help in predicting outcomes of management practices in agricultural and natural systems (Bissett et al., 2011). In the example of the ex-arable land chronosequence, a combination of next generation sequencing and stable isotope tracing was used. These techniques were used to map the species composition in the system and to sample its functional characteristics. Together, these techniques provided valuable insight into the functional and community changes in the soil community during secondary succession (Gilbert et al., 2014). Soil ecologists need to work together to get an accurate view on how the whole soil system works (Fig. 1), and not only focus on the soil group a particular researcher has expertise with. Modellers can help to provide soil ecologists with a wider overview of soil food web functioning where proof is still missing, e.g. help to identify the drivers of change in the soil food web during land use change (Fig. 1). Now is the time to combine new insights from sequencing, stable isotope studies and gut content analyses to develop a new and more dynamic conceptual soil food web system (as proposed in Fig. 1). An extension of similar studies in different ecosystem types could result in an updated and more dynamic view of soil food web dynamics. Additionally, these techniques might also lead to more productive and pest-resistant crops in agricultural systems or can than serve as a useful tool to make more targeted decisions on management practices in the future.

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