

MINI-REVIEW: ECOLOGICAL SOLUTIONS TO GLOBAL FOOD SECURITY

Below-ground connections underlying above-ground food production: a framework for optimising ecological connections in the rhizosphere

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Summary

1. Healthy soils that contain an active microbiome and food web are critical to sustainably produce food for a growing global human population. Many studies have focussed on the role of microbial species diversity and the presence of key functional groups as important controls on the many functions that a sustainable food system relies on.

2. Here, we synthesise recent ecological empirical evidence and theory to propose that the interactions between organisms in the soil food web are the critical determinant of soil function.

3. We propose the Rhizosphere Interactions for Sustainable Agriculture Model, in which crop roots recruit small, modular, highly connected soil rhizosphere networks from large, static, relatively unconnected and diverse bulk soil networks. We argue that conventional agricultural management disrupts the connections between rhizosphere and bulk soil networks.

4. *Synthesis.* We identify future research directions for optimising ecological connections between roots and rhizosphere microbial and faunal networks, and between rhizosphere networks and bulk soil networks in agricultural production systems. Knowledge on these connections can be applied in agricultural systems to sustainably produce food for a growing global population.

Key-words: bacteria, bulk soil, carbon, fungi, microbial community, network, nitrogen, roots, soil fauna, stability

Introduction

Healthy soils are critical to support food production as the human population grows towards 9.7 billion and our planet warms (Paustian *et al.* 2016). But, what are the most important characteristics of healthy soils that support sustainable agriculture? Most definitions of soil health include not only just physiochemical attributes like high organic matter content but also a rich biological component of microbes and soil fauna (Doran & Zeiss 2000). Soils with active microbes and fauna in close interactions with plants support efficient nutrient cycling, pathogen resistance and overall crop health (Bender, Wagg & van der Heijden 2016). However, we lack a rigorous framework for directing future research efforts towards quantifying and optimising interactions between plants and soil organisms to support healthy, productive crops

while reducing our reliance on agrochemicals. Here, we draw on recent ecological evidence and theory to develop a conceptual framework that can support future research efforts to advance our understanding of these interactions. Ultimately, an increased understanding of interactions between plants and soil communities can accelerate new technological and management innovations that harness below-ground interactions to enhance above-ground productivity.

When plants first started extending their roots into primordial soils, they encountered a rich microbiome. Ever since, plants have co-evolved with soil microbes and fauna, and traits that supported beneficial interactions with soil organisms likely incurred a fitness advantage (Lambers *et al.* 2009). For example, plants that enable mycorrhizal colonisation are able to enhance their nutrient acquisition. Plant root exudates also support microbes that release enzymes to depolymerise organic matter and transform it into plant-available forms through mineralisation. This long history of co-evolution

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provides a roadmap for measuring and managing beneficial plant–microbe interactions that are key components of healthy soils. Here, we suggest that rather than overall microbial abundance or species diversity, the structure of the network of interactions between plants and soil organisms and among soil organisms best predicts the functionality of soil communities and provides a framework for assessing and managing soil health.

Plants affect the structure and function of the soil microbiome and food webs directly through beneficial associations with mycorrhizal fungi and *Rhizobia*, and through antagonistic associations with, for example, plant–parasitic nematodes. Indirect controls on soil communities are equally important and act primarily through the quantity and quality of plant above-ground and below-ground litter inputs (Orwin *et al.* 2010; De Vries *et al.* 2012b; Baxendale *et al.* 2014). In the rhizosphere, plant N uptake is a dominant control on bacterial and fungal community composition (Bell *et al.* 2015; Moreau *et al.* 2015; Giagnoni *et al.* 2016; Thion *et al.* 2016). In addition, rhizodeposits and root litter have been shown to strongly influence the composition of soil microbial and faunal communities and soil food webs (Scheunemann *et al.* 2015; Sauvadet *et al.* 2016), and feed back to the performance of neighbouring plant species by altering soil N availability (Meier, Keyserling & Bowman 2009). Root exudates have been hypothesised as an important mechanism driving microbial community and soil food web composition and activity (Bardgett, Mommer & De Vries 2014; De Vries & Caruso 2016), though this has only been experimentally demonstrated for *Arabidopsis* (Shi *et al.* 2011; Badri *et al.* 2013). Finally, antimicrobial compounds isolated from crop plant root exudates can affect the growth and activity of pathogenic soil bacteria (Liu *et al.* 2015; Fang *et al.* 2016). These mechanisms form a tight link between plants, microbes and the soil food web in the rhizosphere.

As a result of these interactions, the rhizosphere and bulk soil host contrasting microbial and faunal communities. The rhizosphere is typically enriched in bacterial taxa that can be classified as copiotrophic, such as Alphaproteobacteria, Betaproteobacteria and Bacteroidetes (Shi *et al.* 2015; Uksa *et al.* 2015), as well as in specialist decomposers and plant growth-promoting bacteria, compared to the bulk soil (Hargreaves, Williams & Hofmockel 2015; Chen *et al.* 2016). Soil animal communities generally have higher biomass and abundance in the rhizosphere, and similar to bacterial communities, the rhizosphere is enriched in species that are able to rapidly use root-derived C (Fujii, Saitoh & Takeda 2014; Scharroba *et al.* 2016). Turner *et al.* (2013) found that the rhizosphere communities of the major crop plants wheat, pea and oat were clearly differentiated despite some overlap. In particular, grain rhizospheres were enriched in cellulolytic bacteria, while peas recruited more plant growth-promoting bacteria. The wheat rhizosphere was strongly enriched in the bacterial-feeding nematode *Acrobeloides*, while the pea rhizosphere was highly enriched in fungi. Recent evidence also shows that bacterial alpha-diversity tends to be lower in the rhizosphere (Hargreaves, Williams & Hofmockel 2015; Chen *et al.* 2016). And while alpha-diversity is often proposed as

an indicator of robust, healthy soil communities, there is little experimental evidence to support this notion.

Rather than species numbers, interactions between organisms appear to be crucial for the functioning of soil communities. Networks of interactions can predict whole ecosystem functioning (Kuiper *et al.* 2015) and drive multiple processes and ecosystem services that underlie this functioning (Hines *et al.* 2015). Soil food webs with a more prominent fungal energy channel (Box 1) are more resistant to, and continue to function better under drought (De Vries *et al.* 2012a). In addition, the ratio between the bacterial and fungal energy channel has been correlated to the rates of soil C and N cycling processes (De Vries *et al.* 2013). The success of pathogen invasion in the rhizosphere has been shown to depend on the network structure of resident bacterial communities (Wei *et al.* 2015). Specifically, pathogen success was lower when resident networks had low nestedness (or modularity, see Box 1) and high connectance, presumably through more efficient consumption of resources. Other recent studies found that associations between methane oxidising bacteria and other microbes were central in modulating methane-oxidation (Ho *et al.* 2016), and that fungal co-occurrence network structure was strongly associated with different stages of litter decomposition (Purahong *et al.* 2016). Thus, new ecological knowledge of the structure of interactive networks among organisms and their environment might be used as an indicator of their functional attributes.

Rhizosphere networks are recruited from bulk soil networks

In the rhizosphere, bacterial networks typically have more nodes, more hubs and stronger connections (see Box 1 for definitions) than those in bulk soil (Mendes *et al.* 2014; Shi *et al.* 2016). In a recent study, Shi *et al.* (2016) found that while bulk soil bacterial communities contained more OTUs, rhizosphere networks of bacterial taxa were larger and more connected. Moreover, rhizosphere networks grew larger and gained more connections and hubs during plant growth, while networks in the bulk soil remained relatively static. Similarly, rhizosphere decomposer soil food webs tend to be dominated by the bacterial energy channel (Thakur & Eisenhauer 2015; Muller *et al.* 2016), which typically has lower diversity than the fungal energy channel (De Vries *et al.* 2012a, 2013). These patterns likely occur because the high-resource rhizosphere ‘recruits’ a subset of species from the bulk soil community. The selected species then share niche space in the rhizosphere and as a result show strong positive associations in networks (Mendes *et al.* 2014; Edwards *et al.* 2015). Importantly, the presence of plant roots has been shown to be as important as land use and soil type for shaping bacterial community composition (Edwards *et al.* 2015; Hargreaves, Williams & Hofmockel 2015).

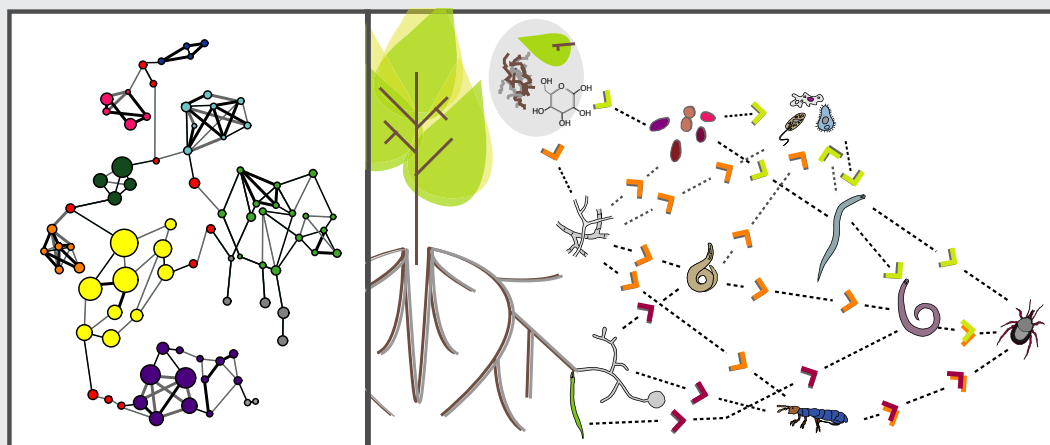
As a result of these different network structures, rhizosphere networks are likely to be less stable under changing environmental conditions than bulk soil networks. Rhizosphere microbial networks are characterised by

Box 1. Networks and food webs – interaction types, configuration and stability

Ecological networks are webs of connections between organisms. Connections in a network can consist of a range of different interaction types, from predator–prey interactions to mutualisms, competition and coexistence. Most studies of microbial networks focus on bacteria and only include significant, positive interactions that might consist of mutualisms, cooperation or niche sharing. In contrast, classical soil food webs only consist of feeding interactions, which can be positive (bottom-up) or negative (top-down) [but see Buchkowski (2016) and Hawlena & Zaguri (2016) for arguments for including non-feeding interactions in soil food webs]. However, networks can include any functional group and type of interaction, and hybrids between microbial networks and traditional soil food webs, including both positive and negative interactions, might be more informative than separate networks.

Seminal work by May (1973) focussed on the number of organisms or species present in a network and the number of connections between these. Counterintuitively, May found that more diverse networks were less stable under perturbations than simpler networks. However, these early networks were randomly created, and since then, multiple studies have shown that the configuration and interaction types within networks determine their stability. For example, networks that consist of many weak links are more stable than those consisting of few strong links (Neutel, Heesterbeek & de Ruiter 2002). Compartmentalisation, as well as the presence of weak connectors between compartments, has also been shown to increase the stability of networks (Moore *et al.* 2003; Rooney *et al.* 2006; Stouffer & Bascompte 2011). Finally, trophic coherence and the presence of negative interactions, such as top-down controls, can increase network stability (Johnson *et al.* 2014; Coyte, Schluter & Foster 2015).

We currently lack enough examples to determine whether there are general configurations in microbial networks, how these networks are affected by changes in agricultural management, and what the implications are for their stability and functioning. In contrast, the effects of agricultural management on soil food webs and their functioning are relatively clear. Traditionally, food webs have been divided into clear energy channels, or compartments: the root energy channel, which is fuelled by live roots through the activities of root-feeding nematodes and mycorrhizal fungi, and two detritus-fuelled compartments: the fungal and the bacterial energy channel. While these compartmentalisations are currently hotly debated and under revision (Ballhausen & de Boer 2016; Geisen 2016; see figure), agricultural intensification reduces the biomass of the root and fungal energy channels, and thereby increases the relative importance of the bacterial energy channel. Experimental and modelling studies have shown that the fungal energy channel, which consists of slow growing organisms and weak interactions, is more stable under disturbance than the bacterial energy channel and continues to function better (Rooney *et al.* 2006; De Vries *et al.* 2012a). It is assumed that the root energy channel and the fungal energy channel are controlled by bottom-up interactions, while the bacterial energy channel is top-down controlled (Moore *et al.* 2003). Organisms that feed on multiple functional groups, such as predatory nematodes and mites, can connect these compartments, and thereby increase food web stability by dampening fluctuations in their prey (Rooney *et al.* 2006).



An example of a network (left) and a soil food web (right). A network consists of nodes (circles) that are connected by edges (lines) through weak and strong, positive and negative interactions; here, strong connections have a heavier line weight than weak connections, positive interactions are grey and negative interactions are black. Modules are indicated by different colours, and connectors between modules are in red. Soil food webs are traditionally represented by three compartments, as indicated by arrow colours. The fungal and bacterial energy channels (yellow and orange arrows respectively) are fuelled by above-ground litter, root litter and root exudates (grey ellipse); the root energy channel (purple arrows) is fuelled by live roots. However, recent evidence suggests that bacteria can feed on fungal hyphae, and protozoa are part of both the fungal and the bacterial energy channel (as indicated by grey dashed arrows), thus increasing the number of connections within the soil food web and challenging the concept of distinct energy channels. [Colour Box can be viewed online at wileyonlinelibrary.com]

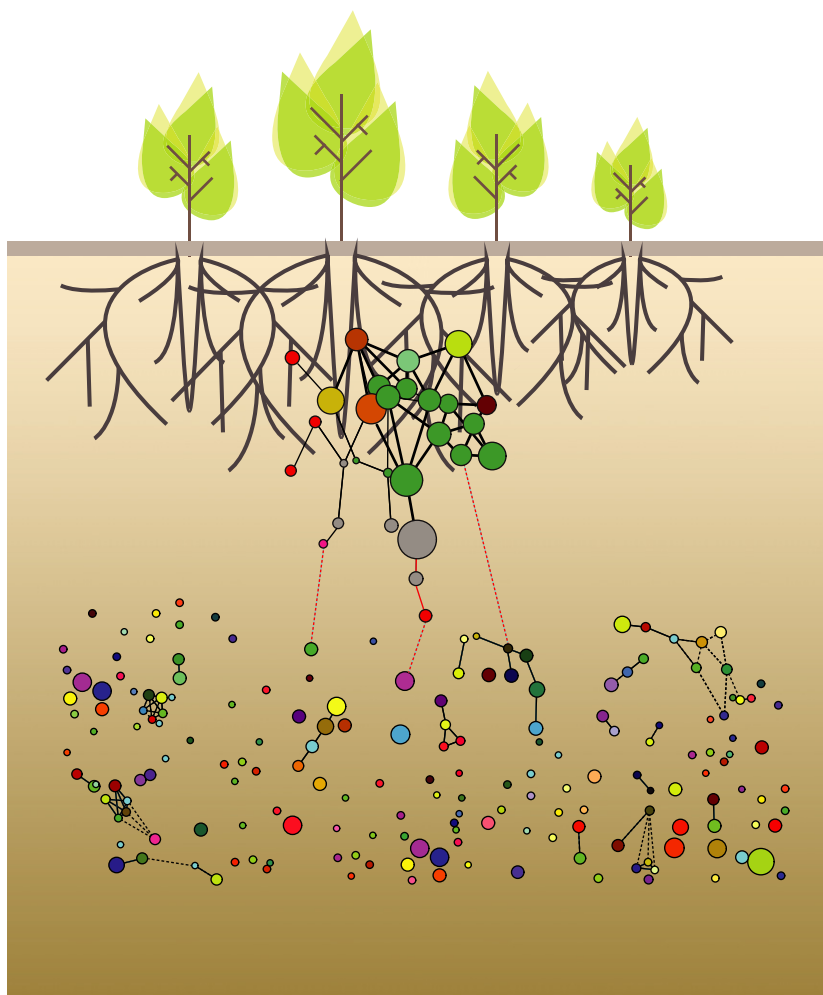


Fig. 1. The Rhizosphere Interactions for Sustainable Agriculture Model. Rhizosphere networks consist of relatively few but highly abundant and connected species (indicated by circles; different colours indicate different taxa) that are recruited from the much more diverse but weakly connected bulk soil network. Connections between rhizosphere and bulk soil networks (indicated by red dotted lines) are crucial for the recruitment of functional rhizosphere networks. Understanding and manipulating network structure of both rhizosphere and bulk soil networks in agricultural soils, and the connections between them, is a promising avenue for optimising healthy soils and the benefits they provide for sustainable food production. [Colour figure can be viewed at wileyonlinelibrary.com]

overwhelmingly strong, positive interactions, which have been shown to compromise network stability (Box 1). In addition, bacterial-dominated rhizosphere soil food webs consist of strong interactions, and a reduction of the fungal energy channel effectively reduces network compartmentalisation, thereby reducing network stability (Box 1). These properties allow rhizosphere networks to respond quickly to changes in resource availability, for example as a result of plant growth stages or agricultural management.

In contrast to the rhizosphere, the bulk soil harbours a large, diverse network of organisms with low abundances that consists of weak interactions. The majority of these organisms are dormant or inactive and are thus highly resistant to environmental stresses (Lennon & Jones 2011) and can persist in soil for long periods of time (Troxler *et al.* 2012). This network of bulk soil organisms is mostly unaffected by the dynamic processes that affect rhizosphere networks and remains relatively static during the growing season (Shi *et al.* 2016), but would be highly stable under changing environmental conditions because of its properties. We propose that this bulk soil network provides the ‘seed bank’ from which rhizosphere networks are recruited, and we argue that crops will be able to recruit a functioning rhizosphere network as long as this seed bank is intact (Fig. 1). The composition and

structure of the recruited rhizosphere network depends on the traits, and in particular root traits, of the crop grown, as well as on the abundance and composition of the bulk soil community. However, we argue that conventional agricultural management reduces the ability of the rhizosphere to recruit from the bulk soil.

Agricultural management affects network structure of, and connections between, rhizosphere and bulk soil networks

Agricultural management directly affects both microbial network and soil food web structure in the rhizosphere. It is well known that agricultural practices such as fertilisation and tillage reduce the diversity of soil organisms (Tsiafouli *et al.* 2015) and shift soil food webs towards being bacterial-dominated rather than fungal-dominated (Beare *et al.* 1997; De Vries *et al.* 2006). Recent evidence also indicates that microbial networks are affected by agricultural management. For example, in a field sampling across China, chemical fertiliser application reduced the size, modularity and number of connections of bacterial networks compared to organic amendments (Ling *et al.* 2016). Similarly, in a field experiment, organic manure amendment increased the modularity of

arbuscular mycorrhizal fungal networks (Zhu *et al.* 2016). But agricultural management also disproportionately reduces the biomass of groups of organisms that form a connection between rhizosphere and bulk soil, and thus facilitate rhizosphere recruitment. For example, fungal hyphae can form a connection between rhizosphere and bulk soil microbial communities and food webs by transporting C and facilitating bacterial movement (Fransson & Rosling 2014; Gahan & Schmalenberger 2015; Pausch *et al.* 2016). Similarly, soil fauna can form a connection between rhizosphere and bulk soil networks. Earthworms incorporate and distribute organic residues into different soil layers and facilitate microbial dispersal (Tao *et al.* 2009). Both fungal and bacterial grazers can carry bacterial cells and fungal spores in their gut and on their surface (Ingham 1999; Renker *et al.* 2005), and facilitate their movement by migrating between soil layers (Lindberg & Bengtsson 2005). In addition, conventional agricultural management can also reduce the movement of soil organisms between rhizosphere and bulk soil by compacting and homogenising the soil (Tao *et al.* 2009; Warmink *et al.* 2011; Ebrahimi & Or 2014). Moreover, the composition and persistence of the bulk soil 'seed bank' can be affected by agricultural amendments seeping to deeper soil layers, such as fertiliser, pesticides, manure and the antibiotics within manure.

The Rhizosphere Interactions for Sustainable Agriculture Model

Drawing on recent advances in understanding of the structure and functioning of ecological networks, we introduce a new conceptual framework to guide future research efforts as well as technological and management innovations that optimise the abilities of soils to support sustainable crop production. Specifically, this framework aims to optimise connections between roots and rhizosphere microbial and faunal networks, and connections between rhizosphere networks and bulk soil networks. Based on the emerging evidence reviewed above, we propose that agricultural bulk soils should contain diverse organismal communities characterised by weak interactions, whereas rhizosphere communities should be less diverse and characterised by a high degree of nodes and strongly positive connections, both within organismal networks and between these network and rhizosphere properties. Most importantly, connections between the rhizosphere and bulk soils should be supported.

Most evidence that organismal network structure underlies soil functioning originates from studies on soil food webs, in which feeding interactions between organisms have empirically been quantified through decades of research (Bradford 2016). While the nature of soil food web interactions are currently under debate (Ballhausen & de Boer 2016; Geisen 2016), existing food web models have successfully predicted C and N fluxes in natural and agricultural systems (De Ruiter *et al.* 1993; Holtkamp *et al.* 2011). In soil microbial networks, correlations between microbial taxa can result from a variety of interaction types (Box 1). To model process rates

from data on interactions within microbial networks, and to predict functioning based on microbial network structure, we need to first elucidate the exact nature of dynamic microbe–microbe interactions (Gottstein *et al.* 2016). Therefore, an important challenge is to identify interaction types between microbial groups or species and how these determine network structure. Here, we can learn from gut microbiologists, who have successfully linked gene transcripts to species–species interactions (Plichta *et al.* 2016). Several covarying transcripts were down-regulated in interacting species pairs, indicating that the functional overlap between species was reduced and that species activities were context specific. A creative alternative to experimentally elucidating the nature of the millions possible specific microbe–microbe interactions might be text-mining of existing literature (Lim *et al.* 2016).

Once we know the functionalities of key nodes and network modules, we can identify nodes and hubs associated with desirable functions such as nutrient mineralisation or plant protection from disease. Taxa that often appear as nodes in structured rhizosphere networks may be promising targets for inoculants, as the addition of just a few species may lead to a structured network. There is a long history of inoculating beneficial microbes either directly into soils or as seed coatings (Calvo, Nelson & Kloepper 2014). Mycorrhizae are often inoculated on tree seedlings and crops to improve establishment and nutrient uptake (du Jardin 2015). *Rhizobium* are inoculated on legumes to ensure nodule formation (Catroux, Hartmann & Revellin 2001; du Jardin 2015). However, along with many other types of plant growth-promoting bacteria, inoculants have had only limited success to date in field agriculture (Calvo, Nelson & Kloepper 2014). There is little evidence that most inoculants are able to persist and compete with other microbes in most soils (Verbruggen *et al.* 2013; Berruti, Lumini & Bianciotto 2016), although one study found that the plant growth-promoting bacterium *Pseudomonas fluorescens* persisted in the bulk soil for months after inoculation (Troxler *et al.* 2012).

In addition to inoculation, mechanistic knowledge on links between plant traits and soil organismal networks could enable another promising approach for promoting soil organismal networks that deliver desirable functions (Kumar *et al.* 2016). While there is accumulating evidence that plant traits, and in particular root traits, can predict soil faunal and microbial community structure and functioning (De Vries *et al.* 2012b; Grigulis *et al.* 2013; De Vries & Bardgett 2016; Legay *et al.* 2016), there is only limited evidence that links plant traits to soil microbial networks. For example, it has been shown that specific compounds in root exudates can promote the formation of bacterial clusters (Thomas & Cebren 2016). In addition, in a mesocosm study with eucalyptus seedlings, networks of ammonia-oxidising archaea were more connected and had more modules in soil under elevated CO₂ than those under control conditions, presumably through changes in below-ground plant C inputs (Hu *et al.* 2016). As future research further elucidates possible linkages between plant traits and microbial functions, plant breeding and engineering could be directed to enhance these interactions.

Many research challenges need to be addressed before we can use the analysis of soil networks to design management interventions that optimise connections between plant roots and soil networks and between rhizosphere and bulk soil. However, the effectiveness of many new agricultural management approaches for improving soil health and agricultural sustainability (Tilman *et al.* 2002) can be explained by our conceptual model. For example, it is well known that no-till or reduced tillage supports active decomposer communities (Arshad *et al.* 1990; Ogle, Swan & Paustian 2012), and they also promote linkages between rhizosphere and bulk soil networks by reducing soil disturbance. Cover crops displace fallow periods with plants that fix N, increase C inputs (Olson, Ebelhar & Lang 2010) and also likely enhance soil network structure. Along with other forms of organic inputs such as manure and compost, cover crops may support diverse bulk soils with weak interactions (Ling *et al.* 2016). Finally, crop rotations that prevent the build-up of diseases have been shown to differ in their fungal network structure from diseased soils under continuous monoculture, with rhizosphere networks in healthy soils showing higher modularity and meta-modularity, and more highly connected generalists (Lu *et al.* 2013). However, it is important to acknowledge that soil organismal networks and their connections with plants are likely to depend on edaphic soil characteristics, such as soil texture and cation exchange capacity (Ma *et al.* 2016a,b). The design of novel management approaches to promote networks will have to take into account context-specificity and be tailored for different crops, soil types and climatic conditions.

Over the years, various indices have been proposed as indicators of healthy soils including soil organic matter content (Reeves 1997), microbial diversity (Lehman *et al.* 2015), fungal:bacterial ratios (De Vries *et al.* 2006), enzyme activities (Bandick & Dick 1999), metabolic quotients (Anderson 2003) or soil respiration burst tests (Morrow *et al.* 2016). These indices do not recognise the importance of interactions among these components, but we expect many of these metrics to be correlated to the structure of soil organismal networks, as has been shown already for certain soil food web characteristics (De Vries *et al.* 2013). While much research is needed to establish links between soil properties, plant traits, network structure and soil functioning, novel understanding of ecological interactions within and between soil communities and plants has tremendous potential to be applied in agricultural systems to sustainability produce food for a growing global population.

Authors' contributions

F.T.d.V. conceived the original idea for this article, after which both authors contributed equally to the manuscript.

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Data accessibility

This article does not use data.

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