



Belowground connections underlying aboveground food production: a framework for optimising ecological connections in the rhizosphere

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**Belowground connections underlying aboveground food
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1 **Belowground connections underlying aboveground food production: a**
2 **framework for optimising ecological connections in the rhizosphere**

3

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13

14 Running headline: **Belowground connections for aboveground food production**

15

16

17 **Summary**

18 1 Healthy soils that contain an active microbiome and food web are critical to
19 sustainably produce food for a growing global human population. Many studies have
20 focussed on the role of microbial species diversity and the presence of key functional
21 groups as important controls on the many functions that a sustainable food system
22 relies on.

23 3 Here, we synthesize recent **ecological** empirical evidence and theory to propose that
24 the interactions between organisms in the soil food web are the critical determinant of
25 soil function.

26 4 We propose the Rhizosphere Interactions for Sustainable Agriculture (RISA) Model, in
27 which crop roots recruit small, modular, highly connected soil rhizosphere networks
28 from large, static, relatively unconnected and diverse bulk soil networks. **We argue that**
29 **conventional agricultural management disrupts the connections between rhizosphere**
30 **and bulk soil networks.**

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

36

37 Keywords: carbon, nitrogen, bacteria, fungi, microbial community, soil fauna, stability,
38 network, bulk soil, roots

39

40 *Introduction*

41 Healthy soils are critical to support food production as the human population grows
42 towards 9.7 billion and our planet warms (Paustian *et al.* 2016). But, what are the most
43 important characteristics of healthy soils that support sustainable agriculture? Most
44 definitions of soil health include not just physiochemical attributes like high organic
45 matter content, but also a rich biological component of microbes and soil fauna (Doran
46 & Zeiss 2000). Soils with active microbes and fauna in close interactions with plants
47 support efficient nutrient cycling, pathogen resistance and overall crop health (Bender,
48 Wagg & van der Heijden 2016). However, we lack a rigorous framework for directing
49 future research efforts towards **quantifying and optimising** interactions between plants
50 and soil organisms to support healthy, productive crops while reducing our reliance on
51 agrochemicals. **Here, we draw on recent ecological evidence and theory to develop a**
52 **conceptual framework that can support future research efforts to advance our**
53 **understanding** of these interactions. **Ultimately, an increased understanding of**
54 **interactions between plants and soil communities can** accelerate new technological and
55 management innovations that harness belowground interactions to enhance
56 aboveground productivity.

57 When plants first started extending their roots into primordial soils, they encountered a
58 rich microbiome. Ever since, plants have co-evolved with soil microbes and fauna, and
59 traits that supported beneficial interactions with soil organisms likely incurred a fitness
60 advantage (Lambers *et al.* 2009). For example, plants that enable mycorrhizal
61 colonisation are able to enhance their nutrient acquisition. Plant root exudates also
62 support microbes that release enzymes to depolymerize organic matter and transform it
63 into plant-available forms through mineralisation. This long history of co-evolution
64 provides a roadmap for measuring and managing beneficial plant-microbe interactions
65 that are key components of healthy soils. Here, we suggest that rather than overall
66 microbial abundance or species diversity, the structure of the network of interactions
67 between plants and soil organisms and among soil organisms best predicts the
68 functionality of soil communities and provides a framework for assessing and managing
69 soil health.

70 Plants affect the structure and function of the soil microbiome and food webs directly
71 through beneficial associations with mycorrhizal fungi and *Rhizobia*, and through
72 antagonistic associations with, for example, plant-parasitic nematodes. Indirect controls
73 on soil communities are equally important and act primarily through the quantity and

74 quality of plant aboveground and belowground litter inputs (Orwin *et al.* 2010; De Vries
75 *et al.* 2012b; Baxendale *et al.* 2014). In the rhizosphere, plant N uptake is a dominant
76 control on bacterial and fungal community composition (Bell *et al.* 2015; Moreau *et al.*
77 2015; Giagnoni *et al.* 2016; Thion *et al.* 2016). In addition, rhizodeposits and root litter
78 have been shown to strongly influence the composition of soil microbial and faunal
79 communities and soil food webs (Scheunemann *et al.* 2015; Sauvadet *et al.* 2016), and
80 feed back to the performance of neighbouring plant species by altering soil N availability
81 (Meier, Keyserling & Bowman 2009). Root exudates have been hypothesised as an
82 important mechanism driving microbial community and soil food web composition and
83 activity (Bardgett, Mommer & De Vries 2014; De Vries & Caruso 2016), though this has
84 only been experimentally demonstrated for *Arabidopsis* (Shi *et al.* 2011; Badri *et al.*
85 2013). Finally, antimicrobial compounds isolated from crop plant root exudates can
86 affect the growth and activity of pathogenic soil bacteria (Liu *et al.* 2015; Fang *et al.*
87 2016). These mechanisms form a tight link between plants, microbes, and the soil food
88 web in the rhizosphere.

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

107 Rather than species numbers, interactions between organisms appear to be crucial for
108 the functioning of soil communities. Networks of interactions can predict whole

109 ecosystem functioning (Kuiper *et al.* 2015) and drive multiple processes and ecosystem
110 services that underlie this functioning (Hines *et al.* 2015). Soil food webs with a more
111 prominent fungal energy channel (Box 1) are more resistant to, and continue to function
112 better under drought (De Vries *et al.* 2012a). In addition, the ratio between the bacterial
113 and fungal energy channel has been correlated to the rates of soil C and N cycling
114 processes (De Vries *et al.* 2013). The success of pathogen invasion in the rhizosphere
115 has been shown to depend on the network structure of resident bacterial communities
116 (Wei *et al.* 2015). Specifically, pathogen success was lower when resident networks had
117 low nestedness (or modularity, see Box 1) and high connectance, presumably through
118 more efficient consumption of resources. Other recent studies found that associations
119 between methane oxidising bacteria and other microbes were central in modulating
120 methane-oxidation (Ho *et al.* 2016), and that fungal co-occurrence network structure
121 was strongly associated with different stages of litter decomposition (Purahong *et al.*
122 2016). Thus, **new ecological knowledge of** the structure of interactive networks among
123 organisms and their environment might be used as an indicator of their functional
124 attributes.

125

126 *Rhizosphere networks are recruited from bulk soil networks*

127 In the rhizosphere, bacterial networks typically have more nodes, more hubs, and
128 stronger connections (see Box 1 for definitions) than those in bulk soil (Mendes *et al.*
129 2014; Shi *et al.* 2016). In a recent study, Shi *et al.* (2016) found that while bulk soil
130 bacterial communities contained more OTUs, rhizosphere networks of bacterial taxa
131 were larger and more connected. Moreover, rhizosphere networks grew larger and
132 gained more connections and hubs during plant growth, while networks in the bulk soil
133 remained relatively static. Similarly, rhizosphere decomposer soil food webs tend to be
134 dominated by the bacterial energy channel (Thakur & Eisenhauer 2015; Muller *et al.*
135 2016), which typically have lower diversity than fungal-dominated soil food webs (De
136 Vries *et al.* 2012a, 2013). These patterns likely occur because the high-resource
137 rhizosphere 'recruits' a subset of species from the bulk soil community. The selected
138 species then share niche space in the rhizosphere and as a result show strong positive
139 associations in networks (Mendes *et al.* 2014; Edwards *et al.* 2015). Importantly, the
140 presence of plant roots has been shown to be as important as land use and soil type for
141 shaping bacterial community composition (Edwards *et al.* 2015; Hargreaves, Williams &
142 Hofmockel 2015).

143 As a result of these different network structures, rhizosphere networks are likely to be
144 less stable under changing environmental conditions than bulk soil networks.
145 Rhizosphere microbial networks are characterised by overwhelmingly strong, positive
146 interactions, which have been shown to compromise network stability (Box 1). In
147 addition, bacterial-dominated rhizosphere soil food webs consist of strong interactions,
148 and a reduction of the fungal energy channel effectively reduces network
149 compartmentalisation, thereby reducing network stability (Box 1). These properties
150 allow rhizosphere networks to respond quickly to changes in resource availability, for
151 example as a result of plant growth stages or agricultural management.

152 In contrast to the rhizosphere, the bulk soil harbours a large, diverse network of
153 organisms with low abundances that consists of weak interactions. The majority of
154 these organisms are dormant or inactive and are thus highly resistant to environmental
155 stresses (Lennon & Jones 2011) and can persist in soil for long periods of time (Troxler
156 *et al.* 2012). This network of bulk soil organisms is mostly unaffected by the dynamic
157 processes that affect rhizosphere networks and remains relatively static during the
158 growing season (Shi *et al.* 2016), but would be highly stable under changing
159 environmental conditions because of its properties. We propose that this bulk soil
160 network provides the 'seed bank' from which rhizosphere networks are recruited, and
161 we argue that crops will be able to recruit a functioning rhizosphere network as long as
162 this seed bank is intact (Fig. 1). The composition and structure of the recruited
163 rhizosphere network depends on the traits, and in particular root traits, of the crop
164 grown, as well as on the abundance and composition of the bulk soil community.
165 However, we argue that conventional agricultural management reduces the ability of the
166 rhizosphere to recruit from the bulk soil.

167

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

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

177 of connections of bacterial networks compared to organic amendments (Ling *et al.*
178 2016). Similarly, in a field experiment, organic manure amendment increased the
179 modularity of arbuscular mycorrhizal fungal networks (Zhu *et al.* 2016). But
180 agricultural management also disproportionately reduces the biomass of groups of
181 organisms that form a connection between rhizosphere and bulk soil, and thus facilitate
182 rhizosphere recruitment. For example, fungal hyphae can form a connection between
183 rhizosphere and bulk soil microbial communities and food webs by transporting C and
184 facilitating bacterial movement (Fransson & Rosling 2014; Gahan & Schmalenberger
185 2015; Pausch *et al.* 2016). Similarly, soil fauna can form a connection between
186 rhizosphere and bulk soil networks. Earthworms incorporate and distribute organic
187 residues into different soil layers and facilitate microbial dispersal (Tao *et al.* 2009).
188 Both fungal and bacterial grazers can carry bacterial cells and fungal spores in their gut
189 and on their surface (Ingham 1999; Renker *et al.* 2005), and facilitate their movement
190 by migrating between soil layers (Lindberg & Bengtsson 2005). In addition,
191 conventional agricultural management can also reduce the movement of soil organisms
192 between rhizosphere and bulk soil by compacting and homogenising the soil (Tao *et al.*
193 2009; Warmink *et al.* 2011; Ebrahimi & Or 2014). Moreover, the composition and
194 persistence of the bulk soil 'seed bank' can be affected by agricultural amendments
195 seeping to deeper soil layers, such as fertiliser, pesticides, manure, and the antibiotics
196 within manure.

197

198 *The Rhizosphere Interactions for Sustainable Agriculture (RISA) Model*

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

211 Most evidence that organismal network structure underlies soil functioning originates
212 from studies on soil food webs, in which feeding interactions between organisms have
213 empirically been quantified through decades of research (Bradford 2016). While the
214 nature of soil food web interactions are currently under debate (Ballhausen & de Boer
215 2016; Geisen 2016), existing food web models have successfully predicted C and N
216 fluxes in natural and agricultural systems (De Ruiter *et al.* 1993; Holtkamp *et al.* 2011).
217 In soil microbial networks, correlations between microbial taxa can result from a variety
218 of interaction types (Box 1). To model process rates from data on interactions within
219 microbial networks, and to predict functioning based on microbial network structure,
220 we need to first elucidate the exact nature of dynamic microbe-microbe interactions
221 (Gottstein *et al.* 2016). Therefore, an important challenge is to identify interaction types
222 between microbial groups or species and how these determine network structure. Here,
223 we can learn from gut microbiologists, who have successfully linked gene transcripts to
224 species-species interactions (Plichta *et al.* 2016). Several covarying transcripts were
225 down-regulated in interacting species pairs, indicating that the functional overlap
226 between species was reduced and that species activities were context specific. A
227 creative alternative to experimentally elucidating the nature of the millions possible
228 specific microbe-microbe interactions might be text-mining of existing literature (Lim *et al.*
229 *et al.* 2016).

230 Once we know the functionalities of key nodes and network modules, we can identify
231 nodes and hubs associated with desirable functions such as nutrient mineralisation or
232 plant protection from disease. Taxa that often appear as nodes in structured
233 rhizosphere networks may be promising targets for inoculants, since the addition of just
234 a few species may lead to a structured network. There is a long history of inoculating
235 beneficial microbes either directly into soils or as seed coatings (Calvo, Nelson &
236 Kloepper 2014). Mycorrhizae are often inoculated on tree seedlings and crops to
237 improve establishment and nutrient uptake (du Jardin 2015). *Rhizobia* are inoculated on
238 legumes to ensure nodule formation (Catroux, Hartmann & Revellin 2001; du Jardin
239 2015). However, along with many other types of plant-growth promoting bacteria,
240 inoculants have had only limited success to date in field agriculture (Calvo, Nelson &
241 Kloepper 2014). There is little evidence that most inoculants are able to persist and
242 compete with other microbes in most soils (Verbruggen *et al.* 2013; Berruti, Lumini &
243 Bianciotto 2016), although one study found that the plant-growth promoting bacterium
244 *Pseudomonas fluorescens* persisted in the bulk soil for months after inoculation (Troxler
245 *et al.* 2012).

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

260 Many research challenges need to be addressed before we can use the analysis of soil
261 networks to design management interventions that optimise connections between plant
262 roots and soil networks and between rhizosphere and bulk soil. However, the
263 effectiveness of many new agricultural management approaches for improving soil
264 health and agricultural sustainability (Tilman *et al.* 2002) can be explained by our
265 conceptual model. For example, it is well known that no-till or reduced tillage supports
266 active decomposer communities (Arshad *et al.* 1990; Ogle, Swan & Paustian 2012), but
267 they also promote linkages between rhizosphere and bulk soil networks by reducing soil
268 disturbance. Cover crops displace fallow periods with plants that fix N, increase C
269 inputs (Olson, Ebelhar & Lang 2010), and also likely enhance soil network structure.
270 Along with other forms of organic inputs such as manure and compost, cover crops may
271 support diverse bulk soils with weak interactions (Ling *et al.* 2016). Finally, crop
272 rotations that prevent the build-up of diseases have been shown to differ in their fungal
273 network structure from diseased soils under continuous monoculture, with rhizosphere
274 networks in healthy soils showing higher modularity and meta-modularity, and more
275 highly-connected generalists (Lu *et al.* 2013). However, it is important to acknowledge
276 that soil organismal networks **and their connections with plants** are likely to depend on
277 edaphic soil characteristics, such as soil texture and cation exchange capacity (Ma *et al.*
278 2016a; Ma *et al.* 2016b). The design of novel management approaches to promote
279 networks will have to take into account context-specificity and be tailored for **different**
280 **crops**, soil types, and climatic conditions.

281 Over the years, various indices have been proposed as indicators of healthy soils
282 including soil organic matter content (Reeves 1997), microbial diversity (Lehman *et al.*
283 2015), fungal:bacterial ratios (De Vries *et al.* 2006), enzyme activities (Bandick & Dick
284 1999), metabolic quotients (Anderson 2003), or soil respiration burst tests (Morrow *et*
285 *al.* 2016). These indices do not recognize the importance of interactions among these
286 components, but we expect many of these metrics to be correlated to the structure of
287 soil organismal networks, as has been shown already for certain soil food web
288 characteristics (De Vries *et al.* 2013). While much research is needed to establish links
289 between soil properties, plant traits, network structure and soil functioning, **novel**
290 **understanding of ecological interactions within and between soil communities and**
291 **plants has tremendous potential to be applied in agricultural systems to sustainability**
292 **produce food for a growing global population.**

293

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

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

306 Seminal work by May (1973) focussed on the number of organisms or species present in
307 a network and the number of connections between these. Counterintuitively, May found
308 that more diverse networks were less stable under perturbations than simpler
309 networks. However, these early networks were randomly created, and since then,
310 multiple studies have shown that the configuration and interaction types within
311 networks determine their stability. For example, networks that consist of many weak
312 links are more stable than those consisting of few strong links (Neutel, Heesterbeek & de
313 Rooter 2002). Compartmentalisation, as well as the presence of weak connectors
314 between compartments, has also been shown to increase the stability of networks

315 (Moore *et al.* 2003; Rooney *et al.* 2006; Stouffer & Bascompte 2011). Finally, trophic
316 coherence and the presence of negative interactions, such as top-down controls, can
317 increase network stability (Johnson *et al.* 2014; Coyte, Schluter & Foster 2015).

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

338

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346

347

348 **References**

- 349 Anderson, T.H. (2003) Microbial eco-physiological indicators to assess soil quality.
350 *Agriculture Ecosystems & Environment*, **98**, 285-293.
- 351 Arshad, M.A., Schnitzer, M., Angers, D.A. & Ripmeester, J.A. (1990) EFFECTS OF TILL VS
352 NO-TILL ON THE QUALITY OF SOIL ORGANIC-MATTER. *Soil Biology &*
353 *Biochemistry*, **22**, 595-599.
- 354 Badri, D.V., Chaparro, J.M., Zhang, R.F., Shen, Q.R. & Vivanco, J.M. (2013) Application of
355 Natural Blends of Phytochemicals Derived from the Root Exudates of
356 *Arabidopsis* to the Soil Reveal That Phenolic-related Compounds Predominantly
357 Modulate the Soil Microbiome. *Journal of Biological Chemistry*, **288**, 4502-4512.
- 358 Ballhausen, M.-B. & de Boer, W. (2016) The sapro-rhizosphere: Carbon flow from
359 saprotrophic fungi into fungus-feeding bacteria. *Soil Biology and Biochemistry*,
360 **102**, 14-17.
- 361 Bandick, A.K. & Dick, R.P. (1999) Field management effects on soil enzyme activities. *Soil*
362 *Biology & Biochemistry*, **31**, 1471-1479.
- 363 Bardgett, R.D., Mommer, L. & De Vries, F.T. (2014) Going underground: root traits as
364 drivers of ecosystem processes. *Trends in Ecology & Evolution*, **29**, 692-699.
- 365 Baxendale, C., Orwin, K.H., Poly, F., Pommier, T. & Bardgett, R.D. (2014) Are plant-soil
366 feedback responses explained by plant traits? *New Phytologist*, **204**, 408-423.
- 367 Beare, M.H., Hu, S., Coleman, D.C. & Hendrix, P.F. (1997) Influences of mycelial fungi on
368 soil aggregation and organic matter storage in conventional and no-tillage soils.
369 *Applied Soil Ecology*, **5**, 211-219.
- 370 Bell, C.W., Asao, S., Calderon, F., Wolk, B. & Wallenstein, M.D. (2015) Plant nitrogen
371 uptake drives rhizosphere bacterial community assembly during plant growth.
372 *Soil Biology & Biochemistry*, **85**, 170-182.
- 373 Bender, S.F., Wagg, C. & van der Heijden, M.G.A. (2016) An Underground Revolution:
374 Biodiversity and Soil Ecological Engineering for Agricultural Sustainability.
375 *Trends in Ecology & Evolution*, **31**, 440-452.
- 376 Berruti, A., Lumini, E. & Bianciotto, V. (2016) AMF components from a microbial
377 inoculum fail to colonize roots and lack soil persistence in an arable maize field.
378 *Symbiosis*, 1-8.
- 379 Bradford, M.A. (2016) Re-visioning soil food webs. *Soil Biology and Biochemistry*, **102**, 1-
380 3.
- 381 Buchkowski, R.W. (2016) Top-down consumptive and trait-mediated control do affect
382 soil food webs: It's time for a new model. *Soil Biology and Biochemistry*, **102**, 29-
383 32.
- 384 Calvo, P., Nelson, L. & Kloepper, J.W. (2014) Agricultural uses of plant biostimulants.
385 *Plant and Soil*, **383**, 3-41.
- 386 Catroux, G., Hartmann, A. & Revellin, C. (2001) Trends in rhizobial inoculant production
387 and use. *Plant and Soil*, **230**, 21-30.
- 388 Chen, L., Brookes, P.C., Xu, J.M., Zhang, J.B., Zhang, C.Z., Zhou, X.Y. & Luo, Y. (2016)
389 Structural and functional differentiation of the root-associated bacterial
390 microbiomes of perennial ryegrass. *Soil Biology & Biochemistry*, **98**, 1-10.
- 391 Coyte, K.Z., Schluter, J. & Foster, K.R. (2015) The ecology of the microbiome: Networks,
392 competition, and stability. *Science*, **350**, 663-666.
- 393 De Ruiter, P.C., Moore, J.C., Zwart, K.B., Bouwman, L.A., Hassink, J., Bloem, J., Devos, J.A.,
394 Marinissen, J.C.Y., Didden, W.A.M., Lebbink, G. & Brussaard, L. (1993) Simulation
395 of Nitrogen Mineralization in the Belowground Food Webs of 2 Winter-Wheat
396 Fields. *Journal of Applied Ecology*, **30**, 95-106.
- 397 De Vries, F.T. & Bardgett, R.D. (2016) Plant community controls on short-term
398 ecosystem nitrogen retention. *New Phytologist*, **210**, 861-874.

- 399 De Vries, F.T. & Caruso, T. (2016) Eating from the same plate? Revisiting the role of
400 labile carbon inputs in the soil food web. *Soil Biology & Biochemistry*, In Press.
- 401 De Vries, F.T., Hoffland, E., van Eekeren, N., Brussaard, L. & Bloem, J. (2006)
402 Fungal/bacterial ratios in grasslands with contrasting nitrogen management.
403 *Soil Biology & Biochemistry*, **38**, 2092-2103.
- 404 De Vries, F.T., Liiri, M., Bjørnlund, L., Bowker, M., Christensen, S., Setälä, H. & Bardgett,
405 R.D. (2012a) Land use alters the resistance and resilience of soil food webs to
406 drought. *Nature Climate Change*, **2**, 276-280.
- 407 De Vries, F.T., Manning, P., Tallowin, J.R.B., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A.,
408 Hobbs, P.J., Quirk, H., Shipley, B., Cornelissen, J.H.C., Kattge, J. & Bardgett, R.D.
409 (2012b) Abiotic drivers and plant traits explain landscape-scale patterns in soil
410 microbial communities. *Ecology Letters*, **15**, 1230-1239.
- 411 De Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Bracht
412 Jørgensen, H., Brady, M.V., Christensen, S., de Ruiter, P.C., d'Hertefeldt, T., Frouz,
413 J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H.,
414 Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V. & Bardgett, R.D.
415 (2013) Soil food web properties explain ecosystem services across European
416 land use systems. *Proceedings of the National Academy of Sciences*, **110**, 14296-
417 14301.
- 418 Doran, J.W. & Zeiss, M.R. (2000) Soil health and sustainability: managing the biotic
419 component of soil quality. *Applied Soil Ecology*, **15**, 3-11.
- 420 du Jardin, P. (2015) Plant biostimulants: Definition, concept, main categories and
421 regulation. *Scientia Horticulturae*, **196**, 3-14.
- 422 Ebrahimi, A.N. & Or, D. (2014) Microbial dispersal in unsaturated porous media:
423 Characteristics of motile bacterial cell motions in unsaturated angular pore
424 networks. *Water Resources Research*, **50**, 7406-7429.
- 425 Edwards, J., Johnson, C., Santos-Medellín, C., Lurie, E., Podishetty, N.K., Bhatnagar, S.,
426 Eisen, J.A. & Sundaresan, V. (2015) Structure, variation, and assembly of the
427 root-associated microbiomes of rice. *Proceedings of the National Academy of
428 Sciences*, **112**, E911-E920.
- 429 Fang, Y., Zhang, L., Jiao, Y., Liao, J., Luo, L., Ji, S., Li, J., Dai, K., Zhu, S. & Yang, M. (2016)
430 Tobacco Rotated with Rapeseed for Soil-Borne Phytophthora Pathogen
431 Biocontrol: Mediated by Rapeseed Root Exudates. *Frontiers in Microbiology*, **7**.
- 432 Fransson, P. & Rosling, A. (2014) Fungal and bacterial community responses to *Suillus*
433 *variegatus* extraradical mycelia and soil profile in Scots pine microcosms. *Plant
434 and Soil*, **385**, 255-272.
- 435 Fujii, S., Saitoh, S. & Takeda, H. (2014) Effects of rhizospheres on the community
436 composition of Collembola in a temperate forest. *Applied Soil Ecology*, **83**, 109-
437 115.
- 438 Gahan, J. & Schmalenberger, A. (2015) Arbuscular mycorrhizal hyphae in grassland
439 select for a diverse and abundant hyphospheric bacterial community involved in
440 sulfonate desulfurization. *Applied Soil Ecology*, **89**, 113-121.
- 441 Geisen, S. (2016) The bacterial-fungal energy channel concept challenged by enormous
442 functional versatility of soil protists. *Soil Biology and Biochemistry*, **102**, 22-25.
- 443 Giagnoni, L., Pastorelli, R., Mocali, S., Arenella, M., Nannipieri, P. & Renella, G. (2016)
444 Availability of different nitrogen forms changes the microbial communities and
445 enzyme activities in the rhizosphere of maize lines with different nitrogen use
446 efficiency. *Applied Soil Ecology*, **98**, 30-38.
- 447 Gottstein, W., Olivier, B.G., Bruggeman, F.J. & Teusink, B. (2016) Constraint-based
448 stoichiometric modelling from single organisms to microbial communities.
449 *Journal of the Royal Society Interface*, **13**.
- 450 Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastl, E., Arnoldi,
451 C., Bardgett, R.D., Poly, F., Pommier, T., Schloter, M., Tappeiner, U., Bahn, M. &
452 Clément, J.-C. (2013) Relative contributions of plant traits and soil microbial

- 453 properties to mountain grassland ecosystem services. *Journal of Ecology*, **101**,
454 47-57.
- 455 Hargreaves, S.K., Williams, R.J. & Hofmockel, K.S. (2015) Environmental Filtering of
456 Microbial Communities in Agricultural Soil Shifts with Crop Growth. *PLoS ONE*,
457 **10**, e0134345.
- 458 Hawlena, D. & Zaguri, M. (2016) Fear and below-ground food-webs. *Soil Biology and*
459 *Biochemistry*, **102**, 26-28.
- 460 Hines, J., van der Putten, W.H., De Deyn, G.B., Wagg, C., Voigt, W., Mulder, C., Weisser,
461 W.W., Engel, J., Melian, C., Scheu, S., Birkhofer, K., Ebeling, A., Scherber, C. &
462 Eisenhauer, N. (2015) Towards an Integration of Biodiversity-Ecosystem
463 Functioning and Food Web Theory to Evaluate Relationships between Multiple
464 Ecosystem Services. *Ecosystem Services: From Biodiversity to Society, Pt 1* (eds G.
465 Woodward & D.A. Bohan), pp. 161-199. Elsevier Academic Press Inc, San Diego.
- 466 Ho, A., Angel, R., Veraart, A.J., Daebeler, A., Jia, Z.J., Kim, S.Y., Kerckhof, F.M., Boon, N. &
467 Bodelier, P.L.E. (2016) Biotic Interactions in Microbial Communities as
468 Modulators of Biogeochemical Processes: Methanotrophy as a Model System.
469 *Frontiers in Microbiology*, **7**.
- 470 Holtkamp, R., van der Wal, A., Kardol, P., van der Putten, W.H., de Ruiter, P.C. & Dekker,
471 S.C. (2011) Modelling C and N mineralisation in soil food webs during secondary
472 succession on ex-arable land. *Soil Biology & Biochemistry*, **43**, 251-260.
- 473 Hu, H.W., Macdonald, C.A., Trivedi, P., Anderson, I.C., Zheng, Y., Holmes, B., Bodrossy, L.,
474 Wang, J.T., He, J.Z. & Singh, B.K. (2016) Effects of climate warming and elevated
475 CO₂ on autotrophic nitrification and nitrifiers in dryland ecosystems. *Soil*
476 *Biology & Biochemistry*, **92**, 1-15.
- 477 Ingham, E.R. (1999) Nematodes. *Soil Biology Primer* (eds A.J. Tugel & A.M.
478 Lewandowski).
- 479 Johnson, S., Domínguez-García, V., Donetti, L. & Muñoz, M.A. (2014) Trophic coherence
480 determines food-web stability. *Proceedings of the National Academy of Sciences*,
481 **111**, 17923-17928.
- 482 Kuiper, J.J., van Altena, C., de Ruiter, P.C., van Gerven, L.P.A., Janse, J.H. & Mooij, W.M.
483 (2015) Food-web stability signals critical transitions in temperate shallow lakes.
484 *Nature Communications*, **6**.
- 485 Kumar, V., Baweja, M., Singh, P.K. & Shukla, P. (2016) Recent Developments in Systems
486 Biology and Metabolic Engineering of Plant Microbe Interactions. *Frontiers in*
487 *Plant Science*, **7**.
- 488 Lambers, H., Mougél, C., Jaillard, B. & Hinsinger, P. (2009) Plant-microbe-soil
489 interactions in the rhizosphere: an evolutionary perspective. *Plant and Soil*, **321**,
490 83-115.
- 491 Legay, N., Lavorel, S., Baxendale, C., Krainer, U., Bahn, M., Binet, M.-N., Cantarel, A.A.M.,
492 Colace, M.-P., Foulquier, A., Kastl, E.-M., Grigulis, K., Mouhamadou, B., Poly, F.,
493 Pommier, T., Schloter, M., Clément, J.-C. & Bardgett, R.D. (2016) Influence of plant
494 traits, soil microbial properties, and abiotic parameters on nitrogen turnover of
495 grassland ecosystems. *Ecosphere*, **7**, e01448-n/a.
- 496 Lehman, R.M., Acosta-Martinez, V., Buyer, J.S., Cambardella, C.A., Collins, H.P., Ducey, T.F.,
497 Halvorson, J.J., Jin, V.L., Johnson, J.M.F., Kremer, R.J., Lundgren, J.G., Manter, D.K.,
498 Maul, J.E., Smith, J.L. & Stott, D.E. (2015) Soil biology for resilient, healthy soil.
499 *Journal of Soil and Water Conservation*, **70**, 12A-18A.
- 500 Lennon, J.T. & Jones, S.E. (2011) Microbial seed banks: the ecological and evolutionary
501 implications of dormancy. *Nature Reviews Microbiology*, **9**, 119-130.
- 502 Lim, K.M.K., Li, C.H., Chng, K.R. & Nagarajan, N. (2016) @Minter: automated text-mining
503 of microbial interactions. *Bioinformatics*, **32**, 2981-2987.
- 504 Lindberg, N. & Bengtsson, J. (2005) Population responses of oribatid mites and
505 collembolans after drought. *Applied Soil Ecology*, **28**, 163-174.

- 506 Ling, N., Zhu, C., Xue, C., Chen, H., Duan, Y.H., Peng, C., Guo, S.W. & Shen, Q.R. (2016)
 507 Insight into how organic amendments can shape the soil microbiome in long-
 508 term field experiments as revealed by network analysis. *Soil Biology &*
 509 *Biochemistry*, **99**, 137-149.
- 510 Liu, Y.X., Li, X., Cai, K., Cai, L.T., Lu, N. & Shi, J.X. (2015) Identification of benzoic acid and
 511 3-phenylpropanoic acid in tobacco root exudates and their role in the growth of
 512 rhizosphere microorganisms. *Applied Soil Ecology*, **93**, 78-87.
- 513 Ma, B., Wang, H.Z., Dsouza, M., Lou, J., He, Y., Dai, Z.M., Brookes, P.C., Xu, J.M. & Gilbert, J.A.
 514 (2016a) Geographic patterns of co-occurrence network topological features for
 515 soil microbiota at continental scale in eastern China. *Isme Journal*, **10**, 1891-
 516 1901.
- 517 Ma, J.C., Ibekwe, A.M., Yang, C.H. & Crowley, D.E. (2016b) Bacterial diversity and
 518 composition in major fresh produce growing soils affected by physiochemical
 519 properties and geographic locations. *Science of the Total Environment*, **563**, 199-
 520 209.
- 521 May, R.M. (1973) *Stability and complexity in model ecosystems*. Princeton University
 522 Press, Princeton.
- 523 Meier, C.L., Keyserling, K. & Bowman, W.D. (2009) Fine root inputs to soil reduce growth
 524 of a neighbouring plant via distinct mechanisms dependent on root carbon
 525 chemistry. *Journal of Ecology*, **97**, 941-949.
- 526 Mendes, L.W., Kuramae, E.E., Navarrete, A.A., van Veen, J.A. & Tsai, S.M. (2014)
 527 Taxonomical and functional microbial community selection in soybean
 528 rhizosphere. *Isme Journal*, **8**, 1577-1587.
- 529 Moore, J.C., McCann, K., Setälä, H. & De Ruiter, P.C. (2003) Top-down is bottom-up: Does
 530 predation in the rhizosphere regulate aboveground dynamics? *Ecology*, **84**, 846-
 531 857.
- 532 Moreau, D., Pivato, B., Bru, D., Busset, H., Deau, F., Faivre, C., Matejicek, A., Strbik, F.,
 533 Philippot, L. & Mougél, C. (2015) Plant traits related to nitrogen uptake influence
 534 plant-microbe competition. *Ecology*, **96**, 2300-2310.
- 535 Morrow, J.G., Huggins, D.R., Carpenter-Boggs, L.A. & Reganold, J.P. (2016) Evaluating
 536 Measures to Assess Soil Health in Long-Term Agroecosystem Trials. *Soil Science*
 537 *Society of America Journal*, **80**, 450-462.
- 538 Muller, K., Kramer, S., Haslwimmer, H., Marhan, S., Scheunemann, N., Butenschon, O.,
 539 Scheu, S. & Kandeler, E. (2016) Carbon transfer from maize roots and litter into
 540 bacteria and fungi depends on soil depth and time. *Soil Biology & Biochemistry*,
 541 **93**, 79-89.
- 542 Neutel, A.M., Heesterbeek, J.A.P. & de Ruiter, P.C. (2002) Stability in real food webs:
 543 Weak links in long loops. *Science*, **296**, 1120-1123.
- 544 Ogle, S.M., Swan, A. & Paustian, K. (2012) No-till management impacts on crop
 545 productivity, carbon input and soil carbon sequestration. *Agriculture Ecosystems*
 546 *& Environment*, **149**, 37-49.
- 547 Olson, K.R., Ebelhar, S.A. & Lang, J.M. (2010) Cover Crop Effects on Crop Yields and Soil
 548 Organic Carbon Content. *Soil Science*, **175**, 89-98.
- 549 Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S. & Bardgett, R.D.
 550 (2010) Linkages of plant traits to soil properties and the functioning of
 551 temperate grassland. *Journal of Ecology*, **98**, 1074-1083.
- 552 Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschon, O., Kandeler, E.,
 553 Marhan, S., Riederer, M., Scheu, S., Kuzyakov, Y. & Ruess, L. (2016) Small but
 554 active - pool size does not matter for carbon incorporation in below-ground food
 555 webs. *Functional Ecology*, **30**, 479-489.
- 556 Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G.P. & Smith, P. (2016) Climate-
 557 smart soils. *Nature*, **532**, 49-57.
- 558 Plichta, D.R., Juncker, A.S., Bertalan, M., Rettedal, E., Gautier, L., Varela, E., Manichanh, C.,
 559 Fouqueray, C., Levenez, F., Nielsen, T., Dore, J., Machado, A.M.D., de Evgrafov,

- 560 M.C.R., Hansen, T., Jorgensen, T., Bork, P., Guarner, F., Pedersen, O., Sommer,
561 M.O.A., Ehrlich, S.D., Sicheritz-Ponten, T., Brunak, S., Nielsen, H.B. &
562 Metagenomics Human Intestinal, T. (2016) Transcriptional interactions suggest
563 niche segregation among microorganisms in the human gut. *Nature*
564 *Microbiology*, **1**.
- 565 Purahong, W., Kruger, D., Buscot, F. & Wubet, T. (2016) Correlations between the
566 composition of modular fungal communities and litter decomposition-associated
567 ecosystem functions. *Fungal Ecology*, **22**, 106-114.
- 568 Reeves, D.W. (1997) The role of soil organic matter in maintaining soil quality in
569 continuous cropping systems. *Soil & Tillage Research*, **43**, 131-167.
- 570 Renker, C., Otto, P., Schneider, K., Zimdars, B., Maraun, M. & Buscot, F. (2005) Oribatid
571 mites as potential vectors for soil microfungi: Study of mite-associated fungal
572 species. *Microbial Ecology*, **50**, 518-528.
- 573 Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006) Structural asymmetry and the
574 stability of diverse food webs. *Nature*, **442**, 265-269.
- 575 Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.A., Villenave, C. & Bertrand, I. (2016) The
576 dynamics of soil micro-food web structure and functions vary according to litter
577 quality. *Soil Biology & Biochemistry*, **95**, 262-274.
- 578 Scharroba, A., Kramer, S., Kandeler, E. & Ruess, L. (2016) Spatial and temporal variation
579 of resource allocation in an arable soil drives community structure and biomass
580 of nematodes and their role in the micro-food web. *Pedobiologia*, **59**, 111-120.
- 581 Scheunemann, N., Maraun, M., Scheu, S. & Butenschoen, O. (2015) The role of shoot
582 residues vs. crop species for soil arthropod diversity and abundance of arable
583 systems. *Soil Biology & Biochemistry*, **81**, 81-88.
- 584 Shi, S., Nuccio, E., Herman, D.J., Rijkers, R., Estera, K., Li, J., da Rocha, U.N., He, Z., Pett-
585 Ridge, J., Brodie, E.L., Zhou, J. & Firestone, M. (2015) Successional Trajectories of
586 Rhizosphere Bacterial Communities over Consecutive Seasons. *mBio*, **6**.
- 587 Shi, S., Nuccio, E.E., Shi, Z.J., He, Z., Zhou, J. & Firestone, M.K. (2016) The interconnected
588 rhizosphere: High network complexity dominates rhizosphere assemblages.
589 *Ecology Letters*, **19**, 926-936.
- 590 Shi, S.J., Richardson, A.E., O'Callaghan, M., DeAngelis, K.M., Jones, E.E., Stewart, A.,
591 Firestone, M.K. & Condon, L.M. (2011) Effects of selected root exudate
592 components on soil bacterial communities. *FEMS Microbiology Ecology*, **77**, 600-
593 610.
- 594 Stouffer, D.B. & Bascompte, J. (2011) Compartmentalization increases food-web
595 persistence. *Proceedings of the National Academy of Sciences*, **108**, 3648-3652.
- 596 Tao, J., Chen, X.Y., Liu, M.Q., Hu, F., Griffiths, B. & Li, H.X. (2009) Earthworms change the
597 abundance and community structure of nematodes and protozoa in a maize
598 residue amended rice-wheat rotation agro-ecosystem. *Soil Biology &*
599 *Biochemistry*, **41**, 898-904.
- 600 Thakur, M.P. & Eisenhauer, N. (2015) Plant community composition determines the
601 strength of top-down control in a soil food web motif. *Scientific Reports*, **5**.
- 602 Thion, C.E., Poirel, J.D., Cornulier, T., De Vries, F.T., Bardgett, R.D. & Prosser, J.I. (2016)
603 Plant nitrogen-use strategy as a driver of rhizosphere archaeal and bacterial
604 ammonia oxidiser abundance. *FEMS Microbiology Ecology*, **92**.
- 605 Thomas, F. & Cebren, A. (2016) Short-Term Rhizosphere Effect on Available Carbon
606 Sources, Phenanthrene Degradation, and Active Microbiome in an Aged-
607 Contaminated Industrial Soil. *Frontiers in Microbiology*, **7**.
- 608 Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. (2002) Agricultural
609 sustainability and intensive production practices. *Nature*, **418**, 671-677.
- 610 Troxler, J., Svercel, M., Natsch, A., Zala, M., Keel, C., Moenne-Loccoz, Y. & Defago, G. (2012)
611 Persistence of a biocontrol *Pseudomonas* inoculant as high populations of
612 culturable and non-culturable cells in 200-cm-deep soil profiles. *Soil Biology &*
613 *Biochemistry*, **44**, 122-129.

- 614 Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H.,
615 Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L.,
616 Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H., Frouz,
617 J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J.,
618 Wolters, V. & Hedlund, K. (2015) Intensive agriculture reduces soil biodiversity
619 across Europe. *Global Change Biology*, **21**, 973-985.
- 620 Turner, T.R., Ramakrishnan, K., Walshaw, J., Heavens, D., Alston, M., Swarbreck, D.,
621 Osbourn, A., Grant, A. & Poole, P.S. (2013) Comparative metatranscriptomics
622 reveals kingdom level changes in the rhizosphere microbiome of plants. *Isme*
623 *Journal*, **7**, 2248-2258.
- 624 Uksa, M., Schloter, M., Endesfelder, D., Kublik, S., Engel, M., Kautz, T., Kopke, U. & Fischer,
625 D. (2015) Prokaryotes in Subsoil-Evidence for a Strong Spatial Separation of
626 Different Phyla by Analysing Co-occurrence Networks. *Frontiers in Microbiology*,
627 **6**.
- 628 Verbruggen, E., van der Heijden, M.G.A., Rillig, M.C. & Kiers, E.T. (2013) Mycorrhizal
629 fungal establishment in agricultural soils: factors determining inoculation
630 success. *New Phytologist*, **197**, 1104-1109.
- 631 Warmink, J.A., Nazir, R., Corten, B. & van Elsas, J.D. (2011) Hitchhikers on the fungal
632 highway: The helper effect for bacterial migration via fungal hyphae. *Soil Biology*
633 *& Biochemistry*, **43**, 760-765.
- 634 Wei, Z., Yang, T.J., Friman, V.P., Xu, Y.C., Shen, Q.R. & Jousset, A. (2015) Trophic network
635 architecture of root-associated bacterial communities determines pathogen
636 invasion and plant health. *Nature Communications*, **6**.
- 637 Zhu, C., Ling, N., Guo, J., Wang, M., Guo, S. & Shen, Q. (2016) Impacts of Fertilization
638 Regimes on Arbuscular Mycorrhizal Fungal (AMF) Community Composition
639 Were Correlated with Organic Matter Composition in Maize Rhizosphere Soil.
640 *Frontiers in Microbiology*, **7**, 1840.
- 641
- 642

643 **Figure captions**644 Figure in Box

645 An example of a network (left) and a soil food web (right). A network consists of nodes
646 (circles) that are connected by edges (lines) through weak and strong, positive and
647 negative interactions; here, strong connections have a heavier line weight than weak
648 connections, positive interactions are grey and negative interactions are black. Modules
649 are indicated by different colours, and connectors between modules are in red. Soil food
650 webs are traditionally represented by three compartments, as indicated by arrow
651 colours. The fungal and bacterial energy channels (yellow and orange arrows
652 respectively) are fuelled by aboveground litter, root litter, and root exudates (grey
653 ellipse); the root energy channel (purple arrows) is fuelled by live roots. However,
654 recent evidence suggests that bacteria can feed on fungal hyphae, and protozoa are part
655 of both the fungal and the bacterial energy channel (as indicated by grey dashed
656 arrows), thus increasing the number of connections within the soil food web and
657 challenging the concept of distinct energy channels.

658

659 Figure 1

660 Rhizosphere networks consist of relatively few but highly abundant and connected
661 species that are recruited from the much more diverse but weakly connected bulk soil
662 network. Connections between rhizosphere and bulk soil networks (indicated by red
663 dotted lines) are crucial for the recruitment of functional rhizosphere networks.
664 Understanding and manipulating network structure of both rhizosphere and bulk soil
665 networks in agricultural soils, and the connections between them, is a promising avenue
666 for optimising healthy soils and the benefits they provide for sustainable food
667 production.

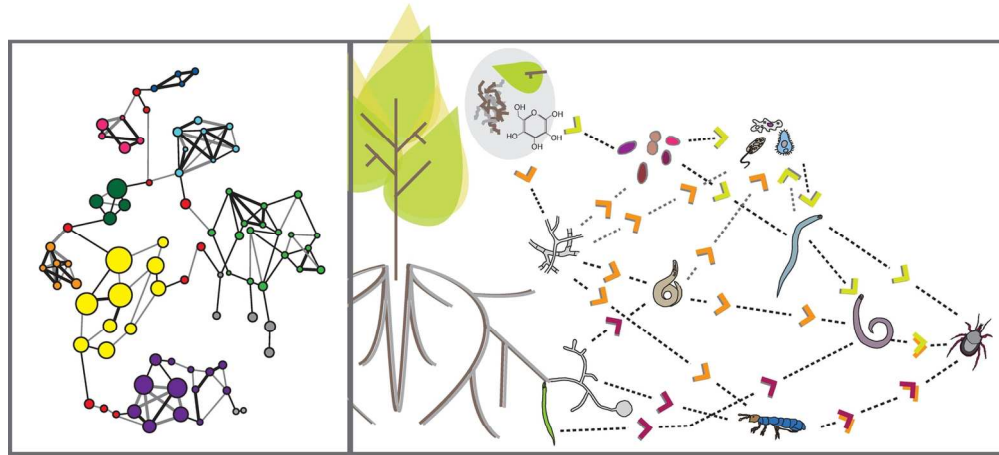


Figure in Box. !! † An example of a network (left) and a soil food web (right). A network consists of nodes (circles) that are connected by edges (lines) through weak and strong, positive and negative interactions; here, strong connections have a heavier line weight than weak connections, positive interactions 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 aboveground 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.!! †

144x82mm (300 x 300 DPI)

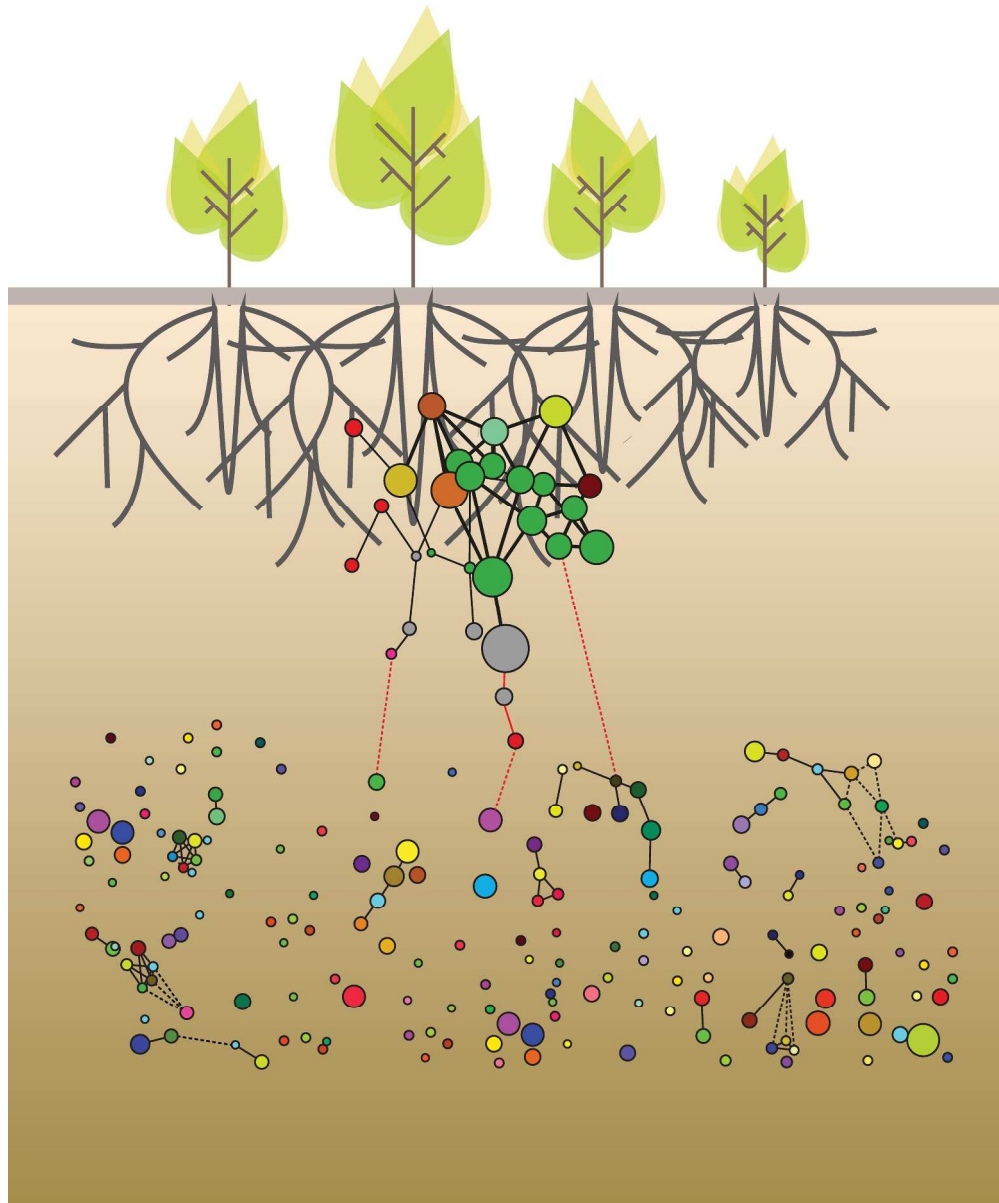


Figure 1. !! + Rhizosphere networks consist of relatively few but highly abundant and connected species that are recruited from the much more diverse but weakly connected bulk soil network. Connections between rhizosphere and bulk soil networks (indicated by red dotted lines) are crucial for the recruitment 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. !! +

258x310mm (300 x 300 DPI)