

1 Plant biodiversity as a tool to steer soil microbial communities for
2 sustainable agriculture

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10 **Abstract**

11 While the positive relationship between plant biodiversity and ecosystem functioning (BEF) is relatively
12 well-established, far less is known about the extent to which this relationship is mediated via below-
13 ground microbial responses to plant diversity. Limited evidence suggests that the diversity of soil
14 microbial communities is sensitive to plant community structure, and that diverse soil microbial
15 communities promote functions desired of sustainable food production systems such as enhanced carbon
16 sequestration and nutrient cycling. Here, we discuss available evidence on how plant diversity could be
17 utilized to purposefully guide soil biodiversity in agricultural systems that are typically depleted of
18 biodiversity, and are notoriously sensitive to both biotic and abiotic stressors. We outline the direct and
19 soil microbe-mediated mechanisms expected to promote a positive BEF relationship both above- and
20 below-ground. Finally, we identify management schemes based on ecological theory and vast empirical
21 support that can be utilized to maximize ecosystem functioning in agroecosystems via biodiversity
22 implementation schemes.

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24 **Keywords:**

25 Agriculture, biodiversity, sustainability, carbon cycling, cropping systems, agroecology

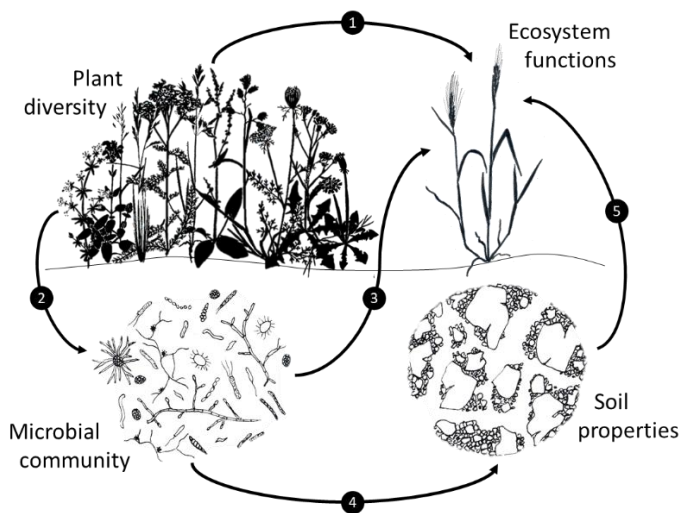
26 **Main**

27 Biodiversity stabilizes ecosystem productivity, and productivity-dependent ecosystem services¹.
28 Increasing evidence confirms that biodiversity stabilizes ecosystem functioning by increasing resistance
29 to climate events², and by diluting disease risks³. In contrast, agricultural systems are depleted of
30 biodiversity, and are notoriously sensitive to pathogens and pests⁴, as well as environmental stress such
31 as drought⁵⁻⁷. To guarantee food security to a growing global population and food habit changes⁸,
32 increases in yields must not further erode the natural capital upon which agriculture relies. Hence,
33 ecological intensification that supports and regulates ecosystem services is increasingly seen as one way
34 of achieving food security in an environmentally sustainable and climate-smart way^{9,10}. This would
35 allow transitioning away from increasing use of synthetic inputs that has characterized global
36 agricultural intensification, causing degradation of agroecosystems and its functions both within
37 agricultural environments¹¹ as well as beyond its boundaries. Currently the mechanisms underpinning
38 the biodiversity-ecosystem functioning relationships are under active discussion. While most research
39 has focused on above-ground mechanisms, current limited evidence suggests that plant diversity
40 interacts with below-ground microbial communities that in turn sustain and promote ecosystem
41 functioning both below- and above-ground¹²⁻¹⁵. Toward this end, here, we present a framework for
42 understanding how plant diversity could be utilized to guide environmentally-friendly agriculture both
43 directly via mechanisms operating above-ground, as well as those mediated by responses in below-
44 ground microbial communities (Figure 1).

45 A variety of mechanisms have been suggested to lead to positive diversity-ecosystem
46 functioning relationships^{31,32}. Primary productivity is the most intensively studied dimension of
47 ecosystem functioning, and biodiversity experiments have shown that with increasing plant diversity
48 productivity also increases³³. While diverse communities produce consistently high amounts of biomass,
49 species-poor communities show much more variability. There are certain species that produce
50 comparable amounts of biomass when grown alone or in diverse communities¹⁷. Including few such
51 productive species in diverse mixtures may promote the productivity through selection effects. In

52 addition, complementary interactions between species can enhance the productivity of most of the
53 species within the community^{34,35}. There is a wide variety of complementary interactions, but they can
54 be broadly classified into resource partitioning (e.g. through different root morphology and depth),
55 biotic feedbacks (e.g. the hosting of pollinators or N-fixation by legumes) and abiotic facilitation (e.g.
56 through the microclimate)^{32,36}. Similar mechanisms are likely to influence other ecosystem functions as
57 well³⁷⁻³⁹. Biodiversity may also promote ecosystem stability and productivity by increasing resistance
58 and resilience to biotic and abiotic stressors (the insurance hypothesis)⁴⁰. An analysis of 46 experiments
59 that manipulated grassland plant diversity found that biodiversity increased ecosystem resistance for a
60 broad range of climate events². Increasing biodiversity is often associated with a reduction in the risk of
61 an individual's disease risk, a phenomenon known as the dilution effect⁴¹. The dilution effect is most
62 commonly observed for biodiversity gradients generated by disturbances resulting in biodiversity loss³.
63 Growing evidence suggests that changes in the structure of host communities and in the composition of
64 functional traits following biodiversity loss rather than species richness *per se*, can explain when a
65 dilution effect should be observed⁴²⁻⁴⁸.

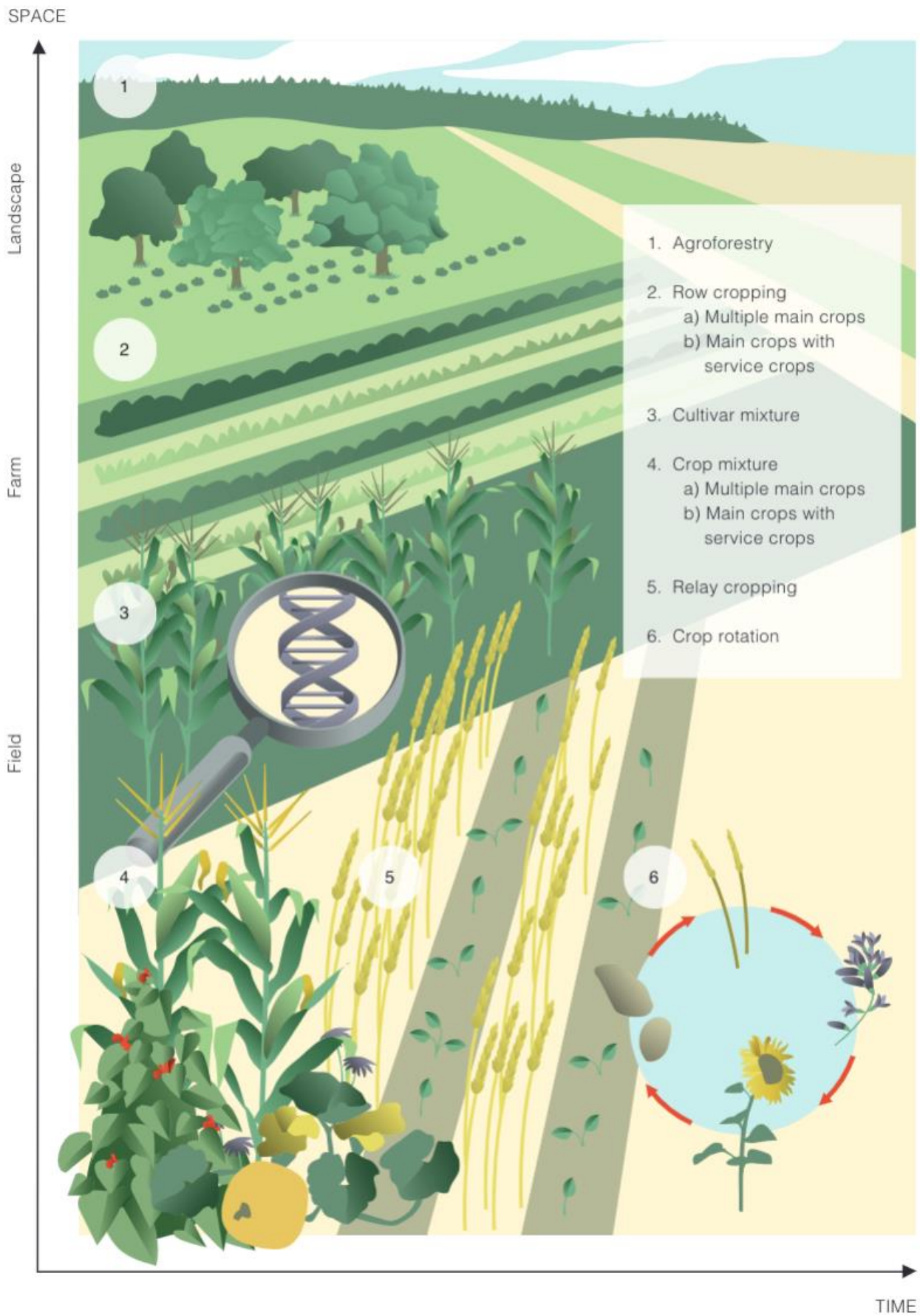
66 The relevance of biodiversity in provisioning ecosystem functions grows when larger spatial and
67 temporal scales are considered^{49,50}. As environmental conditions vary with time, stress intensity changes
68 as well. High levels of stress have been shown to have a greater negative effect on low-diversity than
69 high-diversity communities^{35,51-53}. The relevance of the above-mentioned insurance dimension of
70 diversity also increases when considering the ability of ecosystems to maintain their functions over
71 years or decades^{40,54}. Moreover, complementary interactions between species become increasingly
72 important at longer time scales^{35,50}. More studies and long-term experimental sites are needed not only
73 to further evaluate how complementarity and selection effects change over time but also how other
74 ecosystem functions other than productivity may be impacted by diversity through time.



- 1 Plant diversity is crucial for a stable provisioning of various ecosystem functions.
- 2 Different microbial communities are associated with different plant species. The diversity and composition of the plant community should thus shape the diversity and composition of the soil microbial communities.
- 3 Soil microbial diversity can directly promote ecosystem functions such as decomposition, nutrient cycling or mitigation of greenhouse gas emissions.
- 4-5 The effects of soil microbial diversity on ecosystem function can be indirect via changes in soil properties such as soil aggregation.

75 **Figure 1. The pathways by which plant biodiversity links to ecosystem, functioning via both**
 76 **above- and below-ground.** Plant biodiversity is known to contribute to and stabilize the provisioning of
 77 ecosystem functions, such as biomass production, decomposition, soil carbon storage, dilution of fungal
 78 pathogens and insect herbivores or pollinator abundance^{16,17}. Many of these functions are crucial for
 79 agricultural production. It is becoming increasingly clear that plant community diversity and
 80 composition determines the composition of the soil microbial community. Plant traits such as
 81 productivity, physiology, root architecture, and the composition of root exudates are predictors of how
 82 plant species affect the soil microbial community¹⁸⁻²⁰. The diversity and composition of the plant
 83 community is expected to affect how soil microbial communities are structured. Plant diversity is
 84 associated with increased microbial biomass²¹ and respiration, and plant community functional
 85 composition is a strong predictor of mycorrhizal community composition²². Soil microbial communities
 86 in turn can directly promote ecosystem functions such as decomposition²³, nutrient cycling²⁴ or mitigate
 87 green-house gas emissions from the soil²⁵⁻²⁷. The influence of the soil microbial community on
 88 ecosystem functioning might occur through direct interactions with the plant community or via
 89 alterations in the soil properties, such as soil aggregation, which can impact, for example, water and
 90 oxygen percolation in soil with consequences for plant growth. Soil microbial diversity has been found
 91 to positively affect soil aggregation²⁸, community growth efficiency²⁹ and formation of new soil organic
 92 matter³⁰ that is more persistent to decomposition.

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 100 **Figure 2. Agricultural diversification in space and time.** Modern agriculture often relies on large
 101 fields of uniform crops and thus has large potential for diversification. Diversification can occur at
 102 varying spatial and temporal scales: At a large spatial scale, 1. agroforestry systems incorporating trees
 103 and shrubs on and between the agricultural fields and 2. the spatial arrangement of fields or rows of a)
 104 different main crops or b) main crops and service crops can create diverse landscapes. Within fields, the
 105 mixture of 3) different cultivars of the same crop or 4) multiple different species – be it a) multiple main
 106 crops or b) main crops with service crops – can contribute to local diversification. When different crops
 107 grow on the same field, but temporally separated, diversification occurs in time: 5) in relay cropping
 108 systems a subsequent crop is planted before the prior crop is harvested. Thus, there is a time period
 109 when both crops grow together, but not throughout their entire life cycles, so diversification occurs both
 110 in space and time. 6) In crop rotation, different crops are sown after the harvest of the prior crop and
 111 diversification occurs solely in time.



113 **Can sustainability of agroecosystems be improved by increasing plant diversity?**

114 Many of the ecosystem functions which diverse ecosystems provide, such as pollination, nutrient
115 retention, weed control or disease suppression are important for agricultural crop production^{55,56}.
116 Modern agriculture has been developed to maximize yield per hectare, and current crops produce high
117 yields in monocultures when supplemented with nutrients and controlled by pesticides. In such a
118 scenario, the addition of species will likely provide limited benefits in terms of productivity⁵⁵. Indeed, in
119 many agricultural systems diversification does not increase yield of the main crop⁵⁷. However, diversity
120 has the potential to improve other ecosystem functions in agricultural monocultures, potentially by
121 reducing the need for external inputs such as pesticides, irrigation or fertilization⁵⁵. To date, it is well-
122 established that increasing the diversity of crops - even from a monoculture to a mixture of two cultivars
123 - reduces disease levels significantly⁵⁸⁻⁶⁰. A recent synthesis demonstrated that indices of functional
124 diversity, particularly the distribution of trait abundances, were strong predictors of agricultural
125 ecosystem multifunctionality that included weed suppression, nitrogen (N) retention, inorganic N
126 supply, increase in above-ground biomass, and sometimes even yield⁶¹. In Figure 2 we outline current
127 management options that increase plant diversity in space and time in agricultural cropping systems.

128 While there is more or less evidence that any of these diversification measures are beneficial for
129 the provisioning of one or the other ecosystem function, we lack a general framework to maximize
130 multiple ecosystem functions without compromising crop yields. There is evidence that biodiversity is
131 especially important when multiple ecosystem functions should be provided simultaneously^{62,63}.

132 Often the provisioning of a given ecosystem function depends at least to some degree on the
133 capacity of each species in the community to provide this function and on the relative abundance of
134 these species⁶⁴. Since different species are good at supporting different functions^{37,65,66} and
135 abundance of each species is limited by the presence of multiple other species, “Jack-of-all-trades”
136 effects are likely: diverse communities are good at providing multiple functions at intermediate
137 levels, while low diversity communities are better at maximizing single or few functions⁶⁴.

138 However, complementarity mechanisms between species, such as for example facilitation can help

139 to provide ecosystem functions above simple additive effects in polycultures³². This implies that in
140 agricultural systems, where crop production usually is the main ecosystem function to be
141 maximized, the identity and abundance of the additional species added (thereafter service species)
142 in diversification schemes is essential to enhance functions other than crop production, without
143 simultaneously compromising crop yield. This requires a fundamental ecological understanding, a
144 clear definition of target ecosystem functions for a given agroecosystem and the choice of service
145 species accordingly. A good diversification scheme thus includes a combination of species to
146 enhance target functions and species, which support the crop species to continuously provide
147 relatively high levels of yield (complementarity effects). For example, (local) diversification has
148 been shown to enhance pest control, but this often leads to a trade-off with crop yield. This trade-off
149 can be alleviated by including legume species in the polyculture and pest control can be enhanced
150 while less compromising crop yields. Also, other trade-offs between different ecosystem functions
151 are possible, but can be alleviated by strategic choice of species and management practices⁶⁷.
152 Similar principles likely apply also for the use of different varieties in monoculture crops⁶⁸.

153 **Plant diversity effects on below-ground microbial communities**

154 Processes leading to positive BEF relationships can happen above ground, for example habitat
155 provisioning for natural enemies and pollinators or alterations in the microclimate, but there is also a
156 multitude of mechanisms that occur below ground, for example processes involved in resource
157 partitioning and decomposition or dilution of (below-ground) pathogens. Soil microbial communities
158 are involved in many of these below-ground processes and plant-soil feedbacks likely play a crucial role
159 in shaping BEF relationships as recently discussed by Thakur et al. (2021)¹².

160 Understanding the potential of plant diversity to promote below-ground microbial diversity and
161 ecosystem functions is highly relevant in food production systems where configuration of plant diversity
162 is under strict human control. Currently, there is a pressing need to identify how plant diversity could be
163 utilized to steer soil microbiomes to improve the growth, yield and resistance of crops, as well as

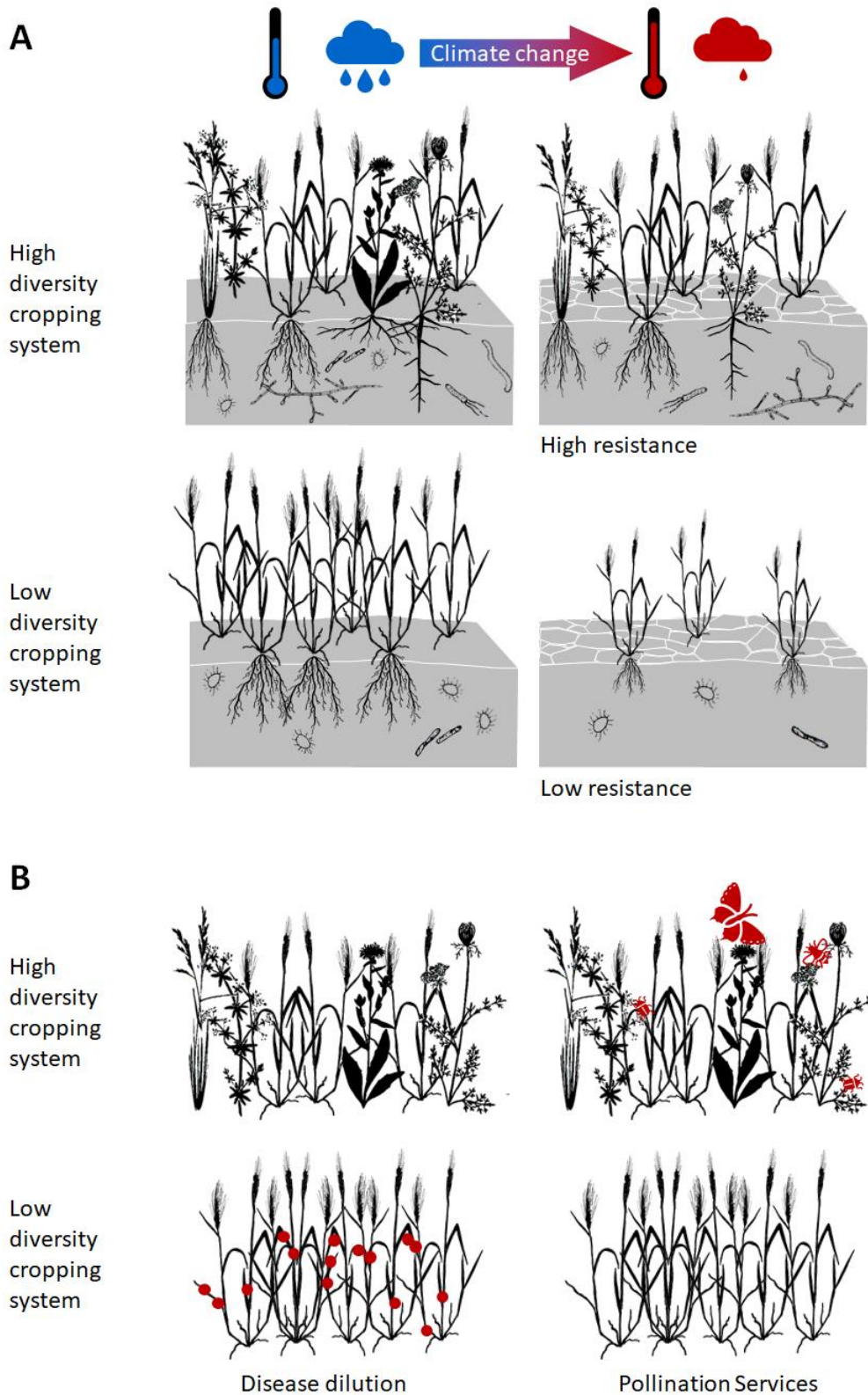
164 ecosystem functioning⁶⁹⁻⁷¹ (Figure 3). Beneficial soil microbes - namely fungi and bacteria - can
165 improve plant nutrient acquisition, defense, and stress tolerance⁷²⁻⁷⁴, as well as community level nutrient
166 capture⁷¹ and productivity⁷⁵. The targeted use of beneficial soil microbes in agricultural systems would
167 not incur the environmental and socioeconomic costs associated with agrichemical inputs used with
168 the same aims⁷⁶. However, agricultural soils typically host low densities of microbial symbionts due to
169 the disruptive impacts of tillage, chemical inputs, crop rotation patterns⁷⁷⁻⁸⁰, as well as potentially due to
170 the lack of plant diversity^{81,82}. While it is generally accepted that below-ground diversity, particularly of
171 fungal symbionts, has the potential to regulate plant assemblages and their diversity^{75,83}, far less is
172 known about how plant diversity in turn regulates below-ground microbial diversity⁷¹.

173 A few pioneering studies have demonstrated the extent to which plant species differ in how they
174 influence their soil microbiome^{18,71}. Numerous host plant traits have been found to associate with root
175 microbial diversity. Among these, root exudates that differ among plant species play a dominant role in
176 shaping the rhizosphere and eventually the soil microbiome^{19,20}. Plant functional type (e.g. for nodule
177 forming bacteria for legumes) can also explain variation in the soil microbiome, even to the extent that it
178 overrides the effects of plant species⁸⁴. In addition, plant productivity, physiology, and root architecture
179 are among traits that are found to associate with diversity of root microbial communities, generating
180 variation in microbial communities associated with different plant species¹⁸. Plant species may also
181 differ considerably in their affinity to form associations with beneficial microbes. Importantly, modern
182 crops are found to be less responsive to symbionts and exerting less robust partner choice than their
183 ancestors and wild relatives⁸⁵.

184 The variation detected among plant species in their associated below-ground microbial
185 communities suggests that above-ground diversity at the community level has the potential to drive
186 below-ground microbial diversity⁷¹. Indeed, the limited evidence to date has demonstrated that the
187 effects of plant diversity on the diversity of soil micro-organisms were most pronounced in the most
188 diverse plant communities, although differences could only be detected after a time lag. Plant species
189 functional grouping at the community level has also been found to be a strong predictor of arbuscular

190 mycorrhizal (AM) community composition²². The effects of plant diversity are not only evident at the
191 contemporary community level; AM fungal community assembly on focal plant species was influenced
192 by a legacy effect of neighboring plant species from the past⁸⁶. This is promising for management
193 schemes that implement diversity through rotations (see Figure 2, point 6).

194 There is a growing consensus that the key to understand the effects of plants on the below-
195 ground communities and their functions lies where the world of plants and soil microbes meet: the
196 rhizosphere^{71,87,88}. Considered one of the most dynamic interfaces of Earth, rhizosphere is the thin zone
197 of soil that encircles and is impacted by plant roots. Rhizodeposits - the rhizosphere products imparted
198 to the surrounding soil - contain a multitude of compounds including sugars, amino acids, organic acids,
199 as well as mucilage (i. e. polymerized sugar) and root dead cells that may strongly impact the activity
200 and composition of the microbial community in the rhizosphere⁷¹. The rhizodeposits signature is
201 species-specific⁸⁹, and chemical temporal succession in the rhizosphere of oat plants (*Avena barbata*)
202 was shown to interact with microbial substrate preference and ultimately drive microbial community
203 assembly⁹⁰. Cropping schemes are predominantly developed under highly-fertile conditions and via
204 suppression of soil pathogens, thus minimizing the potential contribution of interactions in the
205 rhizosphere to plant health and growth. When aiming to develop a more sustainable agriculture that
206 relies less on external inputs of pesticides and fertilizers, it is crucial to capitalize on multitrophic
207 rhizosphere-mediated interactions. The challenge ahead lies on re-establishing these interactions that are
208 weakened or lost due to consequences of breeding⁸⁵ and intensive agricultural practices⁹¹.



209

210 **Figure 3. Cropping system diversity and its ecosystem functions.** Diverse cropping systems are more
 211 resistant to climate perturbations of temperature and precipitation, being able to maintain higher crop
 212 yields even under these disturbances compared to low diverse systems. Plant-microbial interactions
 213 explain in part the capacity of plants to cope with the adverse abiotic conditions (A). High levels of
 214 biodiversity decrease disease risk also known as the dilution effect and ensure pollination services
 215 compared to low diverse systems (B).

216 **The effects of soil microbial diversity on ecosystem functioning**

217 In addition to the effects on microbial diversity, plant diversity is associated with increased microbial
218 activity enhancing biomass, respiration⁹² and carbon storage in soils^{14,93,94}. Biodiversity of soil microbes
219 may interact directly with plants or via their effects on soil properties (Fig. 1). Previously, it was argued
220 that a positive relationship would be observed between soil microbial diversity and soil functions if
221 those were controlled by a phylogenetically restricted group of microorganisms⁹⁵. However, more recent
222 studies are challenging this idea as some general processes of carbon cycling have been shown to be
223 dependent on microbial community composition^{29,96,13}. Thus, growing evidence suggests that soil
224 microbial diversity is associated with crucial functional aspects of soils for sustainable agriculture,
225 including suppression of pathogenic microbes^{97,23}, decomposition of plant matter²³, nutrient cycling⁹⁸,
226 mitigation of greenhouse gases²⁵⁻²⁷ and carbon sequestration (Box 1)⁹⁹. Diversity of soil microorganisms
227 may impact both nutrient cycling crucial for plants as well as soil physical structure¹⁰⁰ that is typically
228 measured as soil aggregation. Soil aggregation reduces erosion and is considered an important
229 component of soil fertility and water retention capacity. There is increasing evidence that beneficial
230 microbes are a crucial component ensuring plant wealth and growth, by recycling nutrients, N fixation,
231 defense benefits, nutrient acquisition⁷¹).

232 During the last decade we've gained understanding in how microbial community composition
233 drive soil functioning, now more recent studies are evaluating the context-dependencies of this
234 relationship. For example, microbial diversity was shown to have a positive impact on carbon use
235 efficiency (CUE) but only in wet soils²⁸, showing that abiotic factors can modulate the diversity –
236 function relationship. The biotic context may also mediate these outcomes - changes in multitrophic
237 interactions between microorganisms and plants was shown to explain temporal variation of diversity
238 effects¹⁰¹. Considering that only 0.3% of soil ecological studies have quantified both diversity and
239 function²⁹, it is important to highlight that more holistic research is needed to increase our understanding
240 of the dependencies between biodiversity and function in soils. However, it is becoming increasingly
241 clear that soil microbial biodiversity is a promising – yet underutilized - component of sustainable

242 agriculture. A recent expert consensus statement concluded that understanding how climate change and
243 other human activities affect microorganisms as well as deciphering how microorganisms affect climate
244 change (including production and consumption of greenhouse gases) is essential for achieving an
245 environmentally sustainable future¹⁰².

Box 1: What is the role of soil microbial communities for the global carbon cycle in agroecosystems?

Soils are the largest and most dynamic terrestrial carbon (C) pool, storing 2000 Pg of C – more than the atmosphere and biosphere combined^{103,104}. While the net C input into soils is due to net primary productivity dominated by higher plants, soil microorganisms greatly contribute to the net C exchange between soil and atmosphere through the processes of decomposition and heterotrophic respiration. Natural CO₂ fluxes from soils are almost seven times higher than emissions due to the combustion of fossil fuels. This suggests that any small changes on these natural fluxes could have major implications for CO₂ concentration in the atmosphere and for the climate. Increases in soil organic matter decomposition and CO₂ emissions can be driven by agricultural practices. For example, deep ploughing enhances decomposition by increasing the oxygen level of soils and making previously inaccessible carbon accessible for microorganisms. Globally, soils could have lost between 40 and 90 Pg of C already due to agriculture¹¹³. As 40% of earth surface is utilized for agriculture¹⁰³, strategies to reduce CO₂ levels in the atmosphere must include management practices aiming to sequester some of this C back into soils.

Empirical evidence is slowly accumulating to demonstrate that high plant diversity results in higher levels of C stocks in soils in both long-term experimental sites^{93,112} and observations in natural ecosystems^{105–111}. While soils with high diversity of plants show high C stocks, it is the microorganisms living in soil that play a central role for this C sequestration¹¹⁵. Previous theories focused on the recalcitrance of less-reactive compounds and physical protection as controls of soil carbon stocks, while more recently the focus has shifted to highlight the importance of microbial-derived soil organic matter (SOM)¹¹³. When microbes metabolize soil C inputs (i.e., leaf litter, root exudates, organic amendments, or pre-existing C compounds), a proportion of C is allocated to growth, and the resulting biomass can contribute to further building the SOC pool once exuded by microbes or upon cell death (Figure 4). In a recent study, Domeignoz-Horta *et al.* (2020) showed that a higher fraction of carbon is allocated to growth in relation to respiration when microbial diversity is high^{94,114}. Thus, if above ground plant diversity or other management practices can be applied to enhance belowground microbial diversity, it is likely that more C will be sequestered due to higher microbial community growth efficiency (Figure

4). With respect to microbial control of SOM formation, emerging theories focus on molecular functional diversity of SOM, spatial heterogeneity and temporal variability^{14,33}. Lehman *et al.*, 2020 recently proposed that greater diversity of C compounds could increase the metabolic costs necessary for its decomposition, resulting in remaining C in soil that could be potentially degraded but is not due to low energetic gains. A recent study corroborates this new theory demonstrating that bacterial community composition explained the signature of newly-formed SOM during microbial growth and that more diverse communities generated more persistent SOM^{14,93}. This same study highlights the importance of fungal x bacterial interactions for the decomposition and generation of new stable SOM. These findings provide insight on how to manage soils for maximum biological diversity as a means of building persistent SOM stocks in agriculture.

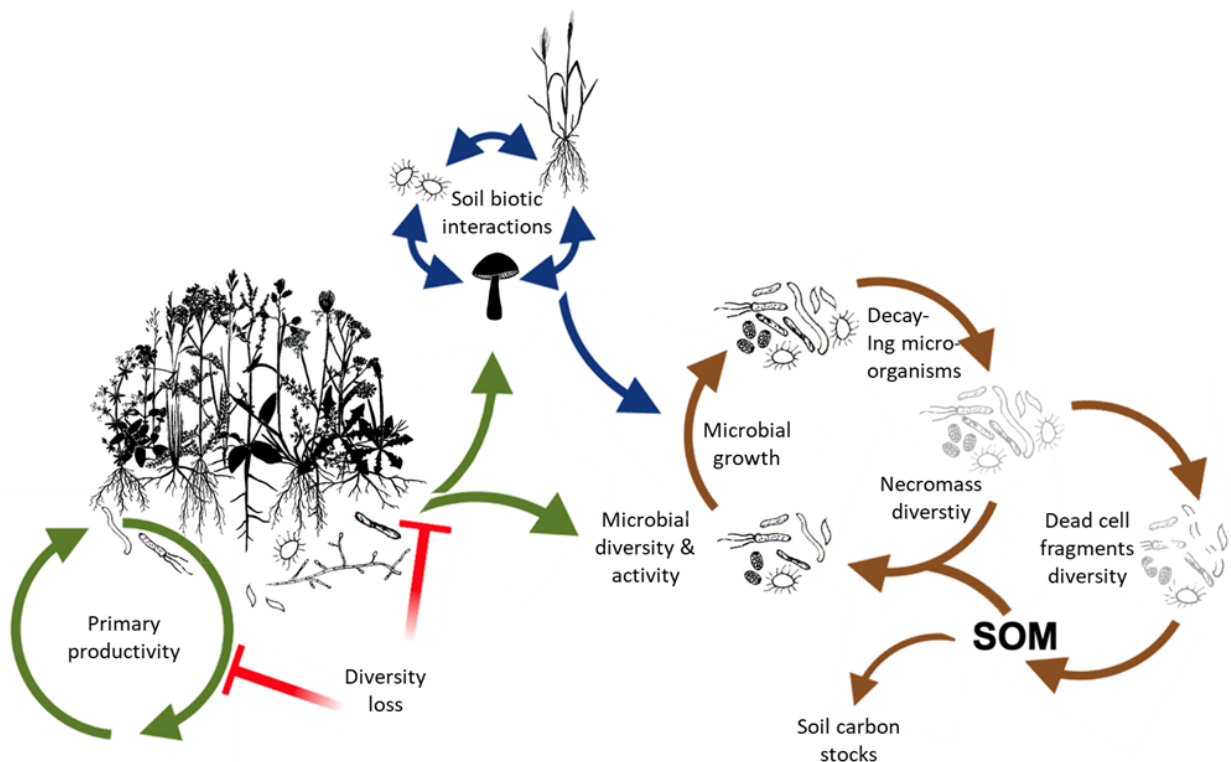


Figure 4. Plant diversity impact on soil carbon cycling. Plant diversity impact multitrophic interactions and microbial community assembly and growth. A more diverse signature of rhizodeposits will result in a more active microbial nutrient cycling, impacting positively microbial community growth efficiency and the formation of more complex necromass, which will form SOM that is more persistent to degradation. Red arrows represent negative impact of plant diversity loss on plant-driven processes (green arrows). A high diverse plant community result in more positive soil multitrophic interactions (blue arrows) which will impact soil carbon cycling (brown arrows).

247 **How to implement diversity into agroecosystems?**

248 Biodiversity-ecosystem functioning relationships often display a positive asymptotic relationship. This
249 means that the biggest benefits of additional species occur in species-poor communities^{65,17}. Large
250 agricultural fields consisting of monoculture have thus large potential for improved ecosystem
251 functioning through diversification⁵⁵. Diversification in agriculture can be achieved through various
252 measures at different spatial and temporal scales (Figure 2). Here, our intent is to highlight the potential
253 of plant diversity for a more sustainable agriculture via both above- and below-ground mechanisms.
254 However, we acknowledge that benefits of diversification will depend on how it is combined with other
255 management practices, including conservation tillage, re-use of crop residues, and integrated pest
256 management¹¹⁶.

257 Agroforestry (Figure 2, point 1), where trees or shrubs are incorporated into crop production,
258 can provide erosion control, enhance soil fertility and promote biodiversity of other organismal groups
259 in agriculture¹¹⁷. Row cropping of different main crops (Figure 2 point 2a) can increase yield, reduce the
260 need for fertilizer¹¹⁸ and promote diversity of mycorrhizal fungi¹¹⁹. Sometimes species other than main
261 crops are needed for the provision of ecosystem services aside from crop production (Figure 2, point
262 2b), for example the use of flower strips to promote pollination or pest control¹²⁰. Within a field,
263 mixtures of different varieties of a crop species (Figure 2, point 3) have been shown to increase crop
264 yield and stress resistance¹²¹, reduce disease pressure⁵⁸ and improve human nutrition¹²². Combinations
265 of functionally distinct varieties have proven especially good at providing stable high yield^{68,121}.
266 Similarly, mixtures of different crop species (Figure 2, point 4) can increase yield¹²³, reduce pest
267 pressure¹²⁴, fertilizer need and nutrient leaching¹²⁵. Sometimes, species other than the main crop, so-
268 called service crops, can help to promote ecosystem functions. For example, undersown Italian ryegrass
269 has been shown to prevent nutrient leaching in cereal fields¹²⁶. It is likely that the mixture of crops with
270 complementary traits provide most benefits⁶⁶.

271 Diversification in time includes relay cropping (Figure 2, point 5) and crop rotation (Figure 2,
272 point 6), which can include the use of cover crops between main crops. Relay cropping can help to gain

273 benefits of row cropping or mixed cropping, while reducing negative effects such as competition
274 between the crops, by growing multiple crops together for only a part of the growing period^{118,127}. Crop
275 rotation can prevent large pest populations from establishing over time, optimize resource use and avoid
276 self-toxicity¹²⁸. Ground-covering crops between intervals of successive cash main crops sustain soil
277 quality and productivity by reducing erosion and nutrient loss and by enhancing soil C and N contents,
278 and microbial biomass^{129,80}. Crop rotations are thus a cornerstone of sustainable agroecosystems^{80,130}
279 with a long-standing history, but developments such as the availability of chemical inputs and
280 specialized machinery together with economic market trends have led to shorter and simpler rotation
281 cycles with often negative consequences for crop yield¹²⁸.

282 Different diversification measures can also be successfully combined. For example, push-pull
283 methods to reduce natural enemy damage combine diversification at two spatial scales: they mix crop
284 species with service species that repel insect pest and have strips of another species, which lures the
285 pests away from the crops surrounding the crop field¹³¹. Another example is the use of diverse cover
286 crop mixtures within crop rotations to provide more ecosystem functions than the use of simpler cover
287 crop mixtures⁶⁶. It seems that there are many cases where diversification at different spatial and
288 temporal scales jointly yield the best outcomes⁵⁶.

289 **Future directions**

290 It is becoming increasingly clear that promoting plant diversity in agricultural systems has the potential
291 to drive soil microbial diversity, and jointly the above- and below-ground diversity are expected to
292 enhance ecosystems functions desired of sustainable cropping systems and their stable provisioning over
293 time– e.g. productivity, disease resistance and nutrient cycling. However, there are still two major
294 knowledge gaps that we discuss below.

295 *Context dependencies of the soil microbial diversity – soil ecosystem functioning relationships*

296 Growing evidence shows that soil microbial diversity promotes single soil ecosystem functions, and
297 overall multifunctionality¹³². It is also known that plant species differ in how they influence the soil

298 microbiome depending on their functional traits¹⁸, plant functional type⁸⁴ and their root exudates¹⁹. It
299 should thus be possible to use plants to modulate the soil microbiome and with this promote ecosystem
300 functioning. However, it is difficult to predict the outcome of these plant-soil feedbacks, which may be
301 highly context dependent⁷¹). For example, bacterial diversity promoted carbon use efficiency only in
302 wet soils, and diverse AMF communities can switch from beneficial to antagonistic under drought
303 conditions for their crop host¹³³. Consequently, further research is needed to (1) delineate the
304 mechanisms responsible for the relationship between diversity and specific soil functions, and to (2)
305 determine the context-dependencies of such relationship for the multiple soil functions. Global change,
306 especially climate change might disrupt the associations between soil microbes and the plants¹³⁴.
307 Understanding the mechanisms behind diversity effects is crucial in order to predict how global changes
308 influence plant-soil feedbacks and to design agroecosystems which are robust to global change.

309 *Application of ecological knowledge to agricultural practices*

310 Despite the reliance of agriculture on ecosystem functions and the large potential for enhanced
311 functioning in agroecosystems, thus far knowledge regarding biodiversity-ecosystem functioning
312 relationships has had little impact on agricultural practices. The reason for this is likely a mismatch
313 between the focus of ecological research and farmers' interests⁷⁶. In order to be implemented,
314 diversification schemes must prove direct economic benefit for crop farming in terms of enhanced yield
315 or reduced need for chemical inputs, without causing implementation costs that exceed the benefits⁷⁶.
316 There is a clear need to bridge that gap between ecological and agricultural research.

317 A factor that might reduce the benefits provided by diversification is that many agricultural
318 species have to some degree lost the ability to cooperate with microbial symbionts, likely because the
319 services provided by these services have been replaced by external inputs. Thus, it remains unclear to
320 what extent agricultural species are responsive to these microbial associations, and can benefit from
321 diversification⁸⁵. Plant breeding research should focus on traits that promote beneficial plant-microbe
322 interactions, as well as plant-plant interactions that are critical for biodiversity-ecosystem functioning
323 relationships.

324 Further, farming practices such as fertilization or tillage on their own affect the diversity and
325 composition of soil microbial communities¹³⁵ and might decouple plant-plant and plant-microbial
326 interactions. For example, overfertilization can inhibit mycorrhizal colonization and the formation of
327 nodules in legumes¹³⁶ and promote greenhouse gas emissions¹³⁷. Such agricultural practices thus add
328 a layer of complexity to the soil-mediated diversity effects on ecosystem functioning that need to be
329 considered when studying and designing diverse agroecosystems.

330 Finally, we see a great need for integrating the knowledge of different disciplines in order to
331 understand how changes in the plant community composition in agroecosystems cascade through soil
332 microbial food webs and ultimately affect the provision of ecosystem functions.

333 **Conclusions**

334 The motivation behind this Perspective was to bring together insights from biodiversity-ecosystem
335 functioning research spanning both plant and microbial ecology to gain understanding of how plant
336 diversity could be used to guide ecosystem functioning not only above- but also below-ground in
337 agricultural settings. The effects of plant diversity on ecosystem functioning above-ground have been
338 previously reviewed³¹, and current theory and empirical support provide a framework for developing
339 sustainable agricultural strategies. However, there are major gaps in current knowledge in how below-
340 ground effects contribute to – and could be managed – to promote sustainable agriculture. These need to
341 be addressed to reliably predict conditions under which we can reach the desired outcomes.

342 Uncertainties include the efficacy related to the different management practises described in Figure 2
343 with respect to below-ground processes, and as well as the context dependency – including abiotic,
344 biotic and cultural – that needs to be accounted for to develop general strategies to guide sustainable
345 agriculture. Nevertheless, limited data emerging from different fields highlight that plant diversity could
346 be purposefully used to guide soil biodiversity, and it would be short-sighted not to take advantage of
347 this potentially highly effective yet environmentally friendly and cost-effective management strategy at
348 a time when the need for sustainable agriculture is in greater demand than ever before.

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