Utilizing principles of Biodiversity Science to Guide Soil Microbial Communities for Sustainable Agriculture

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Abstract

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

Keywords:

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

Main

Biodiversity stabilizes ecosystem productivity, and productivity-dependent ecosystem services[1]. Increasing evidence confirms that biodiversity stabilizes ecosystem functioning by increasing resistance to climate events[2], and by diluting disease risks[3]. In contrast, agricultural systems are depleted of biodiversity, and are notoriously sensitive to pathogens and pests[4], as well as environmental stress such as drought[5–7]. To guarantee food security to a growing global population and food habit changes[8], increases in yields must not further erode the natural capital upon which agriculture relies. Hence, ecological intensification that supports and regulates ecosystem services is increasingly seen as one way of achieving food security in an environmentally sustainable and climate-smart way[9,10]. This would allow transitioning away from increasing use of synthetic inputs that has characterized global agricultural intensification, causing degradation of agroecosystems and its functions both within agricultural environments[11] as well as beyond its boundaries. Currently the mechanisms underpinning the biodiversity-ecosystem functioning relationships are under active discussion. While most research has focused on above-ground mechanisms, current limited evidence suggests that plant diversity interacts with below-ground microbial communities that in turn sustain and promote ecosystem functioning both below- and above-ground[12–15]. Toward this end, here, we present a framework for understanding how plant diversity could be utilized to guide environmentally-friendly agriculture both directly via mechanisms operating above-ground, as well as those mediated by responses in below-ground microbial communities (Figure 1).

A variety of mechanisms have been suggested to lead to positive diversity-ecosystem functioning relationships[31,32]. Primary productivity is the most intensively studied dimension of ecosystem functioning, and biodiversity experiments have shown that with increasing plant diversity productivity also increases[33]. While diverse communities produce consistently high amounts of biomass, species-poor communities show much more variability. There are certain species that produce comparable amounts of biomass when grown alone or in diverse communities[17]. Including few such productive species in diverse mixtures may promote the productivity through selection effects. In addition, complementary interactions between species can enhance the productivity of most of the species within the community[34,35]. There is a wide variety of complementary interactions, but they can be broadly classified into resource partitioning (e.g. through different root morphology and depth), biotic feedbacks (e.g. the hosting of pollinators or N-fixation by legumes) and abiotic facilitation (e.g. through the microclimate)[32,36]. Similar mechanisms are likely to influence other ecosystem functions as well[37–39]. Biodiversity may also promote ecosystem stability and productivity by increasing resistance and resilience to biotic and abiotic stressors (the insurance hypothesis)[40]. An analysis of 46 experiments that manipulated grassland plant diversity found that biodiversity increased ecosystem resistance for a broad range of climate events[2]. Increasing biodiversity is often associated with a reduction in the risk of an individual's disease risk, a phenomenon known as the dilution effect[41]. The dilution effect is most commonly observed for biodiversity gradients generated by disturbances resulting in biodiversity loss[3]. Growing evidence suggests that changes in the structure of host communities and in the composition of functional traits following biodiversity loss rather than species richness *per se*, can explain when a dilution effect should be observed[42–48].

The relevance of biodiversity in provisioning ecosystem functions grows when larger spatial and temporal scales are considered[49050]. As environmental conditions vary with time, stress intensity changes as well. High levels of stress have been shown to have a greater negative effect on low-diversity than high-diversity communities[35,51–53]. The relevance of the above-mentioned insurance dimension of diversity also increases when considering the ability of ecosystems to maintain their functions over years or decades[40,54]. Moreover, complementary interactions between species become increasingly important at longer time scales[35,50]. More studies and long-term experimental sites are needed not only to further evaluate how complementarity and selection effects change over time but also how other ecosystem functions other than productivity may be impacted by diversity through time.

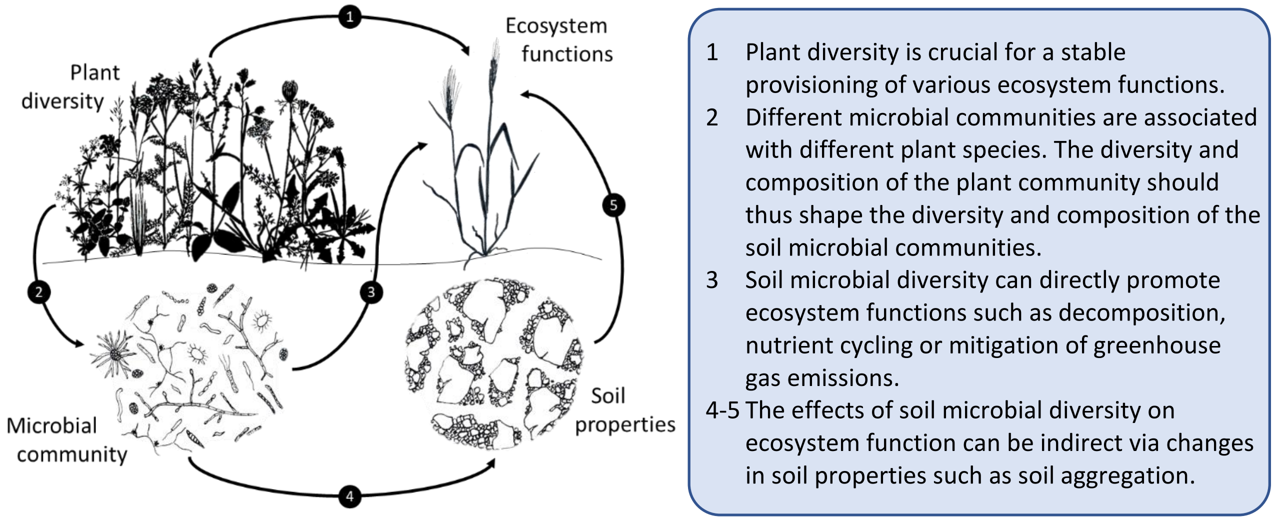
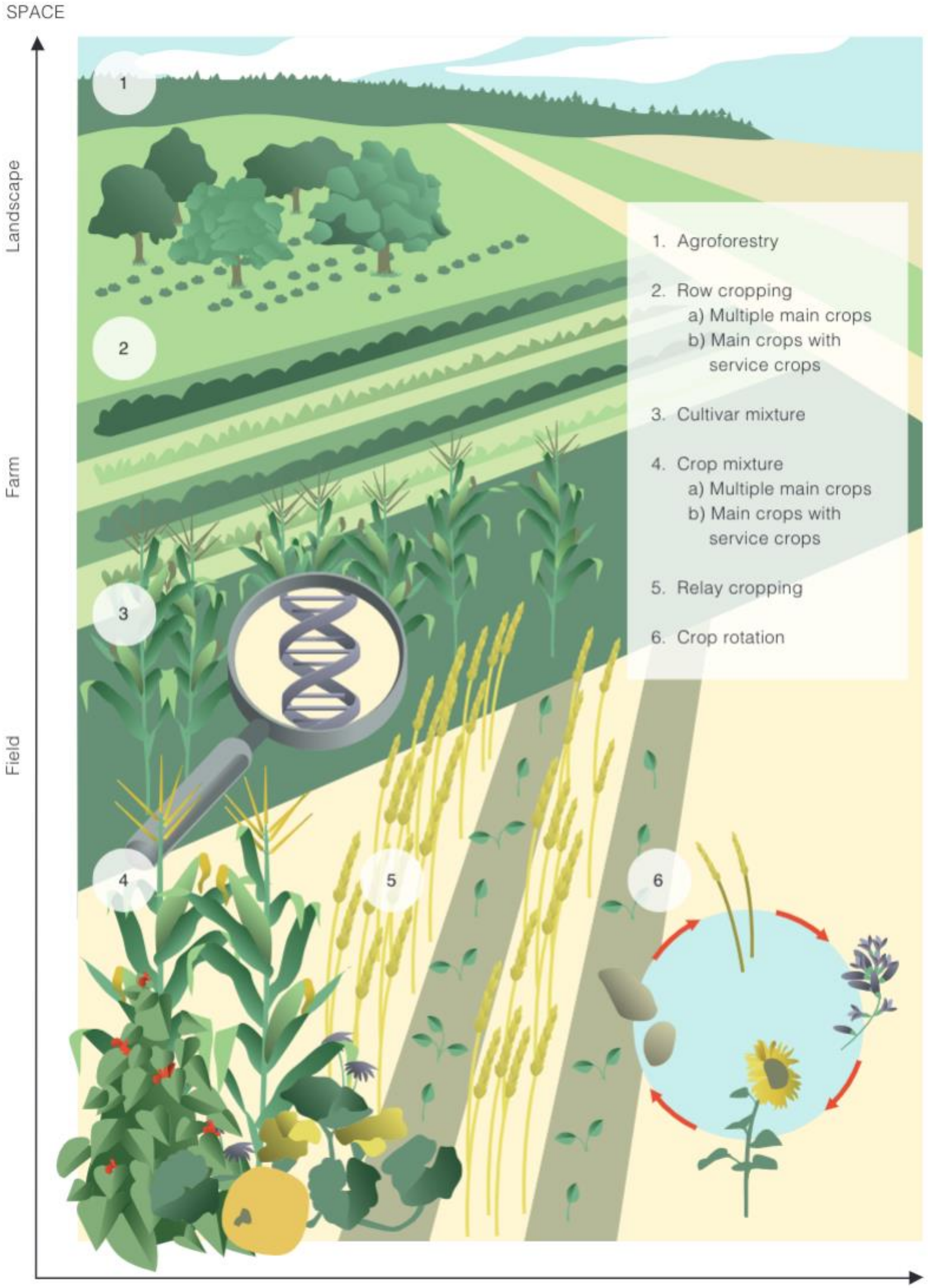


Figure 1. The pathways by which plant biodiversity links to ecosystem, functioning via both above- and below-ground. Plant biodiversity is known to contribute to and stabilize the provisioning of ecosystem functions, such as biomass production, decomposition, soil carbon storage, dilution of fungal pathogens and insect herbivores or pollinator abundance[16,17]. Many of these functions are crucial for agricultural production. It is becoming increasingly clear that plant community diversity and composition determines the composition of the soil microbial community. Plant traits such as productivity, physiology, root architecture, and the composition of root exudates are predictors of how plant species affect the soil microbial community[18–20]. The diversity and composition of the plant community is expected to affect how soil microbial communities are structured. Plant diversity is associated with increased microbial biomass21 and respiration, and plant community functional composition is a strong predictor of mycorrhizal community composition[22]. Soil microbial communities in turn can directly promote ecosystem functions such as decomposition[23], nutrient cycling[24] or mitigate green-house gas emissions from the soil[25–27]. The influence of the soil microbial community on ecosystem functioning might occur through direct interactions with the plant community or via alterations in the soil properties, such as soil aggregation, which can impact, for example, water and oxygen percolation in soil with consequences for plant growth. Soil microbial diversity has been found to positively affect soil aggregation[28], community growth efficiency[29] and formation of new soil organic matter30 that is more persistent to decomposition.

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


SPACE
Landscape
Farm
Field
TIME
1
2
3
4
5
6
1. Agroforestry
2. Row cropping
a) Multiple main crops
b) Main crops with service crops
3. Cultivar mixture
4. Crop mixture
a) Multiple main crops
b) Main crops with service crops
5. Relay cropping
6. Crop rotation

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Can sustainability of agroecosystems be improved by increasing plant diversity?

Many of the ecosystem functions which diverse ecosystems provide, such as pollination, nutrient retention, weed control or disease suppression are important for agricultural crop production[55,56]. Modern agriculture has been developed to maximize yield per hectare, and current crops produce high yields in monocultures when supplemented with nutrients and controlled by pesticides. In such a scenario, the addition of species will likely provide limited benefits in terms of productivity[55]. Indeed, in many agricultural systems diversification does not increase yield of the main crop[57]. However, diversity has the potential to improve other ecosystem functions in agricultural monocultures, potentially by reducing the need for external inputs such as pesticides, irrigation or fertilization[55]. To date, it is well-established that increasing the diversity of crops - even from a monoculture to a mixture of two cultivars - reduces disease levels significantly[58–60]. A recent synthesis demonstrated that indices of functional diversity, particularly the distribution of trait abundances, were strong predictors of agricultural ecosystem multifunctionality that included weed suppression, nitrogen (N) retention, inorganic N supply, increase in above-ground biomass, and sometimes even yield[61]. In Figure 2 we outline current management options that increase plant diversity in space and time in agricultural cropping systems.

While there is more or less evidence that any of these diversification measures are beneficial for the provisioning of one or the other ecosystem function, we lack a general framework to maximize multiple ecosystem functions without compromising crop yields. There is evidence that biodiversity is especially important when multiple ecosystem functions should be provided simultaneously[62,63]. Often the provisioning of a given ecosystem function depends at least to some degree on the capacity of each species in the community to provide this function and on the relative abundance of these species[64]. Since different species are good at supporting different functions[37,65,66] and abundance of each species is limited by the presence of multiple other species, “Jack-of-all-trades” effects are likely: diverse communities are good at providing multiple functions at intermediate levels, while low diversity communities are better at maximizing single or few functions[64]. However, complementarity mechanisms between species, such as for example facilitation can help to provide ecosystem functions above simple additive effects in polycultures[32]. This implies that in agricultural systems, where crop production usually is the main ecosystem function to be maximized, the identity and abundance of the additional species added (thereafter service species) in diversification schemes is essential to enhance functions other than crop production, without simultaneously compromising crop yield. This requires a fundamental ecological understanding, a clear definition of target ecosystem functions for a given agroecosystem and the choice of service species accordingly. A good diversification scheme thus includes a combination of species to enhance target functions and species, which support the crop species to continuously provide relatively high levels of yield (complementarity effects). For example, (local) diversification has been shown to enhance pest control, but this often leads to a trade-off with crop yield. This trade-off can be alleviated by including legume species in the polyculture and pest control can be enhanced while less compromising crop yields. Also, other trade-offs between different ecosystem functions are possible, but can be alleviated by strategic choice of species and management practices[67]. Similar principles likely apply also for the use of different varieties in monoculture crops[68].

Plant diversity effects on below-ground microbial communities

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

Understanding the potential of plant diversity to promote below-ground microbial diversity and ecosystem functions is highly relevant in food production systems where configuration of plant diversity is under strict human control. Currently, there is a pressing need to identify how plant diversity could be utilized to steer soil microbiomes to improve the growth, yield and resistance of crops, as well as ecosystem functioning[69-71] (Figure 3). Beneficial soil microbes - namely fungi and bacteria - can improve plant nutrient acquisition, defense, and stress tolerance[72–74], as well as community level nutrient capture[71] and productivity[75]. The targeted use of beneficial soil microbes in agricultural systems would not concur the environmental and socioeconomic costs associated with agrichemical inputs used with the same aims[76]. However, agricultural soils typically host low densities of microbial symbionts due to the disruptive impacts of tillage, chemical inputs, crop rotation patterns[77–80], as well as potentially due to the lack of plant diversity[81,82]. While it is generally accepted that below-ground diversity, particularly of fungal symbionts, has the potential to regulate plant assemblages and their diversity[75,83], far less is known about how plant diversity in turn regulates below-ground microbial diversity[71].

A few pioneering studies have demonstrated the extent to which plant species differ in how they influence their soil microbiome[18,71]. Numerous host plant traits have been found to associate with root microbial diversity. Among these, root exudates that differ among plant species play a dominant role in shaping the rhizosphere and eventually the soil microbiome[19, 20]. Plant functional type (e.g. for nodule forming bacteria for legumes) can also explain variation in the soil microbiome, even to the extent that it overrides the effects of plant species[84]. In addition, plant productivity, physiology, and root architecture are among traits that are found to associate with diversity of root microbial communities, generating variation in microbial communities associated with different plant species[18]. Plant species may also differ considerably in their affinity to form associations with beneficial microbes. Importantly, modern crops are found to be less responsive to symbionts and exerting less robust partner choice than their ancestors and wild relatives[85].

The variation detected among plant species in their associated below-ground microbial communities suggests that above-ground diversity at the community level has the potential to drive below-ground microbial diversity[71]. Indeed, the limited evidence to date has demonstrated that the effects of plant diversity on the diversity of soil micro-organisms were most pronounced in the most diverse plant communities, although differences could only be detected after a time lag. Plant species functional grouping at the community level has also been found to be a strong predictor of arbuscular mycorrhizal (AM) community composition[22]. The effects of plant diversity are not only evident at the contemporary community level; AM fungal community assembly on focal plant species was influenced by a legacy effect of neighboring plant species from the past[86]. This is promising for management schemes that implement diversity through rotations (see Figure 2, point 6).

There is a growing consensus that the key to understand the effects of plants on the below-ground communities and their functions lies where the world of plants and soil microbes meet: the rhizosphere[71,87,88]. Considered one of the most dynamic interfaces of Earth, rhizosphere is the thin zone of soil that encircles and is impacted by plant roots. Rhizodeposits - the rhizosphere products imparted to the surrounding soil - contain a multitude of compounds including sugars, amino acids, organic acids, as well as mucilage (i. e. polymerized sugar) and root dead cells that may strongly impact the activity and composition of the microbial community in the rhizosphere[71]. The rhizodeposits signature is species-specific[89], and chemical temporal succession in the rhizosphere of oat plants (*Avena barbata*) was shown to interact with microbial substrate preference and ultimately drive microbial community assembly[90]. Cropping schemes are predominantly developed under highly-fertile conditions and via suppression of soil pathogens, thus minimizing the potential contribution of interactions in the rhizosphere to plant health and growth. When aiming to develop a more sustainable agriculture that relies less on external inputs of pesticides and fertilizers, it is crucial to capitalize on multitrophic rhizosphere-mediated interactions. The challenge ahead lies on re-establishing these interactions that are weakened or lost due to consequences of breeding[85] and intensive agricultural practices[91].

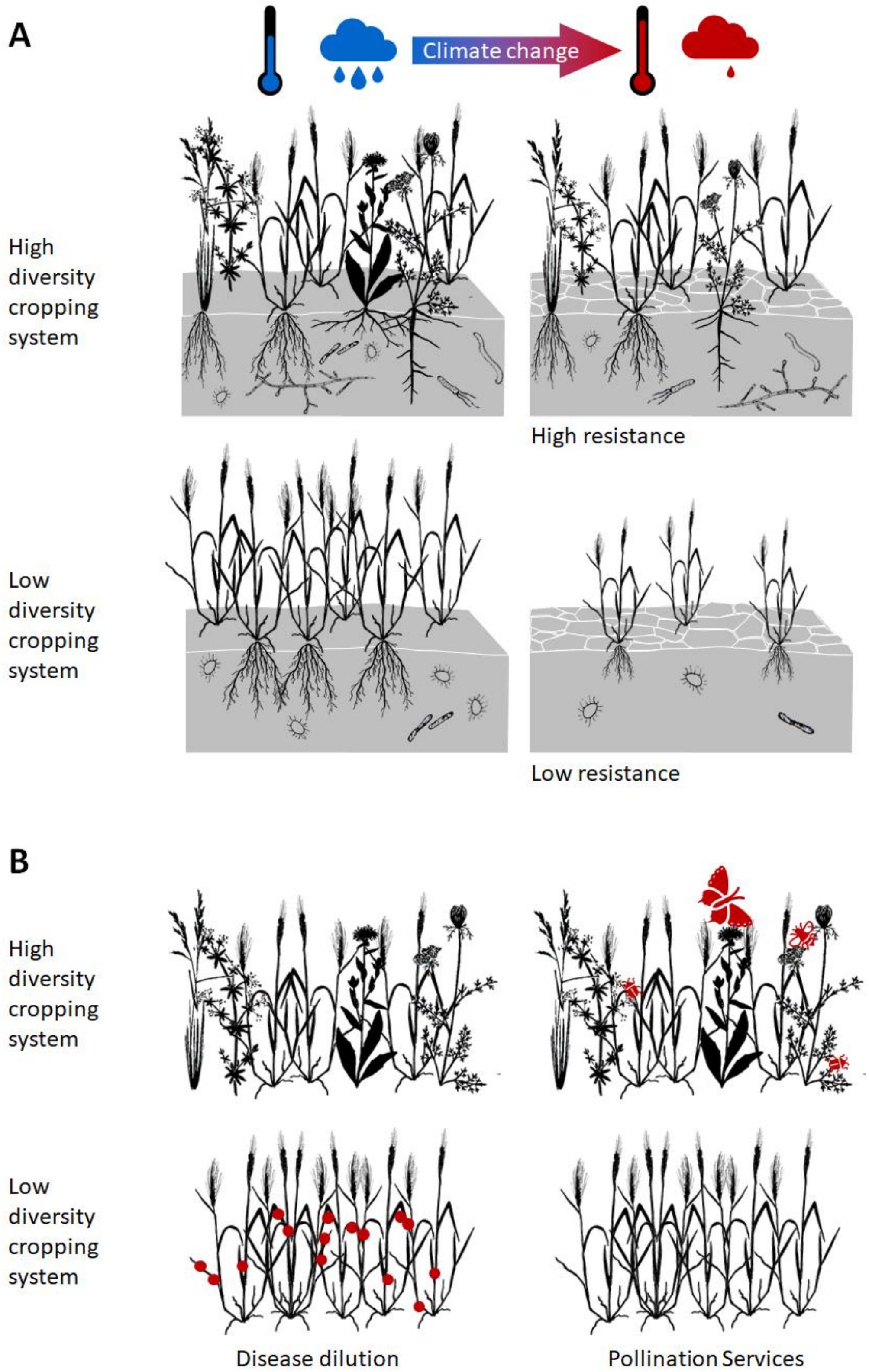

Figure 3. Cropping system diversity and its ecosystem functions. Diverse cropping systems are more resistant to climate perturbations of temperature and precipitation, being able to maintain higher crop yields even under these disturbances compared to low diverse systems. Plant-microbial interactions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

The effects of soil microbial diversity on ecosystem functioning

In addition to the effects on microbial diversity, plant diversity is associated with increased microbial activity enhancing biomass, respiration[92] and carbon storage in soils[14,93,94]. Biodiversity of soil microbes may interact directly with plants or via their effects on soil properties (Fig. 1). Previously, it was argued that a positive relationship would be observed between soil microbial diversity and soil functions if those were controlled by a phylogenetically restricted group or microorganisms[95]. However, more recent studies are challenging this idea as some general processes of carbon cycling have been shown to be dependent on microbial community composition[29,96,13]. Thus, growing evidence suggests that soil microbial diversity is associated with crucial functional aspects of soils for sustainable agriculture, including suppression of pathogenic microbes[97,23], decomposition of plant matter[23], nutrient cycling[98], mitigation of greenhouse gases[25-27] and carbon sequestration (Box 1)[99]. Diversity of soil microorganisms may impact both nutrient cycling crucial for plants as well as soil physical structure[100] that is typically measured as soil aggregation. Soil aggregation reduces erosion and is considered an important component of soil fertility and water retention capacity. There is increasing evidence that beneficial microbes are a crucial component ensuring plant wealth and growth, by recycling nutrients, N fixation, defense benefits, nutrient acquisition[71]).

During the last decade we've gained understanding in how microbial community composition drive soil functioning, now more recent studies are evaluating the context-dependencies of this relationship. For example, microbial diversity was shown to have a positive impact on carbon use efficiency (CUE) but only in wet soils[28], showing that abiotic factors can modulate the diversity – function relationship. The biotic context may also mediate these outcomes - changes in multitrophic interactions between microorganisms and plants was shown to explain temporal variation of diversity effects[101]. Considering that only 0.3% of soil ecological studies have quantified both diversity and function[29], it is important to highlight that more holistic research is needed to increase our understanding of the dependencies between biodiversity and function in soils. However, it is becoming increasingly clear that soil microbial biodiversity is a promising – yet underutilized - component of sustainable agriculture. A recent expert consensus statement concluded that understanding how climate change and other human activities affect microorganisms as well as deciphering how microorganisms affect climate change (including production and consumption of greenhouse gases) is essential for achieving an environmentally sustainable future[102].

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 CO_2 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 CO_2 concentration in the atmosphere and for the climate. Increases in soil organic matter decomposition and CO_2 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 agriculture[113]. As 40% of earth surface is utilized for agriculture[103], strategies to reduce CO_2 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 sequestration[115]. 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 contributes 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.

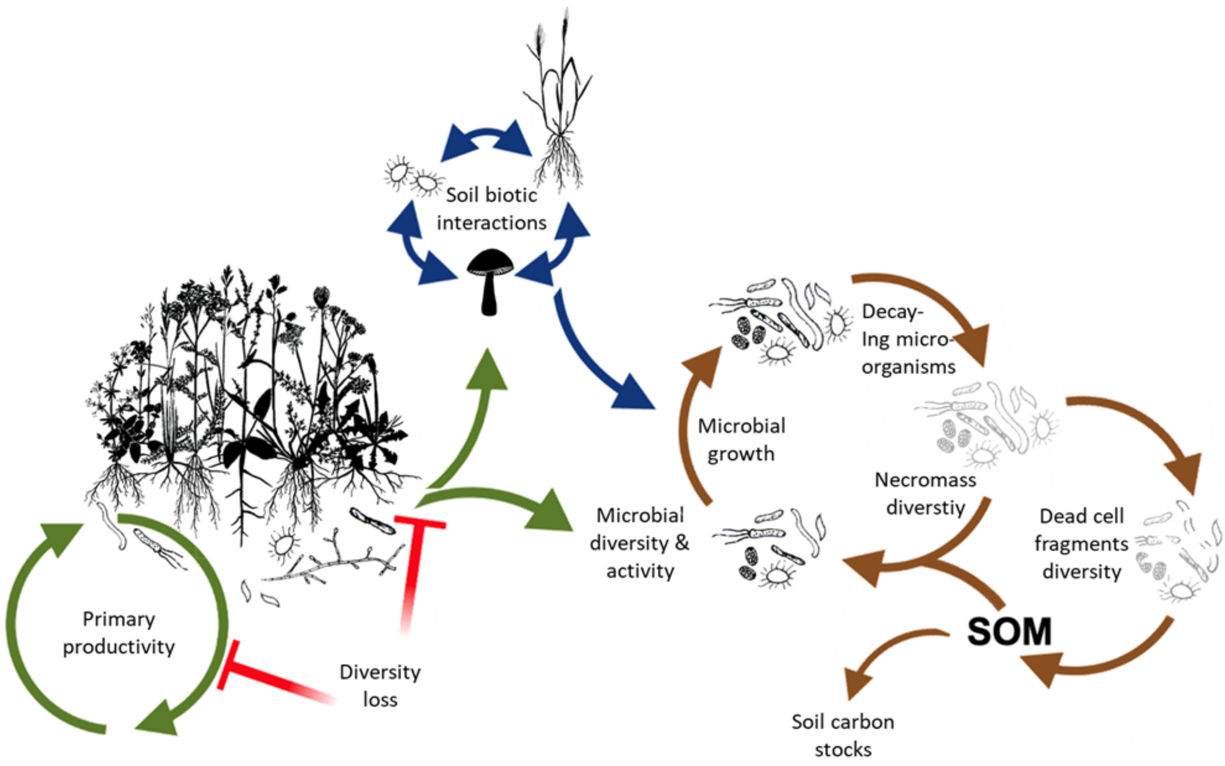

Figure 4. Plant diversity impact on soil carbon cycling. Plant diversity impact multitrophic interactions and microbial community assembly and growth. A more diverse signature of rhizodeposits will result in a more active microbial nutrient cycling, impacting positively microbial community growth efficiency 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).

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How to implement diversity into agroecosystems?

Biodiversity-ecosystem functioning relationships often display a positive asymptotic relationship. This means that the biggest benefits of additional species occur in species-poor communities[65,17]. Large agricultural fields consisting of monoculture have thus large potential for improved ecosystem functioning through diversification[55]. Diversification in agriculture can be achieved through various measures at different spatial and temporal scales (Figure 2). Here, our intent is to highlight the potential of plant diversity for a more sustainable agriculture via both above- and below-ground mechanisms. However, we acknowledge that benefits of diversification will depend on how it is combined with other management practices, including conservation tillage, re-use of crop residues, and integrated pest management[116].

Agroforestry (Figure 2, point 1), where trees or shrubs are incorporated into crop production, can provide erosion control, enhance soil fertility and promote biodiversity of other organismal groups in agriculture[117]. Row cropping of different main crops (Figure 2 point 2a) can increase yield, reduce the need for fertilizer[118] and promote diversity of mycorrhizal fungi[119]. Sometimes species other than main crops are needed for the provision of ecosystem services aside from crop production (Figure 2, point 2b), for example the use of flower strips to promote pollination or pest control[120]. Within a field, mixtures of different varieties of a crop species (Figure 2, point 3) have been shown to increase crop yield and stress resistance[121], reduce disease pressure[58] and improve human nutrition[122]. Combinations of functionally distinct varieties have proven especially good at providing stable high yield[68,121]. Similarly, mixtures of different crop species (Figure 2, point 4) can increase yield[123], reduce pest pressure[124], fertilizer need and nutrient leaching[125]. Sometimes, species other than the main crop, so-called service crops, can help to promote ecosystem functions. For example, undersown Italian ryegrass has been shown to prevent nutrient leaching in cereal fields[126]. It is likely that the mixture of crops with complementary traits provide most benefits[66].

Diversification in time includes relay cropping (Figure 2, point 5) and crop rotation (Figure 2, point 6), which can include the use of cover crops between main crops. Relay cropping can help to gain benefits of row cropping or mixed cropping, while reducing negative effects such as competition between the crops, by growing multiple crops together for only a part of the growing period[118,127]. Crop rotation can prevent large pest populations from establishing over time, optimize resource use and avoid self-toxicity[128]. Ground-covering crops between intervals of successive cash main crops sustain soil quality and productivity by reducing erosion and nutrient loss and by enhancing soil C and N contents, and microbial biomass[129,80]. Crop rotations are thus a cornerstone of sustainable agroecosystems[80,130] with a long-standing history, but developments such as the availability of chemical inputs and specialized machinery together with economic market trends have led to shorter and simpler rotation cycles with often negative consequences for crop yield[128].

Different diversification measures can also be successfully combined. For example, push-pull methods to reduce natural enemy damage combine diversification at two spatial scales: they mix crop species with service species that repel insect pest and have strips of another species, which lures the pests away from the crops surrounding the crop field[131]. Another example is the use of diverse cover crop mixtures within crop rotations to provide more ecosystem functions than the use of simpler cover crop mixtures[66]. It seems that there are many cases where diversification at different spatial and temporal scales jointly yield the best outcomes[56].

Future directions

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

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

Growing evidence shows that soil microbial diversity promotes single soil ecosystem functions, and overall multifunctionality132. It is also known that plant species differ in how they influence the soil microbiome depending on their functional traits18, plant functional type84 and their root exudates19. It should thus be possible to use plants to modulate the soil microbiome and with this promote ecosystem functioning. However, it is difficult to predict the outcome of these plant-soil feedbacks, which may be highly context dependent71). For example, bacterial diversity promoted carbon use efficiency only in wet soils, and diverse AMF communities can switch from beneficial to antagonistic under drought conditions for their crop host133. Consequently, further research is needed to (1) delineate the mechanisms responsible for the relationship between diversity and specific soil functions, and to (2) determine the context-dependencies of such relationship for the multiple soil functions. Global change, especially climate change might disrupt the associations between soil microbes and the plants134. Understanding the mechanisms behind diversity effects is crucial in order to predict how global changes influence plant-soil feedbacks and to design agroecosystems which are robust to global change.

Application of ecological knowledge to agricultural practices

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

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

Further, farming practices such as fertilization or tillage on their own affect the diversity and composition of soil microbial communities[135] and might decouple plant-plant and plant-microbial interactions. For example, overfertilization can inhibit mycorrhizal colonization and the formation of nodules in legumes[136] and promote greenhouse gas emissions[137]. Such agricultural practices thus add a layer of complexity to the soil-mediated diversity effects on ecosystem functioning that need to be considered when studying and designing diverse agroecosystems.

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

Conclusions

The motivation behind this Perspective was to bring together insights from biodiversity-ecosystem functioning research spanning both plant and microbial ecology to gain understanding of how plant diversity could be used to guide ecosystem functioning not only above- but also below-ground in agricultural settings. The effects of plant diversity on ecosystem functioning above-ground have been previously reviewed[31], and current theory and empirical support provide a framework for developing sustainable agricultural strategies. However, there are major gaps in current knowledge in how below-ground effects contribute to – and could be managed – to promote sustainable agriculture. These need to be addressed to reliably predict conditions under which we can reach the desired outcomes. Uncertainties include the efficacy related to the different management practises described in Figure 2 with respect to below-ground processes, and as well as the context dependency – including abiotic, biotic and cultural – that needs to be accounted for to develop general strategies to guide sustainable agriculture. Nevertheless, limited data emerging from different fields highlight that plant diversity could be purposefully used to guide soil biodiversity, and it would be short-sighted not to take advantage of this potentially highly effective yet environmentally friendly and cost-effective management strategy at a time when the need for sustainable agriculture is in greater demand than ever before.

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References

1. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).

2. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577 (2015).

3. Halliday, F. W., Rohr, J. R. & Laine, A.-L. Biodiversity loss underlies the dilution effect of biodiversity. (2020). doi:10.1101/2020.04.20.050377v1

4. Savary, S. *et al.* The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* **3**, 430–439 (2019).

5. Kang, Y., Khan, S. & Ma, X. Climate change impacts on crop yield, crop water productivity and food security - A review. *Progress in Natural Science* **19**, 1665–1674 (2009).

6. Liang, X. Z. *et al.* Determining climate effects on US total agricultural productivity. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E2285–E2292 (2017).

7. Parry, M. L., Rosenzweig, C., Iglesias, A., Livermore, M. & Fischer, G. Effects of climate change on global food production under SRES emissions and socio-economic scenarios. *Glob. Environ. Chang.* **14**, 53–67 (2004).

8. Bruinsma, J. *World agriculture: Towards 2015/2030: an FAO perspective*. (Earthscan, 2003).

9. Jackson, L. E. *et al.* Social-ecological and regional adaptation of agrobiodiversity management across a global set of research regions. *Glob. Environ. Chang.* **22**, 623–639 (2012).

10. Bommarco, R., Kleijn, D. & Potts, S. G. Ecological intensification: Harnessing ecosystem services for food security. *Trends Ecol. Evol.* **28**, 230–238 (2013).

11. Pingali, P. L. Green revolution: Impacts, limits, andthe path ahead. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 12302–12308 (2012).

12. Thakur, M. P. *et al.* Plant–Soil Feedbacks and Temporal Dynamics of Plant Diversity–Productivity Relationships. *Trends in Ecology and Evolution* (2021). doi:10.1016/j.tree.2021.03.011

13. Wagg, C., Bender, S. F., Widmer, F. & Van Der Heijden, M. G. A. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 5266–5270 (2014).

14. Prommer, J. *et al.* Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. *Glob. Chang. Biol.* **26**, 669–681 (2020).

15. Van Der Heijden, M. G. A., Bardgett, R. D. & Van Straalen, N. M. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* **11**, 296–310 (2008).

16. van der Plas, F. Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.* **94**, 1220–1245 (2019).

17. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).

18. Fitzpatrick, C. R. *et al.* Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc. Natl. Acad. Sci. U. S. A.* **115**, E1157–E1165 (2018).

19. Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S. & Vivanco, J. M. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* **57**, 233–266 (2006).

20. Hu, L. *et al.* Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat. Commun.* **9**, 1–13 (2018).

21. Chen, C., Chen, H. Y. H., Chen, X. & Huang, Z. Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. *Nat. Commun.* **10**, 1–10 (2019).

22. Šmilauer, P., Košnar, J., Kotilínek, M. & Šmilauerová, M. Contrasting effects of host identity, plant community, and local species pool on the composition and colonization levels of arbuscular mycorrhizal fungal community in a temperate grassland. *New Phytol.* **225**, 461–473 (2020).

23. Glassman, S. I. *et al.* Decomposition responses to climate depend on microbial community composition. *Proc. Natl. Acad. Sci. U. S. A.* **115**, 11994–11999 (2018).

24. Miki, T., Ushio, M., Fukui, S. & Kondoh, M. Functional diversity of microbial decomposers facilitates plant coexistence in a plant-microbe-soil feedback model. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 14251–14256 (2010).

25. Domeignoz-Horta, L. . *et al.* Peaks of *in situ* N_2O emissions are influenced by N_2O producing and reducing microbial communities across arable soils. *Glob. Chang. Biol.* **24**, 360–370 (2018).

26. Domeignoz-Horta, L. A. *et al.* The diversity of the N2O reducers matters for the N2O:N2 denitrification end-product ratio across an annual and a perennial cropping system. *Front. Microbiol.* **6**, 971 (2015).

27. Jones, C. M. *et al.* Recently identified microbial guild mediates soil N2O sink capacity. *Nat. Clim. Chang.* **4**, 801–805 (2014).

28. Lehmann, A., Zheng, W. & Rillig, M. C. Soil biota contributions to soil aggregation. *Nat. Ecol. Evol.* **1**, 1828–1835 (2017).

29. Domeignoz-Horta, L. A. *et al.* Microbial diversity drives carbon use efficiency in a model soil. *Nat. Commun.* **11**, 1–10 (2020).

30. Kallenbach, C. & Grandy, A. S. Controls over soil microbial biomass responses to carbon amendments in agricultural systems: A meta-analysis. *Agric. Ecosyst. Environ.* **144**, 241–252 (2011).

31. Tilman, D., Isbell, F. & Cowles, J. M. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* **45**, 471–493 (2014).

32. Barry, K. E. *et al.* The Future of Complementarity: Disentangling Causes from Consequences. *Trends in Ecology and Evolution* **34**, 167–180 (2019).

33. Weisser, W. W. *et al.* Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic Appl. Ecol.* **23**, 1–73 (2017).

34. Loreau M. & Hector. A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).

35. Fargione, J. *et al.* From selection to complementarity: Shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proc. R. Soc. B Biol. Sci.* **274**, 871–876 (2007).

36. Guimarães-Steinicke, C. *et al.* Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities. *J. Ecol.* **00**, 1–17 (2021).

37. Cappelli, S., Pichon, N., Mannall, T. & Allan, E. Consistent biodiversity effects across ecosystem functions. *Authorea Prepr.* (2020). doi:10.22541/AU.158981096.65644572

38. Pires, A. P. F. *et al.* Interactive effects of climate change and biodiversity loss on ecosystem functioning. *Ecology* **99**, 1203–1213 (2018).

39. Grossiord, C. *et al.* Application of Loreau & Hector's (2001) partitioning method to complex functional traits. *Methods Ecol. Evol.* **4**, 954–960 (2013).

40. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* **96**, 1463–1468 (1999).

41. Keesing, F., Holt, R. D. & Ostfeld, R. S. Effects of species diversity on disease risk. *Ecol. Lett.* **9**, 485–498 (2006).

42. Johnson, P. T. J., Preston, D. L., Hoverman, J. T. & Richgels, K. L. D. Biodiversity decreases disease through predictable changes in host community competence. *Nature* **494**, 230–233 (2013).

43. Johnson, P. T. J., Calhoun, D. M., Riepe, T., McDevitt-Galles, T. & Koprivnikar, J. Community disassembly and disease: Realistic-but not randomized-biodiversity losses enhance parasite transmission. *Proc. R. Soc. B Biol. Sci.* **286**, (2019).

44. Joseph, M. B., Mihaljevic, J. R., Orlofske, S. A. & Paull, S. H. Does life history mediate changing disease risk when communities disassemble? *Ecol. Lett.* **16**, 1405–1412 (2013).

45. Liu, X., Chen, F., Lyu, S., Sun, D. & Zhou, S. Random species loss underestimates dilution effects of host diversity on foliar fungal diseases under fertilization. *Ecol. Evol.* **8**, 1705–1713 (2018).

46. Halliday, F. W. & Rohr, J. R. Measuring the shape of the biodiversity-disease relationship across systems reveals new findings and key gaps. *Nat. Commun.* **10**, 1–10 (2019).

47. Mihaljevic, J. R., Joseph, M. B., Orlofske, S. A. & Paull, S. H. The scaling of host density with richness affects the direction, shape, and detectability of diversity-disease relationships. *PLoS One* **9**, e97812 (2014).

48. Strauss, A. T. *et al.* Habitat, predators, and hosts regulate disease in Daphnia through direct and indirect pathways. *Ecol. Monogr.* **86**, 393–411 (2016).

49. Qiu, J. & Cardinale, B. J. Scaling up biodiversity–ecosystem function relationships across space and over time. *Ecology* **101**, e03166 (2020).

50. Cardinale, B. J. *et al.* Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 18123–18128 (2007).

51. Mori, A. S., Osono, T., Cornelissen, J. H. C., Craine, J. & Uchida, M. Biodiversity–ecosystem function relationships change through primary succession. *Oikos* **126**, 1637–1649 (2017).

52. Wang, G. *et al.* Soil microbiome mediates positive plant diversity-productivity relationships in late successional grassland species. *Ecol. Lett.* **22**, 1221–1232 (2019).

53. Steudel, B. *et al.* Biodiversity effects on ecosystem functioning change along environmental stress gradients. *Ecol. Lett.* **15**, 1397–1405 (2012).

54. Isbell, F. *et al.* Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecol. Lett.* **21**, 763–778 (2018).

55. Manning, P. *et al.* Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems. in *Advances in Ecological Research* **61**, 323–356 (Academic Press Inc., 2019).

56. Duru, M. *et al.* How to implement biodiversity-based agriculture to enhance ecosystem services: a review. *Agronomy for Sustainable Development* **35**, 1259–1281 (2015).

57. Letourneau, D. K. *et al.* Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* **21**, 9–21 (2011).

58. Zhu, Y. *et al.* Genetic diversity and disease control in rice. *Nature* **406**, 718–722 (2000).

59. Mundt, C. C. Use of multiline cultivars and cultivar mixtures for disease management. *Annual Review of Phytopathology* **40**, 381–410 (2002).

60. Karasov, T. L., Shirsekar, G., Schwab, R. & Weigel, D. What natural variation can teach us about resistance durability. *Current Opinion in Plant Biology* **56**, 89–98 (2020).

61. Finney, D. M., White, C. M. & Kaye, J. P. Biomass production and carbon/nitrogen ratio influence ecosystem services from cover crop mixtures. *Agron. J.* **108**, 39–52 (2016).

62. Hector, A. & Bagchi, R. Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188–190 (2007).

63. Zavaleta, E. S., Pasari, J. R., Hulvey, K. B. & Tilman, G. D. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 1443–1446 (2010).

64. Van Der Plas, F. *et al.* Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. *Nat. Commun.* **7**, 11 (2016).

65. Isbell, F. *et al.* Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology* **105**, 871–879 (2017).

66. Finney, D. M. & Kaye, J. P. Functional diversity in cover crop polycultures increases multifunctionality of an agricultural system. *J. Appl. Ecol.* **54**, 509–517 (2017).

67. German, R. N., Thompson, C. E. & Benton, T. G. Relationships among multiple aspects of agriculture's environmental impact and productivity: A meta-analysis to guide sustainable agriculture. *Biol. Rev.* **92**, 716–738 (2017).

68. Montazeaud, G. *et al.* Multifaceted functional diversity for multifaceted crop yield: Towards ecological assembly rules for varietal mixtures. *J. Appl. Ecol.* **57**, 2285–2295 (2020).

69. Badri, D. V., Zolla, G., Bakker, M. G., Manter, D. K. & Vivanco, J. M. Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New Phytol.* **198**, 264–273 (2013).

70. Pineda, A., Kaplan, I., Hannula, S. E., Ghanem, W. & Bezemer, T. M. Conditioning the soil microbiome through plant–soil feedbacks suppresses an aboveground insect pest. *New Phytol.* **226**, 595–608 (2020).

71. Philippot, L., Raaijmakers, J. M., Lemanceau, P. & Van Der Putten, W. H. Going back to the roots: The microbial ecology of the rhizosphere. *Nature Reviews Microbiology* **11**, 789–799 (2013).

72. Busby, P. E. *et al.* Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.* **15**, e2001793 (2017).

73. Finkel, O. M., Castrillo, G., Herrera Paredes, S., Salas González, I. & Dangl, J. L. Understanding and exploiting plant beneficial microbes. *Curr. Opin. Plant Biol.* **38**, 155–163 (2017).

74. Mueller, U. G. & Sachs, J. L. Engineering Microbiomes to Improve Plant and Animal Health. *Trends in Microbiology* **23**, 606–617 (2015).

75 Van Der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).

76. Kleijn, D. *et al.* Ecological Intensification: Bridging the Gap between Science and Practice. *Trends in Ecology and Evolution* **34**, 154–166 (2019).

77. Zhang, S., Lehmann, A., Zheng, W., You, Z. & Rillig, M. C. Arbuscular mycorrhizal fungi increase grain yields: a meta-analysis. *New Phytol.* **222**, 543–555 (2019).

78. Rillig, M. C. *et al.* Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist* **222**, 1171–1175 (2019).

79. Thilakarathna, M. S. & Raizada, M. N. A meta-analysis of the effectiveness of diverse rhizobia inoculants on soybean traits under field conditions. *Soil Biology and Biochemistry* **105**, 177–196 (2017).

80. Bowles, T. M., Jackson, L. E., Loeher, M. & Cavagnaro, T. R. Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover crop effects. *J. Appl. Ecol.* **54**, 1785–1793 (2017).

81. McDaniel, M. D., Tiemann, L. K. & Grandy, A. S. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecol. Appl.* **24**, 560–570 (2014).

82. Vukicevich, E., Lowery, T., Bowen, P., Urbez-Torres, J. R. & Hart, M. Cover crops to increase soil microbial diversity and mitigate decline in perennial agriculture. A review. *Agron. Sustain. Dev.* **36**, (2016).

83. Hooper, D. U. *et al. Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks*. *BioScience* **50**, (Oxford Academic, 2000).

84. Hannula, S. E., Ma, H.-K., Perez-Jaramillo, J. E., Pineda, A. & Bezemer, T. M. Structure and ecological function of the soil microbiome affecting plant-soil feedbacks in the presence of a soil-borne pathogen. *Environ. Microbiol.* doi:10.1111/1462-2920.14882

85. Porter, S. S. & Sachs, J. L. Agriculture and the Disruption of Plant–Microbial Symbiosis. *Trends in Ecology and Evolution* **35**, 426–439 (2020).

86 Bittebiere, A. K. *et al.* Past spatial structure of plant communities determines arbuscular mycorrhizal fungal community assembly. *J. Ecol.* **108**, 546–560 (2020).

87. Korenblum, E. *et al.* Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 3874–3883 (2020).

98. Lau, J. A. & Lennon, J. T. Evolutionary ecology of plant-microbe interactions: Soil microbial structure alters selection on plant traits. *New Phytol.* **192**, 215–224 (2011).

89. Garbeva, P., Van Elsas, J. D. & Van Veen, J. A. Rhizosphere microbial community and its response to plant species and soil history. *Plant Soil* **302**, 19–32 (2008).

90. Zhalnina, K. *et al.* Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* **3**, 470–480 (2018).

91. Banerjee, A. & Roychoudhury, A. Strigolactones: multi-level regulation of biosynthesis and diverse responses in plant abiotic stresses. *ACTA Physiol. Plant.* **40**, (2018).

92. Chen, X. *et al.* Minor responses of soil microbial biomass, community structure and enzyme activities to nitrogen and phosphorus addition in three grassland ecosystems. *Plant Soil* **444**, 21–37 (2019).

93. Lange, M. *et al.* Plant diversity increases soil microbial activity and soil carbon storage. *Nat. Commun.* **6**, (2015).

94. Chen, S. *et al.* Plant diversity enhances productivity and soil carbon storage. *Proc. Natl. Acad. Sci. U. S. A.* **115**, 4027–4032 (2018).

95. Nemergut, D., Shade, A. & Violle, C. When, where and how does microbial community composition matter? *Front. Microbiol.* **5**, 497 (2014).

96. Liebich, J., Schloter, M., Schäffer, A., Vereecken, H. & Burauel, P. Degradation and humification of maize straw in soil microcosms inoculated with simple and complex microbial communities. *Eur. J. Soil Sci.* **58**, 141–151 (2007).

97. Ou, Y. *et al.* Deciphering Underlying Drivers of Disease Suppressiveness Against Pathogenic Fusarium oxysporum. *Front. Microbiol.* **10**, 2535 (2019).

98. Philippot, L. *et al.* Loss in microbial diversity affects nitrogen cycling in soil. *ISME J.* **7**, 1609–19 (2013).

99. Guerra, C. A. *et al.* Blind spots in global soil biodiversity and ecosystem function research. *Nat. Commun.* **11**, 1–13 (2020).

100. Ramankutty, N. *et al.* Trends in Global Agricultural Land Use: Implications for Environmental Health and Food Security. *Annual Review of Plant Biology* **69**, 789–815 (2018).

101. Lynch, J. M. & Bragg, E. Microorganisms and soil aggregate stabililty. *Adv. soil Sci. Vol. 2* 133–171 (1985). doi:10.1007/978-1-4612-5088-3_3

102. Guerrero-Ramírez, N. R. *et al.* Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* **1**, 1639–1642 (2017).

103. Köchy, M., Hiederer, R. & Freibauer, A. Global distribution of soil organic carbon – Part 1: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *SOIL* **1**, 351–365 (2015).

104. IPCC, 2013. *CLIMATE CHANGE 2013 The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2013).

105. Kallenbach, C. M., Frey, S. D. & Grandy, A. S. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nat. Commun.* **7**, 1–10 (2016).

106. Miltner, A., Bombach, P., Schmidt-Brücken, B. & Kästner, M. SOM genesis: Microbial biomass as a significant source. *Biogeochemistry* **111**, 41–55 (2012).

107. Hu, Y., Zheng, Q., Noll, L., Zhang, S. & Wanek, W. Direct measurement of the in situ decomposition of microbial-derived soil organic matter. *Soil Biol. Biochem.* **141**, 107660 (2020).

108. Delgado-Baquerizo, M. *et al.* Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat. Ecol. Evol.* **4**, 210–220 (2020).

109. Liang, C., Amelung, W., Lehmann, J. & Kästner, M. Quantitative assessment of microbial necromass contribution to soil organic matter. *Glob. Chang. Biol.* **25**, 3578–3590 (2019).

110. Berhongaray, G., Cotrufo, F. M., Janssens, I. A. & Ceulemans, R. Below-ground carbon inputs contribute more than above-ground inputs to soil carbon accrual in a bioenergy poplar plantation. *Plant Soil* **434**, 363–378 (2019).

111. Lehmann, J. *et al.* Persistence of soil organic carbon caused by functional complexity. *Nat. Geosci.* **13**, 529–534 (2020).

112. Domeignoz-Horta, L. A. *et al.* The role of microbial diversity in the formation of soil organic matter quality and persistence. *bioRxiv* 2021.04.23.441131 (2021). doi:10.1101/2021.04.23.441131

113. Cavicchioli, R. *et al.* Scientists' warning to humanity: microorganisms and climate change. *Nature Reviews Microbiology* **17**, 569–586 (2019).

114. Chen, X. *et al.* Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biol. Rev.* **95**, 167–183 (2020).

115. Lal, R. Soil carbon sequestration to mitigate climate change. *Geoderma* **123**, 1–22 (2004).

116. Tamburini, G. *et al.* Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci. Adv.* **6**, eaba1715 (2020).

117. Torralba, M., Fagerholm, N., Burgess, P. J., Moreno, G. & Plieninger, T. Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. *Agriculture, Ecosystems and Environment* **230**, 150–161 (2016).

118. Li, C. *et al.* Syndromes of production in intercropping impact yield gains. *Nat. Plants* **6**, 653–660 (2020).

119. Guzman, A. *et al.* Crop diversity enriches arbuscular mycorrhizal fungal communities in an intensive agricultural landscape. *New Phytol.* nph.17306 (2021). doi:10.1111/nph.17306

120. Albrecht, M. *et al.* The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* **23**, 1488–1498 (2020).

121. Reiss, E. R. & Drinkwater, L. E. Cultivar mixtures: A meta-analysis of the effect of intraspecific diversity on crop yield: A. *Ecol. Appl.* **28**, 62–77 (2018).

122. Snyder, L. D., Gómez, M. I. & Power, A. G. Crop Varietal Mixtures as a Strategy to Support Insect Pest Control, Yield, Economic, and Nutritional Services. *Frontiers in Sustainable Food Systems* **4**, 60 (2020).

123. Zhang, C., Postma, J. A., York, L. M. & Lynch, J. P. Root foraging elicits niche complementarity-dependent yield advantage in the ancient ‘three sisters’ (maize/bean/squash) polyculture. *Ann. Bot.* **114**, 1719–1733 (2014).

124. Iverson, A. L. *et al.* Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *J. Appl. Ecol.* **51**, 1593–1602 (2014).

125. Jensen, E. S., Carlsson, G. & Hauggaard-Nielsen, H. Intercropping of grain legumes and cereals improves the use of soil N resources and reduces the requirement for synthetic fertilizer N: A global-scale analysis. *Agronomy for Sustainable Development* **40**, 1–9 (2020).

126. Valkama, E., Lemola, R., Känkänen, H. & Turtola, E. Meta-analysis of the effects of undersown catch crops on nitrogen leaching loss and grain yields in the Nordic countries. *Agriculture, Ecosystems and Environment* **203**, 93–101 (2015).

127. Wezel, A. *et al.* Agroecological practices for sustainable agriculture. A review. *Agronomy for Sustainable Development* **34**, 1–20 (2014).

128. Bennett, A. J., Bending, G. D., Chandler, D., Hilton, S. & Mills, P. Meeting the demand for crop production: The challenge of yield decline in crops grown in short rotations. *Biol. Rev.* **87**, 52–71 (2012).

129. Blanco-Canqui, H. *et al.* Cover crops and ecosystem services: Insights from studies in temperate soils. *Agron. J.* **107**, 2449–2474 (2015).

130. Cloutier, M. L. *et al.* Fungal community shifts in soils with varied cover crop treatments and edaphic properties. *Sci. Rep.* **10**, 1–14 (2020).

131. Khan, Z. R., Midega, C. A. O., Bruce, T. J. A., Hooper, A. M. & Pickett, J. A. Exploiting phytochemicals for developing a 'push-pull' crop protection strategy for cereal farmers in Africa. *J. Exp. Bot.* **61**, 4185–4196 (2010).

132. Wagg, C., Schlaeppi, K., Banerjee, S., Kuramae, E. E. & van der Heijden, M. G. A. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nat. Commun.* **10**, 1–10 (2019).

133. Sendek, A. *et al.* Drought modulates interactions between arbuscular mycorrhizal fungal diversity and barley genotype diversity. *Sci. Rep.* **9**, (2019).

134. Classen, A. T. *et al.* Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *ECOSPHERE* **6**, (2015).

135. de Graaff, M. A., Hornslein, N., Throop, H. L., Kardol, P. & van Diepen, L. T. A. Effects of agricultural intensification on soil biodiversity and implications for ecosystem functioning: A meta-analysis. in *Advances in Agronomy* **155**, 1–44 (Academic Press Inc., 2019).

136. Treseder, K. K. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytol.* **164**, 347–355 (2004).

137. Snyder, C. S., Bruulsema, T. W., Jensen, T. L. & Fixen, P. E. Review of greenhouse gas emissions from crop production systems and fertilizer management effects. *Agric. Ecosyst. Environ.* **133**, 247–266 (2009).