Trends in
Plant Science

CellPress

Opinion

Belowground facilitation and trait matching: two or three to tango?

Rui-Peng Yu,[1] Hans Lambers,[2,3] Ragan M. Callaway,[4]
Alexandra J. Wright,[5] and Long Li[1,*]

High biodiversity increases ecosystem functions; however, belowground facilitation remains poorly understood in this context. Here, we explore mechanisms that operate via 'giving–receiving feedbacks' for belowground facilitation. These include direct effects via root exudates, signals, and root trait plasticity, and indirect biotic facilitation via the effects of root exudates on soil biota and feedback from biota to plants. We then highlight that these two- or three-way mechanisms must affect biodiversity–ecosystem function relationships via specific combinations of matching traits. To tango requires a powerful affinity and harmony between well-matched partners, and such matches link belowground facilitation to the effect of biodiversity on function. Such matching underpins applications in intercropping, forestry, and pasture systems, in which diversity contributes to greater productivity and sustainability.

Highlights

Belowground facilitation is a vital mechanism underlying ecosystem function in diverse plant communities.

A bottleneck to linking theory to application is that interspecific belowground facilitation processes are incompletely understood.

Here, we explore direct and indirect facilitation, which requires matching specific belowground responses between the facilitated species and the facilitator.

Understanding and integrating the processes of interspecific facilitation helps to design sustainable diverse plant communities with compatible ecosystem functions.

Biodiversity, ecosystem function, and belowground facilitation

Many experiments in natural ecosystems and agroecosystems have shown that experimentally increased biodiversity enhances various ecosystem functions [1–4]. The preeminent mechanism for this effect of biodiversity is **resource complementarity** (see Glossary) and niche partitioning, which occurs when species in diverse polycultures have unique traits and requirements that lead to greater resource capture than that of any single species in monoculture. However, resource partitioning alone does not always explain **biodiversity–ecosystem function** (BEF) relationships [5,6]. In addition to partitioning, **facilitation** has received increasing attention as another important mechanism driving BEF, and this occurs when one or more species in polycultures increase a functional metric (e.g., biomass) of one or more other species [3,7,8] (Box 1). To date, most studies interpret facilitation in BEF by calculating relative interaction intensities [9] or diversity effects [10], for example, complementarity effect (consequences), in which facilitation is framed, often appropriately, as a distinct alternative to resource complementarity. However, this integration does not shed light on mechanisms by which polycultures of species interact, and often cannot separate facilitation from resource complementarity (causes) [4,10].

More recently, researchers have focused on belowground facilitative mechanisms underlying positive BEF relationships [3]. For example, it is widely accepted that legumes may facilitate neighbours via dinitrogen (N_2) fixation and increasing nitrogen (N) availability in soil [3,4,7]. However, beyond N facilitation, belowground facilitation has received little attention in BEF research. For example, a study showed that 40% more root biomass was produced in polycultures than predicted from monocultures, and this was not due to spatial partitioning. They argued that root responses were consistent with species-specific root recognition, but this was not demonstrated [11]. Other studies also reported striking decreases in the occurrence of pathogenic fungi in plant polycultures (indirect biotic facilitation), while the plant-beneficial microbe–pathogen interaction was underexplored [12,13].

[1]Key Laboratory of Plant-Soil Interactions, Ministry of Education, Beijing Key Laboratory of Biodiversity and Organic Farming, College of Resources and Environmental Sciences, China Agricultural University, 2 Yuan Ming Yuan West Road, Beijing 100193, PR China
[2]School of Biological Sciences and Institute of Agriculture, The University of Western Australia, 35 Stirling Highway, Crawley, Perth, WA 6009, Australia
[3]National Academy of Agriculture Green Development, China Agricultural University, 2 Yuan Ming Yuan West Road, Beijing 100193, PR China
[4]Division of Biological Sciences and Institute on Ecosystems, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
[5]Department of Biological Sciences, California State University Los Angeles, 5151 State University Drive, Los Angeles, CA 90032, USA

*Correspondence:
lilong@cau.edu.cn (L. Li).

https://doi.org/10.1016/j.tplants.2021.07.014
© 2021 Elsevier Ltd. All rights reserved.

Box 1. Linking facilitation to ecosystem function in BEF experiments

Facilitative mechanisms can explain the greater ecosystem function in BEF experiments by direct abiotic facilitation (e.g., microclimate amelioration and resource enrichment) and indirect biotic facilitation (e.g., microbe-mediated pathogen protection, nutrient mobilisation, and biotic feedback) [4,7]. Direct abiotic facilitation may operate via emergent effects associated with unique properties of a more diverse community, that is, community-scale facilitative effect [18]. For instance, in aboveground facilitation, it can drive greater canopy architecture complementarity, which leads to unique microclimate effects that protect drought-/cold-sensitive species [66,75]. Or, direct abiotic belowground facilitation may operate in a universal fashion through resource enrichment (e.g., N and water facilitation) [4,7,76,77] and greater root biomass creating soils with greater porosity that enhances oxygen diffusion in soils which alleviates the negative effect of flooding or compaction on productivity [17]. Indirect biotic belowground facilitation through common mycorrhizal networks may also play universal roles in increasing plant nutrient uptake and enhancing defence against pathogens of their hosts [19,21]. Belowground facilitation may also function in a species-specific manner, that is, members of polycultures facilitating species that possess traits that benefit only certain other species [14,42]. This matching of ‘complementary’ traits can be crucial for facilitation to function. To understand this matching and potential conceptual overlap between resource complementarity and facilitation, we must understand the mechanisms by which facilitation affects BEF.

Recent studies without a focus on BEF have explored the role of belowground direct and indirect facilitation in plant–plant [14], plant–microbiome [15] and cross–kingdom interactions [16], providing opportunities to better conceptualise facilitative interactions that might underlie how biodiversity increases ecosystem functions. Here, we synthesise these recent advances. We also highlight the importance of intimate matches among interacting species that enhance not only direct abiotic facilitation via **root exudates**, **signalling molecules**, and species-specific root **phenotypic plasticity**, but also indirect biotic facilitation via plant–microbiome combinations. As tango requires a powerful affinity and harmony between well-matched partners, so do these belowground processes. However, tango is officially and logistically limited to two partners, but facilitative interactions that drive BEF are not. A deeper understanding of how these processes allow facilitation, and matches among species, can advance conceptual ecological theory and bridge the gap between biodiversity theory and application.

How does belowground facilitation work?

First, we acknowledge that facilitation in highly diverse plant communities may operate via emergent effects associated with unique properties of a more diverse community (direct abiotic facilitation or indirect biotic facilitation via soil biota) [7,17,18] (Box 1). For instance, higher diversity plant communities may have more complete occupation of belowground root space and this can lead to increased soil porosity and enhanced aeration of soils during a flooding event; as a result, all constituent species benefit from living in a higher diversity soil during a flood [17]. Mycorrhizal fungi- and beneficial microbe-mediated indirect abiotic facilitation may play universal roles in increasing plant nutrient uptake via **common mycorrhizal networks** (e.g., N and P), and benefiting their hosts by enhancing their defence against pathogens in diverse plant communities [13,19–21]. However, for the purpose of this review, we focus on specific two- and three-way interactions between neighbouring species (Box 1). In particular, we explore direct abiotic facilitation via nutrient-mobilising root exudates and signalling molecules, direct facilitation due to trait plasticity in response to neighbours, and indirect facilitation via root–soil biota interactions.

Direct facilitation via root exudates and signalling molecules

Nutrient-mobilising root exudates and signalling molecules may mediate belowground plant–plant interactions via direct abiotic facilitation (Figure 1). In faba bean (*Vicia faba*)/maize (*Zea mays*) intercrops, root exudates from maize include flavonoids, which are signalling compounds for the rhizobial symbiosis with legume plants [22]. These exudates increase nodulation and nodule activity in neighbouring faba bean, whereas root exudates from wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), which do not produce the signalling flavonoids, do not increase

Glossary

Biodiversity–ecosystem function: the effect of species, genotype, and functional diversity on the function of communities.

Common mycorrhizal networks: hyphal networks established by mycorrhizal fungi that connect plant individuals and transfer nutrients, signals, and water.

Facilitation: process by which the target species (facilitated species) benefits from the presence of another species (facilitator).

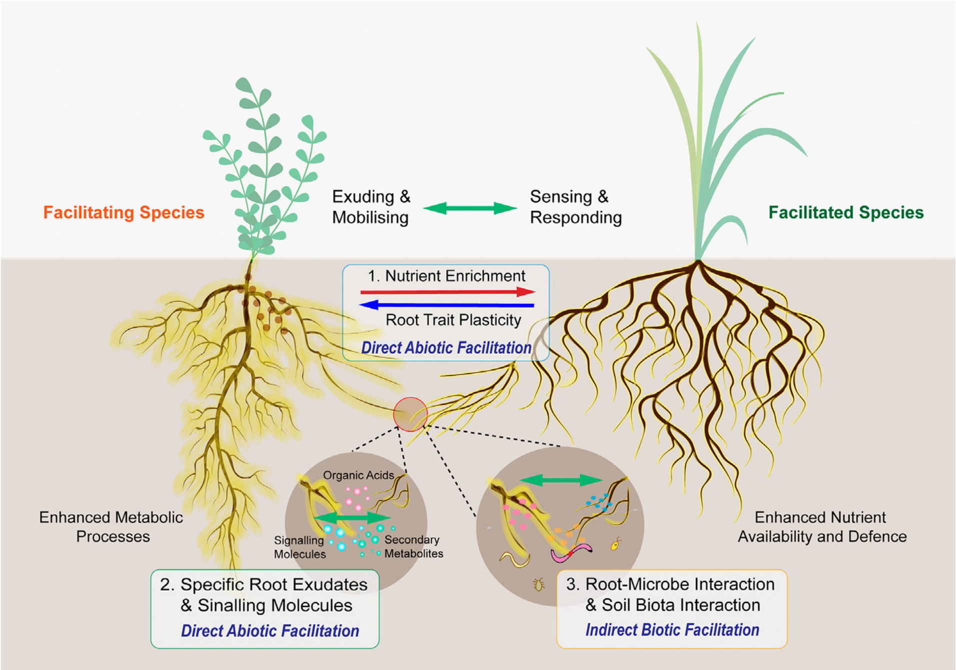
Phenotypic plasticity: the ability of a particular genotype to express different phenotypes in response to environmental variation.

Resource complementarity: partitioning of resources among species because all species specialise on different resources. This can lead to increased performance of a higher-diversity community.

Rhizosphere: the narrow zone of soil directly affected by root activity and the root microbiome.

Root exudate: substance released by plant roots into the rhizosphere.

Signalling molecules: compounds that are neither nutrients nor enzymes, but transmit information between cells and species.



Trends in Plant Science

Figure 1. Belowground interspecific facilitation that requires matching of benefactors and beneficiaries. The red arrow indicates the processes exhibited by facilitating species that affect facilitated species. The blue arrow indicates the processes expressed by facilitated species that respond to facilitators; the green arrows represent bidirectional effects between facilitating and facilitated species. There are three groups of facilitative mechanisms that require the matching of belowground processes: (1) facilitating species that are efficient in mobilising nutrients and facilitated species that exhibit greater root trait plasticity; (2) communication among species via specific nutrient-mobilising root exudates and signalling molecules, and the process might be bidirectional; and (3) root exudate-induced microbial interactions and specific soil biota that may enhance nutrient availability or defence.

nodulation. In return, the enhanced N_2 fixation process of faba bean also acidifies soils and increases the availability of P, which facilitates N and P acquisition by nearby maize [22,23].

Allelopathy and chemical facilitation via root exudates affect belowground interactions in a species- and dose-specific manner, and are common in both natural and agricultural ecosystems [24]. Some chemicals may enhance plant performance at low concentrations, and inhibit performance at relatively high concentrations. For example, in a mixed-species forest, *Michelia macclurei* (Magnoliaceae) reduces the release of a cyclic dipeptide, an autotoxic compound, from the roots of its neighbour Chinese fir (*Cunninghamia lanceolata*), and thus enhances the growth of neighbouring Chinese fir via chemical facilitation [25]. Recent studies have shown that root-secreted chemical signals, such as jasmonic acid, (–)-loliolide, and strigolactones, contribute to root–root communications and trigger chemical responses among plant species [26–28], and root-secreted N-rich allantoin may be responsible for recognition among rice (*Oryza sativa*) genotypes [29]. By integrating these kinds of species-specific root exudates and signals that drive belowground facilitation, we may increase our understanding of BEF. In turn, this may contribute to functioning in species- or genotype-diverse agroecosystems and the restoration of degraded communities.

Direct facilitation via trait plasticity in response to neighbours

Trait plasticity may be associated with a greater potential for giving–receiving facilitation (Figure 1). A recent study showed that grassland species that are facilitated tend to exhibit greater phenotypic plasticity of specific root traits in response to root exudates released by the facilitator on P-deficient soils than non-facilitated neighbours [14]. For example, when the roots of two facilitated species, *Cleistogenes squarrosa* and *Bromus inermis*, interact with a P-mobilising facilitator, they show greater plasticity in root proliferation and rhizosheath acid phosphatase activity than do co-occurring non-P-mobilising species that do not experience facilitation [14]. Root trait plasticity in response to neighbours may also be shaped by nutrient availability and particular neighbour species or genotypes [30–33]. Thus, specific genotypes and species combinations appear to enhance belowground facilitation through trait matching, which may increase some metrics of ecosystem function.

The studies reviewed above emphasise that facilitation predominates when facilitated species exhibit greater phenotypic plasticity in root traits (e.g., specific root length and root-secreted phosphatases [14,30]) in ways that permit better matches with specific benefits from a facilitator. However, quantifying the role of root trait plasticity in diverse plant communities is a challenge. Multispecies genotyping by sequencing [34] and Fourier-transform infrared spectroscopy [35] can quantify relative root abundance of multispecies or multigenotype communities; the combination of zymography, planar optodes, and image processing is a promising tool to image and quantify **rhizosphere** processes *in situ* in multispecies communities [36,37]. However, the plasticity of root traits for multispecies and whole root systems has not been linked to ecosystem functioning. A promising alternative approach to sampling highly variable root exudates is easily measured leaf [Mn] as a proxy for interspecific P facilitation via rhizosheath carboxylates [20,38,39].

Indirect facilitation via root–soil biota interactions

Evidence is mounting that root exudate-induced shifts of soil microbial composition and microbe–microbe interactions may contribute to enhancing ecosystem functioning in diverse plant communities [40,41]. For example, species-specific chemical signals and phytohormones that are involved in plant–plant recognition alter soil microbial composition [24,42]. A recent study showed that ethylene synthesis and release from the roots of peanut (*Arachis hypogaea*) are enhanced by cyanide released from neighbouring cassava (*Manihot esculenta*) [15]. Here, ethylene has a dual role in species-specific recognition as a gaseous signal and inducing a shift of microbial composition in the peanut rhizosphere. The increased abundance of an actinobacterial species enhances soil nutrient availability and facilitates peanut fruit productivity [15].

Signals among plants mediated by volatile organic compounds in the rhizosphere may occur through common mycorrhizal networks or specific microbes, protecting them against degradation and enhancing plant-to-plant transmission [43–45] or directing root placement [46]. For example, kin pairs of *Pseudotsuga menziesii* share more carbon from donor to recipient through ectomycorrhizal networks than non-kin pairs, mediated by root-secreted signalling molecules [47].

Communication among species might be species specific and bidirectional (Figure 1). Wang *et al.* [48] demonstrated that root exudate differentiation may trigger positive microbial legacy effects that suppress pathogens and increase beneficial microbes, attenuating negative plant–soil feedbacks [48]. This appears to enhance the performance of wheat–faba bean and maize–faba bean combinations, but not of the wheat–maize combination. The outcome of root–microbiome interactions depends on spatial and temporal patterns of root exudates, management practices, and genotype identity [49–52]. Therefore, selecting specific species or genotype combinations to match phenotype, microbiome function, and plant–soil feedback are possible routes to enhance BEF.

Specific soil microbe–microbe and interkingdom interactions also provide new insights into indirect belowground interspecific facilitation. For instance, mycelia of *Phomopsis liquidambaris* promote migration of rhizobia from bulk soil to the rhizosphere of peanuts which then triggers nodulation [53]. In a combination of particular mycorrhizal fungi and bacteria, extraradical hyphae of arbuscular mycorrhizal fungi carry phosphate-solubilising bacteria via water film to organic P patches and enhance organic P mineralisation by hyphal exudates [54]. Multikingdom interactions also play a vital role in plant performance by communications mediated by root nutrient-mobilising exudates and signalling molecules [16,55]. However, the importance of these soil biota interactions in plant–plant interactions remains unexplored. Diverse communities may benefit from matches between certain root traits and soil microbiome combinations among plant species in ways that enhance nutrient acquisition and defence against pathogens [56–58] (Figure 2). To better understand this, or to develop productive managed systems, we need to integrate high-throughput cultivation and identification of root microbiota and multi-omics analyses to understand the complicated belowground facilitative network [59,60]. For instance, we first need to show facilitation mediated by belowground processes, and then identify the changes in root exudates, root trait plasticity, and microbial composition. Then, we can further explore the molecular mechanisms of root–microbe interactions [50] or manipulate the microbial community to study the interactions between root traits and specific microbes [59].

Why do some combinations show stronger facilitative interactions than others?

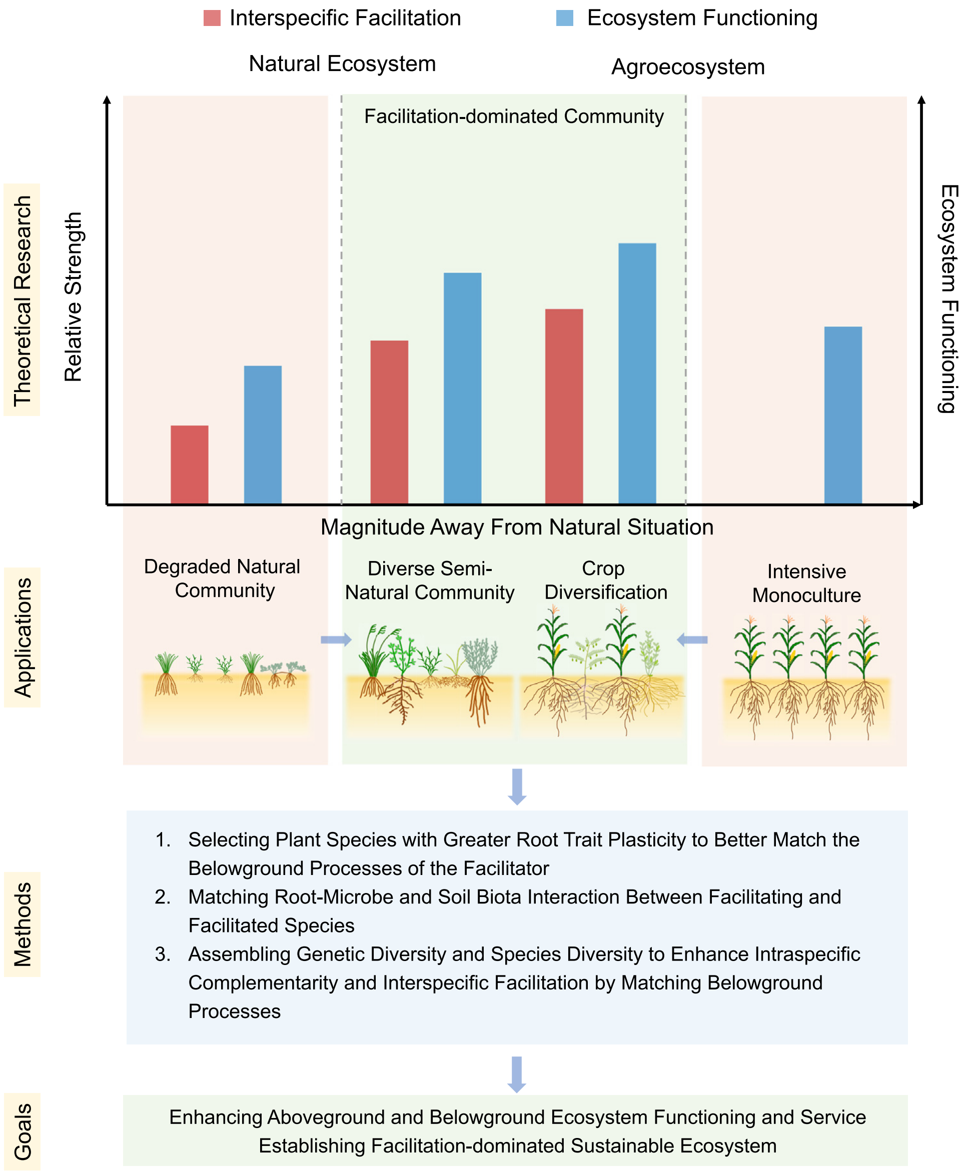
Both competition and facilitation play roles in shaping community patterns, but the net outcome is determined by the relative strength of different mechanisms [61]. These mechanisms are often determined by species-specific traits (e.g., variation in the ability to perform N_2 fixation or P-mobilisation, deep versus shallow roots, variation in detection of different species). For some combinations, facilitation is overridden by competition, because of the strong competitive ability of the facilitator or facilitated species [61,62]. Besides, in plant communities that experience multiple abiotic stresses simultaneously (e.g., water and N limitation), N facilitation between N-fixing species and neighbours may occur only when the root traits exhibit greater dissimilarity in accessing water sources from different depths, and the facilitated species have greater stomatal control in response to water stress [63,64]. Therefore, we also need to understand how facilitation and competition interact under multiple stresses; this would allow us to strengthen facilitation for the primary factors that limit growth and avoid competition for another by trait matching when establishing managed communities.

Inspirations for BEF relationships and managed ecosystems

To fully understand the mechanisms of belowground facilitation in BEF experiments, we need to know: (1) how more diverse plant communities structurally change the environment in a way that benefits many of the constituent species (reviewed in [4,7]), as well as (2) what determines a good match between species with facilitating and facilitated traits. Below, we illustrate the links between belowground facilitative mechanisms and BEF relationships, and the approaches that might establish productive and sustainably managed systems based on facilitation theory.

Linking belowground facilitation and enhanced BEF relationships

Based on the stress-gradient hypothesis, we expect the strength of facilitation to increase in environments with relatively greater abiotic stresses, but this depends on the species involved and the type of stress. This increase may be due to more important microclimate amelioration by nurse plants or resource enrichment in harsh conditions [3,65,66]. Undisturbed plant communities at equilibrium usually harbour more plant species than those not at equilibrium (e.g., N-deposition communities [67]) which in turn corresponds to increases in some metrics of ecosystem functions in the former. In degraded communities, commonly not at equilibrium, establishing artificial grasslands and reforestation by transplanting or reseeding facilitating species (e.g., legume establishment [68]) might be more efficient than natural succession. By matching belowground processes we



1. Selecting Plant Species with Greater Root Trait Plasticity to Better Match the Belowground Processes of the Facilitator
2. Matching Root-Microbe and Soil Biota Interaction Between Facilitating and Facilitated Species
3. Assembling Genetic Diversity and Species Diversity to Enhance Intraspecific Complementarity and Interspecific Facilitation by Matching Belowground Processes

Enhancing Aboveground and Belowground Ecosystem Functioning and Service
Establishing Facilitation-dominated Sustainable Ecosystem

Trends in Plant Science

Figure 2. Linking theoretical research and application in diverse plant communities to enhance belowground interspecific facilitation and ecosystem functioning. The x-axis represents a relative distance from natural communities. At the far left of the x-axis is a degraded natural community with low ecosystem function and without human efforts towards restoration. To the far right of the x-axis is monoculture. Interspecific facilitation (red columns) may increase via matching plant traits of artificial assemblages of particular plant species, increasing ecosystem function in seminatural communities and diverse cropping systems compared with degraded natural communities (theoretical research). There is no interspecific facilitation in monocultures. The diverse seminatural communities and agroecosystems in the green centre of the x-axis represent goals (blue arrows) for sustainable artificial communities (applications) with enhanced ecosystem function and stability. To link theoretical research and applications, we need to consider the methods in the blue box between matching facilitating and facilitated species via belowground processes.

discussed above, we predict increases in some ecosystem functions in such ‘giving–receiving’ managed plant communities compared with those in naïvely designed managed communities due to more efficient interspecific facilitation.

In agroecosystems, continuous monocropping systems usually exhibit inferior ecosystem functions in comparison with diverse cropping systems. Intercropping, cultivar-diversity mixtures, agroforestry, and crop rotations are practices to increase biodiversity in agroecosystems that increase ecosystem function and stabilise food production [69]. By selecting appropriate species or cultivar combinations, belowground facilitation can strengthen facilitative interactions and enhance the grain yield of facilitated species via direct root exudate-mediated or indirect microbe-mediated nutrient enrichment under greater nutrient stress [20,70]; or disease suppression through dilution effects or antagonism between beneficial and pathogenic microbiomes in high-input agroecosystems [3] (Figure 2).

How to establish a facilitation-based managed community?

How to design sustainably functioning managed communities is an ongoing question. Previous studies have focused on temporal and spatial complementarity and productivity. We suggest that the kinds of belowground interspecific facilitation mechanisms we review might contribute to the designs of managed communities. This would entail matching belowground processes among genotypes and species to enhance facilitation and ecosystem functions (Figure 2). Species that exhibit a greater response to a facilitator via root trait plasticity and enrichment of beneficial microbiomes in the rhizosphere will likely benefit more from facilitators. For instance, in the reciprocal faba bean–maize and faba bean–wheat systems, cereals usually exhibit greater root length plasticity in response to P mobilised by neighbouring faba bean [30]. In return, the root exudates of maize may stimulate N_2 fixation of neighbouring faba bean [22]; root exudates of wheat may alleviate soil-borne diseases of faba bean in intercropping [48]. As a result, both species may exhibit yield advantages in intercropping [23,48]. Such species-specific facilitation may also result from greater biochemical plasticity of tree species in mixed-species forest plantations [42]. Facilitated species may also benefit more from the facilitator when specific traits exhibit greater phenotypic distance from those of its facilitator [71]. In addition, harnessing beneficial soil biota interactions and signals to strengthen positive effects of microbe-mediated root–root interactions and override negative effects (e.g., allelopathy, pathogen and insect attack; Figure 2) is desirable in facilitative networks in temporal (e.g., rotation) and spatially diverse (e.g., intercropping and agricultural mixtures) plant communities [48,58,60,72]. When establishing a rotation system or restoring a degraded community, manipulating the order of arrival of species or functional groups is important to influence competition and facilitation between earlier- and later-arriving species by root exudates and legacy effects [48,73,74].

Others have found that optimising resource (e.g., P) and temporal complementarity by specific species/genotype combinations can reduce competition and enhance ecosystem functioning [4], but such combinations are difficult to identify [5,6,62]. We argue that searching for these combinations in the context of direct and indirect facilitative interactions may contribute to trait matching and improve the establishment of managed communities. Adopting an understanding of biotic and abiotic stress gradients on the relative strength of facilitation and competition may also contribute to managing ecosystems [65].

Concluding remarks and future perspectives

A key challenge for ecologists and plant scientists is to close the gap between ecological principles and applications in agroecosystems and other managed systems. We suggest that biodiversity research has the potential to unveil secrets of species-specific responses of root traits as well as metabolic and interkingdom interactions between facilitating and facilitated species in ways that maximise facilitation in plant communities. The insights gained from such studies would inform selection of species/genotype combinations and breeding that might promote facilitation in diverse systems. The next frontier of belowground facilitation in BEF research, particularly as

Outstanding questions

How can we quantitatively separate facilitation and niche differentiation (cause) from complementarity effects (consequence)?

How do facilitated species recognise, respond to, and match a facilitator via root exudates, signalling molecules, and soil biota?

How can we measure interspecific facilitation in more diverse plant communities (more than two species) via functional traits (e.g., leaf manganese concentration) and new technology (e.g., image processes and multiomic analyses) to better understand mechanisms of facilitation?

How can we engineer belowground facilitation processes to design more productive and sustainable cropping systems (e.g., intercropping and agroforestry) and seminatural systems (e.g., managed forests and sown grasslands)?

applied to agroecosystems, will be the identification of intricately intertwined two- and three-species interactions that enhance ecosystem functions. These two- and three-way ecological 'tangos' might be harnessed in ecologically and economically groundbreaking ways (see Outstanding questions).

Acknowledgements

R-P.Y. and L.L. were supported by the National Key Research and Development Program of China (Project No. 2016YFD0300202), National Natural Science Foundation of China (NSFC) (Project No. 31430014), and National Key Basic Research Program of China (Project No. 2014CB138801). Funding was provided by Australian Research Council Discovery Grants (Nos DP130100005 and DP200101013) to H.L. and the Deputy Vice Chancellor (Research) at the University of Western Australia. R.M.C. acknowledges support from the National Science Foundation EPSCoR Cooperative Agreement OIA-1757351. Funding was provided from a California State University Los Angeles start-up grant to A.J.W.

Declaration of interests

No interests are declared.

References

1. Tilman, D. *et al.* (2014) Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. S.* 45, 471–493
2. Li, L. *et al.* (2014) Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol.* 203, 63–69
3. Brooker, R.W. *et al.* (2021) Facilitation and biodiversity ecosystem function (BEF) relationships in crop production systems and their role in sustainable farming. *J. Ecol.* 109, 2054–2067
4. Barry, K.E. *et al.* (2019) The future of complementarity: disentangling causes from consequences. *Trends Ecol. Evol.* 34, 167–180
5. Jesch, A. *et al.* (2018) Below-ground resource partitioning alone cannot explain the biodiversity-ecosystem function relationship: a field test using multiple tracers. *J. Ecol.* 106, 2002–2018
6. Barry, K.E. *et al.* (2019) Limited evidence for spatial resource partitioning across temperate grassland biodiversity experiments. *Ecology* 101, e02905
7. Wright, A.J. *et al.* (2017) The overlooked role of facilitation in biodiversity experiments. *Trends Ecol. Evol.* 32, 383–390
8. Losapio, G. *et al.* (2021) Facilitation and biodiversity jointly drive mutualistic networks. *J. Ecol.* 109, 2029–2037
9. Armas, C. *et al.* (2004) Measuring plant interactions: a new comparative index. *Ecology* 85, 2682–2686
10. Loreau, M. and Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76
11. Mommer, L. *et al.* (2010) Unveiling below-ground species abundance in a biodiversity experiment: a test of vertical niche differentiation among grassland species. *J. Ecol.* 98, 1117–1127
12. Mommer, L. *et al.* (2018) Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. *New Phytol.* 218, 542–553
13. van Ruijven, J. *et al.* (2020) Do soil-borne fungal pathogens mediate plant diversity-productivity relationships? Evidence and future opportunities. *J. Ecol.* 108, 1810–1821
14. Yu, R. *et al.* (2020) Phosphorus facilitation and covariation of root traits in steppe species. *New Phytol.* 226, 1285–1298
15. Chen, Y. *et al.* (2020) Root ethylene mediates rhizosphere microbial community reconstruction when chemically detecting cyanide produced by neighbouring plants. *Microbiome* 8, 4
16. Jiang, Y. *et al.* (2020) Trophic interactions as determinants of the arbuscular mycorrhizal fungal community with cascading plant-promoting consequences. *Microbiome* 8, 142
17. Wright, A.J. *et al.* (2017) Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytol.* 213, 645–656
18. Liancourt, P. *et al.* (2021) Community-scale effects and strain: facilitation beyond conspicuous patterns. *J. Ecol.* 109, 19–25
19. van der Heijden, M.G. and Horton, T.R. (2009) Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J. Ecol.* 97, 1139–1150
20. Pang, J. *et al.* (2021) Advances in understanding plant root uptake of phosphorus. In *Understanding and Improving Crop Root Function* (Gregory, P., ed.), pp. 321–372, Burleigh Dodds Science Publishing Limited
21. Lambers, H. *et al.* (2018) How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impoverished hyperdiverse ecosystems. *Plant Soil* 424, 11–33
22. Li, B. *et al.* (2016) Root exudates drive interspecific facilitation by enhancing nodulation and N_2 fixation. *Proc. Natl. Acad. Sci. U. S. A.* 113, 6496–6501
23. Li, L. *et al.* (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proc. Natl. Acad. Sci. U. S. A.* 104, 11192–11196
24. Wang, N. *et al.* (2021) Root exudate signals in plant-plant interactions. *Plant Cell Environ.* 44, 1044–1058
25. Xia, Z. *et al.* (2016) A broadleaf species enhances an autotoxic conifers growth through belowground chemical interactions. *Ecology* 97, 2283–2292
26. Lopez-Raez, J.A. *et al.* (2017) Strigolactones in plant interactions with beneficial and detrimental organisms: the Yin and Yang. *Trends Plant Sci.* 22, 527–537
27. Li, L. *et al.* (2020) (–)-Loliolide, the most ubiquitous lactone, is involved in barnyardgrass-induced rice allelopathy. *J. Exp. Bot.* 71, 1540–1550
28. Kong, C. *et al.* (2018) Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. *Nat. Commun.* 9, 3867
29. Yang, X. *et al.* (2018) Kin recognition in rice (*Oryza sativa*) lines. *New Phytol.* 220, 567–578
30. Zhang, D. *et al.* (2016) Increased soil phosphorus availability induced by faba bean root exudation stimulates root growth and phosphorus uptake in neighbouring maize. *New Phytol.* 209, 823–831
31. Zhang, D. *et al.* (2020) Neighbouring plants modify maize root foraging for phosphorus: coupling nutrients and neighbours for improved nutrient-use efficiency. *New Phytol.* 226, 244–253
32. Schneider, H.M. and Lynch, J.P. (2020) Should root plasticity be a crop breeding target? *Front. Plant Sci.* 11, 546
33. Abakumova, M. *et al.* (2016) Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytol.* 211, 455–463
34. Wagemaker, C.A.M. *et al.* (2021) msGBS: A new high-throughput approach to quantify the relative species abundance in root samples of multispecies plant communities. *Mol. Ecol. Resour.* 21, 1021–1036
35. Streit, J. *et al.* (2019) Above- and belowground biomass in a mixed cropping system with eight novel winter faba bean genotypes and winter wheat using FTIR spectroscopy for root species discrimination. *Plant Soil* 436, 141–158

36. Tegtmeier, J. *et al.* (2021) Root-o-Mat: a novel tool for 2D image processing of root-soil interactions and its application in soil zymography. *Soil Biol. Biochem.* 157, 108236
37. Ma, X. *et al.* (2021) Phosphatase activity and acidification in lupine and maize rhizosphere depend on phosphorus availability and root properties: coupling zymography with planar optodes. *Appl. Soil Ecol.* 167, 104029
38. Yu, R. *et al.* (2020) Linking shifts in species composition induced by grazing with root traits for phosphorus acquisition in a typical steppe in Inner Mongolia. *Sci. Total Environ.* 712, 136495
39. Lambers, H. *et al.* (2021) Leaf manganese concentrations as a tool to assess belowground plant functioning in phosphorus-impoverished environments. *Plant Soil* 461, 43–61
40. Wagg, C. *et al.* (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* 111, 5266–5270
41. Epihov, D.Z. *et al.* (2021) Legume-microbiome interactions unlock mineral nutrients in regrowing tropical forests. *Proc. Natl. Acad. Sci. U. S. A.* 118, e202224118
42. Xia, Z. *et al.* (2019) Broadleaf trees mediate chemically the growth of Chinese fir through root exudates. *Biol. Fertil. Soils* 55, 737–749
43. Mhlongo, M.I. *et al.* (2018) The chemistry of plant-microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. *Front. Plant Sci.* 9, 112
44. Li, X. *et al.* (2020) *Atractylodes lancea* volatiles induce physiological responses in neighboring peanut plant during intercropping. *Plant Soil* 453, 409–422
45. Li, X. *et al.* (2018) Suppression of soil-borne *Fusarium* pathogens of peanut by intercropping with the medicinal herb *Atractylodes lancea*. *Soil Biol. Biochem.* 116, 120–130
46. de Britto Costa, P. *et al.* (2021) Root positioning and trait shifts in *Hibbertia racemosa* as dependent on its neighbour's nutrient-acquisition strategy. *Plant Cell Environ.* 44, 1257–1267
47. Pickles, B.J. *et al.* (2017) Transfer of ^{13}C between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas. *New Phytol.* 214, 400–411
48. Wang, G. *et al.* (2021) Soil microbial legacy drives crop diversity advantage: linking ecological plant-soil feedback with agricultural intercropping. *J. Appl. Ecol.* 58, 496–506
49. Zhang, X. *et al.* (2019) Spatial pattern of enzyme activities depends on root exudate composition. *Soil Biol. Biochem.* 133, 83–93
50. Zhang, J. *et al.* (2019) NRT1.1B is associated with root microbiota composition and nitrogen use in field-grown rice. *Nat. Biotechnol.* 37, 676–684
51. Zhalnina, K. *et al.* (2018) Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480
52. Chen, S. *et al.* (2019) Root-associated microbiomes of wheat under the combined effect of plant development and nitrogen fertilization. *Microbiome* 7, 136
53. Zhang, W. *et al.* (2020) Mycelial network-mediated rhizobial dispersal enhances legume nodulation. *ISME J.* 14, 1015–1029
54. Jiang, F. *et al.* (2021) Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. *New Phytol.* 230, 304–315
55. Suleiman, A.K.A. *et al.* (2019) Organic amendment strengthens interkingdom associations in the soil and rhizosphere of barley (*Hordeum vulgare*). *Sci. Total Environ.* 695, 133885
56. Li, M. *et al.* (2019) Facilitation promotes invasions in plant-associated microbial communities. *Ecol. Lett.* 22, 149–158
57. Korenblum, E. *et al.* (2020) Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc. Natl. Acad. Sci. U. S. A.* 117, 3874–3883
58. Geddes, B.A. *et al.* (2019) Engineering transkingdom signalling in plants to control gene expression in rhizosphere bacteria. *Nat. Commun.* 10, 3430
59. Zhang, J. *et al.* (2021) High-throughput cultivation and identification of bacteria from the plant root microbiota. *Nat. Protoc.* 16, 988–1012
60. Song, C. *et al.* (2021) Designing a home for beneficial plant microbiomes. *Curr. Opin. Plant Biol.* 62, 102025
61. Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*, Springer
62. Li, C. *et al.* (2018) Testing for complementarity in phosphorus resource use by mixtures of crop species. *Plant Soil* 439, 163–177
63. Wei, L. *et al.* (2015) Nitrogen sharing and water source partitioning co-occur in estuarine wetlands. *Funct. Plant Biol.* 42, 410–417
64. Tang, Y. *et al.* (2019) Water source partitioning and nitrogen facilitation promote coexistence of nitrogen-fixing and neighbor species in mixed plantations in the semiarid Loess Plateau. *Plant Soil* 445, 289–305
65. Bertness, M.D. and Callaway, R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193
66. Callaway, R.M. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848
67. Tian, Q. *et al.* (2016) A novel soil manganese mechanism drives plant species loss with increased nitrogen deposition in a temperate steppe. *Ecology* 97, 65–74
68. Zhou, J. *et al.* (2019) Following legume establishment, microbial and chemical associations facilitate improved productivity in degraded grasslands. *Plant Soil* 443, 273–292
69. Renard, D. and Tilman, D. (2019) National food production stabilized by crop diversity. *Nature* 571, 257–260
70. Cong, W. *et al.* (2020) Tightening the phosphorus cycle through phosphorus-efficient crop genotypes. *Trends Plant Sci.* 25, 967–975
71. Navarro-Cano, J.A. *et al.* (2021) Phenotypic structure of plant facilitation networks. *Ecol. Lett.* 24, 509–519
72. Bakker, P. *et al.* (2020) The soil-borne identity and microbiome-assisted agriculture: looking back to the future. *Mol. Plant* 13, 1394–1401
73. Delory, B.M. *et al.* (2019) When history matters: the overlooked role of priority effects in grassland overyielding. *Funct. Ecol.* 33, 2369–2380
74. Delory, B.M. *et al.* (2021) Soil chemical legacies trigger species-specific and context-dependent root responses in later arriving plants. *Plant Cell Environ.* 44, 1215–1230
75. Gómez-Aparicio, L. *et al.* (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* 14, 1128–1138
76. Dawson, E.T. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95, 565–574
77. Bayala, J. and Prieto, I. (2019) Water acquisition, sharing and redistribution by roots: applications to agroforestry systems. *Plant Soil* 453, 17–28