

Opinion

Steering Soil Microbiomes to Suppress Aboveground Insect Pests

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Soil-borne microbes affect aboveground herbivorous insects through a cascade of molecular and chemical changes in the plant, but knowledge of these microbe–plant–insect interactions is mostly limited to one or a few microbial strains. Yet, the soil microbial community comprises thousands of unique taxa interacting in complex networks, the so-called ‘microbiome’, which provides plants with multiple beneficial functions. There has been little exploration of the role and management of whole microbiomes in plant–insect interactions, calling for the integration of this complexity in aboveground–belowground research. Here, we propose holistic approaches to select soil microbiomes that can be used to protect plants from aboveground attackers.

Microbes Conferring Immunity in the Phytobiome

The late entomologist, Thomas Eisner, once famously stated, ‘Bugs are not going to inherit the Earth. They own it now’ [1]. However, in light of on-going discoveries in microbial taxonomy and ecology, we can probably affirm that in fact ‘Microbes own the Earth’. The complex network of microorganisms inhabiting an area (e.g., soil, plant, or animal), referred to as the **microbiome** (see [Glossary](#)), imparts crucial functions to all living organisms. For instance, the chemical defences that were previously considered an innate genetic feature of many animals and plants are in fact produced by microbial symbionts [2,3] and we expect more examples to be revealed in the near future. In humans, immunity and even behavior are influenced by the intestinal microbiome [4,5]. Interestingly, the **rhizosphere**, a thin interface between roots and soil, can be considered the plant equivalent to the human intestinal tract [6].

Soil is the major source of microbes, which determine the plant-associated microbiome [7]. Soil microbes are not only crucial for enhancing plant survival, growth, and tolerance to abiotic stress, but also induce systemic resistance against pathogens and insects both aboveground [8–11] and belowground [12]. Thus, the soil microbiome has emerged as a key component of plant immunity [8,9,13], and shapes how plants interact with their abiotic and biotic environments, in the so-called ‘**phytobiome**’ [14,15]. Most of the work on aboveground plant defence, so far, focuses on the impact of individual microbial species or strains. This is in contrast to DNA-sequencing techniques that are revealing an astonishing taxonomic diversity in soils, not only in the rhizosphere, but also the plant itself [7,16,17]. Given that the beneficial effects for the plant are often provided by a consortium of microbes [18], there is an urgent need for approaches that incorporate the wider diversity that exists in nature into microbe-mediated plant protection strategies [19].

Impact of Soil Microbiomes on Aboveground Herbivores

Evidence for how belowground microbial communities, as a whole, impact aboveground insects is scarce; however, given the typically strong responses to only one or two

Trends

Soil microbes are a major source of the plant microbiome and recent advances show that they are key components of plant resistance against aboveground attackers.

However, most of our knowledge of how belowground microbes affect aboveground pests is limited to single strain effects, calling for research that incorporates the full potential of the entire soil microbiome.

Soil microbiomes can be manipulated, as has been done for centuries through agricultural practices such as crop rotation or the use of amendments. Conditioned soils can also be transplanted to restore ecological functions in other ecosystems.

The role of the plant in shaping soil microbiomes and in how plants respond to those microbiomes can be maximized but we need to increase our mechanistic understanding at the genetic, physiological, and ecological levels.

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experimentally augmented microbes, we anticipate that the community-wide effects are substantial. Soil microbiomes can impact aboveground insects indirectly through plant-mediated mechanisms, or directly through pathogenic or mutualistic interactions. A recent study showed that increases in the population of the specialist foliar-feeding aphid *Aphis jacobaea* depended on the composition of microbial communities inhabiting the soil used by its host plant ragwort (*Senecio jacobaea*). The soils maintained different fungal communities that influenced the concentration of amino acids in the phloem sap, which the authors proposed influenced, in turn, the aphids [20]. Similarly, inoculation of distinct microbiomes collected from soils with different plant species altered the leaf metabolome of arabidopsis (*Arabidopsis thaliana*) and resistance of the plant to the caterpillar *Trichoplusia ni* [21]. Via removal of the majority of microorganisms using a filter of 0.45 μm , this study further confirmed the contribution of the microbial component of the soil (instead of the presence of chemical compounds that could pass the filter) to plant performance. These studies illustrate that exposure to particular microbiomes alters the resistance of plants to aboveground insects (Figure 1, Key Figure). However, the underlying molecular plant mechanisms in microbiome-induced systemic resistance (ISR, Box 1) are probably more complex than predicted.

Soil microbes can have direct interactions with aboveground herbivores. Recent studies have shown that leaf and soil microbiomes are linked [22–24] and, thus, soils could influence the composition of insect pathogenic or symbiotic microbes present in or on the leaves. Entomopathogenic fungi, such as *Beauveria bassiana* and *Metarhizium anisopliae*, for example, are not only common in the soil, but also exhibit an **endophytic** phase that can promote plant growth and insect resistance [25]. Remarkably, these fungi not only provide a benefit to plants by killing their herbivores, but can also translocate nitrogen from aboveground insect cadavers to the plant via fungal mycelia [26]. Other fungi historically considered to be limited to soils (e.g., *Trichoderma*) are now known to colonize leaves as endophytes, where they can suppress insect pests, such as thrips [27]. Insect symbionts provide their host with functions such as the ability to suppress plant defences or mobilize nutrients [28,29], and these symbionts can be acquired via the soil. For example, the soybean insect pest *Riptortus pedestris* acquires *Burkholderia* strains from the soil that metabolize an organophosphate that confers resistance to insecticides [30].

Given the substantial evidence that soil communities affect aboveground plant interactions, we argue that agricultural scientists should start to think more about reshaping microbiomes to increase crop resistance to insect pests. Managed systems allow a large amount of flexibility in inputs or other design strategies that shape soil life. Here, we focus on three specific strategies that are known to generate community-scale impacts on microbiomes and, thus, can be adapted for sustainable pest control aboveground.

Transplanting New Microbiomes into the Soil

A major advancement in microbe–plant interaction research was the development and commercialization of microbial inoculants for agricultural use. These inocula usually comprise one to several species that are phylogenetically clustered within a few genera (e.g., *Bacillus* or *Trichoderma*). However, many of these microbial inoculants that are successful under laboratory conditions fail when applied in the field. Recent studies have argued that this is probably due to competition of single strains with the existing microbiome in the donor soil [9,31]. A potential solution to this problem would be to inoculate microbiomes that are more complex than currently used [19]. Large-scale cultivation of microbes and their introduction in complex synthetic microbiomes may help maximize the beneficial functions of certain microbes by introducing taxa interactions [22,32]. For instance, some microbes alter their metabolism when involved in microbial interactions, and produce compounds (e.g., volatiles or antibiotics) that are not produced when growing as single strains. These compounds could, for example, act

Glossary

Endophytic: colonizes inside above- and/or belowground plant organs, without causing evident disease symptoms.

Endosphere: microbial habitat inside plant organs.

Induced systemic resistance (ISR): enhanced resistance in the entire plant against pathogens and herbivores, characterized by priming, and triggered by beneficial microbes.

Microbiome: totality of microbial genomes present in a particular environment; for example, soil, rhizosphere, phyllosphere, or endophytic compartment.

Phyllosphere: the surface of aerial plant organs, dominated by the leaves.

Phytobiomes: plants, their environment, and their associated communities of organisms, including microbes, animals, and other plants.

Plant–soil feedbacks: changes induced by a plant of the biotic and abiotic characteristics of the soil in which they grow that influence the next generation of plants growing in the same soil.

Plant–soil–insect feedbacks: plant–soil feedbacks that have effects on insects, or that are affected by insect feeding on the plant creating the soil legacy.

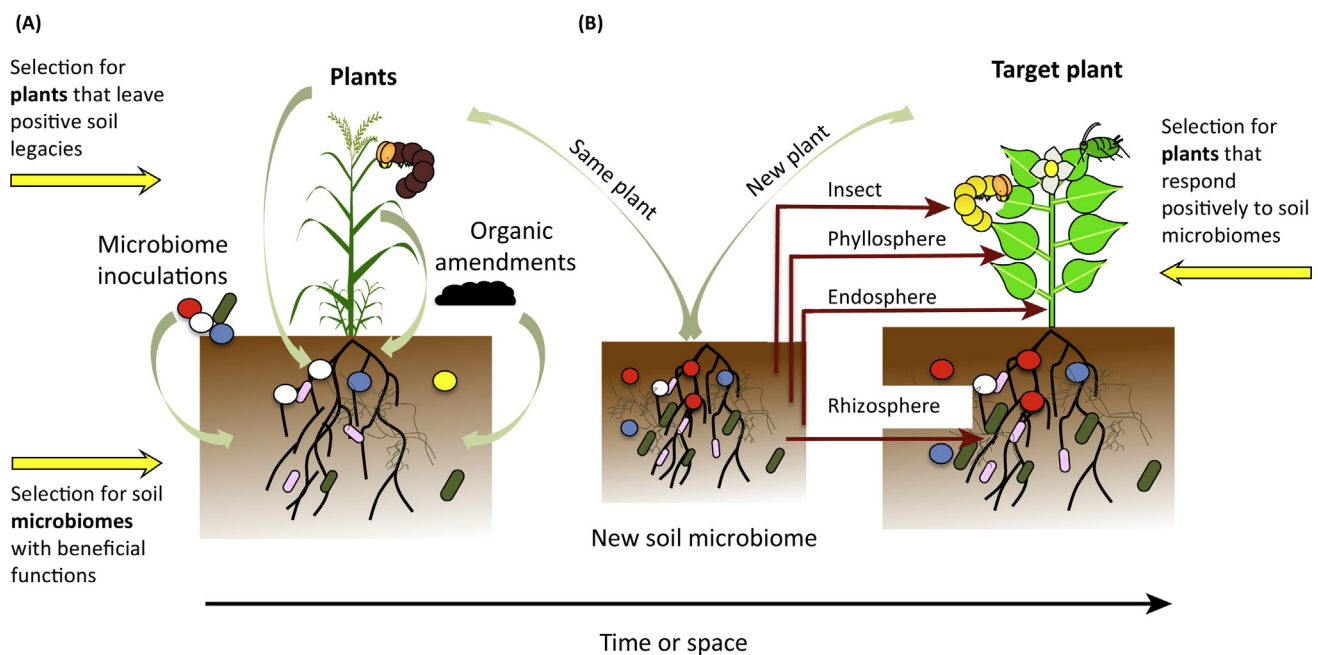
Priming: alert state after certain stimuli that allows plants to mount a stronger and/or faster defensive response upon attack.

Rhizosphere: thin layer of soil in contact with roots that is directly influenced by root exudates and soil microbes.

Root exudates: molecules released by plant roots; include, among others, organic acids and sugars.

Key Figure

Soil Microbiome Manipulation to Induce Resistance in Plants to Aboveground Insects



Trends in Plant Science

Figure 1. (A) Soil microbiomes can be steered by different strategies, such as inoculating new microbiomes, adding organic amendments, or growing certain plants. Interactions of the plant with antagonists, such as aboveground insect herbivores, will further shape the soil microbial community. Different components of the system can be selected for desirable traits. For instance, through plant breeding, cultivars that recruit beneficial soil microbiomes can be developed. Soil microbiomes can also be engineered, selecting through several generations those soils that confer plants with certain functions. (B) The new microbiome can affect plant growth and resistance to aboveground attackers of not only the plant that is already growing in the soil, but also that of plants growing later in the soil. The new soil microbiome is an important source of the microbial assembly of the rhizosphere, endosphere, and phyllosphere of plants. Microbes inhabiting those habitats can suppress aboveground insect pests, either directly (e.g., insect pathogens) or indirectly via changes in the immunity of the host plant. Cultivars that show strong positive responses (in terms of plant growth, resistance, etc.) to soil microbiomes could be developed. The suggested pattern of events could occur along a temporal (e.g., in a crop rotation system) or spatial axis (e.g., during intercropping).

antagonistically to other microbes that are prohibiting the establishment, enhance plant colonization, or have a direct effect on plant growth or resistance [33]. Soil microbial diversity is a major driver of ecosystem multifunctionality [34,35] and, due to the contribution of soil microbes to multiple functions, such as nutrient cycling, biological control, or food production, soil microbiomes are a multifunctional component of terrestrial ecosystems. Entire microbiomes can also be introduced via soil transplantation. A recent field experiment showed that introducing a thin layer of soil (5 mm) resulted in accelerated nature restoration in a degraded ecosystem, and that composition of the bacterial and fungal communities 6 years after application was still different from those where no soil had been added [36]. Other studies showed that soils with disease-suppressive properties can be successfully transplanted and remain disease suppressive in the new area [9, 17]. Agricultural soils, in particular in commercial glasshouses, are regularly sterilized (e.g., by steaming). This practice eradicates much of the existing microbial community [37], a situation that is ideal for the introduction of a new microbiome.

Box 1. Microbial-Induced Systemic Resistance against Insects

Plants can induce several types of resistance upon interacting with herbivores, pathogens, or beneficial microbes. From those, ISR is the enhanced defensive capacity of the entire plant against a broad spectrum of attackers triggered upon local induction by beneficial microbes [69]. Plants then enter a primed state that allows them to respond faster and stronger upon further herbivore or pathogen attack [11]. Our knowledge of the molecular mechanisms of ISR against insects has substantially increased in recent years. Several microbes, including plant growth-promoting rhizobacteria, mycorrhizal fungi, and free-living fungi, such as *Trichoderma*, can trigger ISR against insect herbivores, especially generalist leaf chewers. Interestingly, the mechanisms appear to be conserved across microbial groups. However, although ISR against insects is regulated by JA and ET signaling pathways in most cases [69,71], some microbial strains require other signaling pathways to be functional [72]. Genes, such as *LOX2*, *PDF1.2*, and *HEL*, are often more strongly induced after herbivory in arabidopsis that is inoculated with plant growth-promoting rhizobacteria [71,73,74]. However, the effects and underlying mechanisms of microbes on insects are diverse, and two aspects in particular suggest that the established paradigm of ISR needs to be re-evaluated: (i) direct induction instead of priming: soil microbes can also directly induce plant defence responses in the absence of an attacker. Genes in the ET pathway, such as *ORA59* and *PDF1.2*, for example, are induced by rhizobacteria colonization in arabidopsis [71], as are the JA-regulated genes *GhAOS*, *GhLOX1* and *GhOPR3* in cotton [75]. Associated with this, plant growth-promoting rhizobacteria or their volatiles directly induced the synthesis of glucosinolates in arabidopsis [71,72,76] and gossypol in cotton [75]; (ii) induced systemic susceptibility: insect performance often increases upon soil inoculation with beneficial microbes. This is especially common in phloem feeders, such as aphids and whiteflies, probably due to their behavior, whereby they avoid damaging cells and feed on phloem sap, which has lower levels of defensive compounds than the overall leaf tissue [10]. However, microbe-induced susceptibility has also been observed in generalist caterpillars [77,78]. Elucidating the factors causing this variability will be a major breakthrough in our knowledge and application of microbe–plant–insect interactions. Similar to microbial interaction networks, insects and plants are also structured in interaction networks. Systems approaches coupling microbial, insect, and plant signaling networks will allow scientists to design predictive models of microbiome–plant–insect interactions.

There is a unique opportunity here to forge collaborative and mutually beneficial relationships among those studying plant and animal microbiomes. Fecal microbiota transplantation is now frequently used to suppress diseases and alter immune responses in humans, while soil inoculation and transplantation is still in its infancy. Hence, those studying human health consequences of gut microbiome transplantation are far ahead of those working in plant health. Yet, the two approaches, while differing in practical aspects of implementation, are identical in theory. In fact, direct analogies between these two areas have been highlighted for characteristics such as nutrient uptake, pathogen defence, and immune function [6,38].

Steering Existing Soil Microbiomes

Apart from introducing a new microbiome, the residing soil community can also be steered to a desired beneficial state [39,40]. This could be accomplished by stimulating particular subgroups of the microbiome via manipulations of environmental factors, such as soil temperature or moisture levels [37], via the application of chemical compounds or manipulating resource availability through organic amendments. It is well known that amelioration of soils with manure or plant residues alters the soil microbiome, thereby suppressing belowground pathogens [9,40,41]. Different studies have shown that the addition of biochar (pyrolyzed plant residues) to soil, for example, increases bacterial diversity and microbial biomass [42], as well as the resistance of plants to aboveground pests and diseases [43,44]. Interestingly, the response that biochar causes in the plant to the pathogen *Botrytis cinerea* resembles microbial-ISR, including **priming** of defence-related genes associated with the early oxidative burst via the jasmonic acid (JA) signaling pathway [43]. These sets of studies highlight how soil amendment could impact aboveground attackers through changes in the soil microbiome and plant defences. However, evidence linking how soil amendments alter the soil microbiome, and how this cascades to induce systemic resistance in plants is still missing.

Certain ‘keystone’ microbes are highly connected with other taxa and have a key ecological role in the microbiome. By targeting keystone species, the entire microbial network can be adapted, as supported by recent discoveries [32,45,46]. Introduction of the oomycete pathogen *Albugo* sp. and the basidiomycete yeast fungus *Dioszegia* sp., for example, altered the microbiome

network in the **phyllosphere** of arabidopsis [45]. The important role of these keystone taxa suggests that they should be present in high abundance in the microbiome. However, keystone species can also have an important role at low densities and even rare microbes, which have been shown to induce resistance against aphids [47], can act as keystone players in microbiomes [48]. Whether a microbial function, such as ISR, is driven by changes in the microbiome network following the introduction a keystone taxon, rather than by the introduced taxa itself, is still unknown.

Using Plants to Steer the Soil Microbiome

By growing in the soil, plants modify the microbiome, either directly, or indirectly via influencing the abiotic environment [7]. Host factors, such as plant species, ontogeny, and exposure to antagonists, all shape microbiomes. Even different genotypes imprint unique microbial signatures on the soil [7,24,49–51]. Plant roots release compounds, such as sugars, organic acids, phytohormones, and secondary metabolites, and this **exudation** influences the soil community [52,53]. For instance, specific compounds (e.g., malic acid, benzoxiacinoids, and strigolactones) can enhance or recruit certain beneficial soil microbes in the rhizosphere [54–57]. Interestingly, the exudation of some of these compounds increases following aboveground herbivory, suggesting that this is an active strategy whereby plants recruit beneficial microbes for protection. The impact of herbivory on the soil can also influence the susceptibility of plants that are later exposed to this microbiome [58,59]. For example, the soil fungal community in the rhizosphere of ragwort that suffered from belowground or aboveground herbivory differed considerably from communities in unexposed plants. Plants that grew later in the soil with a belowground herbivory legacy displayed higher resistance to the leaf-chewer *Mamestra brassicae*, and this was associated with a modified profile of pyrrolizidine alkaloids in the foliage [59]. These two examples illustrate a closed feedback loop in interactions between plants, soil microbes, and insects, a term that we propose to call '**plant–soil–insect feedbacks**'.

The concept of plants changing the soil microbiome, which subsequently influences the performance of other plants that grow later in the soil, is one of the main mechanisms of '**plant–soil feedback**' [60,61] and is the basis for ancient agricultural practices, such as crop rotation, intercropping, or cover crops. However, this concept has primarily been used in the context of avoidance of soil pathogen build-up and autotoxicity, or to increase nutrient availability by using leguminous crops. We argue that plants displaying positive feedback effects on crop immunity to pests through their effect on the soil microbiome should be selected for and included in rotation systems, as 'engineers' of beneficial soil microbiomes. Plants that create a beneficial microbiome with positive effects on plant health could also be used to produce inocula that can be then be introduced during or at the start of cultivation. Surprisingly, the contribution of soil microbiomes to plant–soil feedbacks and their application in agriculture is largely unknown [62]. There is an urgent need for studies that improve our understanding of the mechanisms by which plants influence soil microbiomes and that predict how plants respond to these changes (Box 2). This will enable us to design optimal combinations of succeeding plants in rotation schemes and enable breeding for optimal crop responses to soil manipulations [63].

The genetic traits that underlie the responses of plants to changes in soil microbiomes are also largely unknown. However, a recent genome-wide association study in arabidopsis identified ten genetic loci that were highly associated with the ability of the plant to respond to the growth-promotion effect of volatiles from a soil-derived *Pseudomonas simiae* strain [64]. In crop plants, breeding for resistance to pathogens in combination with high inputs of fertilizers and pesticides that suppress pathogens and herbivores, may have selected for poorly responding genotypes, and even for genotypes that suppress beneficial microbes [49,65]. Therefore, incorporating

Box 2. Plant–Soil and Plant–Soil–Insect Feedbacks

Plants as primary producers provide the basic resources for soil biota, including insects, nematodes, and microbes [79]. They contribute litter originating from dead shoots or roots to the soil, and living plant roots release an array of metabolites. Via these effects, plants shape the soil biotic communities that use these compounds or are influenced by them, and alter the physical and chemical properties of soils. These plant-mediated changes to the soil can influence the performance of other plants that grow later in the same soil [60,61]. This phenomenon is called ‘plant–soil feedback’ and is now receiving considerable attention because of its relevance in vegetation dynamics and invasion ecology. Plants can affect individuals of the same species (known as direct or conspecific feedback) or of different species (indirect or heterospecific feedback). Most examples of conspecific plant–soil feedbacks are negative, but heterospecific soil feedbacks are often positive, since many species perform better in soil conditioned by species other than its own [60,61]. Outcomes also vary widely between plant species and soils, and more research is needed to predict these patterns. Plant functional traits, such as growth rate, specific root length, and even aboveground characteristics, such as specific leaf area, have been used to predict plant soil feedbacks in natural ecosystems. For instance, soil conditioned by fast-growing plant species or those with higher belowground biomass produced more positive feedbacks due to increased nitrogen availability [80,81]. One of the most straightforward predictions is that closely related plant species are more likely to be attacked by similar pathogenic microbes, and negative feedbacks would be expected in this case. However, studies so far show inconsistent effects of the relationship between phylogenetic relatedness and plant–soil feedbacks [81–83]. Another layer of complexity in plant–soil feedbacks is the presence of herbivorous insects attacking the plants involved in the feedback, a concept that we define as ‘plant–soil–insect feedback’. A first possibility is that herbivory on plants that condition the soil alters soil legacies [59]. The second possibility is that plant–soil feedback effects cascade to insects interacting with the responding plant during the feedback phase [20]. Both scenarios may occur in a single plant–insect system [59]. Thus, ecological knowledge of plant–soil feedback effects on the natural enemies of plants has strong potential for future implementation in agricultural ecosystems.

Outstanding Questions

Can we develop a universal approach to manage soil and plant microbiomes to achieve higher yields, tolerance to abiotic stress, and enhanced resistance to pests?

What genetic, molecular, and chemical plant mechanisms are responsible for how plants shape and respond to soil microbiomes?

What are the mechanisms that underlie microbiome-induced systemic resistance to aboveground attackers and what are the consequences for higher trophic levels?

How do soil microbiomes interact with plant- and herbivore-associated microbiomes to influence plant–insect interactions?

knowledge of microbiomes during the crop selection process may improve traits such as plant productivity and resistance. By growing plants repeatedly in the soil and selecting in each generation for specific plant traits, such as early onset of flowering or more efficient induction of defences, beneficial soil microbiomes can also be selected and, therefore, further steered, so that they become more effective [17,66,67].

Concluding Remarks and Future Perspectives

Unraveling the mechanisms that govern species interactions is a major challenge in ecology. In this opinion, we have emphasized that soil microbiomes can be manipulated to enhance plant performance and resistance to aboveground pests, and that plants have pivotal roles in this. Given that soil microbiomes are complex entities, the mechanisms involved are diverse, including priming for enhanced defensive responses, induction of plant secondary metabolites, as well as direct interactions between soil microbes and insects (via direct contact of insects with the soil or via colonization of plant by soil microbes). We propose three areas for future research that are essential if we aim to steer microbiomes to alter aboveground plant–insect interactions (also see Outstanding Questions).

First, fundamental knowledge of the mechanisms of how plants shape soil and plant microbiomes will help to develop new approaches and products. For instance, cultivars emitting higher levels of compounds that enrich certain groups of beneficial microbes could be selected, or products based on those of compounds could be developed. Also, breeding programs could select plants to enhance microbe-mediated functions, from leaving positive soil legacies to strongly responding to those legacies by increasing growth or inducing resistance in aboveground tissues [63]. Therefore, knowledge of soil, plant, and insect microbiomes should be integrated into established research on insect–plant interactions to fully understand the functioning of these interactions within the phytobiome.

Second, in a similar way as gut microbiome transplantation in humans has been a major breakthrough in overcoming recurrent *Clostridium difficile* infection [68], we propose that soil microbiome transplantation can be successful to induce resistance in plants against insects. Plant–soil feedback concepts can be used to create specific donor soils. We envisage that, in

agriculture, plants will be grown with the clear purpose of conditioning soil, which can then be transplanted, or that soil conditioning will be incorporated into crop rotation systems. A major challenge is to predict which plant species or genotypes can be used to obtain desired soils. Understanding microbiome assembly and function in different plants, coupled with empirical knowledge of agricultural practices, and of microbe–plant–insect interactions, will be essential for the development of such predictive models.

Third, we propose that, since insect herbivores can severely impact productivity in terrestrial ecosystems, plant resistance to insects should be seen as a key service of microbiomes, and microbiome–insect interactions should be included in agricultural management strategies. Many of the ecosystem services of soil microbiomes may not be effective under current production systems with a high input of pesticides and chemical fertilizers, and only become apparent when plants are exposed to abiotic stress conditions [19]. Based on current global changes in agriculture and nutrient supplies, we expect that beneficial soil microbiomes will have an even more important role in plant productivity in the future. The increased availability of nutrients in agriculture was the basis for the first green revolution, which led to a boost in yields worldwide. We are now on the verge of a second green revolution, which will utilize the potential of microbiomes to boost plant health and productivity [69,70]. The use of plant and soil microbiomes to induce resistance in plants to insect pests should be an essential part of this second revolution.

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References

1. Berenbaum, M.R. (2011) Thomas Eisner: interpreter extraordinaire of nature's chemistry. *Proc. Natl. Acad. Sci. U. S. A.* 108, 19482–19483
2. Florez, L.V. *et al.* (2015) Defensive symbioses of animals with prokaryotic and eukaryotic microorganisms. *Nat. Prod. Rep.* 32, 904–936
3. Saikonen, K. *et al.* (2013) Chemical ecology mediated by fungal endophytes in grasses. *J. Chem. Ecol.* 39, 962–968
4. Thaiss, C.A. *et al.* (2016) The microbiome and innate immunity. *Nature* 535, 65–74
5. Eisenstein, M. (2016) Microbiome: bacterial broadband. *Nature* 533, 104–106
6. Selosse, M.-A. *et al.* (2014) Microbial priming of plant and animal immunity: symbionts as developmental signals. *Trends Microbiol.* 22, 607–613
7. Bulgarelli, D. *et al.* (2013) Structure and functions of the bacterial microbiota of plants. *Annu. Rev. Plant Biol.* 64, 807–838
8. Pieterse, C.M.J. *et al.* (2016) The soil-borne supremacy. *Trends Plant Sci.* 21, 171–173
9. Raaijmakers, J.M. and Mazzola, M. (2016) Soil immune responses. *Science* 352, 1392–1393
10. Pineda, A. *et al.* (2010) Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends Plant Sci.* 15, 507–514
11. Martínez-Medina, A. *et al.* (2016) Recognizing plant defense priming. *Trends Plant Sci.* 21, 818–822
12. Martínez-Medina, A. *et al.* (2017) Shifting from priming of salicylic acid- to jasmonic acid-regulated defences by *Trichoderma* protects tomato against the root knot nematode *Meloidogyne incognita*. *New Phytol.* 213, 1363–1377
13. Alvisatos, A.P. *et al.* (2015) A unified initiative to harness Earth's microbiomes. *Science* 350, 507–508
14. Leach, J.E. *et al.* (2017) Communication in the phytobiome. *Cell* 169, 587–596
15. Beattie, G.A. (2015) Microbiomes: curating communities from plants. *Nature* 528, 340–341
16. Lundberg, D.S. *et al.* (2012) Defining the core *Arabidopsis thaliana* root microbiome. *Nature* 488, 86–90
17. Mendes, R. *et al.* (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* 332, 1097–1100
18. Santhanam, R. *et al.* (2015) Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proc. Natl. Acad. Sci. U. S. A.* 112, E5013–E5020
19. Busby, P.E. *et al.* (2017) Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.* 15, e2001793
20. Kos, M. *et al.* (2015) Species-specific plant–soil feedback effects on above-ground plant–insect interactions. *J. Ecol.* 103, 904–914
21. Badri, D.V. *et al.* (2013) Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New Phytol.* 198, 264–273
22. Bai, Y. *et al.* (2015) Functional overlap of the *Arabidopsis* leaf and root microbiota. *Nature* 528, 364–369
23. de Souza, R.S.C. *et al.* (2016) Unlocking the bacterial and fungal communities assemblages of sugarcane microbiome. *Sci. Rep.* 6, 28774
24. Wagner, M.R. *et al.* (2016) Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. *Nat. Commun.* 7, 12151
25. Jaber, L.R. and Enkerli, J. (2016) Effect of seed treatment duration on growth and colonization of *Vicia faba* by endophytic *Beauveria bassiana* and *Metarhizium brunneum*. *Biol. Control* 103, 187–195
26. Behie, S.W. *et al.* (2012) Endophytic insect-parasitic fungi translocate nitrogen directly from insects to plants. *Science* 336, 1576–1577

27. Muvea, A.M. *et al.* (2014) Colonization of onions by endophytic fungi and their impacts on the biology of *Thrips tabaci*. *PLoS One* 9, e108242
28. Chung, S.H. *et al.* (2013) Herbivore exploits orally secreted bacteria to suppress plant defenses. *Proc. Natl. Acad. Sci. U. S. A.* 110, 15728–15733
29. Giron, D. *et al.* (2017) Influence of microbial symbionts on plant–insect interactions. *Adv. Bot. Res.* 81, 225–257
30. Kikuchi, Y. *et al.* (2012) Symbiont-mediated insecticide resistance. *Proc. Natl. Acad. Sci. U. S. A.* 109, 8618–8622
31. Gadhav, K.R. *et al.* (2016) Developing soil microbial inoculants for pest management: can one have too much of a good thing? *J. Chem. Ecol.* 42, 348–356
32. Niu, B. *et al.* (2017) Simplified and representative bacterial community of maize roots. *Proc. Natl. Acad. Sci. U. S. A.* 114, 2450–2459
33. Schmidt, R. *et al.* (2015) Volatile affairs in microbial interactions. *ISME J.* 9, 2329–2335
34. Wagg, C. *et al.* (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* 111, 5266–5270
35. Delgado-Baquerizo, M. *et al.* (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.* 7, 10541
36. Wubs, E.R.J. *et al.* (2016) Soil inoculation steers restoration of terrestrial ecosystems. *Nat. Plants* 2, 16107
37. van der Voort, M. *et al.* (2016) Impact of soil heat on reassembly of bacterial communities in the rhizosphere microbiome and plant disease suppression. *Ecol. Lett.* 19, 375–382
38. Berendsen, R.L. *et al.* (2012) The rhizosphere microbiome and plant health. *Trends Plant Sci.* 17, 478–486
39. Chaparro, J.M. *et al.* (2012) Manipulating the soil microbiome to increase soil health and plant fertility. *Biol. Fertility Soils* 48, 489–499
40. Dessaux, Y. *et al.* (2016) Engineering the rhizosphere. *Trends Plant Sci.* 21, 266–278
41. Mazzola, M. *et al.* (2015) *Brassica* seed meal soil amendments transform the rhizosphere microbiome and improve apple production through resistance to pathogen reinfestation. *Phytopathology* 105, 460–469
42. Kolton, M. *et al.* (2017) Biochar-stimulated plant performance is strongly linked to microbial diversity and metabolic potential in the rhizosphere. *New Phytol.* 213, 1393–1404
43. Mehari, Z.H. *et al.* (2015) Induced systemic resistance in tomato (*Solanum lycopersicum*) against *Botrytis cinerea* by biochar amendment involves jasmonic acid signaling. *Plant Soil* 395, 31–44
44. Hou, X. *et al.* (2015) Biochar amendment to soils impairs developmental and reproductive performances of a major rice pest *Nilaparvata lugens* (Homoptera: Delphacidae). *J. Appl. Entomol.* 139, 727–733
45. Agler, M.T. *et al.* (2016) Microbial hub taxa link host and abiotic factors to plant microbiome variation. *PLoS Biol.* 14, e1002352
46. van der Heijden, M.G.A. and Hartmann, M. (2016) Networking in the plant microbiome. *PLoS Biol.* 14, e1002378
47. Hol, W.H.G. *et al.* (2010) Reduction of rare soil microbes modifies plant–herbivore interactions. *Ecol. Lett.* 13, 292–301
48. Jousset, A. *et al.* (2017) Where less may be more: how the rare biosphere pulls ecosystems strings. *ISME J.* 11, 853–862
49. Bulgarelli, D. *et al.* (2015) Structure and function of the bacterial root microbiota in wild and domesticated barley. *Cell Host Microbe* 17, 392–403
50. Peiffer, J.A. *et al.* (2013) Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6548–6553
51. Chaparro, J.M. *et al.* (2014) Rhizosphere microbiome assemblage is affected by plant development. *ISME J.* 8, 790–803
52. van Dam, N.M. and Bouwmeester, H.J. (2016) Metabolomics in the rhizosphere: tapping into belowground chemical communication. *Trends Plant Sci.* 21, 256–265
53. Bais, H.P. *et al.* (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* 57, 233–266
54. Rudrappa, T. *et al.* (2008) Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiol.* 148, 1547–1556
55. Neal, A.L. *et al.* (2012) Benzoxazinoids in root exudates of maize attract *Pseudomonas putida* to the rhizosphere. *PLoS One* 7, e35498
56. Lakshmanan, V. *et al.* (2014) Functional soil microbiome: belowground solutions to an aboveground problem. *Plant Physiol.* 166, 689–700
57. López-Ráez, J.A. *et al.* (2017) Strigolactones in plant interactions with beneficial and detrimental organisms: the Yin and Yang. *Trends Plant Sci.* 22, 527–537
58. Bezemer, T.M. *et al.* (2013) Above- and below-ground herbivory effects on below-ground plant–fungus interactions and plant–soil feedback responses. *J. Ecol.* 101, 325–333
59. Kostenko, O. *et al.* (2012) Legacy effects of aboveground–belowground interactions. *Ecol. Lett.* 15, 813–821
60. van der Putten, W.H. *et al.* (2013) Plant–soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276
61. Kulmatiski, A. *et al.* (2008) Plant–soil feedbacks: a meta-analytical review. *Ecol. Lett.* 11, 980–992
62. Dias, T. *et al.* (2015) Accounting for soil biotic effects on soil health and crop productivity in the design of crop rotations. *J. Sci. Food Agric.* 95, 447–454
63. Gopal, M. and Gupta, A. (2016) Microbiome selection could spur next-generation plant breeding strategies. *Front. Microbiol.* 7, 1971
64. Wintermans, P.C. *et al.* (2016) Natural genetic variation in *Arabidopsis* for responsiveness to plant growth-promoting rhizobacteria. *Plant Mol. Biol.* 90, 623–634
65. Pérez-Jaramillo, J.E. *et al.* (2016) Impact of plant domestication on rhizosphere microbiome assembly and functions. *Plant Mol. Biol.* 90, 635–644
66. Panke-Buisse, K. *et al.* (2015) Selection on soil microbiomes reveals reproducible impacts on plant function. *ISME J.* 9, 980–989
67. Mueller, U. and Sachs, J. (2015) Engineering microbiomes to improve plant and animal health. *Trends Microbiol.* 23, 606–617
68. Fuentes, S. *et al.* (2014) Reset of a critically disturbed microbial ecosystem: faecal transplant in recurrent *Clostridium difficile* infection. *ISME J.* 8, 1621–1633
69. Pieterse, C.M.J. *et al.* (2014) Induced systemic resistance by beneficial microbes. *Annu. Rev. Phytopathol.* 52, 347–375
70. Bender, S.F. *et al.* (2016) An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol. Evol.* 31, 440–452
71. Pangesti, N. *et al.* (2016) Jasmonic acid and ethylene signaling pathways regulate glucosinolate levels in plants during rhizobacteria-induced systemic resistance against a leaf-chewing herbivore. *J. Chem. Ecol.* 42, 1212–1225
72. van de Mortel, J.E. *et al.* (2012) Metabolic and transcriptomic changes induced in *Arabidopsis* by the rhizobacterium *Pseudomonas fluorescens* SS101. *Plant Physiol.* 160, 2173–2188
73. Pangesti, N. *et al.* (2014) Variation in plant-mediated interactions between rhizobacteria and caterpillars: potential role of soil composition. *Plant Biol.* 17, 474–483
74. van Oosten, V.R. *et al.* (2008) Differential effectiveness of microbially induced resistance against herbivorous insects in *Arabidopsis*. *Mol. Plant-Microbe Interact.* 21, 919–930
75. Zebelo, S. *et al.* (2016) Rhizobacteria activates (+)- δ -cadinene synthase genes and induces systemic resistance in cotton against beet armyworm (*Spodoptera exigua*). *Plant Cell Environ.* 39, 935–943
76. Aziz, M. *et al.* (2016) Augmenting sulfur metabolism and herbivore defense in *Arabidopsis* by bacterial volatile signaling. *Front. Plant Sci.* 7, 458
77. Megali, L. *et al.* (2013) Fertilization with beneficial microorganisms decreases tomato defenses against insect pests. *Agron. Sustain. Dev.* 34, 649–656

78. Fernández de Bobadilla, M. *et al.* (2017) Does drought stress modify the effects of plant-growth promoting rhizobacteria on an aboveground chewing herbivore? *Insect Sci.* Published online May 12, 2017. <http://dx.doi.org/10.1111/1744-7917.12477>
79. Bardgett, R.D. and Wardle, D.A. (2010) *Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*, Oxford University Press
80. Baxendale, C. *et al.* (2014) Are plant–soil feedback responses explained by plant traits? *New Phytol.* 204, 408–423
81. Fitzpatrick, C.R. *et al.* (2017) Phylogenetic relatedness, phenotypic similarity and plant–soil feedbacks. *J. Ecol.* 105, 786–800
82. Mehrabi, Z. and Tuck, S.L. (2015) Relatedness is a poor predictor of negative plant–soil feedbacks. *New Phytol.* 205, 1071–1075
83. Anacker, B.L. *et al.* (2014) Phylogenetic conservatism in plant–soil feedback and its implications for plant abundance. *Ecol. Lett.* 17, 1613–1621