Microbial Population and Community Dynamics on Plant Roots and Their Feedbacks on Plant Communities

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Abstract

The composition of the soil microbial community can be altered dramatically due to association with individual plant species, and these effects on the microbial community can have important feedbacks on plant ecology. Negative plant-soil feedback plays primary roles in maintaining plant community diversity, whereas positive plant-soil feedback may cause community conversion. Host-specific differentiation of the microbial community results from the trade-offs associated with overcoming plant defense and the specific benefits associated with plant rewards. Accumulation of host-specific pathogens likely generates negative feedback on the plant, while changes in the density of microbial mutualists likely generate positive feedback. However, the competitive dynamics among microbes depends on the multidimensional costs of virulence and mutualism, the fine-scale spatial structure within plant roots, and active plant allocation and localized defense. Because of this, incorporating a full view of microbial dynamics is essential to explaining the dynamics of plant-soil feedbacks and therefore plant community ecology.

Keywords

rhizosphere; competition; trade-offs; mutualism; pathogen; specificity

INTRODUCTION

Ecologists have historically focused on resource partitioning as the primary force structuring communities (83). Communities of competing species can be stabilized by strong negative intraspecific interactions relative to interspecific interactions (30). Traditionally, strong negative intraspecific interactions have been thought to result from high resource use overlap (83, 131), a framework that has been successful at explaining patterns of animal communities (28). A variant of resource partitioning theory, built around the Monod model of microbial growth (95), has been effectively used for explaining the dynamics of microbial communities (145). Resource partitioning also explains patterns of microbial communities in evolving laboratory communities (63) and in the field (124). The Monod models of resource partitioning have also been developed into an influential framework for understanding plant community dynamics (131). However, years of plant competition studies have produced only limited evidence of coexistence of competing plant species through resource partitioning (36, 91).

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The limited success of resource partitioning theory in explaining the dynamics of plant communities may result from neglecting soil microorganisms, which act as drivers of terrestrial ecology, as shown by a growing body of work. The composition of soil microbial communities has large impacts on plant-plant interactions (47, 96) and consequently on plant diversity and composition (134, 135, 140). Therefore, a complete understanding of plant community structure and plant dynamics requires integrating microbial perspectives into our conceptual frameworks.

Several frameworks for integrating microbes into plant community dynamics have been developed (14, 118, 119). The framework of plant-soil community feedback (10, 13, 17) has become increasingly influential in plant ecology, as it is instrumental in explanations of plant diversity and community structure (13, 69, 85, 104, 108), plant species invasion (25, 34, 37, 69, 117, 139), and succession dynamics (62, 89, 136). Here, we review the conceptual framework of plant-soil feedback, and the evidence of its importance in structuring plant communities, and then dissect the microbial interactions that drive these feedbacks.

SOIL COMMUNITY FEEDBACK AND PLANT COMMUNITY DYNAMICS

The plant-soil feedback framework builds on the well-established observation that plant species differ in their response to individual microbial species, as both the negative effects of soil pathogens and the positive effects of root symbionts are host specific. Growth rates of microbes are also host specific; components of the soil biota rapidly change in response to plant identity, and this change in microbial composition generates a feedback on plant relative performance that defines the long-term influence of soil microbes on plant species coexistence (13, 17).

Soil community feedback involves two steps: First, the density and/or composition of the soil community changes in response to the composition of the plant community, and second, the change in composition alters the relative growth rates of individual plant species (Figure 1). As plant-microbe interactions likely occur at a local scale, the feedbacks can be analyzed at the scale of individual plants. Changes in the microbial community due to the identity of the resident plant can not only alter a plant's growth rate, but also affect survival, reproduction, and the likelihood of being replaced by an individual of the same species. These influences may be identified as the direct feedbacks of the soil community on the fitness of the resident species, represented by α_A and β_B in Figure 2. The microbial change may also alter the likelihood that the resident plant species is replaced by an individual of a second species, which can be measured as indirect feedbacks represented by α_B and β_A in Figure 2. The net pairwise dynamics depends on the relative magnitude of the direct and indirect feedbacks (13, 17). Accumulation of soil microbes that promote their hosts' fitness better than that of neighboring competitor plants generates a positive-feedback dynamic that leads to a loss of local-scale diversity and contributes to alternative stable states (Figure 1). In contrast, a negative-feedback dynamic that allows for the coexistence of competing plant species results when plants promote the growth of soil microbes that antagonize their own fitness relative to that of their competitors (Figure 1).

Evidence of Plant-Soil Feedbacks in Shaping Plant Communities

Mounting empirical evidence suggests that soil community feedbacks are major determinants of plant species coexistence. Pot studies, which isolate the microbial effects, have demonstrated negative soil feedbacks among co-occurring plant species (10, 69, 70, 85, 108). Further, seedling performance in the field frequently declines with proximity to conspecific adults (32, 51, 85, 104, 144). This is a pattern frequently referred to as the Janzen-Connell hypothesis. Janzen originally imagined that this pattern was driven by

species-specific seed predation (56); however, empirical work demonstrates that host-specific soil pathogens play a dominant role (7, 85, 104). Moreover, the strength of measured feedbacks positively correlates with relative plant species abundance (32, 69, 85), and simulation models identify that this pattern is expected only when the soil community feedbacks maintain plant diversity (85).

Soil feedbacks may also represent an important dimension of the success of invasive species. Consistent with this, several studies have shown that invading plant species benefit from escape from host-specific soil pathogens (25, 52, 117). Positive soil community feedback is also important in the success of invasive plant species (14, 100, 114, 139), potentially contributing to a self-accelerating decline in community composition known as invasion meltdown (125).

Both positive and negative feedbacks contribute to plant community change during succession (62, 89). Early successional plant species tend to have limited defenses and therefore are vulnerable to a buildup of pathogens that later successional species can resist (136). Early successional plant species also tend to have a low dependence on mycorrhizal fungi, the buildup of which generates a positive feedback that promotes the success of later successional species (55, 89).

In agricultural settings, negative soil community feedbacks drive the seasonal rotation of monocrops throughout the world (23, 68). Management of soil pathogens through chemical means is often not economical. Rather, as most soil pathogens are host specific, their population densities are managed by rotation with nonhost crops. The corn-soybean rotation that dominates much of agriculture in the United States, for example, is motivated by the escape of host-specific pathogens (bacterial, fungal, and oomycete) and nematodes (19, 23, 98, 112).

Microbial Agents of Plant-Soil Feedback

Although there is growing conceptual clarity on, and accumulating empirical support for, the importance of microbial feedbacks on plant community dynamics, there has been less explicit focus on the microbial agents of these feedbacks in unmanaged systems. In part, this results from the challenge imposed by the stunning taxonomic and functional diversity present in soil microbial communities (115). Which members of these diverse communities are the agents driving plant-soil feedbacks?

THEORY OF PLANT-SOIL FEEDBACKS

An exponential model of plant-soil feedback (17) identified that net pairwise dynamics depend upon an interaction coefficient I_S, where I_S equals the difference in the direct feedbacks and the indirect feedbacks ($I_S = (\alpha_A + \beta_B) - (\alpha_B + \beta_A)$). When I_S is positive, the change in microbial composition increases the relative performance of the locally abundant plant species, generating a positive feedback dynamic that would lead to loss of diversity at a local scale. Conversely, competing plant species can coexist when the change in microbial composition decreases the relative performance of the locally abundant plant species, generating a net negative feedback, as reflected by a negative I_S (17).

The basic conclusions of the simple exponential model (17) are generally upheld by inclusion of greater complexities. The inclusion of negative density dependence and interspecific competition among plant species demonstrates that microbial dynamics can contribute to plant species coexistence, even of strong competitors such as plants utilizing the same resources (13). Spatially explicit models reveal that negative feedback leads to coexistence regardless of the scale of interaction, though the resulting spatial

pattern can vary with the spatial scale of interaction and dispersal (94). Conversely, while positive feedback always leads to loss of diversity at the local scale, local interactions can contribute to the stability of uniform patch types and therefore to heterogeneity at the larger geographic scale (93).

Negative feedbacks result from an accumulation of host-specific bacterial and fungal pathogens (23, 68); oomycetes are particularly important in both grassland and forest systems (7, 92, 104). Negative feedbacks may also result from changes in the composition of other components of the soil community (17, 133). For example, shifts in the composition of beneficial arbuscular mycorrhizal (AM) fungi can generate negative feedback on plant growth (12, 26).

Conversely, positive feedback commonly results from changes in the density of host-specific mutualists, including AM fungi, ectomycorrhizal (EM) fungi and symbiotic nitrogen-fixing bacteria, as depicted in Figure 1. However, pathogen accumulation on a tolerant host may generate net positive effects on its own growth when pathogen accumulation suppresses competing plants, as has been found with invasive plant species (38, 86). Reciprocal changes in the pathogen composition of this type would generate positive feedback (13).

A MICROBIAL PERSPECTIVE ON PLANT-SOIL FEEDBACK

Given the great taxonomic and functional diversity of microbes and the potentially complex and counterintuitive ways they can generate dynamically equivalent net pairwise feedbacks, one may question the predictability of soil microbial dynamics. However, similar net feedback dynamics may be driven by a set of forces common across microbial communities. We outline a general conceptual framework for understanding the forces that structure microbial population dynamics on plant roots and how these processes generate positive and negative feedbacks on plant growth. Our intent is to find commonalities across functionally distinct categories of microbes such as pathogens and symbionts and to build toward the common factors that influence their dynamics. To do this, we first identify common features of the plant-microbe system that make feedback on plant growth likely.

- Microbes are likely to differ in their growth rates on plant roots because plants are defended both by chemicals and by specific immune responses. Trade-offs associated with overcoming specific defenses generate host-specific differentiation of microbial communities.

- Microbes have high rates of turnover, so small differences in fitness are amplified, making microbial dynamics and microbial specialization on their host fast relative to changes in the plant community.

- Soil is a viscous medium, leading to high spatial structure and patchy distributions of microbes, so changes in microbial communities are likely to feed back on the growth of that same plant type on which they accumulated.

- The sign of these feedbacks is generated by the relationship between the microbe's competitive ability on the roots and the effect of that microbe on that plant. Competitive ability of microbes is determined by the interplay of costs of mutualism and virulence, the burden of overcoming plant defenses, benefits of plant allocation, and fine-scale microbial spatial structure.

In the remaining sections, we discuss first the selective forces that drive differentiation of the microbial community on plant roots, and then the consequences of this differentiation on plants. Throughout this review, we identify essential instabilities that will likely generate

turnover within the microbial community. The rate of this turnover will be a function of the rate of (re)introduction of new microbial types. Accordingly we discuss the means by which microbes can be introduced or reintroduced into a root system.

Microbial Specialization on Plant Roots

The interface of plant roots and the surrounding soil, the rhizosphere, harbors a diverse and dynamic microbial community (115). Plant roots exude a wide range of molecules into the rhizosphere, thereby altering soil chemistry and providing nutrient sources that resident microbes can utilize. However, plant roots are not passive targets, as a significant portion of plant exudates include a diversity of defensive secondary metabolites (141). The suite of molecules exuded by roots shape the rhizosphere environment and consequently also help shape the composition of microbial communities (20). Root exudates generally vary substantially between different plant species and genotypes and can depend on a variety of factors such as nutrient levels, disease, stress, and even the microbial community itself (74, 147). This variation can have dramatic effects on the composition and dynamics of microbial communities, as the microbes present must be able to tolerate or utilize the plant's exudates. Trade-offs associated with tolerating host defenses structure microbial competition on hosts, thereby determining the differentiation of microbial communities on different host species. In fact, there is extensive evidence of such host specialization, in which particular microbial communities, species, or strains associate with specific plant species or genotypes (5, 6, 20).

Specific and sometimes reciprocal responses between plants and microbes often influence the differentiation of symbiotic microbes. The interaction between rhizobial bacteria and leguminous plants offers one of the best-characterized examples. During the mutualistic association of nitrogen-fixing bacteria and leguminous plants, the microbe produces chemical cues that elicit developmental and exudate changes within the plant, and the bacteria also respond to root exudates secreted by the plant to alter its behavior. Plant-exuded flavonoids trigger its bacterial partner to express numerous genes involved in nodulation (Nod) (60). The resulting Nod factors vary among rhizobial species and strains (107) and trigger plant host changes necessary for nodulation such as root hair curling. Further, plant and bacterial factors contribute to the subsequent maturation of the legume-rhizobia symbiosis (60). The specificity of these factors determines which plant and rhizobial species/genotypes can associate (48). AM fungi use a set of host recognition cues similar to that used by rhizobia, and preliminary work suggests that EM fungi do as well (50). The degree of specificity of these cues appears to be low in AM fungi; however, after infection, the growth rates of AM fungal species differ across host species, generating distinct AM fungal community composition on different host plants (12, 15).

Agrobacterial plant pathogens are close relatives of rhizobial mutualists (39), and the benefits provided to the infecting bacteria also depend on manipulation of plant host exudates (111). These pathogens respond to plant-dependent cues such as low pH and release of plant phenolics by expressing genes involved with the genetic transformation of plant cells (146). The resultant genetic manipulation causes the plant cell to misregulate its growth hormones, resulting in tumor production. The transformed plant cells are also induced to exude unusual metabolites called opines, which promote the fitness of the infecting agrobacterial pathogen's relatives (44, 45, 111).

Plants are also sometimes able to shunt resources to, or away from, particular symbionts. The dynamics of mutualists can be influenced by plant control of nutrient flow into the rhizosphere, which uses sanctions or preferential allocation to promote the growth of particular mutualists (16, 65, 66, 103). The two-tiered plant immune system provides plants a means of diverting resources away from pathogens by undergoing targeted apoptosis of

pathogen-associated cells (31, 59). The first tier of the plant immune system depends on the recognition of slowly evolving pathogen-associated molecular patterns (PAMPs) by transmembrane pattern recognition receptors (101). The perception of PAMPs triggers an immune defense that can prevent the pathogen from establishing an infection. Pathogens may subvert host defenses by injecting effector proteins that interfere with the immune response into the plant cell. The second tier of the plant immune system depends on the recognition of the pathogen's effector proteins by *R* (resistance) proteins (31, 59). Detection of bacterial effectors by *R* proteins results in an amplified PAMP-triggered response and a hypersensitive cell death response, preventing further infection by the pathogen. This effector-triggered immunity involves a high degree of specificity between *R* proteins and the cognate effectors.

The gene-for-gene interactions between the plant's *R* loci and the pathogen's *avr* (avirulence) loci encoding the effector proteins can generate host-specific differentiation of associated microbial pathogens (9, 73, 130). Differentiation of the pathogen community depends on trade-offs emerging from the costs associated with overcoming host defenses. Although the existence of these costs has been controversial, several studies give direct evidence of their significance (57, 130). Moreover, in the absence of costs of virulence, one would expect pathogens to evolve the ability to infect many hosts. Contrary to this, alleles conferring the ability to infect hosts are rapidly lost when those hosts are no longer available (41, 106, 137).

Feedback on Plant Growth from Differentiated Microbial Communities

The change in microbial composition with host plant feeds back onto plant dynamics when the components of the microbial community exert differential effects on plant growth. Although mutualists and pathogens can generate similar net pairwise feedbacks (17), they likely differ in their basic tendencies (e.g., Figure 1). We address the forces structuring these feedbacks by discussing the dynamics of mutualists and pathogens.

Dynamics of microbial mutualists—The differential accumulation of microbial mutualists, as expected from host recognition systems, should positively affect the growth of compatible hosts, compared to incompatible hosts, thereby generating positive feedback. Positive feedback is also generated among plant hosts that differ in their degree of responsiveness to microbial symbionts when there is a positive correlation between the quality of the plant as a host and the dependence of that plant on the symbionts (133). Alternatively, changes in density of microbial mutualists could generate a negative feedback if the most responsive plant species were also a poorer host for AM fungi (133). However, although more data are needed, the few studies suggest that responsive host plants are also better hosts for their mutualists (122). Moreover, positive feedback via changes in mutualist density has been observed.

Positive feedback through changes in mutualist density is important at early stages of succession, where many colonizing species do not associate or have weak associations with mycorrhizal fungi, whereas later successional species can have strong dependence (55). Concomitantly, invasive plants with low dependence on AM fungi may decrease the density of mycorrhizal mutualists, thereby inhibiting re-establishment of native species. For example, high levels of glucosinolates produced by *Alliaria petiolata*, an invasive species of North American forests, inhibit AM fungi and thereby impede establishment of native plants (24, 74, 128). Similarly, dominance by nonnative species in California grasslands can decrease the density of mycorrhizal fungi, which may limit the growth of native species that tend to be highly dependent on these fungi (114, 139). By degrading soil microbial mutualisms, nonnative plants transform terrestrial communities. A similar transformation

can occur when nonnative plants species are paired with locally novel microbial symbiosis, e.g., the invasive EM fungal association with invasive pines in South America (100) and *Frankia* association with invasive *Myrica faya* in Hawaii (138).

Host-specific changes in symbiont composition can also feed back positively or negatively on net pairwise plant dynamics if the competitively dominant symbionts improve or decrease plant growth, respectively (11). Experimental evidence suggests that plants can use rhizobial cues to preferentially associate with superior mutualists (42, 49), generating a positive correlation between plant and fungal relative fitness and positive feedback. Recognition cues involved in specificity of association may also generate positive feedback in EM fungal communities (22).

However, given that all plant root mutualists' associations may involve individual plants simultaneously associating with multiple symbionts that vary in their benefit, the overall feedback will be a function of the microbial competitive dynamics within plant roots. The most competitive symbionts may be the least beneficial because of the energetic cost of providing resources to the host (i.e., there is a substantial cost of mutualism). For example, it is energetically costly for an AM fungus to acquire phosphorus, transport it along its hyphae, and then deliver it to the host plant. Consistent with such costs, several studies have shown that the least beneficial AM fungi are the most competitive (8, 12). A negative correlation between measures of host and rhizobium fitness suggests that a similar cost operates within this interaction (48); however, tests with EM fungi have produced mixed results (64). In AM fungi, the competitive shift on hosts generates negative feedback on plant growth (12, 26). Similarly, *Bacillus mycoides* generally improves plant growth but is detrimental when interacting with the host species from which it is isolated (143). Further work is required to evaluate whether this dynamic occurs within other communities of beneficial plant microbes.

Because the spread of less beneficial "cheater" strains could degrade the mutualism, the processes maintaining mutualists have been an area of active investigation. Plant hosts have been observed to sanction ineffective rhizobia (66, 103) and preferentially allocate the most effective AM fungal mutualists (16, 65). The ability of plants to sanction and preferentially allocate likely varies among plant species (42, 49) and the quality of the mutualist (16, 49, 103). The potential of sanctions and preferential allocation to overcome the competitive advantage of the poorer mutualists may depend on the level of mixing of the symbionts within the plant roots. As an extreme example, sanctioning would be ineffective if all nodules contained mixed infections of good and bad rhizobia. In an empirical test with AM fungi, the most beneficial symbiont dominated when symbionts were spatially separated within the root system (16). However, nonbeneficial fungi dominated (16) and negative feedback was observed (12) when beneficial and nonbeneficial fungi were well mixed within the root system of their host. Nodules occupied by nitrogen-fixing bacteria and root tips associated with EM fungi represent discrete spatial structures that plants can manipulate. Whether the dominance of better mutualists enabled by sanctions and preferential allocation will generate positive feedback depends upon whether microbial dynamics are coupled with host-specific differences in growth promotion—an area that requires additional research. Several studies have found evidence that host-specific changes in the composition of AM fungal communities can generate positive feedback on plant growth (84, 149).

Dynamics of plant pathogens—The accumulation of a specialist pathogen on its host generates feedbacks that favor the growth of nonhost plant species. Local accumulation of pathogens is a common cause of negative feedback in nature and is important in grassland (92) and forest systems (7, 105). Although more work is needed on the dynamics of soil pathogens in unmanaged systems, studies of soil-borne diseases in agricultural systems

show that a great taxonomic diversity of microbial pathogens have sufficient host specificity to generate negative feedbacks.

Despite the specificity of these interactions, plant root systems are exposed to numerous microbes simultaneously, and the competitive dynamics among these microorganisms likely influences net feedbacks on plants. Epidemiological models predict that multiple infections can result in greater virulence when virulence is correlated with increased efficiency of exploitation of the host (2, 126). To the extent that this is true with root pathogens, we would expect competition among multiple infecting pathogens to increase negative feedbacks provided that different plant species or genotypes are differentially affected by the pathogen. However, selective dynamics can lead to the evolution of either increased or decreased virulence, depending on the interplay of the selective pressures acting on the pathogens (1, 3, 21).

Although costs associated with overcoming individual host defenses can drive differentiation of microbial communities on hosts (see Microbial Specialization on Plant Roots, above), these costs and other costs of virulence (110) can also alter the dynamics of pathogens within hosts. Once the host or a root of that host has been compromised by a virulent pathogen, other microbes that do not bear the costs of virulence may have a competitive advantage in exploiting that resource. For example, virulent *Agrobacterium tumefaciens* strains harbor costly virulence plasmids and are burdened by large costs of expressing the machinery required to infect plant tissues (110). These costs create a strong selective pressure favoring the evolution of avirulent, freeloading strains that have lost the ability to infect plants but maintain the ability to catabolize the opine nutrients exuded by infected plants (110, 111). One such avirulent freeloader is *Agrobacterium radiobacter* strain K84, which agriculturalists have been using for decades as a potent biocontrol agent of crown gall disease. Its freeloading makes K84 a resource competitor of *A. tumefaciens*, but in addition to this, K84 interferes with the pathogen via the production of a targeted toxin, allowing it to effectively suppress the disease on its host (67, 116).

The suppression of virulent pathogens through interactions with other microbes commonly occurs in agricultural systems with repeated monocropping. This phenomenon, called suppressive soil, has been observed with numerous soil-borne plant diseases such as take-all wheat (120), potato scab (80), and tobacco black root rot (72). Although trade-offs between virulence and saprophytic growth in facultative pathogens (68, 110) make virulent pathogens vulnerable to suppression, the antagonistic activities of members of the rhizosphere microbiome can be mediated by several phenotypes including the production of antibiotics, siderophores, and surfactants by microbes in the disease-suppressive community (68). Many bacterial taxa tend to be associated with disease-suppressive soils, indicating that this phenomenon depends on consortia of microbes (88, 120).

Establishment of Plant-Associated Microbial Diversity

The plant-soil microbial dynamics that we have described are dependent on and generate spatial structure in the microbial community. At the continental scale, the success of invasive species often depends on release from microbial antagonists (25, 117). Within communities, positive plant-soil microbial feedback reinforces spatial separation of microbial communities (93), and negative feedback results in plant replacement, which necessitates recolonization of locally novel roots. At the smallest scale within the root system of an individual plant, the interplay of plant defense, plant allocation, and microbial competition determines the direction of feedbacks. At each of these scales, several facets of microbial ecology and evolution determine the ability of prior or new microbial variants to establish themselves. We discuss the importance of dormancy and storage effects, dispersal, horizontal gene transfer, and mutation in this establishment process.

Dormancy—All soil microbes, ranging from oomycetes, nematodes, AM fungi, to bacteria, have the ability to enter a dormant state under stressful or unsuitable conditions (61, 129). Dormancy allows microbes to persist during unfavorable conditions, increasing local-scale microbial diversity. Surveys estimate that over 80% of the bacterial cells in the soil are dormant (77). Moreover, the community of physiologically active bacteria within the soil are distinct from those that are dormant (77). Similar distinctions are likely in other groups such as AM fungi (113). As a result, estimates of microbial composition using standard DNA extractions from soil may not provide measures that reflect the active players in the plant-microbe interaction, potentially obscuring field attempts to identify the agents of microbial feedbacks.

For plant-associated microbes, shifts into and out of dormancy may be determined by the availability of suitable plants. Dormancy can be triggered by resource deprivation, change in nutrient composition of the soil (increased carbon or phosphorus), or other environmental conditions (e.g., pH, water content), all factors that can be affected by plants. Interactions with other members of the microbial community also stimulate microbial dormancy, as competitors may deplete resources or inhibit growth through antibiotic production (35, 78). The ecology and evolution of microbial dormancy are also influenced by predation in the dormant state (61), which can be significant for groups with large, edible dormant structures, such as spores of AM fungi.

Dispersal—If plant-associated microbes are not already present when the plant begins to grow, then dispersal can introduce new microbes. Wind, water, animals, and insects are major dispersers of soil microorganisms (71). Over smaller scales, soil microbes can facilitate the spread of one another (53, 142). In addition, microbes have evolved a number of strategies to sense changes in the environment and move accordingly. In the rhizosphere, plant-exuded resources such as carbohydrates, amino acids, phenolics, and inorganic ions are accessible to the surrounding microflora, and bacteria will chemotax toward these root-associated exudates (33, 79). For example rhizobia chemotax toward legume-excreted flavonoids prior to the development of symbiotic nodules (60).

Horizontal gene transfer—Horizontal gene transfer is rampant in the microbial world, both within and between species, occurring at such high frequencies that the definition of a species can be blurred (102). A single conjugation event between two species of bacteria can alter the total genetic content by over 10% (18, 29). Many bacterial virulence determinants are associated with mobile genetic elements (46, 121), as are genes for symbiosis and the ability to overcome or even utilize plant exudates and defenses. In fact, facultative symbionts have the greatest concentration of mobile elements in their genome, suggesting that horizontal gene transfer can be particularly important to this group (99). Conjugation, transduction, or transformation can convert free-living microbes to plant pathogens or symbionts and generate novel combinations of specificity factors and virulence or mutualist functions (27, 40, 148). Genes for nitrogen fixation by the plant symbionts *Sinorhizobium meliloti* and *Rhizobium etli* are on mobile plasmids (97, 132), as are the genes encoding the effectors that determine host specificity of the pathogen *Pseudomonas syringae* (43, 54). Genetic transfers can be important in soil fungi as well. There is strong evidence that the pathogenicity genes of *Nectria haematococca*, the fungal causative agent of pea footrot disease, were horizontally acquired (81). Conjugation of plant-associated plasmids can be induced by proximity to hosts, which increases the likelihood that recombinants resulting from horizontal gene transfer will be important at shorter time frames (40).

Mutation—Mutation is another important force generating microbial variants that can interact differently with plant hosts. Mutations affecting virulence-associated genes have

significant consequences for the evolution of virulence in a wide variety of pathogens (87, 127). One clear target of selection are mutants that can evade host defenses (109, 150), though other possible targets include mutations that influence the fitness of the pathogen in the rhizosphere, such as those conferring the ability to catabolize plant-produced resources (75). Similar effects are likely in mutualistic plant-microbe interactions. For example, sequence variation in the *nod* gene of *R. etli* determines the host range of this mutualist (123). Although mutations occur at low rates, microbial population sizes on plant roots are potentially large. Consequently, mutation combined with gene exchange may shape the evolution of host-pathogen interactions (82).

Relative importance of modes of microbe (re)introduction—At the scale of a single root, plant defense response and preferential allocation can change at rapid timescales —in as short as hours (16, 59, 66). At these small spatial and temporal scales, new variants are likely to be reintroduced by local dispersal and reactivation of dormant cells. Over the lifetime of an individual plant, these local processes are likely to be supplemented by evolutionary creation of new variants (109). Within agrobacteria, for example, mutation might create freeloading variants that could suppress virulent types (111). Over large spatial and temporal scales, evolution of local resident microbial populations can overcome the novel defenses of introduced plant species. This may have contributed to the increased negative feedbacks accumulated over hundreds of years following the invasion of *Cerastium alpinum* in New Zealand (34).

SIGNIFICANCE AND FUTURE DIRECTIONS

Microbial Drivers of Plant-Soil Feedback

In this review we have sketched major forces that drive microbial feedbacks on plant growth with the goal of working toward a predictive theory of plant-soil feedback. While doing so, we have identified several areas where further work is required to better understand the microbial drivers of feedbacks. For example, to what extent do plant secondary chemicals influence the relative growth rates and host-specific differentiation of antagonistic or beneficial symbiont species? And to what extent do processes and tensions central to within-host evolution of virulence or mutualism generate differential effects and net pairwise feedbacks between two plant species? To what extent are microbial phenotypes that drive feedbacks introduced through dispersal across space or time, or through mutation or recombination within the resident microbial community?

This review has focused primarily on microbes with direct effects on plant growth through mutualisms or pathogens. However, differentiation of saprophytic components of the soil microbial community may also generate feedbacks on plant growth. Saprophyte communities respond to changes in litter quality associated with plant secondary chemicals. Further, differences in rates of host tissue decomposition could accelerate nutrient cycling, thereby potentially altering plant-plant interactions if the plant species differed in their dependence on and uptake of these nutrients (4, 14, 90, 119). Further work is required to assess the importance of host-specific differentiation of the saprophytic community relative to that of pathogens and mutualists on net pairwise feedbacks.

Microbial Mediation of Feedbacks in the Plant Ecology Context

Much progress has been made through phenomenological investigations of plant-soil feedbacks (14). Given this progress, plant ecologists may ask why they should care about the details of the microbial population and community dynamics that generate these feedbacks. However, there are several important conceptual issues on the impact of

microbes on plant ecology, which will not be addressed without understanding the details of microbial dynamics.

Given the evidence of the central role of microbial feedbacks in plant community structure, other aspects of microbial life history may have cascading impacts on plant ecology. Microbes vary in their tolerance to types of environmental stress, such as salt, drought, and temperature. For example, oomycetes depend on moisture to complete their life cycle. Because oomycetes are important host-specific pathogens that generate negative feedbacks in natural systems (92, 104), the strength of negative feedback may increase along a moisture gradient. Such constraints on microbial ecology could mediate the increase in conspecific negative density dependence observed in areas with greater plant productivity, which may contribute to continental patterns of tree diversity (58).

Moreover, the nuance of microbial dynamics on plant roots is critical to the underlying assumptions of the feedback framework. For example, the accumulation of competitively dominant saprophytes and antagonists can suppress root pathogens after repeated monocropping in agricultural systems (76). Such suppressive soils are unlikely to develop in communities of annual or short-lived perennial plants, as a particular host will likely die and be replaced by a second species prior to the buildup of suppressors of host-specific pathogens. It is possible, however, that suppression of host-specific pathogens is an important process that limits negative feedbacks on long-lived perennial plants. Conceptually, this may generate nonlinear temporal dynamics of negative feedbacks, in which strong negative feedbacks would be experienced at intermediate ages of plants, perhaps contributing to their replacement. However, in older plants the strength of negative feedback may be reduced.

Acknowledgments

Glossary

Feedback	a process whereby the plant alters its environment (e.g., the microbial community) in such a way that it in turn affects the plant's growth and fitness
AM	arbuscular mycorrhizal
EM	ectomycorrhizal
Trade-off	a negative correlation between two aspects of fitness such as growth rate on one host and growth rate on a second host
Cost of mutualism	the metabolic and fitness costs associated with delivering benefit to a second species
Virulence	the ability of a pathogenic agent to cause disease (often measured as the negative effect on host fitness)
Rhizosphere	region in the soil surrounding plant roots
Apoptosis	host-initiated programmed cell death in response to stimulus such as a pathogen
PAMP	pathogen-associated molecular patterns
R	resistance

Dormancy	a reversible state of extremely low metabolic activity that is characterized by the cessation of phenotypic development

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SUMMARY POINTS

1. Negative soil microbial feedback on plant growth can contribute to the maintenance of plant species diversity, whereas positive soil community feedback can contribute to plant community conversion.

2. Host-specific differentiation of microbial communities can be driven by trade-offs in microbial responses to specific plant defenses and exudates.

3. The accumulation of microbial mutualists likely generates positive plant-soil feedback, whereas the accumulation of host-specific pathogens likely generates negative feedback.

4. Change in mutualist competition can generate negative feedback when the cost of mutualism dominates within host dynamics.

5. Preferential allocation can offset the cost of mutualism, potentially generating positive feedback through changes in mutualist composition.

6. Competition and trophic interactions within the microbial community can influence the fitness of host-specific pathogens and thereby potentially suppress negative feedbacks.

7. Feedbacks are driven by, and generate, spatial structure in microbial composition.

8. New microbial variants can arise within a plant-associated microbial community via evolution of the resident populations or dispersal across space or time.
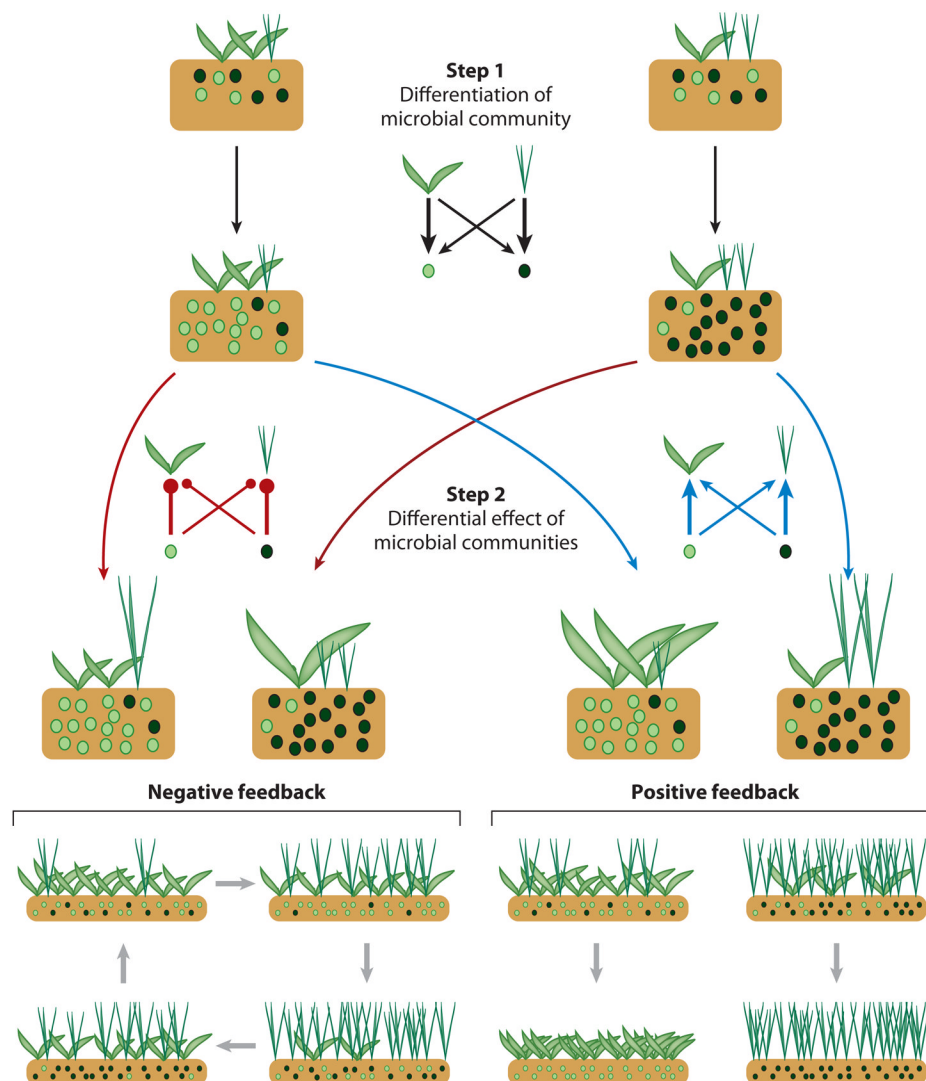
Figure 1.

Soil microbial feedback involves two steps. First, the composition of the microbial community differentiates on the plants because of host-specific microbial growth rates. In this illustration, the light green microbe has higher growth rates on the broad-leaved grass and the dark green microbe has higher growth rates on the narrow-leaved grass. The relative benefit to the microbes is represented by the thickness of the arrows in the fitness diagram. The second step involves differential effects of the microbes on the plant species. (*Left*) For host-specific pathogens, the light and dark green microbes have strongest negative effects on the broad- and narrow-leaved plants, respectively, with relative virulence represented by the thickness of the red clubs. As a result, the plants that were initially most abundant have the lowest growth rates. The net consequence of this negative feedback on plant communities is illustrated at the bottom left, with both species maintained in the community over time. (*Right*) However, for host-specific mutualists, the light and dark green microbes have strongest positive effects on the broad- and narrow-leaved plants, respectively. As a result, the plants that were initially most common grow best. The net result of this positive feedback on the community is a loss of diversity on a local scale with a potential for the community to reach alternate stable states.
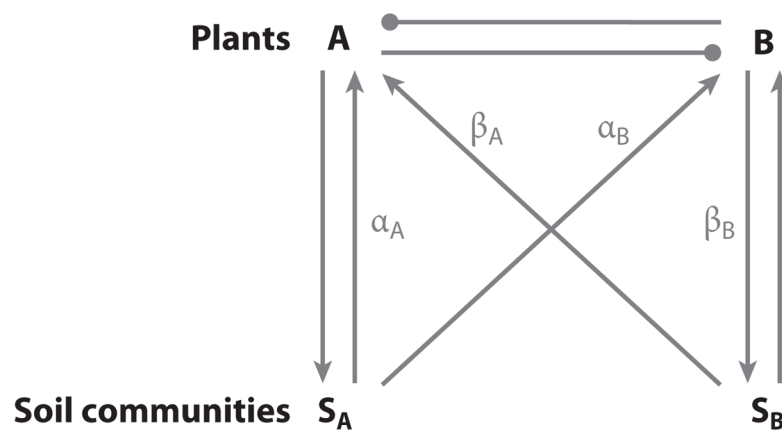
Figure 2.
In this conceptual representation of soil community feedback, the presence of Plant A causes a change in the composition of the soil community, represented by S_A. This change in the soil community can directly alter the population growth rate of Species A (represented by α_A) and it can alter the growth rate (α_B) of competing plant Species B. Similarly, the presence of Plant B can cause a change in the composition of the soil community (S_B), which can directly feed back (β_B) on the population growth rate of Plant B or indirectly feed back on the growth rate of Plant B through changes in the growth rate (β_A) of competing Plant A. The exponential model predicts that the net effect of soil community dynamics on plant species coexistence is determined by the sign and magnitude of an interaction coefficient $I_S = (\alpha_A + \beta_B) - (\alpha_B + \beta_A)$, which represents the net pairwise feedback. Adapted with permission from References 13 and 17.