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Microbial eco-evolutionary dynamics in the plant rhizosphere

Bryden Fields and Ville-Petri Friman

Microbial communities are vital for plant health and productivity. While most studies have underlined the ecology of plant–microbe interactions, accumulating evidence suggests rapid microbial evolution is also important, often occurring at ecological timescales within and between plant generations. We review current evidence and mechanisms of rapid microbial evolution in the rhizosphere, focusing on examples along the mutualism–parasitism continuum. We consider how evolution can change the ecology and plant–microbe ecosystem functioning via eco-evolutionary dynamics and highlight the importance of intraspecies diversity as the product and raw material for natural selection. We conclude that acknowledging rapid evolution is not only crucial for understanding the complex plant–microbiota interplay but also an important prerequisite for harnessing the benefits of soil microbes for sustainable agriculture.

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Introduction

The rhizosphere is the section of soil closest to the plant root where interactions between soil microorganisms and the plant influence plant growth, protection from pathogens, resilience to environmental stresses, competition for resources, and nutrient cycling [1,2]. Reciprocally, microorganisms can benefit from secreted root exudates and plant litter as energy sources. As a result, plants actively influence the composition of rhizosphere communities by stimulating and repressing specific microorganisms for their productive benefit [3–7]. This host filtering can be mediated by secretion of

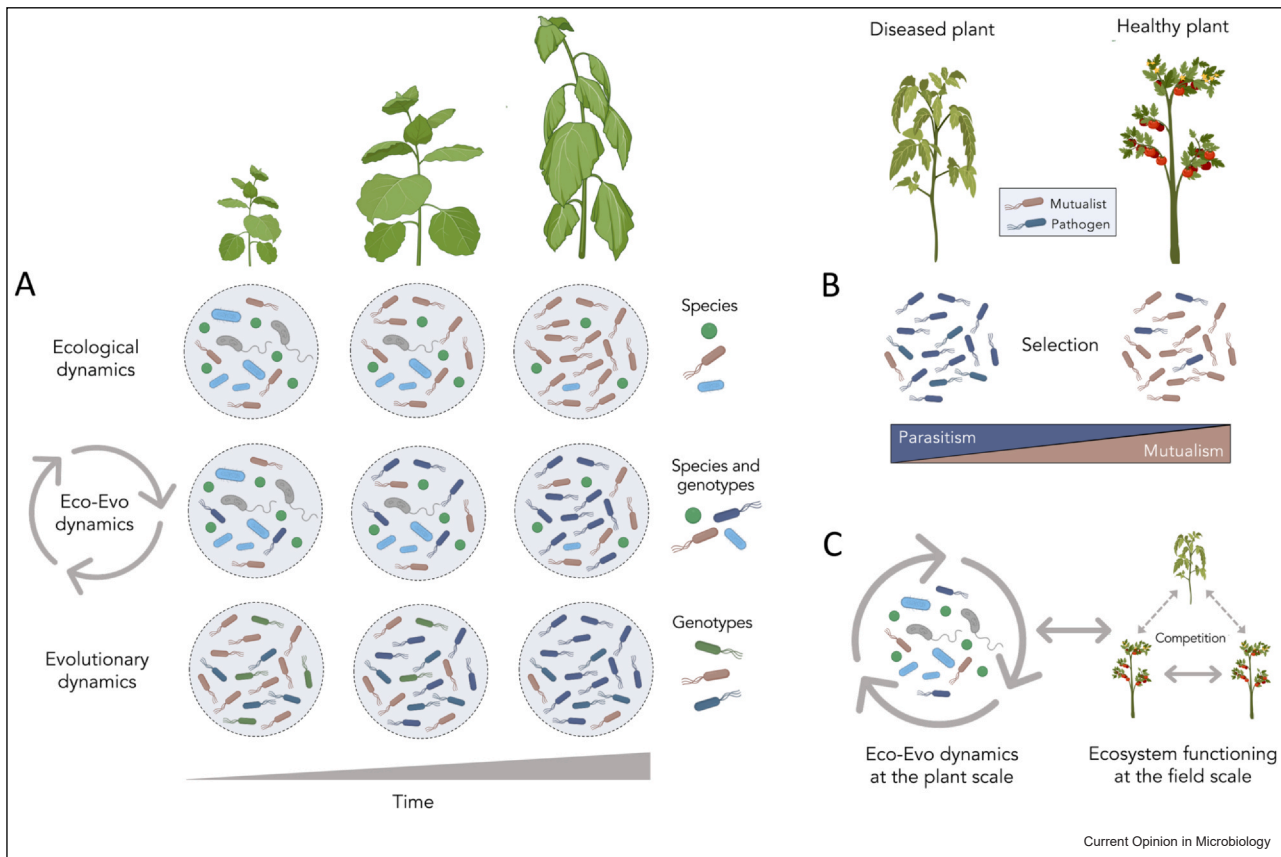
root exudates which enable microbe–plant signalling and the activation of microbe recognition systems to distinguish pathogenic and non-pathogenic microbes [2,8]. Consequently, agricultural practices have been developed to manipulate rhizosphere microbiome communities to improve plant health by encouraging interactions with beneficial symbionts, such as rhizobia bacteria and mycorrhiza fungi, and plant growth-promoting rhizobacteria that can boost plant growth and provide protection against pathogenic bacteria [9–11].

Most of these manipulations are based on ecological theory. For example, maximising competition and niche overlap between pathogenic and non-pathogenic bacteria could help to protect plants from infections [12], while using species that antagonise pathogen-facilitating species [13] could indirectly provide beneficial effects for plant health. Overall, promotion of microbial diversity has been linked to improved rhizosphere ecosystem functioning, which can be explained by (1) selection effects, where community performance is determined by its most productive member, or by (2) complementarity effects, where there is an inherent benefit to diversity that is greater than the combined individual effects of the community members [14]. While the positive relationship between species diversity and ecosystem functioning is well documented, the importance of within-species (intraspecies) diversity is less studied [15] despite its significance for plant–microbe interactions and functioning of host-associated microbiomes [16–19]. Moreover, as the product and raw material for natural selection, acknowledging intraspecies diversity is paramount for understanding the role of rapid microbial evolution in microbe–plant interactions.

Microbes can evolve rapidly in plant-associated microbiomes

Microbial diversity is a result of natural selection driving diversification and speciation via *de novo* mutations and recombination. While microbes are known to evolve rapidly in the lab, we are only beginning to understand microbial adaptation in natural environments and plant-associated microbiomes [20]. Seminal studies conducted in soil microcosms in the absence of plants have established that bacteria can diversify [21] and coevolve with bacteria-specific viruses (phages) [22], and that such local adaptations can have as strong effect as the

Figure 1



Both ecological and evolutionary processes are important in determining the composition and functioning of rhizosphere microbiomes. **(a)** Ecological dynamics can lead to species sorting and changes in rhizosphere microbiota composition, while evolutionary dynamics lead to changes in species genotype frequencies. When ecological and evolutionary processes occur at the same timescale, rhizosphere microbiota composition could be determined by eco-evolutionary dynamics. **(b)** Selection on standing genetic variation can shift microbe–plant interactions along the mutualism–parasitism continuum by selecting for mutualistic or pathogenic bacterial genotypes. **(c)** Microbial Eco-Evo dynamics within individual plants could alter the functioning of plant ecosystems, for example, via effects on plant competition (solid arrow: competition; dashed arrows: loss of competition). Changes in plant species abundances and frequencies could in turn alter the selection on rhizosphere microbiota.

presence of a given focal species for the surrounding community [23]. The effect of intraspecies variation is often neglected in most plant–microbe studies that focus on changes in species richness and abundance based on species-specific amplicon sequencing. As a result, we often only observe changes in species relative abundances and can only make ecological inference of the effects of microbes on the plants and vice versa (Figure 1a: Ecological dynamics). Most microbial species inhabiting the rhizosphere are not clonal but show certain degree of intraspecies diversity [24,25]. Such genetic variation will provide the raw material for natural selection, which can change genotype frequencies within microbial species during plant growth (Figure 1a: Evolutionary dynamics). When these ecological and evolutionary processes occur at the same timescale, they can result in eco-evolutionary dynamics, where evolution changes the ecology of interacting species, which can

further feedback to the process of adaptation by changing the strength of initial selection pressures [26,27] (Figure 1a: Eco-Evo dynamics). While eco-evolutionary dynamics are well documented in several systems [20,26,28–34], research on their importance in an agricultural context is only emerging [7,35–38]. In this review, we will highlight the importance of rapid microbial evolution and eco-evolutionary feedbacks for plant–microbe interactions in the rhizosphere. Specifically, we review the current evidence by using examples of rapid microbial evolution along the mutualism–parasitism continuum and discuss how evolution could change the ecology and functioning of plant–microbe ecosystems.

Evolution of mutualism in plant–microbe interactions

While mutually beneficial interactions between microbes and plants are commonly observed, we still poorly

understand how, and at what timescale, they evolve. Macroevolutionary studies suggest that symbiotic interactions are old and likely originally evolved in relation to plant terrestrialisation as a major evolutionary transition [39]. Recent experimental evolution studies suggest that microbe–plant mutualisms can also evolve rapidly at much shorter timescales. In a recent study, Batstone *et al.* [40] showed that *Ensifer meliloti*, the nitrogen-fixing rhizobial symbiont, can adapt to become more beneficial to its legume host (*Medicago truncatula*) because of *de novo* mutations in putative genes involved in signalling and survival in symbiotic plant root nodules. Interestingly, this adaptation was host genotype-specific and only seen when the symbiont and the host had shared evolutionary history, indicative of rapid evolution of a specialist mutualism [40]. In another study, rhizobial symbionts evolved in cycles with different novel legume genotypes with which they initially provide negligible benefits [41]. Researchers found that rhizobial strains evolved to provide plants with more benefits, and displayed altered infection, proliferation and survival in legume nodules [41]. However, these evolutionary outcomes were specific to host–symbiont combinations and while candidate mutations were identified, these did not reach fixation in evolved populations [41]. Plant host-specific adaptation has also been shown in the case of plant growth-promoting *Bacillus subtilis* rhizobacterium, which rapidly diversified and evolved improved root colonisation in the *Arabidopsis* rhizosphere in a hydroponic system [42]. Similar to the first example, this adaptation was host specific and did not improve root colonisation in unrelated tomato hosts [42]. Furthermore, diversified bacterial morphotypes showed improved productivity when cultured together, indicative of evolution of ecological complementarity [42]. Rapid bacterial evolution has also been shown to cause shifts along the mutualism–parasitism continuum (Figure 1b); for instance, an initially plant-antagonistic *Pseudomonas protegens* bacterium evolved to be more benign on *Arabidopsis thaliana* roots [43]. Mechanistically, this was linked with increased resistance to plant-secreted antimicrobials and improved resource catabolism, which made evolved *P. protegens* genotypes more competitive in the rhizosphere compared to ancestral bacterial clones. Similar to *B. subtilis*, clear phenotypic and genotypic bacterial diversification was observed, which was due to mutations in the GacS-GacA two-component regulatory system [43]. Crucially, improved bacterial competition in the rhizosphere was coupled with improved plant growth promotion by the evolved bacterial genotypes, which suggest that adaptation was beneficial for both parties, and hence, mutualistic [43].

While mutualism is common, it might not always be an evolutionary stable strategy. For example, rhizobial strains interacting with legumes can range from highly mutualistic, beneficial nitrogen-fixers to non-fixing unbeneficial

'cheater' genotypes [44]. Moreover, non-fixers can hide in the nodule alongside nitrogen-fixing genotypes in mixed-strain nodules and thereby benefit from the plant without providing any benefits in return [45,46]. As a result, legume hosts often use partner choice (symbiotic selection based on recognition signalling between plant and microbe) or sanctioning mechanisms (restriction of nutrient supply to poor symbiotic performers and non-fixing 'cheater' strains) to differentiate between beneficial and non-beneficial symbionts [47]. To what extent evolution of cheating destabilises legume–rhizobia mutualism in natural environments is however still debated [48–50]. It is also likely that rhizobial evolution in the rhizosphere goes beyond infection and nodule formation and several lifestyle adaptations linked to competition via rhizosphere growth and root colonisation have recently been identified [51], including that closely related rhizobium strains can show indirect and direct antagonism towards each other [52]. Together, current evidence suggests that while mutualistic plant–microbe interactions are evolutionarily old, they are still refining and changing via selection and rapid bacterial evolution in the plant rhizosphere. Crucially, these changes can occur just within a few plant generations, having potential implications on the ecology and functioning of plant–microbe ecosystems.

Evolution of antagonism in plant–microbe interactions

Similar to mutualism, antagonistic interactions are common in the rhizosphere and can occur between microbes, or between plants and microbes. Evolution of competitive microbial interactions could have indirect effects on the plant via changes in the composition and functioning of rhizosphere microbiomes [53], while certain antimicrobials used in bacterial interference competition are also phytotoxic [43]. Microbial competition can be mediated indirectly via competition for the same resources that often limit microbial growth [19,54] or directly by contact-dependent and contact-independent microbial warfare [55]. How rapidly microbial competition evolves in the rhizosphere is however still unclear. Indirect evidence suggests that *Streptomyces* bacteria and *Fusarium* fungi can be locally adapted and show higher inhibition when in sympatry, which could have resulted from past co-evolutionary history [56]. Furthermore, a recent microbial transplantation study showed that *Curtobacterium* can adapt to its local soil environment through mutations in genes related to nutrient acquisition, stress response, and exopolysaccharide production, indicating that bacteria can rapidly evolve in response to shifts in microbial community composition at relatively short timescale [57]. While microbial competition could have indirect positive effects on plant health via intensified competition with the pathogen [54,58], it could also potentially promote infections if antagonising mutualistic or plant growth-promoting bacteria.

Plant–bacteria interactions are also indirectly shaped through selection by parasitic phages [59]. For example, phages have been shown to control plant pathogenic *Ralstonia solanacearum* bacterium via density reduction and selection for phage-resistant mutants that suffer reduced growth and competitiveness [37]. Furthermore, the negative effects of phages are amplified in the presence of antibiotics-producing *Bacillus amyloliquefaciens* bacterium because evolution of phage resistance sensitises *R. solanacearum* to antibiotics [60]. Phage selection can also have community-wide effects in the rhizosphere by changing bacterial community diversity, composition and functioning in terms of soil suppressiveness [37] and nitrogen cycling [61]. In addition to phages, protist predators can also drive bacterial evolution in the rhizosphere by providing a selective advantage to bacterial genotypes that can avoid predation [62–65]. Evolution of antipredatory defences could also indirectly shape bacterial competitiveness as secondary metabolites that are toxic to protists can improve *P. protegens* establishment into a native rice rhizosphere community [62,66]. While more direct evidence on the evolution of anti-protist defences in the rhizosphere is still required, the above examples together suggest that microbial trophic interactions can play an important role for the ecology and evolution of bacteria–plant interactions in the rhizosphere.

Besides adapting via microbial interactions, bacteria can also rapidly evolve to be more antagonistic towards their plant host (Figure 1b). Guidot et al. [67] used *in planta* serial transfers to adapt soil-borne *R. solanacearum* pathogen to two native (tomato and eggplant) and distant (bean and cabbage) plant hosts for 300 bacterial generations. They found increases in bacterial fitness compared to ancestral clones when in direct competition during xylem colonisation, which was driven by only a few mutations in genes linked with the PhcS-PhcR two-component regulatory system and EfpR transcription regulator protein. In another study, *R. solanacearum* was serially transferred in the xylem of resistant tomato cultivar named ‘Hawaii 7996’ [68]. While no resistance breakdown was observed, improved xylem colonisation was associated with non-parallel mutations that led to parallel rewiring of the virulence gene network between replicate selection lines [68]. Although these experiments did not consider pathogen evolution in the rhizosphere per se, they clearly demonstrate that successive rounds of plant infections can select for increased pathogen fitness.

Effects of eco-evolutionary dynamics on plant–microbe ecosystems

Rapid microbial evolution could affect the ecology of rhizosphere microbiomes and associated plant communities. For example, evolution of plant beneficial or

pathogenic bacteria might change the relative plant species abundances via indirect effects on plant–plant competition, while virulent pathogens could select for resistant or tolerant plant genotypes (Figure 1c). Changes in plant species frequencies and abundances could in turn affect plant community productivity, diversity, stability and aboveground trophic interactions with insects and animals. Such changes could further alter the selection on rhizosphere microbiota [69], leading to evo-eco-evo feedbacks in plant–microbe ecosystems and potentially influencing the processes of range expansion, coevolution and phyllosymbiosis. For example, host–microbiome coevolution has been suggested to have occurred during domestication of the apple [70] which could over time lead to phyllosymbiosis, that is, significant associations between host phylogenetic relatedness and similarity of associated microbiomes [71]. While coevolutionary arms races could also lead to specialised interactions and phylogenetic associations between pathogens and their plant host lineages, host jumps and host range expansions via hybridisation or changes in regulatory networks are also possible [72]. Additionally, in the future, more work is required to better understand how spatial and temporal variation in abiotic physicochemical soil properties, such as nutrient availability, pH and soil type, might determine the cold and hot spots of evolution. Moreover, although microbial evolution is likely to drive such eco-evo feedbacks due to their relatively faster generation times, the role of past plant evolution and plant–microbe coevolution should be acknowledged when inferring current ecological interactions.

Future perspectives

While the reviewed examples suggest that rapid microbial evolution is often observed in association with plants, there are several outstanding questions. Although these questions range from methodological issues of quantifying absolute microbial abundances to identifying who is doing what [73], here we highlight the challenges of moving beyond a ‘focal-species’ approach to study the evolution of microbial communities at different scales. Firstly, it is unclear to what extent the species diversity of a community affects the evolution of its members. Most experimental evidence comes from studies focusing on ‘focal species’ that can be reisolated from microbial communities and evolutionary changes quantified in the laboratory [20,23,74]. However, only a few studies have tried to address microbial evolution at the community level [75–77] or used experimental designs that can disentangle the effects caused by genetic and species diversity [38]. Secondly, while current evidence suggests that evolution of a focal species can change the ecology of communities [37,43,61], it is unclear if these changes might alter the strength of future selection, highlighting the need for longer term

experiments [38]. Finally, although evolution has been shown to take place in conditions that mimic natural conditions, field transplantation experiments are required to understand the relative importance of microbial evolution in spatially heterogeneous environments at the landscape level (Figure 1c). Acknowledging that the strength of selection varies in space and time is crucial to identify evolutionary cold and hot spots that are likely to determine eco-evolutionary outcomes across the natural and agricultural environments. Moreover, understanding the rapid evolution of mutualism and pathogenicity at agriculturally relevant timescales between the harvests and seasons could help harnessing the evolutionary potential of soil microbes and guide the development of experimentally evolved biofertilizers or evolutionary-proof pathogen control strategies.

Conflict of interest statement

Nothing declared.

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