# Functional team selection: a framework for local adaptation in plants and their belowground microbiomes

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## Abstract

Plants and their microbiomes are complex adaptive systems consisting of host plants and a dynamic network of associated microorganisms inside and around plant tissues. This article introduces Functional Team Selection (FTS) as a framework to help envision and study the movement of matter, energy, and information within plant-microbiome systems. FTS embraces the fact that belowground, plants are surrounded by trillions of soil organisms that may help or hinder the function of roots to provide essential resources for photosynthetic production. We describe how limited resources and antagonistic biotic interactions drive host-mediated microbiome engineering and how the function of belowground microbiomes can be selected -even during the host's lifespan- to generate plant adaptation in stressful but not benign environments. The FTS framework provides guidelines for how to work with, rather than against, evolutionary and ecological forces to generate durable cooperation and mutualism in plants and their microbiome.

**Keywords:** Complex adaptive systems, Host-mediated microbiome engineering, Mycorrhizae, Plant growth-promoting bacteria, Plant-soil feedbacks.

## Glossary of terms (underlined in the text)

- Complex adaptive systems (CAS) - Dynamic systems of components that interact and adapt (Holland 2006).
- Cry-for-help hypothesis – Predicts that stressed plants manipulate microbial communities in their rhizosphere through the release of specific compounds in root exudates that enhance populations of beneficial microbes and inhibit pathogens and herbivores (Rolfe et al. 2019).
- Functional teams – Groups of microorganisms that work together to create functions that generate adaptive traits for the host plant.
- Functional team selection (FTS) - Mechanistic framework that links evolutionary and ecological processes in space and time to account for the generation of locally adapted plant-microbiome systems.
- Horizontal gene transfer - Exchange of genetic material from donor to recipient cells in organisms that are not in a parent–offspring relationship (van Elsas et al. 2003, Soucy et al. 2015).
- Host-mediated microbiome engineering – Artificial selection of microbiomes through cyclical propagation of hosts and selection of the microbiome to increase or decrease certain host traits in each subsequent generation (Swenson et al. 2000, Jochum et al. 2019, Yu et al. 2023).
- Hyphosphere – Region in soil that is adjacent to and impacted by the hyphae of mycorrhizal fungi.
- Law of increasing functional information – The premise that a system will evolve if many different configurations of the system undergo selection for one or more functions (Wong et al. 2023).
- Microbe-mediated local adaptation – Enhanced host relative fitness that is partially or entirely the result of evolutionary interactions among local microorganisms (Petipas et al. 2021).
- Microbe-mediated adaptive plasticity – Enhanced host relative fitness resulting from plasticity generated by interactions with local microorganisms (Petipas et al. 2021).
- Microbiome – Community of microscopic organisms living inside, on the surface, and in close proximity to a larger host organism.
- Plant Growth-Promoting Bacteria (PGPB) – Bacteria that enhance plants' growth and protect them from biotic and abiotic stresses through a wide variety of mechanisms (Souza et al. 2015).
- Rhizosphere – Region in the soil adjacent to and impacted by the roots of a plant.
- Syntropy – When two (or more) species cooperatively exchange essential resources through cross-feeding (D’Souza et al. 2018).

## The definition of an individual plant is not as simple as it seems

Innovations in high throughput molecular techniques have revealed a surprising diversity of fungi and bacteria inside and surrounding plant tissues (Vandenkoornhuyse et al. 2007). This discovery led to the recognition that microbiomes composed of diverse microbial communities can shape plant phenotypes (Vandenkoornhuyse et al. 2015, Lyu et al. 2021, Koide 2023). Mycorrhizal fungi and plant growth promoting bacteria (PGPB) are important components of root microbiomes that are known to improve plant nutrition and resistance to biotic and abiotic stress (Trivedi et al. 2020). Arbuscular mycorrhizal (AM) symbioses occur in over 72% of all plants including nearly all crops (Zhang et al. 2019, Meng et al. 2023), and ectomycorrhizal (EM) symbioses are present in over 12% of plant species (Meng et al. 2023) and occur in dominant forest trees that cover an estimated 60% of the Earth's tree stems (Steidinger et al. 2019). The burgeoning plant growth promotion industry sells inoculum containing mycorrhizal fungi and PGPB aimed at harnessing the benefits of these associations, but there is controversy about whether the use of these commercial products is necessary or even desirable (Salomon et al. 2022, Vahter et al. 2023). Understanding the mechanisms by which plant microbiomes assemble, evolve, and function will inform the debate about their use in commercial inoculants, and facilitate their conservation and management in natural and agricultural systems (Martin and van der Heijden 2024). We argue that a better understanding of how microbiomes influence plant phenotypes and fitness is essential before farmers and land managers can sustainably harness them to increase plant yield, survival, and stability in the face of environmental change.

There is fossil evidence that AM symbioses pre-date the evolution of plant roots and helped terraform Earth about 450-500 million years ago (Cairney 2000, Kenrick and Strullu-Derrien 2014, Field et al. 2015, Brundrett and Tedersoo 2018). EM symbioses evolved during the Jurassic period about 150-200 million years ago, concurrently with the rise of pines and other conifer families (Cairney 2000, Brundrett and Tedersoo 2018, Strullu-Derrien et al. 2018). Consequently, it can be assumed that many root traits evolved to house and nurture mycorrhizal fungi and associated bacterial communities (Martin et al. 2017). Plants invest 10 to 30% of their photosynthetic production to mycorrhizal fungi and an additional 5 to 21% to root exudates (Wen et al. 2022). This tremendous investment of organic substrate belowground fosters a dynamic network of fungi, bacteria, and other microbes.

There is solid evidence that root-associated microbiomes play a central role in shaping plant phenotypes and that plants derive adaptive traits from their associations with rhizosphere fungi and bacteria (Friesen et al. 2011, de la Fuente Cantó et al. 2020, Bai et al. 2022, Koide 2023, Wang et al. 2024). The function of mycorrhizae along a mutualism-parasitism continuum varies among plant and fungal taxa and across environmental gradients (Johnson et al. 1997, Hoeksema et al. 2010). This variation in mycorrhizal function has been linked to local adaptation of plants to their environment (Johnson et al. 2010, Remke et al. 2020, 2021, 2022). For over four decades, research has suggested that selection pressures encountered by host plants, such as drought, may drive the evolution of local adaptations involving AM symbioses (Stahl and Smith 1984, Bethlenfalvay et al. 1989). Geographic isolates of both AM and EM fungi and associated communities of microbes have been shown to improve plant performance to a greater extent in their home environments compared to novel environments (Pickles et al. 2015, Rúa et al. 2016, Remke et al. 2020, 2021). There is strong evidence that plants can actively select for the most beneficial mycorrhizal fungi (Bever 2015, Chagnon et al. 2015, Werner and Kiers 2015, Bogar et al. 2019), but there is still little understanding about the mechanisms by which plants assemble and control their microbiomes to help them adapt to local environmental conditions.

Hyphae of mycorrhizal fungi extend the absorptive surface area of plant roots by several orders of magnitude (Hobbie and Hobbie 2008, Frey 2019) and associated bacteria further enhance the capability of mycorrhizal fungi to acquire resources for plant hosts. Studies indicate that both AM and EM fungi support their own <u>hyphosphere</u> microbiome such that bacteria and mycorrhizal fungi synergistically enhance the nutrition of their host plants (Wang et al. 2023, Zhang et al. 2023, Zhang et al. 2024). This hierarchically nested arrangement of symbionts within symbionts challenges traditional evolutionary paradigms that rely on a restricted definition of organismal individuality and of units of selection. It also challenges the traditional modeling of cooperation in the mycorrhizal symbioses as involving only two actors (the host and the fungus). A better understanding of how multilevel selection generates functioning plant, and mycorrhizal microbiomes is needed (Johnson and Gibson 2021). This article explores how ecological and evolutionary processes interact across space and time to generate <u>microbe-mediated local adaption</u> in plants (Petipas et al. 2021). We introduce <u>Functional Team Selection</u> (FTS) as a framework to test hypotheses about the mechanisms by which plants recruit mycorrhizal fungi and other microbes to ameliorate environmental stresses. This framework melds ecological and evolutionary mechanisms to predict the conditions necessary to assemble microbiomes that function as cooperating teams, improving the fitness of their host plant while generating local adaptation (**Box 1**). The extended evolutionary synthesis (Laland et al. 2015), disentanglement of units of selection (Suárez and Lloyd 2023), directed evolution of microbial communities (Sanchez et al. 2021), and the evolutionary law of increasing functional information (Wong et al. 2023) provide the theoretical foundation for FTS.

**Box 1: Assumptions of Functional Team Selection in plants and their belowground microbiomes**

1. To a certain extent, plants can recognize and cultivate beneficial microbes and suppress pathogenic microbes. This trait is heritable.
2. Plants and their associated microbiomes are complex adaptive systems (CAS) composed of an autotrophic host living in close association with communities of fungi, bacteria, viruses, nematodes and other soil-borne organisms.
3. Plant adaptations are emergent properties of CAS.
4. The function of plant microbiomes is context-dependent, and microbiomes may generate beneficial, neutral, or even detrimental (pathogenic) impacts on plants because environmental conditions influence the fitness outcome of CAS.
5. Rhizosphere microbiomes are spatially and temporally dynamic.
6. The law of increasing functional information drives evolution of innovation and adaptation in plants and their associated microbiome.

## Assumptions of Functional Team Selection

***Plants can recognize and cultivate beneficial microbes and suppress pathogenic microbes***

Plants exert a considerable level of control over the composition of their microbiome and this trait ability appears to be heritable (Gehring et al. 2014). Studies show that plants preferentially allocate photosynthate to the most beneficial root symbionts (Bever 2015, Chagnon et al. 2015, Werner and Kiers 2015). The well supported ‘cry-for-help’ hypothesis posits that in response to stresses caused by pathogens, herbivores, pollution, drought or other factors, plant roots release certain metabolites that ameliorate the stress through the selection or recruitment of beneficial microbes (Rolfe et al. 2019). In addition to releasing chemical signals through root exudates, plants may take an even more active role in cultivating their rhizosphere microbiome. The discovery of the rhizophagy cycle hints at the astounding level of control that plants may exert on the bacterial communities surrounding their roots (White et al. 2018). The rhizophagy cycle is analogous to bacterial farming by plants in which certain bacteria enter root tips, are propagated inside root cells as wall-less protoplasts that appear to provide nutrients to the plant, and some surviving bacteria are exuded back into the soil through root hairs (White et al. 2018). Through this mechanism, plants enrich their rhizosphere with high densities of plant-selected bacterial populations which can potentially partner with other roots in the neighborhood.

### *Plants and their microbiomes are complex adaptive systems*

It is likely that plants have never existed in the absence of microbial associates (Berg et al. 2016), and it is useful to envision plants and their microbiomes as complex adaptive systems (CAS) composed of a host plant and diverse communities of interacting fungi, bacteria, viruses, and other soil-borne organisms. Many challenging problems in artificial intelligence, economics, anthropology, and biology may be understood as CAS. According to Holland (2006), all CAS share four features: 1) they consist of a large number of agents that interact simultaneously through sending and receiving signals, 2) they respond to signals through conditional action, 3) sub-groups of agents may combine to create novel building blocks that are tested frequently in a wide range of situations so that their usefulness within the system can be rapidly determined, and 4) agents evolve over time and usually generate adaptations that improve performance of the system. An additional characteristic of CAS is that they are usually open, non-equilibrium systems that interact readily with their environment (Cilliers 1998).

### *Plant adaptations are emergent properties*

If plants and their microbiomes are complex adaptive systems, then adaptations to local conditions are emergent properties of the system (Geesink et al. 2024) because they are expressions of interactions among host plants, associated microorganisms, and the surrounding biotic and abiotic environment. This is a useful insight for guiding experimental designs that aim to elucidate plant adaptations. Results from reductionist laboratory and greenhouse experiments may not extrapolate well for predicting and understanding the performance of CAS in agricultural and natural ecosystems because emergent properties can only be observed (and studied) when the whole system is investigated (Cilliers 1998).

### *Plant-microbiome phenotypes are context dependent*

There is increasing evidence that host plants send and receive chemical signals to and from the microbes in their rhizosphere and that this exchange guides the transaction of resources between hosts and symbionts (Venturi and Keel 2016, van Dam and Bouwmeester 2016, Mhlongo et al. 2018). These dynamic interactions generate emergent properties that may be manifested as beneficial adaptive traits for host plants, but also, they may have neutral or even detrimental (pathogenic) impacts on host plant fitness. Environmental conditions influence the costs and benefits of host plant interactions with their microbiome (Johnson et al. 1997, Bever 2015). Decades of empirical evidence suggest that resource-limited soil generally favors the selection and proliferation of communities of soil-borne microbes that improve plant nutrition (**Figure 1**). In contrast, benign environments with luxury supplies of soil resources do not favor the proliferation of beneficial communities of microbes (**Figure 1)**, but instead the accumulation of organisms with neutral or even antagonistic relationships with plants (Johnson 1993, Bertness and Callaway 1994, Hammarlund and Harcombe 2019, Jochum et al. 2019, Lekberg et al. 2021). Conventional agricultural practices involving fertilizers and tillage appear to inadvertently select for less mutualistic, or even parasitic AM fungi (Johnson et al. 1992, Peng et al. 2024).

### *Microbiomes are spatially and temporally dynamic*

Rhizosphere habitats vary in space and time because of heterogeneity in soil properties, seasonal variation, and different lifespans of the component organisms. Plant roots vary in the rate at which they grow and decompose, ranging from woody structural roots that may live for the entire life of a tree, to fine roots that turn over within months or even weeks (Chen and Brassard 2013). The spatial structure created by networks of mycorrhizal fungal hyphae provide hyphosphere habitats for bacterial communities which may form biofilms that provide substrates for additional microorganisms (Miquel Guennoc et al. 2018). The composition of microbial communities inhabiting different regions of the rhizosphere and hyphosphere are expected to differ considerably and provide different goods and services to host plants throughout the growing season (Gao et al. 2019).

Plant roots engineer their own physical, chemical, and biotic environment because they repeatedly explore the same spaces in the soil. Each growing season, plants inherit the biotic and abiotic legacy of soil properties from the previous year. As nanoimaging technologies continue to develop, more attention should be paid to determining the detailed locations of microbes around plant roots because ecological and evolutionary processes are impacted by spatial structure (Mack 2012). Mutualistic interactions are more likely to assemble and evolve in spatially structured environments compared to well mixed environments due to increased frequency of contact between mutually beneficial partners (Kinzig and Harte 1998; Bever and Simms 2000). Furthermore, spatial structure may facilitate long-term interactions among neighboring rhizosphere organisms which will facilitate the various processes involved with horizontal gene transfer (Soucy et al. 2015, Ku et al. 2021), a potentially important source of genetic diversity for evolution that should not be underestimated (Boto 2010, Quistad et al. 2020, Arnold et al. 2022) – especially for microbiome dynamics. In this regard, adaptive traits can be inherited through spatial memory as well as genetic memory (Rosenberg and Zilber-Rosenberg 2022).

Selection can occur rapidly or slowly within the rhizosphere and the distinction between the ecological process of community assembly and the evolutionary process of natural selection can become fuzzy. Differences in the lifespans of plants and their microbiome organisms creates some interesting evolutionary opportunities for plants. The pace of evolutionary change is typically dictated by the generational time of organisms (Wright 1932), and this could significantly limit the ability of long-lived plants such as trees to adapt to changing environments. However, if long-lived plants gain adaptive traits from their belowground microbiome, they may respond much faster to environmental fluctuations (Gehring et al. 2014, Petipas et al. 2021). Within a single growing season, rhizosphere microbial communities can diverge substantially from adjacent soil communities (Shi et al. 2015). Enhanced host performance within one generation resulting from a legacy of beneficial microorganisms has been classified as microbe-mediated adaptive plasticity to distinguish it from microbe-mediated local adaptation, which entails an evolutionary process involving enhanced host fitness that is partially or entirely the result of co-evolutionary interactions with local microorganisms (Petipas et al. 2021). Differentiating between these two phenomena may be more academic than practical, but the distinction in terms of inheritance is important because it highlights the fact that associations with local communities of microorganisms may benefit plants as much as genetically inherited adaptations involving host-microbiome interactions.

***Teams evolve because of selection for functions that enhance host performance***

Variation in functional traits provides the raw material for natural selection, and in the case of plants and their microbiomes, the traits are emergent properties of a CAS. Advances in evolutionary theory accommodate the potential for multilevel selection to generate cooperative groups of unrelated individuals (Swenson et al. 2000, Lloyd and Wade 2019, Roughgarden 2023). Furthermore, the extended evolutionary synthesis (Laland et al. 2015) provides useful constructs for understanding plant-microbiome teams as CAS. Additional theoretical support for FTS is provided by the "law of increasing functional information" which posits that evolving systems share three characteristics (Wong et al. 2023): 1) they form from numerous interacting components; 2) the components can generate many different configurations; and 3) certain configurations are preferentially selected because they display useful functions. Plant-microbiome teams fulfill all three of these requirements as they are composed of a host and a network of many interacting microbes, their composition can create many different configurations, and certain combinations of plant hosts and associated microbes will function better than others in terms of increasing the productivity, survival, and reproductive success of the host plant.

The astronomical diversity of soil microorganisms, and consequently the extent to which root microbiomes can generate many different functional configurations should be emphasized. One gram of soil can contain 200 m of fungal hyphae and one billion bacteria, both belonging to several thousands of species (FAO et al. 2020). The immense abundance and diversity of soil microorganisms surrounding plant roots increases the probability of selecting beneficial microbiome functions. Certain configurations of the CAS are preferentially selected because they display useful functions, and in this case, the function is to enhance the productivity and relative fitness of the host plant. Rhizosphere and hyphosphere microbes are all directly or indirectly supported by the host plant's production of organic compounds. The bottom line is, if the host plant does well, then populations of microorganisms associated with roots and mycorrhizal hyphae will increase, but if the host does poorly and dies, then these microbial habitats and substrates will dwindle and eventually disappear. This fact establishes the focus of selection for a common function that drives the assembly and evolution of teams of disparate microbial players that are cultivated by a plant host.

Evidence for FTS in plant microbiomes has been accumulating. For example, a grass capable of surviving extreme heat at Yellowstone National Park was discovered to gain thermal tolerance through its symbiotic association with an endophytic fungus which in turn hosted a virus and it was noted that all three players in this tripartite symbiosis were required for the grass' survival in geothermal soils (Marquez et al. 2007). It is now well established that a core set of bacteria inhabit the hyphosphere of AM fungi and that these bacteria are critical for the mobilization of nitrogen (Rozmoš et al. 2022) and phosphorus (Wang et al. 2023, Jin et al. 2024) compounds, which are transferred to the fungus, and in turn, to the host plant. Adding a protist to the experimental system was shown to further increase the nitrogen gained by the AM fungus by at least 65% (Rozmoš et al. 2022), which illustrates how trophic complexity within microbial communities can enhance nutrient availability and ultimately, host plant performance. Lastly, a recent study by Lastovetsky et al. (2024) found that a single AM fungus spore can contain up to 227 endobacterial taxa, most of which have unknown functions but are proposed to be both parasitic and conditional mutualists.

## Host-mediated microbiome engineering and local adaptation

Darwin gained insights about evolution and evidence for natural selection by studying artificial selection of domesticated plants and animals. Similarly, artificial selection of functional plant-microbiome teams can be studied to uncover the mechanisms by which soil microorganisms may contribute to plant adaptations. The key factor in these studies is that plant performance acts as the selective force in microbial community assembly and evolution. Swenson et al. (2000) pioneered the concept of artificial ecosystem selection as a method to select communities of soil microbes based on plant performance. This approach involves exposing multiple generations of plants to a particular selection pressure and at the end of each growing cycle, selecting for the best performing microbiomes to continue to the next generation (Mueller and Sachs 2015). The genetic basis of the host plant remains the same, so the effects can be truly attributed to the belowground microbiome. Host-mediated microbiome engineering that enhance specific plant traits has successfully engineered belowground communities that increase plant tolerance to drought (Lau and Lennon 2012, Jochum et al. 2019), soil salinity (Mueller et al. 2021), and leaf greenness (Jacquiod et al. 2022), among several others (reviewed in Sanchez et al. 2021, 2023 and Yu et al. 2023). Understanding how artificial selection can generate rhizosphere microbiomes that enhance plant performance may illuminate how multilevel selection can generate local adaptation of plant-microbiome teams in natural ecosystems.

Plant-microbiome teams are analogous to human teams composed of actively interacting players surrounded by a bench of inactive (dormant) potential players that may join or leave the team at any time. Plant-microbiome teams compete with their neighbors for resources, are impacted by various environmental stresses, and are attacked by pathogens and herbivores. Winning teams are defined in space and time as the plant-microbiome systems that either maintain their geographic location for years to centuries, as with perennial plants, or in the case of annual plants, recolonize the same location over many years. In the same way that human teams have specialists for different functions related to winning their game, plants may maintain microbiome teams composed of dormant as well as actively cooperating networks of specialist organisms that generate functions which help plants win in terms of survival and reproductive success. In this regard, the diversity of belowground microbiome communities has been observed to be positively correlated with the stability of the functional responses of plant-microbiome systems to disturbances (Bennett et al. 2020). We hypothesize that this occurs because a higher diversity of microbial species increases the probability of the emergence of interactions and epistatic traits with functional significance.

Both plant hosts and AM fungi may actively cultivate beneficial microbes through providing rewards in the form of essential substrates and/or habitat (Jin et al. 2024). Such trophic interactions may initiate a cascade of opportunities for metabolically diverse members of the microbiome. Over time, this dynamic can generate teams of interdependent plant-microbiome systems that function to improve host plant performance in local environments. The process of syntropy may be important in the assembly of plant-microbiome teams. Syntropy, which literally means “feeding together,” occurs when microbes cooperatively exchange essential resources through cross-feeding (D’Souza et al. 2018). In spatially structured environments, syntrophic partnerships may evolve over time to become obligate associations if the partner organisms become increasingly dependent on each other and lose the metabolic capabilities for independent living (Zengler and Zaramela 2018). This phenomenon occurred in the evolution of AM fungi which are obligate biotrophs that have lost the genes required for fatty acid and sugar biosynthesis, and consequently, they must get these compounds through symbiosis with a living plant host (Kameoka and Gutjahr 2022). Environmental omics combined with confocal microscopy have revealed widespread syntrophic relationships involving diverse combinations of bacteria and archaea (D’Souza et al. 2018). It is likely that functional teams are composed of many layers of syntrophic associations, and that these associations may assemble and evolve *in situ* to generate communities of plant genotypes and microbes that are locally adapted to their local environment and to each other.

It is important to keep in mind that the trillions of diverse rhizosphere and hyphosphere organisms have the potential to interact directly and indirectly as competitors, pathogens, commensals, and mutualists. The emergent properties of these interactions may either benefit or hinder the plant host. Microbial interactions are also network-dependent: a cooperative interaction can become non-cooperative in the presence or absence of another microorganism. A large-scale experiment involving 54 fields found that the response of maize to inoculation with AM fungi ranged from -12% (growth depression) to +40% (growth enhancement; Lutz et al. 2023). The best predictor of this wide range of mycorrhizal growth responses was the abundance of pathogenic fungi in the field soil (Lutz et al. 2023). This result strongly supports the idea that the focus of microbiome engineering should be at the level of whole communities and not individual microorganisms.

A rich literature on plant-soil-feedback documents how belowground microbiomes can have positive, neutral, or negative effects on plant fitness (van der Putten et al. 2013, Dudenhöffer et al. 2017, de Long et al. 2020). Positive plant-soil-feedback will maintain the dominant plant taxa within communities (e.g. Wubs et al. 2016), while a negative plant-soil-feedback is an engine for plant succession in natural ecosystems (Bever et al. 1997) and yield decline in agroecosystems (Modjo and Hendrix 1986). It has long been recognized that the key to harnessing mycorrhizae for more sustainable agricultural is to maximize their role in positive plant-soil-feedbacks (Johnson et al. 1992). We must understand the factors that determine whether root microbiomes will improve plant performance and function as mutualisms or antagonize plant performance and cause growth depressions before microbiomes can be successfully managed in agriculture (Lutz et al. 2023). But how is this accomplished? Empirical studies have revealed certain principles that are associated with mutualistic AM symbioses (Hoeksema et al. 2010, Johnson and Gibson 2021). Perhaps these principles can help guide the development of agricultural management practices that enhance the benefits of microbiomes in plants and their associated microbiomes (**Box 2**).

**Box 2. Agricultural Principles to Selection for Beneficial AM symbioses (modified from Johnson and Gibson 2021)**

1. Choose crop cultivars that are adapted *in situ* to the local abiotic environment and co-adapted with the local soil microorganisms.

2. Use ecological stoichiometry to determine fertilizer application. Aim to provide enough nutrients so that AM fungi are not resource limited, while simultaneously maintaining host plant limitation for these resources (Treseder and Allen 2002). A nutrient shortfall for plants, but not AM fungi will encourage a stable mutualism (Johnson 2010).

3. Maintain soil water availability so that mycorrhizal enhancement of drought tolerance can be manifested, but not so low that AM fungi are chronically water limited.

4. Minimize tillage and other disturbances that disrupt intact networks of AM fungi (Peng et al. 2024).

5. If crop yield declines due to negative plant soil feedback, rotate crops to disrupt the accumulation of antagonistic organisms through altering soil habitats and encouraging the proliferation of different groups of soil microbes.

## Next steps

Functional Team Selection envisions plant-microbiome associations as CAS that are assembled and maintained through dynamic processes. Understanding the mechanisms that generate these systems requires melding multiple perspectives that encompass the totality of interactions among plants, microbes, and their environment. This is necessary because the outcome that we desire - improved plant performance - is an emergent property of the entire system. 'Consilience' (Wilson 1998) best describes this melding of multiple perspectives through the lenses of disparate disciplines. To effectively select and engineer beneficial plant-microbiome teams that are durable in a constantly changing environment may require transdisciplinary teams of researchers in disciplines like systems biology, evolutionary biology, microbiology, virology, biochemistry, community ecology, plant pathology, agronomy, soil science, and artificial intelligence. The FTS framework may help structure the consilience of researchers working towards this goal.

Studying local adaptation in natural ecosystems may be a good place to seek insights about the mechanisms responsible for the creation of durable mutualisms among plants and their belowground microbiome. These insights can inform the management and restoration of natural areas and help guide the engineering of crop-microbe systems that require lower inputs of irrigation and fertilizer. Recent advances in omics technologies combined with statistical methods and computational capacity will help reveal patterns in nature that have previously been obscured by the overwhelming diversity and complexity of microbial communities. The FTS framework developed here is focused on understanding the evolution and functioning of plants and their belowground microbiome. It is possible that this framework may also be applicable to animal systems, including humans and their microbiomes. Scientific consilience may help us better understand and manage all kinds of microbiome teams that provide essential functions for humans.

## Acknowledgments

Funding for this article was provided to N.C.J. by the US Department of Energy program in Systems Biology Research to Advance Sustainable Bioenergy Crop Development (DE-FOA-0002214) and to C.M. by the Fondo Nacional de Desarrollo Científico y Tecnológico (Fondecyt Regular No. 1240186, ANID – Chile, convocatoria 2024). C.M. also thanks the ANID + Convocatoria Nacional Subvención a Instalación en la Academia Convocatoria Año 2021 + Folio (SA77210019) project.

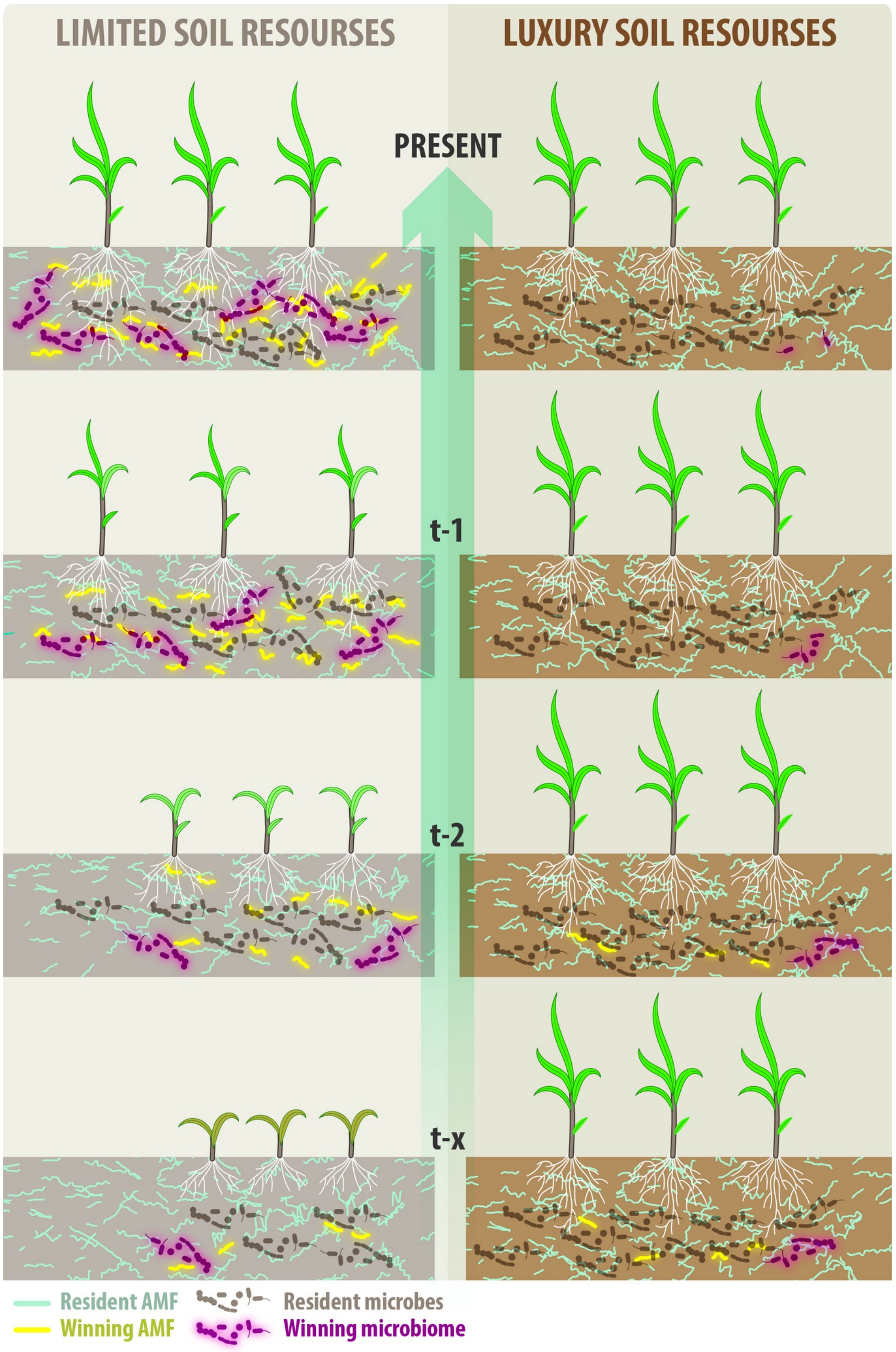

**Figure 1.** Over time (t – x to the present), **limited soil resources** favor the selection of winning teams of soil microbes that function to improve plant nutrition. In contrast, there is no selection for winning teams when plants are not limited by belowground resources (**luxury soil resources)**.

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