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REVIEW

Theory of microbial coexistence in promoting soil–plant ecosystem health

Na Zhang[1,2] · Naoise Nunan[3,4] · Penny R. Hirsch[5] · Bo Sun[1] · Jizhong Zhou[6] · Yuting Liang[1,2]

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Abstract

A healthy soil plant continuum is critical for maintaining agroecosystem functions and ensuring food security, which is the basis of sustainable agricultural development. Diverse soil microorganisms form a complex assembly and play an important role in agroecosystems by regulating nutrient cycling, promoting plant growth, and alleviating biotic and abiotic stresses. Improving microbial coexistence may be an effective and practical solution for the promotion of soil–plant ecosystem health in the face of the impacts of anthropogenic activities and global climate change. Modern coexistence theory is a useful theoretical framework for studying the coexistence of species that are competing for resources. Here, we briefly introduce the basic framework of modern coexistence theory, including the theoretical definitions and mathematical calculations for niche difference and fitness difference, as well as ways to test for these differences empirically. The possible effects of several major biotic and abiotic factors, such as biological interactions, climate change, environmental stress, and fertilization, on microbial niche and fitness differences are discussed. From the perspective of stabilizing and equalizing mechanisms, the potential roles of microbe–microbe interactions and plant–microbe interactions in promoting healthy soil–microbe–plant continuum are presented. We suggest that the use of the coexistence theory framework for the design and construction of microbial communities in agricultural production can provide a solid basis for the biological improvement of agroecosystems.

Keywords Modern coexistence theory · Niche and fitness differences · Stabilizing and equalizing mechanisms · Species interactions · Soil health

Introduction

Global demand for crops is growing rapidly and is likely to continue for decades to come, due to increases in both the global population and per capita consumption (Godfray and Garnett 2014; Tilman et al. 2011). However, global crop yields are predicted to be insufficient to meet the projected demand in 2050 (Ray et al. 2013). Agricultural crop productivity is under tremendous pressure from a variety of abiotic stresses, due to intensive use of chemical fertilizers and pesticides, climate change and environmental pollution, and biotic stresses from pests and pathogens (Molotoks et al. 2020; Pandey et al. 2017). Increasing the productivity of agroecosystems remains a huge challenge, and there is an urgent need for more sustainable ways to increase crop yields.

The phytobiome is composed of plants, their environment, and diverse interacting microscopic and macroscopic organisms, which together profoundly influence plant and agroecosystem health and productivity (Leach et al. 2017).

✉ Yuting Liang
ytliang@issas.ac.cn

[1] State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, No. 71 East Beijing Road, Nanjing 210008, China

[2] University of Chinese Academy of Sciences, No.19A Yuquan Road, Beijing 100049, China

[3] CNRS, IRD, INRA, P7, UPEC, Institute of Ecology and Environmental Sciences—Paris, Sorbonne Université, 4 place Jussieu, 75005 Paris, France

[4] Department of Soil and Environment, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden

[5] Rothamsted Research, Harpenden AL5 2JQ, Herts, UK

[6] Institute for Environmental Genomics, Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA

In the phytobiome, complex networks of interactions that links crops with microorganisms, animals, plants, soil, climate, and other environmental factors are established and regulated through physical and chemical cues (Korenblum and Aharoni 2019; Leach et al. 2017). Historically, agroecosystems have been managed by focusing on individual components of the phytobiome, such as nutrient applications and pesticides. However, managing the phytobiome as an integrated system of diverse interacting components may offer greater opportunities to achieve optimal and sustainable crop productivity (Bell et al. 2019). Phytobiome studies that consider the complex network of interactions inside and outside the plant have demonstrated their potential in crop improvement (Hale et al. 2014; Macias-Bobadilla et al. 2020).

Soil and phytobiome microbes provide essential ecosystem services for agricultural crop production by regulating nutrient cycling, promoting plant growth, controlling pests and pathogens, and alleviating abiotic stress (Begum et al. 2019; Goswami and Deka 2020; Vimal et al. 2017). Microbes are rarely observed as single species populations in the soil environment. They form complex consortia through various types of interactions, including mutualism (two partners A and B have mutual benefit), commensalism (A takes profit, whereas B gains no disadvantage), amensalism (A is limited by B), parasitism (A takes profit of B), predation (A consumes B), and competition (A and B compete for a limiting factor) (Faust and Raes 2012; van Elsas et al. 2019). Thus, the interactions can be either mutualistic (or cooperative, leading to a positive effect on partners of the interaction) or antagonistic (in which a negative effect on at least one partner of the interaction can be seen) (van Elsas et al. 2019). These interactions involve ecological processes such as physiochemical changes, metabolite exchanges, and signaling, which allow different niches to be occupied and affect the competitiveness of communities (Braga et al. 2016). On the one hand, mutualistic interactions between plants and arbuscular mycorrhizal fungi provide several benefits for plant growth and yield by increasing the availability of nutrients, improving soil structure and texture, and enhancing stress resistance of plants (Begum et al. 2019). Plant growth-promoting rhizobacteria generally promote plant growth by producing plant hormones such as auxins and cytokinins, improving nutrition acquisition, enhancing the antioxidant system, and inducing resistance against plant pathogens, production of siderophore, volatile organic compounds, and protection enzymes (Vejan et al. 2016). One the other hand, antagonistic interactions between plants and pathogens have detrimental effects on plant growth and account for a major loss in global crop productivity (Oerke 2006; Strange and Scott 2005).

Many plant growth-promoting microorganisms have been isolated from soil or rhizosphere to study their beneficial effects on soil and plant (De-Bashan et al. 2020; Le Mire et al. 2016; Mahanty et al. 2017). Microbiome engineering is an emerging field of synthetic biology, which may provide a sustainable strategy to improve crop productivity (Ahkami et al. 2017; Orozco-Mosqueda et al. 2018; Qiu et al. 2019). The synthetic community builds on complementary ecological functions of microorganisms and aims to engineer synthetic microbial communities to promote beneficial plant–microbe interactions (Ke et al. 2020). A synthetic microbial community is designed by mixing selected microbial strains that perform a given function better than the sum of individual performances and applying it to plants to study various aspects of plant–microbe interactions (Vorholt et al. 2017). The challenge of microbiome engineering is not only to design synthetic microbial consortia with multiple plant growth-promoting functions, but also to stabilize them under field conditions (Arif et al. 2020; Sessitsch et al. 2019). It is necessary, therefore, to understand the mechanism of both microbe–microbe interactions and plant–microbe interactions (including how microbes affect plants and how plants manipulate microbes) based on the theory of species coexistence (Arif et al. 2020; Vorholt et al. 2017).

Species coexistence has been studied for decades, resulting in two prevailing views on the mechanisms involved. One is the classical niche-based viewpoint that focuses on the demands of species and emphasizes niche differentiation among species to reduce interspecific competition and allow coexistence (Grinnell 1917; Hardin 1960; Macarthur and Levins 1967). The other is the neutral viewpoint, which assumes that different species are functionally equivalent and that coexistence is driven by stochasticity and dispersal (Bell 2001; Hubbell 2001). The modern coexistence theory developed by Peter Chesson reconciles these two perspectives and provides a more comprehensive theoretical framework for studying the coexistence of species in competition for resources (Chesson 2000, 2013, 2018). In the past two decades, modern coexistence theory has been widely used in the theoretical and empirical research on the coexistence of plant species. Here, we review the basic framework of modern coexistence theory, including the theoretical definitions and empirical approaches to test the theory, discuss the main biotic and abiotic factors that influence microbial species' coexistence within this framework, and highlight the potential application of modern coexistence theory in agricultural soil–microbe–plant systems.

The framework of modern coexistence theory

In order to understand and predict species coexistence quantitatively on the basis of mechanistic theory, Chesson (2000) proposed two ecological differences among species, namely, niche difference and average fitness difference. Here, ecological niche is not a Hutchinsonian hypervolume (Leibold 1995) but instead is defined by the relationship between organisms and the physical and biological environment, taking into account both time and space. A particular combination of physical factors (e.g., temperature and moisture) and biological factors (e.g., predated food resources, predators, and natural enemies) at a particular point in time and space defines a point in niche space. A modern definition of a species' ecological niche is the response that the species has to each point in the niche space and the effect that the species has at each point (Chesson 2000; Shea and Chesson 2002). Responses are defined in terms of demographic variables, such as survival and individual growth; but of most importance is the overall outcome of these responses, the per capita rate of increase. Effects include consumption of resources, interference with access to resources by other organisms, support of natural enemies, and occupancy of space. Niche difference reflects the spatial and temporal differences in resource utilization of species. Niche differences arise when intraspecific competition is greater than interspecific competition and prevents any species from becoming completely dominant or extinct in the community, thus stabilizing coexistence. By contrast, fitness difference is competitive asymmetry, which can result in one species excluding another species, regardless of their relative abundance, thus limiting the possibility of coexistence. Examples of fitness difference include differences of species in fecundity, susceptibility to generalist predators, resistance to fluctuating environment, and ability to take up limited resources (Chesson and Kuang 2008). The joint effects of niche difference and fitness difference determine whether each species in a competitive pair can increase from low density when the other is abundant, thus leading to coexistence or exclusion (Fig. 1). Niche difference supports coexistence by limiting the overexpansion of species when they rise to dominance and protecting them from exclusion when they become rare (Adler et al. 2007). Fitness difference drives competitive exclusion when species share the same niche. When niche difference between competitors is larger than fitness difference, the two species will coexist stably. Otherwise, the species with higher fitness will exclude other species.

Increasing niche difference between species and/or decreasing fitness difference, referred to as stabilizing and equalizing mechanisms, respectively, can promote coexistence (Chesson 2000). In other words, the stability mechanism tends to restrict species to interactions within their own population while limiting those with competitors, and the equalizing mechanism tends to make species more similar in competitiveness. For example, resource partitioning (the specialization of species on different resources) is a stabilizing mechanism that increases niche differences. Many trade-offs (a negative correlation between traits because the cell resources allocated to one trait result in a decrease in the fitness of another trait) can be seen as equalizing mechanisms, because doing well in one respect often means doing less well in another (Chesson 2013). For example, in order to survive in a harsh environment, a species may reduce its reproduction rate in exchange for survival (i.e., survival-reproduction trade-offs), thus limiting the fitness differences between species.

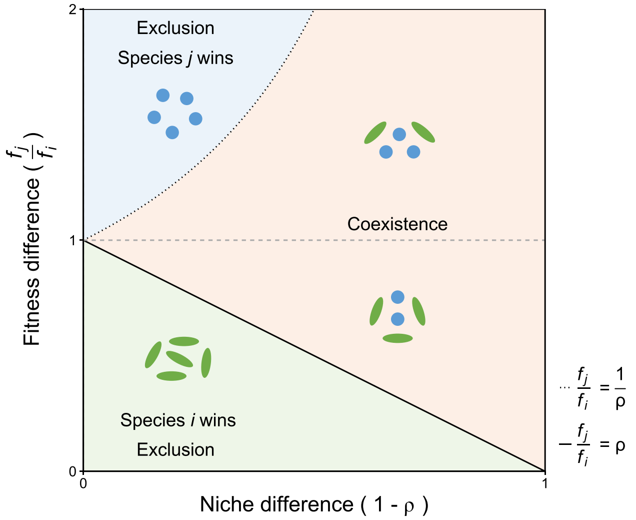

Fig. 1 The conceptual diagram of modern coexistence theory. The competitive outcome is determined by the balance between niche difference and fitness difference, which can be calculated based on the Lotka–Volterra competition model (Chesson 2000, 2013) or MacArthur's consumer-resource model (Carroll et al. 2011). The dotted and solid lines represent the boundaries where f_j/f_i equals $1/\rho$ and ρ, respectively. The right area indicates the region where coexistence occurs; the top and bottom areas indicate where species *j* and *i* is dominant, respectively. Figure modified from Ke and Letten (2018)

Within the framework of modern coexistence theory, there are two methods to estimate niche difference and fitness difference. The first is based on the Lotka–Volterra competition model (Chesson 2000, 2013). Niche difference and fitness difference between species can be estimated by intraspecific and interspecific competition coefficients, which represent a species dependence on its own density and the density of other species, respectively. The equations are as follows:

$$\text{Niche difference} = 1 - \rho = 1 - \sqrt{\frac{\alpha_{ij} \times \alpha_{ji}}{\alpha_{jj} \times \alpha_{ii}}}$$

$$\text{Fitness difference} = \frac{f_j}{f_i} = \sqrt{\frac{\alpha_{ii} \times \alpha_{ij}}{\alpha_{jj} \times \alpha_{ji}}}$$

where α_{ij} describes the per capita effect of species *j* on species *i*, as a proportion of the maximum per capita growth rate of species *i* is decreased by increasing the density of species *j* by one unit. The coefficient measures intraspecific density dependence if $i=j$ and interspecific density dependence if j is different from i. The niche overlap, ρ, is a measure of the relative strength of density-dependent feedback between species and within species. Niche difference reflects the degree of intraspecific competition (denominator) relative to interspecific competition (numerator). Fitness difference between competitors, f_j/f_i, describes the degree to which species i is more sensitive to intraspecific and interspecific competitions than species j. The larger the ratio, the greater the fitness advantage of species j relative to i, and the faster species j can exclude i in the absence of niche difference. Two species coexist stably when their growth (and therefore their increase in density) has a greater inhibitory effect within their own population than on the population of the other species. In other words, when the intraspecific competition coefficient exceeds the interspecific competition coefficient, that is, when fitness difference is between ρ and $1/\rho$, stable coexistence occurs.

Another way to measure niche difference and fitness difference is based on MacArthur's consumer-resource model (Carroll et al. 2011). In this model, niche difference and fitness difference are calculated by the effect of interspecific interaction on population dynamics, that is, the invasion rate. The proportional reduction in the growth rate of an invader i due to interspecific competition is called i's sensitivity (S_i) to the native species j, which is defined as $S_i=\frac{\mu_{i,0}-\mu_{i,j}}{\mu_{i,0}}$, where $\mu_{i,0}$ and $\mu_{i,j}$ are the per capita growth rate of invader i in the absence and presence of the native species j, respectively. When $S_i<1$, i can invade j, but invasion is not possible when $S_i>1$ (i.e., negative growth as invader). For S_i approaches 1, a species would show a sharp drop in growth rate when invading, while $S_i<0$ indicates facilitation (i.e., a special case in which the invader grows better in the presence of the resident than in monoculture). The niche difference and fitness difference between the invasive and local species can be calculated by the geometric mean and geometric standard deviation of their sensitivities to competition. The formulae are as follows:

$$\text{Niche difference} = 1-\prod\nolimits_{i=1}^{n} S_i^{1/n}$$

$$\text{Fitness difference} = \exp\left[\left(\overline{(\ln S)^2}-\overline{(\ln S)^2}\right)^{1/2}\right]$$

when both species are sensitive to interspecific competition, a negative invasion growth rate and an unsuccessful invasion (i.e., the invader dies, and in this case, there is no invasion) occur. It means that $S_i>1$ and a negative niche difference in the calculated values, suggesting strong competition between invasive and local species. When the growth of a species as an invader is as good as that of the species alone, $S_i \rightarrow 0$ and niche difference $\rightarrow 1$, it indicates that species are not negatively affected by interspecific competition. Niche difference reduces the competition, corresponding to the decrease of S_i. If fitness difference >1, the fitness of invaders is greater than that of native species, while fitness difference <1 is the opposite. If fitness difference is close to 1, the growth rates of the two species are affected equally by each other, which makes it possible to coexist stably, even with a small niche difference.

Most of the empirical tests of modern coexistence theory are carried out in annual plant communities by calculating niche difference and fitness difference based on parametric competition models. These models need field estimations of species germination fractions, per-germinant fecundities without neighbors, seed survival in soil, and all pairwise competition coefficients (Godoy et al. 2014; Godoy and Levine 2014; Kraft et al. 2015). Some studies have also determined niche difference and fitness difference between pairs of microbes by measuring invasion growth rates in mutual invasion experiments with bacterial strains (Li et al. 2019; Tan et al. 2017), yeast (Grainger et al. 2019), and green algae (Narwani et al. 2013). Based on the monoculture and invasive growth rates, the sensitivity of each species to competition was evaluated, and the niche difference and fitness difference were determined using the equation described by Carroll et al. (2011). However, in complex soil environments, microbial communities are characterized by multi-species interactions. A key obstacle to using these methods to measure the rate of invasion growth is that it is difficult to do so in the soil microbiome. Empirical testing of modern coexistence theory frameworks in the microbiomes of agricultural ecosystems faces great practical challenges. Here, we suggest that future research on microbial interactions involving two or more species in microcosms should be conducted not only in pure culture but also with surface-reactive particles of soils, such as different clay minerals, in order to test the modern coexistence theory (Bairey et al. 2016; Stotzky 1986).

Effects of biotic and abiotic factors on niche difference and fitness difference

In agricultural ecosystems, the effects of biotic interactions, climate change, environmental stress, fertilization, and soil constraints on the outcome of species competition have long been the focus of research (Valladares et al. 2015; Wardle 2006). In the framework of modern coexistence theory, these factors may act as stabilizing or/and equalizing forces for coexistence (Fig. 2). Biotic interactions, including mutualistic and antagonistic interactions, have positive or negative on the species involved, so they play different roles in determining the competitive outcome within communities (Faust and Raes 2012). In theory, mutualistic interactions promote coexistence by increasing niche difference (i.e., enabling access to other unavailable nutrients) and

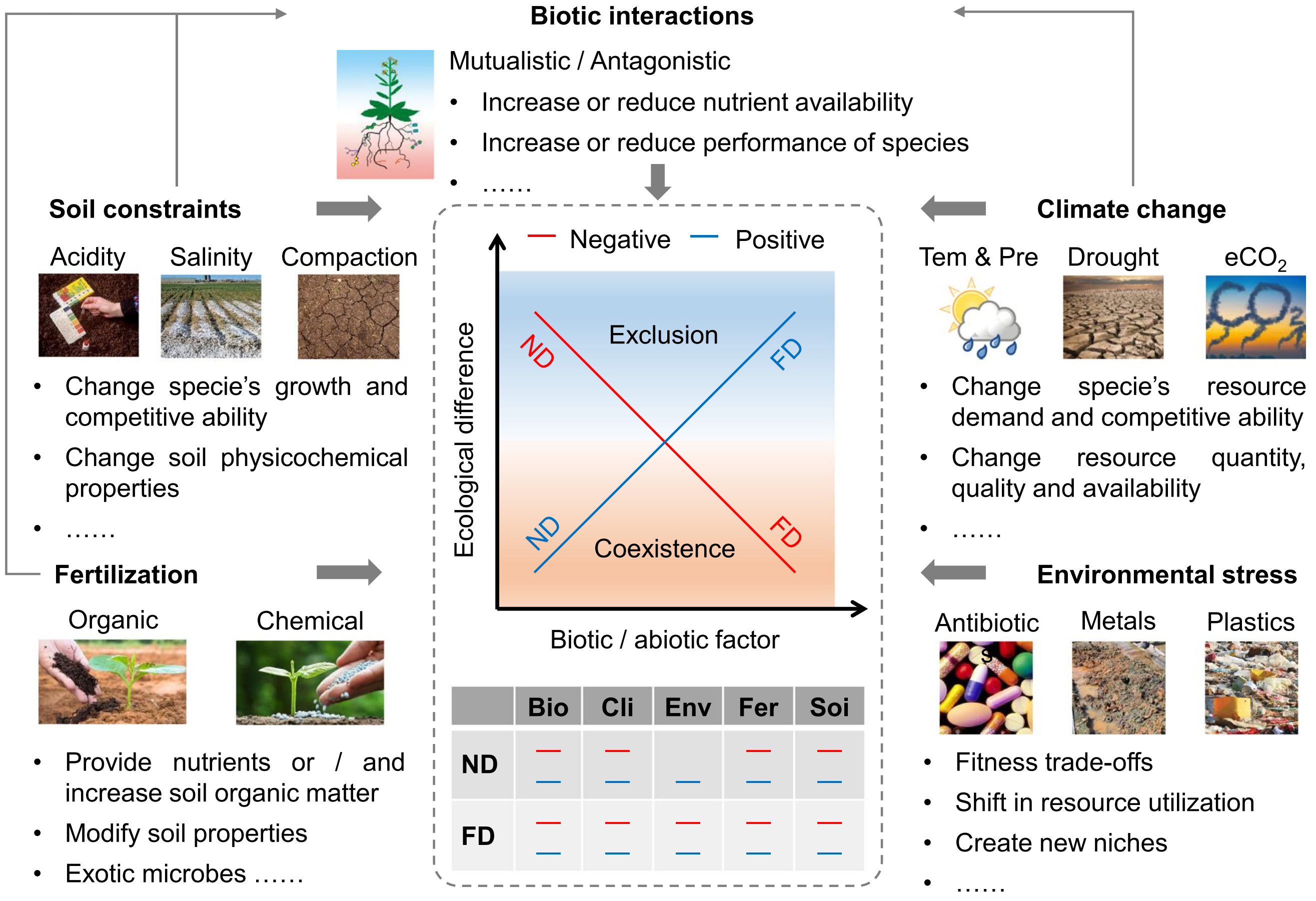

Fig. 2 Graphical presentation of the possible effects of biotic and abiotic factors on niche and fitness differences. ND, niche difference; FD, fitness difference; Bio, biotic interactions; Cli, climate change; Env, environmental stress; Fer, fertilization; Soi, soil constraints. Red and blue lines indicate negative and positive relationships, respectively. Gray thin arrows indicate indirect impact pathways

equalizing fitness difference (i.e., increasing the fitness of inferior species more than that of the dominant species). However, they may also result in competitive exclusion by reducing niche difference (due to increasing interspecific to intraspecific competition, since the mutualistic commodities are themselves limited) and increasing fitness difference (i.e., increasing the fitness of the superior competitor more than that of the inferior) (Bartomeus and Godoy 2018; Johnson 2021). The effects of mutualistic interactions on competitive outcomes and the mechanisms by which they occur depend on the response of species to the interactions. For example, using pollination and mycorrhizal mutualisms as illustrative systems, Johnson (2021) empirically quantifies niche and fitness differences between competitors and demonstrates that species might appear to coexist on resources alone, when the simultaneous incorporation of mutualisms actually drives competitive exclusion or competitive exclusion might occur under resource competition, when in fact, the incorporation of mutualisms generates coexistence. Arbuscular mycorrhizal fungi-dependent plant species are more phenotypically similar to each other and thus compete more strongly than arbuscular mycorrhizal fungi-independent plant species, and different mycorrhizal dependent plant species are more likely to coexist (Veresoglou et al. 2018). Mutualistic interactions between plants and arbuscular mycorrhizal fungi act as both stabilizing and equalizing forces in plant competition. Plant pathogens have antagonistic interactions with plants. However, these interactions can act as a stabilizing force, thus promoting plant species coexistence. They achieve this by enhancing intraspecific negative interactions: density-dependent diseases are more likely to spread through dense host populations and reduce their dominance (Parker et al. 2018). In addition, plant pathogens can act as an equalizing force by reducing the competitive advantage of better competitors. For example, plants with high growth rates, large seeds, and fast leaf turnovers have advantages in resource acquisition strategies. However, there are often trade-offs associated with such resource acquisition strategies, in the form of lower investments in the protection against pathogens, which can result in reductions in their competitive advantage due to antagonistic interactions (Maron et al. 2018; Petry et al. 2018). Indeed, fast-growing plant species experience greater fungal infection rates than slow-growing species (Blumenthal et al. 2009; Parker et al. 2018). By changing the fitness hierarchies of competitors, antagonistic interactions may therefore promote coexistence or exclusion.

Climate change (i.e., rising temperature, drought, and elevated CO_2 [eCO_2]) is expected to have a profound impact on the coexistence of species by changing niche and fitness differences (Valladares et al. 2015). Higher temperatures can change the feeding and population growth rates of species (Brown et al. 2004; Zhou et al. 2016). The asymmetric responses of species' resource requirements as a function of rising temperature can change both niche partitioning and competitive hierarchies (Lewington Pearce et al. 2019). For example, a study using experimentally derived energy budgets and field temperature data show that temperature-dependent asymmetries in energetic performance between *Hemimysis anomala* (which increases its feeding rate with temperature in parallel with growing metabolic demand) and *Mysis salemaai* (which maintains a constant feeding rate with temperature leading to diminishing energy assimilation) are an important mechanism determining invasion success under warming climates (Penk et al. 2016). Temperature can affect the growth and competition among *Microcystis aeruginosa*, *Planktothrix agardhii*, and *Cyclotella meneghiniana*, but the response is dependent on the species (Gomes et al. 2015). Because different temperatures may result in the production of distinct compounds that affect the competition, the vulnerability of target species to these compounds may also depend on the temperature. Therefore, the sensitivity and the physiological status of competing species can determine their lasting coexistence. On the other hand, higher temperatures may lead to increases in resource inputs or decreases in resource availability (due to higher decomposition rates), resulting in differences in the quantity and quality of resources and thus directly changing the ecological habitat (Davidson and Janssens 2006; Liang et al. 2017).

The soil water status controls microbial activities directly or indirectly by affecting the availability of nutrients (Keitt et al. 2016). Due to changes in precipitation or to long-term drought under climate change, the fitness of soil microorganisms may be reduced by investment in resources to tolerate drying and rewetting stress (Evans et al. 2014). Bacteria may be more negatively affected by drought than fungi, which may be attributed to their different tolerances to water stress (Preece et al. 2019). A number of traits, including osmolytes, thick cell walls, β1,3-glucan, trehalose, melanin, and budding growth, can allow fungi to maintain activity during drought (Treseder and Lennon 2015). Filamentous fungi can produce hyphae that extend up to meters and forage for water across small matrix of dry soil (Klein and Paschke 2004). Also, drought can cause changes in nutrient cycling and C allocation in soils, which may influence the niche for microorganisms (Pugnaire et al. 2019). Mutualistic symbionts such as N-fixing bacteria, plant growth-promoting rhizobacteria, and arbuscular mycorrhizal fungi may increase under water stress to enhance nutrient acquisition and drought tolerance (Ngumbi and Kloepper 2016; Suri et al. 2017).

Elevated CO_2 undoubtedly alters belowground C and nutrient allocation, resulting in either positive or negative changes in growth rates and competitive abilities of soil microorganisms (Castro et al. 2010). Heterotrophic decomposers and mutualistic mycorrhizal fungi are the two main groups of soil microbes that respond to changes in C and nutrient cycling under eCO_2 (Pugnaire et al. 2019). High concentration of CO_2 undermines energy acquisition of syntrophic microorganisms but not that of the aceticlastic methanogen in a model microbial consortium, resulting in the dominance of aceticlastic methanogen in the competitive interaction (Kato et al. 2014). In addition, climate change can indirectly affect niche difference and fitness difference among competing species by changing biotic interactions. For example, climate change is expected to alter host–pathogen interactions by increasing pathogen reproduction and host–plant modulation such as altering host tissue size and texture (Singh et al. 2019). Furthermore, the effects of climate change on soil microbes may be stronger under multiple climate change factors, such as the additive or interactive effects of rising temperature, drought, and eCO_2 (Gray et al. 2011; Thakur et al. 2019).

Environmental pollutant stress (such as antibiotics, metals, and microplastics) is known to affect the soil biome and soil functions. Environmental stress can cause fitness trade-offs in microorganisms, that is, a loss of competitiveness (i.e., a reduction in growth rate or yield) due to greater investment in resistance (Andersson and Levin 1999; Hall et al. 2015). The reduction of fitness is highly specific and environment dependent. A species may be resistant in one environment but sensitive in another, and the fitness cost of microbial resistance usually increases under more stressful growth conditions (Hall et al. 2011; Petersen et al. 2009). From the perspective of resistance evolution, stress affects not only fitness difference, but also the niche overlap between species. There are frequently trade-offs between resistance genes and metabolism (Martinez and Rojo 2011; Perkins and Nicholson 2008). The niche difference produced by the change of resource utilization pattern may be sufficient to offset the fitness cost of resistant mutations and allow coexistence. Unlike antibiotics and metals, the effects of microplastics on microorganisms seem to be mediated by physical parameters, such as particle shape and size, rather than by significant chemical-mediated toxicity (Rillig and Lehmann 2020). Therefore, microplastics can act as stabilizing factors by changing the spatial structure of microbial activities, providing adsorbed nutrients and organics, and influencing the flow of gas and water (Dussud et al. 2018; Yang et al. 2020).

Fertilization is a major anthropogenic activity in agricultural production. The direct effect of fertilization is to create niches for soil microbes and plants by providing nutrients that increase the metabolic activity of specific bacteria (Jia et al. 2020; Lin et al. 2020; Yu et al. 2019). The addition of large quantities of nutrients can favor r-strategists, while K-strategists prevail in nutrient-poor soils (Malý et al. 2009). In addition, fertilization may indirectly affect microbial fitness and niche by changing soil properties such as soil pH and aggregates (Geisseler and Scow 2014; Lin et al. 2019). Physiological and ecological studies have demonstrated that fertilization-induced changes in soil pH may drive niche specialization of microorganisms, such as ammonia oxidizers, as bacteria have rather narrow pH ranges for optimal growth, while fungi generally exhibit wider pH ranges for optimal growth (Geisseler and Scow 2014; Rousk et al. 2010; Zhao et al. 2020). Long-term manure application could increase soil aggregation and thus create more ecological niches, because macroaggregates can result in more heterogeneous habitats and labile substrates than microaggregates (Lin et al. 2019; Ye et al. 2021). Organic fertilizers, such as animal manure, compost, or sewage sludge, may introduce exogenous microorganisms into the soil that are either beneficial or detrimental to the growth of soil native organisms and plant, resulting in short-term positive or negative effects on microbial interactions, although the microorganisms added to soil by fertilizers may be unable to survive in the soil conditions (Lourenço et al. 2018; Suleiman et al. 2019). Such effects due to long-term fertilizations have also been frequently reported (Ling et al. 2016; Windisch et al. 2021). Moreover, fertilization has a profound impact on plant–microbial interactions by changing soil pH, organic C content, and nutrient availability (Huang et al. 2019). For example, flavonoids are important signaling molecules in the interactions between plants and N-fixing bacteria (best known as the legume-rhizobia symbiosis), as well as between plants and mycorrhizal and phytopathogenic fungi (Cesco et al. 2012). Soil organic amendments may interrupt flavonoid signaling pathways through metal-mediated reaction between flavonoids and dissolved organic C and weaken the effectiveness of plant–microbe interactions based on flavonoids (Del et al. 2020). Due to the high availability of nutrients and competition for limited C resources, N and P fertilization may reduce arbuscular mycorrhizal fungi colonization and increase fungal pathogen infection (Verbruggen and Toby 2010; Veresoglou et al. 2013). It should be noted that the effects of long-term fertilizer application on soil microbial interactions may have legacy effects in subsequent seasons even if fertilizer application has been discontinued (Liu et al. 2020).

Soil acidity, salinity, and compaction are important soil constraints for agricultural productivity and sustainability. Such stress conditions may significantly change soil physicochemical properties and fertility, resulting in impacts on species coexistence. Soil acidity can influence microbial niche and fitness as the consequence of different optimal pH ranges for microbial growth and activity (Rousk et al. 2010). Soil pH is a key factor in regulating soil organic matter turnover, nutrient bioavailability, and metal transformation (Kemmitt et al. 2006). Increasing soluble and exchangeable Al in the soil with acidity may affect species coexistence by reducing nutrient bioavailability and inducing toxicity to microorganisms and plants (Singh et al. 2017). Also, soil salinity has direct effects on microbial niche and fitness due to their different salinity preferences and tolerances (Rath et al. 2019; Zhang et al. 2019, 2021). Microbial species with specialized physiologies adapted to the high extracellular osmotic pressure may be resistant to soil salinity stress (Oren 2008). In addition, soil salinity can affect the availability of water, organic C decomposition, and the biogeochemical cycling of nutrients and thus may indirectly be a destabilizing factor for plants and microorganisms (De León-Lorenzana et al. 2018; Zhao et al. 2019). Soil compaction mainly affects soil physical properties such as bulk density, strength, and porosity, thereby reducing water infiltration, air permeability, and aggregate stability, altering elements mobility, and changing N and C cycling (Nawaz et al. 2013; Shah et al. 2017). This can change the niche properties for both soil microorganisms and plant roots. On the other hand, these soil constraints may change some biotic interactions among microbes and/or plants. For example, legumes and their rhizobia exhibit diverse tolerances and responses to soil acidity and salinity (Zahran 2010). In general, strains of *Bradyrhizobium* are more acid tolerant than those of *Rhizobium* (Castro et al. 2016).

Here, we only discuss some major factors affecting ecological niche difference and fitness difference and their possible pathways. It is not a comprehensive survey of all of the factors involved; however, it may help the reader to understand the coexistence of soil microorganisms and plants in agricultural ecosystems under climate change and human activities.

Modern coexistence theory in agricultural soil–microbe–plant systems

Numerous studies have reported complex interactions between soil microbes and plants in agroecosystems. Here, we attempt to disentangle the underlying mechanisms driving these interactions from the perspective of modern coexistence theory (Fig. 3). Soil harbors vast numbers of microbes, including bacteria, archaea, fungi, protozoa, and

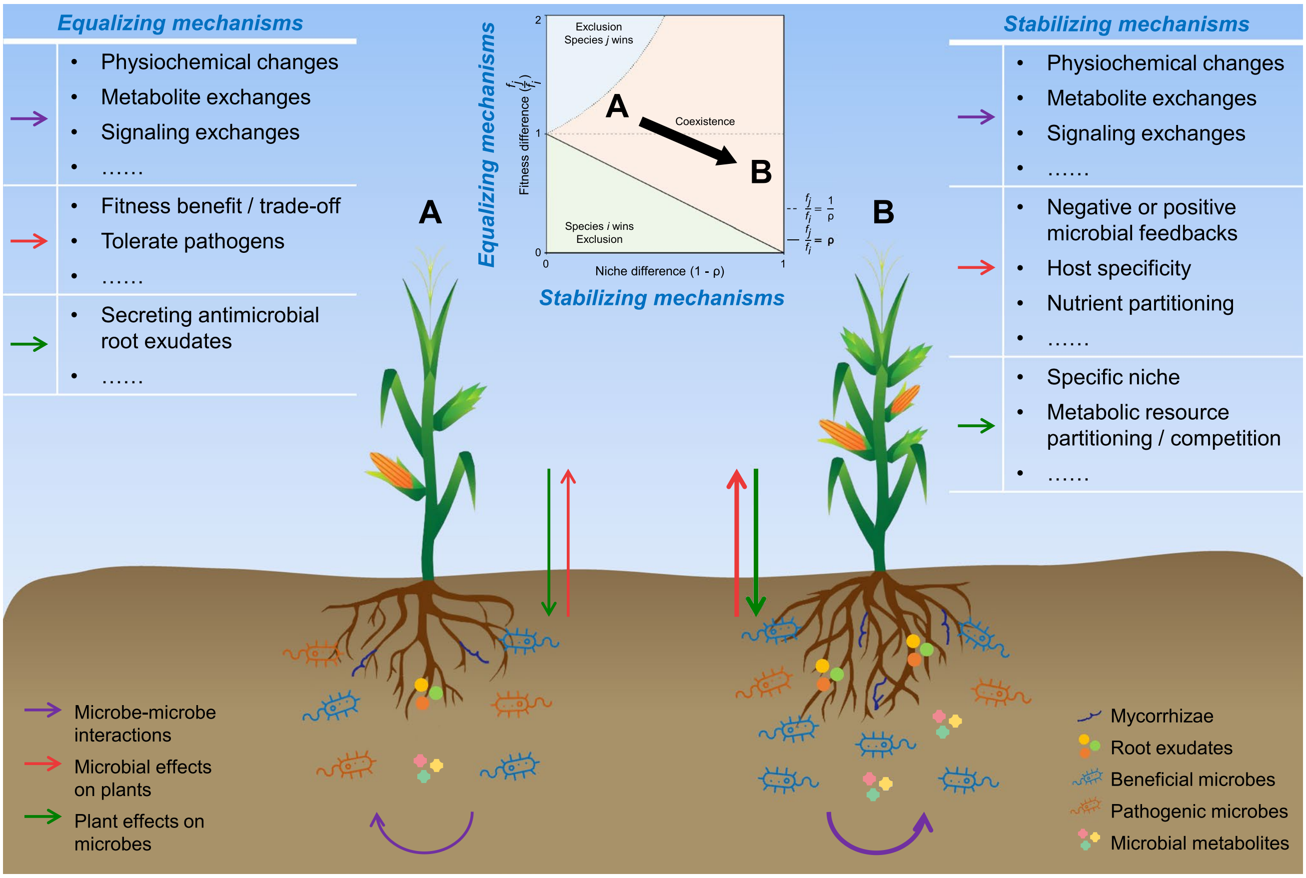

Fig. 3 Schematic illustrating soil microbe–microbe interactions and plant–microbe interactions through modern coexistence theory. The conceptual model of microbe–microbe interactions and plant–microbe interactions is modified after Bever's model of pairwise plant–soil feedback and its derived framework (Bever 2003; Bever et al. 1997; Kandlikar et al. 2019; Ke and Wan 2019). The purple arrows represent microbe–microbe interactions, which can be either mutualistic or antagonistic. The upward red arrows and downward green arrows represent the microbial effects on plants and plant effects on microbes, respectively, which both can be either positive or negative. Thick arrows indicate stronger interactions/effects than thin arrows

viruses, which participate in many ecological processes in agroecosystems, such as organic matter decomposition, nutrient cycling, pesticide degradation, soil-borne pathogen control, and abiotic stress tolerance (Sahu et al. 2019). Microbe–microbe interactions can occur through the transfer of molecular and genetic information, such as secondary metabolites, siderophores, cellular transduction signaling and quorum sensing, and biofilm formation (Braga et al. 2016). It has been suggested that the unculturability of many soil bacteria is due to the establishment of intercellular metabolic networks, which might be a form of coexistence that can potentially have major consequences for microbial functioning (Pande and Kost 2017). Mutualistic interactions and niche creation, which contribute to coexistence, can occur through metabolic cross-feeding, where some microorganisms excrete available metabolites to form new niches that can be occupied by others for their growth (Douglas 2020; D'Souza et al. 2018; San Roman and Wagner 2018). Antagonistic interactions can occur through exploitative competition for nutrients or produce antagonistic metabolites through interference competition (Ghoul and Mitri 2016; Hibbing et al. 2010). The types and extents of these interactions are largely influenced by various abiotic and biotic factors, which in turn change the activities of soil microorganisms and the ecological processes involved (Saleem and Moe 2014).

Using multiple microbial consortia consisting of bacteria and fungi that are beneficial to plants and manipulating rhizosphere microbes to improve crop growth and resistance are expected to contribute to sustainable agricultural production (Ahkami et al. 2017). Simple consortia (simple mixtures of plant beneficial bacteria and/or fungi grown separately before inoculation or growth of more than one plant beneficial bacteria and/or fungi together in a medium suitable for each one) and complex consortia (reconstructing functional metaorganisms based of microbiomes/metagenomics analyses and/or combined with culture-dependent approaches) are two known types of consortia formation (Bashan et al.

2020). The various steps involved in designing the ideal artificial microbial consortia include selecting the origin of the microbes, obtaining and culturing the core microorganisms, optimizing microbial interactions according to their compatibility, and assessing the efficacy of these consortia (Kong et al. 2018). One of the main challenges of such consortia is to explore the interactions between microbial members and specific interactions within plant holobiont (Bashan et al. 2020). The more species in the consortia, the more complex the outcomes of interactions as each member of a consortium can potentially affect the growth and production of metabolites of other members. It has been shown experimentally that defined microscale spatial structure is both necessary and sufficient for the stable coexistence of interacting microbial species in the synthetic community (Kim et al. 2008). In addition to the compatibility of multiple microorganisms and plant holobiont, more practical factors such as initial cell dosages and ratios, physiological activity, growth conditions of the strains, suitable formulations for survival and shelf-life of microorganisms, delivery approaches, colonization capacity, interaction with native microbiota, and potential influence of abiotic and biotic conditions of the soil/plant environment are bottlenecks for the successful establishment of consortia (Sessitsch et al. 2019). Nevertheless, some successful consortia have been achieved to improve crop growth and stress tolerance. For example, a consortium of four bacterial taxa (*Pseudomonas putida*, *Citrobacter freundii*, *Enterobacter cloacae*, and *Comamonas testosteroni*) has been reported to mobilize soil P and increase crop productivity up to twofold (Baas et al. 2016). A bacterial consortium containing four compatible and desiccation-tolerant strains (*Pseudomonas putida* KT2440, *Sphingomonas* sp. OF178, *Azospirillum brasilense* Sp7, and *Acinetobacter* sp. EMM02) was able to colonize the rhizosphere of plants and enhance desiccation stress tolerance in maize (Molina-Romero et al. 2017).

Soil microbes may have stabilizing or destabilizing effects on plants by generating negative or positive density-dependent feedbacks, thus facilitating or hindering coexistence (Bagchi et al. 2014, 2010). Plant growth-promoting rhizobacteria such as N-fixing bacteria (e.g., some species in the genera *Rhizobia*, *Azospirillum*, *Azotobacter*, *Azoarcus*, and Cyanobacteria) and P-solubilizing bacteria (e.g., some species in the genera *Azospirillum*, *Azotobacter*, *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Enterobacter*, and *Streptomyces*) may increase the availability of nutrients and expand the niche partitioning for plants and/or other microorganisms (Gamalero and Glick 2019). Host specificity in plant–microbe interactions may contribute to the niche differentiation and nutrient allocation of mycorrhizal plants and fungi (Tedersoo et al. 2020). Compared with intraspecific competition, it is expected to reduce interspecific competition and provide a stabilizing mechanism for promoting coexistence. On the other hand, plant–microbe interactions can provide different fitness benefits for plants and act as equalizing factors. Root microbiota are an important factor influencing host plants' performance and competition in response to biotic and abiotic stressors (Berendsen et al. 2012; Hodge and Fitter 2013). Microbial-mediated fitness differences in plants may be due to their different tolerance to soil-borne pathogens or the different benefits they get from the interacting soil microorganisms (Kandlikar et al. 2019). Some plant growth-promoting rhizobacteria are able to tolerate abiotic stress and maintain plant fitness by regulating hormonal and nutritional balance and producing plant growth regulators (Kumar and Verma 2018). If host immunity shapes the associated microbiota or if host–microbiota affect immunity, highly similar root microbiota between host plants may reduce plant performance due to transfer and coinfection with shared pathogenic bacteria, while specific microbial taxa in the root may influence competitive interactions among plants (Castrillo et al. 2017; Fitzpatrick et al. 2018; Hacquard et al. 2017). The plant-associated microbiota depend not only on host species but also on soil properties, which then in turn regulate plant performance under biotic and abiotic stresses. For example, among 30 angiosperm species, 40% of the variation in endosphere microbial diversity depends on the host species but only 17% in the rhizosphere soil, and drought shifts the composition of these root microbiomes, with host-specific changes in the relative abundance of specific bacterial taxa associated with increased drought tolerance of host plants (Fitzpatrick et al. 2018). In arbuscular mycorrhizal fungi plant systems, mycorrhizal fungi and hyphal networks tend to enhance plant intraspecific competition and alleviate interspecific competition by promoting the performance of inferior competitors and suppressing superior competitors (Tedersoo et al. 2020). In the context of modern coexistence theory, the extent to which plants coexist or repel is affected by microbial density-dependent feedbacks and niche differentiation, as well as fitness advantages provided by microbes for plant species (Kandlikar et al. 2019).

The rhizosphere is a unique niche for microorganisms that are influenced by plant root exudates (Pinton et al. 2001). When the rhizosphere microorganisms with different substrate uptake patterns undergo niche differentiation of metabolic resource allocation, it leads to stabilizing coexistence (Baran et al. 2015). On the contrary, competition for the same resource may occur when microorganisms have similar substrate preferences, leading to competitive exclusion (Freilich et al. 2011). Also, the substrate concentration is important because microorganisms with low Michaelis–Menten kinetics constant (K_m) values of uptake for the target substrate can prevail at low concentration and the opposite for microorganisms with high K_m values. For example, the slow-growing K-strategic microorganisms with enzymes of high substrate affinity are better adapted for growth on poorly available substrates but are uncompetitive against the r-strategic microorganisms with higher K_m values in the rhizosphere (Tian et al. 2020). The kinetic analysis suggested that comammox *Nitrospira* had higher affinity for ammonia than ammonia-oxidizing archaea and bacteria and thus might be more competitive under oligotrophic conditions (Kits et al. 2017). Some root exudates, such as phenolics and terpenoids, play an antimicrobial role in selecting beneficial microbes and resisting soil-borne pathogens (Baetz and Martinoia 2014). Phenolic compounds can be used as specific substrates or signaling molecules for some bacterial groups and benefit the community by creating specific chemical niches (Badri et al. 2013). In addition, plants can also indirectly affect soil microbes by secreting exudates such as organic acids, thus changing soil pH and nutrient availability (Chen et al. 2016; Dakora and Phillips 2002).

Taken together, the effects of microbe–microbe interactions and plant–microbe interactions on species competitive outcomes in agroecosystem can be understood by Bever's model of pairwise plant–soil feedback model (Bever 2003; Bever et al. 1997; Kandlikar et al. 2019; Ke and Wan 2019). Firstly, microbial mutualistic and antagonistic interactions can affect the niche difference and fitness difference among competing microbes, which is crucial for maintaining soil microbial diversity and ecosystem functioning. Secondly, both beneficial and pathogenic microbes can modify niche difference and fitness difference between competing plants, thus affecting plant growth and yield. Thirdly, plants change niche difference and fitness difference among competing microbes by secreting root exudates that are beneficial or harmful to soil microbes. By integrating niche competition and interaction between microorganisms and plants, we can better understand the effects of interactions between microorganisms and plants on plant fitness. Although these processes are mainly stabilizing or/and equalizing, their impact on coexistence is integrative rather than singular and varies with environmental conditions. Therefore, it is difficult to draw a general conclusion about the influence of soil microorganism on plant coexistence or the influence of plant on soil microorganism coexistence. However, this framework provides an insight into integrating the roles of multiple soil microorganisms and determining their contribution to plant coexistence, which can be applied to the utilization of beneficial microorganisms in plants and the control of soil-borne diseases in crop production. More empirical studies are suggested to test the framework in mesocosms involving two or more microbial species with and without plants.

Conclusion and future perspectives

The modern coexistence theory framework improves our understanding of coexistence and can be applied to microbial communities under different biotic and abiotic conditions. Microbial coexistence plays an important role in promoting soil–plant ecosystem health by stabilization and equalization. Here, we focus on the theory underlying coexistence in soil microbe–plant ecosystems and emphasize some challenges in the future. First of all, for empirical testing, it is difficult to estimate experimentally the population growth rate of microorganisms in the community and their sensitivity to intraspecific and interspecific densities. Population dynamics is the result of complex species interactions in multiple species communities. It remains a big challenge to assess the interaction coefficients among co-occurring microbes, especially in the natural range of high population density and heterogeneous environment. Therefore, one of the next steps is to develop experimental methods to quantitatively estimate the niche difference and fitness difference between competing microorganisms in a community and to predict the competitive outcome of pairwise interactions between species to more complex high-order interactions, even across multiple scales of space and time.

Second, modern coexistence theory provides an abstract concept of coexistence, but it is difficult to apply to empirical studies. Niche difference and fitness difference are simplified functional traits of species and lack specific information. By linking the niche and fitness of plants and microorganisms with specific functional characteristics, physiological characteristics, and biotic or abiotic factors that affect population growth rate, we can deepen our understanding of coexistence. For example, temperature has a significant effect on the metabolic rate and motility of organisms, which can have a special contribution to the population growth rate, thus promoting species coexistence. The explanation of functional traits and physiological attributes can be associated with niche difference and fitness difference among species and explain the potential mechanism of coexistence.

When expanding the application of modern coexistence theory in soil microbe–plant ecosystems, it is necessary to incorporate microbe–microbe interactions and plant–microbe interactions into stabilizing and equalizing mechanisms. Both model and experimental studies should consider more thoroughly the role of plants in mediating microbial interactions and the effects of microbes on plant niche and fitness. It has important practical significance and application value for maintaining microbial and plant diversity and its function in agricultural ecosystems. In plant microbiome engineering, various microbial strains that promote plant growth are usually screened for under highly artificial conditions. Successful field application requires further consideration of the coexistence of synthetic microbial communities and native soil microorganisms, as well as their diversity and ecological functions under the influence of plant root exudates and other environmental factors. The application of modern coexistence theory for plant microbiome research can bridge the gap between laboratory results and field performance.

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Declarations

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