

1 **Theory of microbial coexistence in promoting soil-plant ecosystem**  
2 **health**

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17 **Abstract**

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

38 **Keywords:** modern coexistence theory, niche and fitness differences, stabilizing and  
39 equalizing mechanisms, species interactions, soil health

## 40 **Introduction**

41 Global demand for crops is growing rapidly and is likely to continue for decades to  
42 come, due to increases in both the global population and per capita consumption  
43 (Godfray and Garnett 2014; Tilman et al. 2011). However, global crop yields are  
44 predicted to be insufficient to meet the projected demand in 2050 (Ray et al. 2013).  
45 Agricultural crop productivity is under tremendous pressure from a variety of abiotic  
46 stresses, due to intensive use of chemical fertilizers and pesticides, climate change and  
47 environmental pollution, and biotic stresses from pests and pathogens (Molotoks et al.  
48 2020; Pandey et al. 2017). Increasing the productivity of agroecosystems remains a  
49 huge challenge and there is an urgent need for more sustainable ways to increase crop  
50 yields.

51 The phytobiome is composed of plants, their environment, and diverse interacting  
52 microscopic and macroscopic organisms, which together profoundly influence plant  
53 and agroecosystem health and productivity (Leach et al. 2017). In the phytobiome,  
54 complex networks of interactions that links crops with microorganisms, animals,  
55 plants, soil, climate, and other environmental factors are established and regulated  
56 through physical and chemical cues (Korenblum and Aharoni 2019; Leach et al.  
57 2017). Historically, agroecosystems have been managed by focusing on individual  
58 components of the phytobiome, such as nutrient applications and pesticides. However,

59 managing the phytobiome as an integrated system of diverse interacting components  
60 may offer greater opportunities to achieve optimal and sustainable crop productivity  
61 (Bell et al. 2019). Phytobiome studies that consider the complex network of  
62 interactions inside and outside the plant have demonstrated their potential in crop  
63 improvement (Hale et al. 2014; Macias-Bobadilla et al. 2020).

64 Soil and phytobiome microbes provide essential ecosystem services for agricultural  
65 crop production by regulating nutrient cycling, promoting plant growth, controlling  
66 pests and pathogens, and alleviating abiotic stress (Begum et al. 2019; Goswami and  
67 Deka 2020; Vimal et al. 2017). Microbes are rarely observed as single species  
68 populations in the soil environment. They form complex consortia through various  
69 types of interactions, including mutualism (two partners A and B have mutual  
70 benefit), commensalism (A take profit, whereas B gains no disadvantage), amensalism  
71 (A is limited by B), parasitism (A takes profit of B), predation (A consumes B) and  
72 competition (A and B compete for a limiting factor) (Faust and Raes 2012; van Elsas  
73 et al. 2019). Thus, the interactions can be either mutualistic (or cooperative, leading to  
74 a positive effect on partners of the interaction) or antagonistic (in which a negative  
75 effect on at least one partner of the interaction can be seen) (van Elsas et al. 2019).  
76 These interactions involve ecological processes such as physiochemical changes,  
77 metabolite exchanges, and signaling, which allow different niches to be occupied and  
78 affect the competitiveness of communities (Braga et al. 2016). On the one hand,  
79 mutualistic interactions between plants and arbuscular mycorrhizal fungi provide

80 several benefits for plant growth and yield by increasing the availability of nutrients,  
81 improving soil structure, and enhancing stress resistance of plants (Begum et al.  
82 2019). Plant growth-promoting rhizobacteria generally promote plant growth by  
83 producing plant hormones such as auxins and cytokinins, improving nutrition  
84 acquisition, enhancing the antioxidant system, inducing resistance against plant  
85 pathogens, production of siderophore, volatile organic compounds and protection  
86 enzymes (Vejan et al. 2016). On the other hand, antagonistic interactions between  
87 plants and pathogens have detrimental effects on plant growth and account for a major  
88 loss in global crop productivity (Oerke 2006; Strange and Scott 2005).

89 Many plant growth-promoting microorganisms have been isolated from soil or  
90 rhizosphere to study their beneficial effects on soil and plant (De-Bashan et al. 2020;  
91 Le Mire et al. 2016; Mahanty et al. 2017). Microbiome engineering is an emerging  
92 field of synthetic biology, which may provide a sustainable strategy to improve crop  
93 productivity (Ahkami et al. 2017; Orozco-Mosqueda et al. 2018; Qiu et al. 2019). The  
94 synthetic community builds on complementary ecological functions of  
95 microorganisms and aims to engineer synthetic microbial communities to promote  
96 beneficial plant-microbe interactions (Ke et al. 2020). A synthetic microbial  
97 community is designed by mixing selected microbial strains that perform a given  
98 function better than the sum of individual performances, and applying it to plants to  
99 study various aspects of plant-microbe interactions (Vorholt et al. 2017). The  
100 challenge of microbiome engineering is not only to design synthetic microbial

101 consortia with multiple plant growth promoting functions, but also to stabilize them  
102 under field conditions (Arif et al. 2020; Sessitsch et al. 2019). It is necessary,  
103 therefore, to understand the mechanism of both microbe-microbe interactions and  
104 plant-microbe interactions (including how microbes affect plants and how plants  
105 manipulate microbes) based on the theory of species coexistence (Arif et al. 2020;  
106 Vorholt et al. 2017).

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

122 application of modern coexistence theory in agricultural soil-microbe-plant systems.

### 123 **The framework of modern coexistence theory**

124 In order to understand and predict species coexistence quantitatively on the basis of  
125 mechanistic theory, Chesson (2000) proposed two ecological differences among  
126 species, namely niche difference and average fitness difference. Here, ecological  
127 niche is not a Hutchinsonian hypervolume (Leibold 1995), but instead is defined by  
128 the relationship between organisms and the physical and biological environment,  
129 taking into account both time and space. A particular combination of physical factors  
130 (e.g. temperature and moisture) and biological factors (e.g. predated food resources,  
131 predators and natural enemies) at a particular point in time and space defines a point  
132 in niche space. A modern definition of a species' ecological niche is the response that  
133 the species has to each point in the niche space and the effect that the species has at  
134 each point (Chesson 2000; Shea and Chesson 2002). Responses are defined in terms  
135 of demographic variables, such as survival and individual growth; but of most  
136 importance is the overall outcome of these responses, the per-capita rate of population  
137 increase. Effects include consumption of resources, interference with access to  
138 resources by other organisms, support of natural enemies and occupancy of space.  
139 Niche difference reflects the spatial and temporal differences in resource utilization of  
140 species. Niche differences arise when intraspecific competition is greater than  
141 interspecific competition and prevents any species from becoming absolutely  
142 dominant or extinct in the community, thus stabilizing coexistence. By contrast,

143 fitness difference is competitive asymmetry, which can result in one species excluding  
144 another species, regardless of their relative abundance, thus limiting the possibility of  
145 coexistence. Examples of fitness difference include differences of species in  
146 fecundity, susceptibility to generalist predators, resistance to fluctuating environment,  
147 and ability to take up limited resources (Chesson and Kuang 2008). The joint effects  
148 of niche difference and fitness difference determine whether each species in a  
149 competitive pair can increase from low density when the other is abundant, thus  
150 leading to coexistence or exclusion (Figure 1). Niche difference supports coexistence  
151 by limiting the over expansion of species when they rise to dominance and protecting  
152 them from exclusion when they become rare (Adler et al. 2007). Fitness difference  
153 drives competitive exclusion when species share the same niche. When niche  
154 difference between competitors is larger than fitness difference, the two species will  
155 coexist stably. Otherwise, the species with higher fitness will exclude other species.

156 Increasing niche difference between species and/or decreasing fitness difference,  
157 referred to as stabilizing and equalizing mechanisms, respectively, can promote  
158 coexistence (Chesson 2000). In other words, the stability mechanism tends to restrict  
159 species to interactions within their own population whilst limiting those with  
160 competitors, and the equalizing mechanism tends to make species more similar in  
161 competitiveness. For example, resource partitioning (the specialization of species on  
162 different resources) is a stabilizing mechanism that increases niche differences. Many  
163 trade-offs (a negative correlation between traits because the cell resources allocated to



164 one trait result in a decrease in the fitness of another trait) can be seen as equalizing  
165 mechanisms, because doing well in one respect often means doing less well in another  
166 (Chesson 2013). For example, in order to survive in a harsh environment, a species  
167 may reduce its reproduction rate in exchange for survival (i.e., survival-reproduction  
168 trade-offs), thus limiting the fitness differences between species.

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

175

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

176

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

177 where  $\alpha_{ij}$  describes the per capita effect of species  $j$  on species  $i$ , as a proportion of the  
178 maximum per capita growth rate of species  $i$  is decreased by increasing the density of  
179 species  $j$  by one unit. The coefficient measures intraspecific density dependence if  $i =$   
180  $j$ , and interspecific density dependence if  $j$  is different from  $i$ . The niche overlap,  $\rho$ , is  
181 a measure of the relative strength of density-dependent feedback between species and  
182 within species. Niche difference reflects the degree of intraspecific competition

183 (denominator) relative to interspecific competition (numerator). Fitness difference  
184 between competitors,  $f_j/f_i$ , describes the degree to which species  $i$  is more sensitive to  
185 intraspecific and interspecific competitions than species  $j$ . The larger the ratio, the  
186 greater the fitness advantage of species  $j$  relative to  $i$ , and the faster species  $j$  can  
187 exclude  $i$  in the absence of niche difference. Two species coexist stably when their  
188 growth (and therefore their increase in density) has a greater inhibitory effect within  
189 their own population than on the population of the other species. In other words, when  
190 the intraspecific competition coefficient exceeds the interspecific competition  
191 coefficient, that is, when fitness difference is between  $\rho$  and  $1/\rho$ , stable coexistence  
192 occurs.

193 Another way to measure niche difference and fitness difference is based on  
194 MacArthur's consumer-resource model (Carroll et al. 2011). In this model, niche  
195 difference and fitness difference are calculated by the effect of interspecific  
196 interaction on population dynamics, that is, the invasion rate. The proportional  
197 reduction in the growth rate of an invader  $i$  due to interspecific competition is called

198  $i$ '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  $\mu_{i,0}$

199 and  $\mu_{i,j}$  is the per capita growth rate of invader  $i$  in the absence and presence of the  
200 native species  $j$ , respectively. When  $S_i < 1$ ,  $i$  can invade  $j$ , but invasion is not possible  
201 when  $S_i > 1$  (i.e., negative growth as invader). For  $S_i$  approaches 1, a species would  
202 show a sharp drop in growth rate when invading, whilst  $S_i < 0$  indicates facilitation

203 (i.e., a special case in which the invader grows better in presence of the resident than  
204 in monoculture). The niche difference and fitness difference between the invasive and  
205 local species can be calculated by the geometric mean and geometric standard  
206 deviation of their sensitivities to competition. The formulae are as follows:

$$207 \quad \text{Niche difference} = 1 - \prod_{i=1}^n S_i^{1/n}$$

$$208 \quad \text{Fitness difference} = \exp\left[\left(\overline{(\ln S)^2} - (\overline{\ln S})^2\right)^{1/2}\right]$$

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

220 Most of the empirical tests of modern coexistence theory are carried out in annual  
221 plant communities by calculating niche difference and fitness difference based on  
222 parametric competition models. These models need field estimations of species

224 germination fractions, per-germinant fecundities without neighbors, seed survival in  
225 soil and all pairwise competition coefficients (Godoy et al. 2014; Godoy and Levine  
226 2014; Kraft et al. 2015). Some studies have also determined niche difference and  
227 fitness difference between pairs of microbes by measuring invasion growth rates in  
228 mutual invasion experiments with bacterial strains (Li et al. 2019; Tan et al. 2017),  
229 yeast (Grainger et al. 2019) and green algae (Narwani et al. 2013). Based on the  
230 monoculture and invasive growth rates, the sensitivity of each species to competition  
231 was evaluated, and the niche difference and fitness difference were determined using  
232 the equation described by Carroll et al. (2011). However, in complex soil  
233 environments, microbial communities are characterized by multi-species interactions.  
234 A key obstacle to using these methods to measure the rate of invasion growth is that it  
235 is difficult to do so in the soil microbiome. Empirical testing of modern coexistence  
236 theory frameworks in the microbiomes of agricultural ecosystems faces great practical  
237 challenges. Here, we suggest that future research on microbial interactions involving  
238 two or more species in microcosms should be conducted not only in pure culture but  
239 also with surface-reactive particles of soils, such as different clay minerals, in order to  
240 test the modern coexistence theory (Bairey et al. 2016; Stotzky 1986).

## 241 **Effects of biotic and abiotic factors on niche difference and fitness** 242 **difference**

243 In agricultural ecosystems, the effects of biotic interactions, climate change,  
244 environmental stress, fertilization and soil constraints on the outcome of species

245 competition have long been the focus of research (Valladares et al. 2015; Wardle  
246 2006). In the framework of modern coexistence theory, these factors may act as  
247 stabilizing or/and equalizing forces for coexistence (Figure 2). Biotic interactions,  
248 including mutualistic and antagonistic interactions, have positive or negative on the  
249 species involved, so they play different roles in determining the competitive outcome  
250 within communities (Faust and Raes 2012). In theory, mutualistic interactions  
251 promote coexistence by increasing niche difference (i.e., enabling access to other  
252 unavailable nutrients) and equalizing fitness difference (i.e., increasing the fitness of  
253 inferior species more than that of the dominant species). However, they may also  
254 result in competitive exclusion by reducing niche difference (due to increasing  
255 interspecific to intraspecific competition, since the mutualistic commodities are  
256 themselves limited) and increasing fitness difference (i.e., increasing the fitness of the  
257 superior competitor more than that of the inferior) (Bartomeus and Godoy 2018;  
258 Johnson 2021). The effects of mutualistic interactions on competitive outcomes and  
259 the mechanisms by which they occur depend on the response of species to the  
260 interactions. For example, using pollination and mycorrhizal mutualisms as  
261 illustrative systems, Johnson (2021) empirically quantify niche and fitness differences  
262 between competitors, and demonstrate that species might appear to coexist on  
263 resources alone, when the simultaneous incorporation of mutualisms actually drives  
264 competitive exclusion, or competitive exclusion might occur under resource  
265 competition when in fact, the incorporation of mutualisms generates coexistence.

266 Arbuscular mycorrhizal fungi dependent plant species are more phenotypically similar  
267 to each other and thus compete more strongly than arbuscular mycorrhizal fungi  
268 independent plant species, and different mycorrhizal dependent plant species are more  
269 likely to coexist (Veresoglou et al. 2018). Mutualistic interactions between plants and  
270 arbuscular mycorrhizal fungi act as both stabilizing and equalizing forces in plant  
271 competition. Plant pathogens have antagonistic interactions with plants. However,  
272 these interactions can act as a stabilizing force, thus promoting plant species  
273 coexistence. They achieve this by enhancing intraspecific negative interactions:  
274 density dependent diseases are more likely to spread through dense host populations  
275 and reduce their dominance (Parker et al. 2018). In addition, plant pathogens can act  
276 as an equalizing force by reducing the competitive advantage of better competitors.  
277 For example, plants with high growth rates, large seeds and fast leaf turnovers have  
278 advantages in resource acquisition strategies. However, there are often trade-offs  
279 associated with such resource acquisition strategies, in the form of lower investments  
280 in the protection against pathogens, which can result in reductions in their competitive  
281 advantage due to antagonistic interactions (Maron et al. 2018; Petry et al. 2018).  
282 Indeed, fast-growing plant species experience greater fungal infection rates than slow-  
283 growing species (Blumenthal et al. 2009; Parker et al. 2018). By changing the fitness  
284 hierarchies of competitors, antagonistic interactions may therefore promote  
285 coexistence or exclusion.

286 Climate change (i.e., rising temperature, drought and elevated CO<sub>2</sub> [eCO<sub>2</sub>]) is

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

308 (Davidson and Janssens 2006; Liang et al. 2017).

309 The soil water status controls microbial activities directly or indirectly by affecting  
310 the availability of nutrients (Keitt et al. 2016). Due to changes in precipitation or to  
311 long term drought under climate change, the fitness of soil microorganisms may be  
312 reduced by investment in resources to tolerate drying and rewetting stress (Evans et  
313 al. 2014). Bacteria may be more negatively affected by drought than fungi, which may  
314 be attributed to their different tolerances to water stress (Preece et al. 2019). A number  
315 of traits, including osmolytes, thick cell walls,  $\beta$ 1,3-glucan, trehalose, melanin, and  
316 budding growth, can allow fungi to maintain activity during drought (Treseder and  
317 Lennon 2015). Filamentous fungi can produce hyphae that extend up to meters and  
318 forage for water across small matrix of dry soil (Klein and Paschke 2004). Also,  
319 drought can cause changes in nutrient cycling and carbon allocation in soils, which  
320 may influence the niche for microorganisms (Pugnaire et al. 2019). Mutualistic  
321 symbionts such as N-fixing bacteria, plant growth-promoting rhizobacteria and  
322 arbuscular mycorrhizal fungi may increase under water stress to enhance nutrient  
323 acquisition and drought tolerance (Ngumbi and Kloepper 2016; Suri et al. 2017).

324 Elevated CO<sub>2</sub> undoubtedly alters belowground C and nutrient allocation, resulting  
325 in either positive or negative changes in growth rates and competitive abilities of soil  
326 microorganisms (Castro et al. 2010). Heterotrophic decomposers and mutualistic  
327 mycorrhizal fungi are the two main groups of soil microbes that respond to changes in  
328 C and nutrient cycling under eCO<sub>2</sub> (Pugnaire et al. 2019). High concentration of CO<sub>2</sub>



329 undermine energy acquisition of syntrophic microorganisms, but not that of the  
330 acetoclastic methanogen in a model microbial consortium, resulting in dominance of  
331 acetoclastic methanogen in the competitive interaction (Kato et al. 2014). In addition,  
332 climate change can indirectly affect niche difference and fitness difference among  
333 competing species by changing biotic interactions. For example, climate change is  
334 expected to alter host pathogen interactions by increasing pathogen reproduction and  
335 host plant modulation such as altering host tissue size and texture (Singh et al. 2019).  
336 Furthermore, the effects of climate change on soil microbes may be stronger under  
337 multiple climate change factors, such as the additive or interactive effects of rising  
338 temperature, drought and eCO<sub>2</sub> (Gray et al. 2011; Thakur et al. 2019).

339 Environmental pollutant stress (such as antibiotics, metals, microplastics, etc.) is  
340 known to affect the soil biome and soil functions. Environmental stress can cause  
341 fitness trade-offs in microorganisms, that is, a loss of competitiveness (i.e., a  
342 reduction in growth rate or yield) due to greater investment in resistance (Andersson  
343 and Levin 1999; Hall et al. 2015). The reduction of fitness is highly specific and  
344 environment dependent. A species may be resistant in one environment, but sensitive  
345 in another, and the fitness cost of microbial resistance usually increases under more  
346 stressful growth conditions (Hall et al. 2011; Petersen et al. 2009). From the  
347 perspective of resistance evolution, stress affects not only fitness difference, but also  
348 the niche overlap between species. There are frequently trade-offs between resistance  
349 genes and metabolism (Martinez and Rojo 2011; Perkins and Nicholson 2008). The

350 niche difference produced by the change of resource utilization pattern may be  
351 sufficient to offset the fitness cost of resistant mutations and allow coexistence.  
352 Unlike antibiotics and metals, the effects of microplastics on microorganisms seem to  
353 be mediated by physical parameters, such as particle shape and size, rather than by  
354 significant chemical mediated toxicity (Rillig and Lehmann 2020). Therefore,  
355 microplastics can act as stabilizing factors by changing the spatial structure of  
356 microbial activities, providing adsorbed nutrients and organics, and influencing the  
357 flow of gas and water (Dussud et al. 2018; Yang et al. 2020).

358 Fertilization is a major anthropogenic activity in agricultural production. The direct  
359 effect of fertilization is to create niches for soil microbes and plants by providing  
360 nutrients that increase the metabolic activity of specific bacteria (Jia et al. 2020; Lin et  
361 al. 2020; Yu et al. 2019). The addition of large quantities of nutrients can favor r-  
362 strategists, while K-strategists prevail in nutrient-poor soils (Malý et al. 2009). In  
363 addition, fertilization may indirectly affect microbial fitness and niche by changing  
364 soil properties such as soil pH and aggregates (Geisseler and Scow 2014; Lin et al.  
365 2019). Physiological and ecological studies have demonstrated that fertilization  
366 induced changes in soil pH may drive niche specialization of microorganisms, such as  
367 ammonia oxidizers, as bacteria have rather narrow pH ranges for optimal growth,  
368 while fungi generally exhibit wider pH ranges for optimal growth (Geisseler and  
369 Scow 2014; Rousk et al. 2010; Zhao et al. 2020). Long-term manure application could  
370 increase soil aggregation and thus create more ecological niches, because

371 macroaggregates can result in more heterogeneous habitats and labile substrates than  
372 microaggregates (Lin et al. 2019; Ye et al. 2021). Organic fertilizers, such as animal  
373 manure, compost or sewage sludge, may introduce exogenous microorganisms into  
374 the soil that are either beneficial or detrimental to the growth of soil native organisms  
375 and plant, resulting in short-term positive or negative effects on microbial  
376 interactions, although the microorganisms added to soil by fertilizers may be unable to  
377 survive in the soil conditions (Lourenço et al. 2018; Suleiman et al. 2019). Such  
378 effects due to long-term fertilizations have also been frequently reported (Ling et al.  
379 2016; Windisch et al. 2021). Moreover, fertilization has a profound impact on plant-  
380 microbial interactions by changing soil pH, organic C content and nutrient availability  
381 (Huang et al. 2019). For example, flavonoids are important signaling molecules in  
382 interactions between plants and N-fixing bacteria (best known as the legume-rhizobia  
383 symbiosis), as well as between plants and mycorrhizal and phytopathogenic fungi  
384 (Cesco et al. 2012). Soil organic amendments may interrupt flavonoid signaling  
385 pathways through metal-mediated reaction between flavonoids and dissolved organic  
386 C, and weaken the effectiveness of plant-microbe interactions based on flavonoids  
387 (Del et al. 2020). Due to the high availability of nutrients and competition for limited  
388 C resources, N and P fertilization may reduce arbuscular mycorrhizal fungi  
389 colonization and increase fungal pathogen infection (Verbruggen and Toby 2010;  
390 Veresoglou et al. 2013). It should be noted that the effects of long-term fertilizer  
391 application on soil microbial interactions may have legacy effects in subsequent

392 seasons even if fertilizer application has been discontinued (Liu et al. 2020).

393 Soil acidity, salinity and compaction are important soil constraints for agricultural  
394 productivity and sustainability. Such stress conditions may significantly change soil  
395 physicochemical properties and fertility, resulting in impacts on species coexistence.  
396 Soil acidity can influence microbial niche and fitness as the consequence of different  
397 optimal pH ranges for microbial growth and activity (Rousk et al. 2010). Soil pH is a  
398 key factor in regulating soil organic matter turnover, nutrient bioavailability and metal  
399 transformation (Kemmitt et al. 2006). Increasing soluble and exchangeable Al in the  
400 soil with acidity may affect species coexistence by reducing nutrient bioavailability  
401 and inducing toxicity to microorganisms and plants (Singh et al. 2017). Also, soil  
402 salinity has direct effects on microbial niche and fitness due to their different salinity  
403 preferences and tolerances (Rath et al. 2019; Zhang et al. 2019; Zhang et al. 2021).  
404 Microbial species with specialized physiologies adapted to the high extracellular  
405 osmotic pressure may be resistant to soil salinity stress (Oren 2008). In addition, soil  
406 salinity can affect the availability of water, organic carbon decomposition and the  
407 biogeochemical cycling of nutrients, and thus may indirectly be a destabilizing factor  
408 for plants and microorganisms (De León-Lorenzana et al. 2018; Zhao et al. 2019).  
409 Soil compaction mainly affects soil physical properties such as bulk density, strength,  
410 and porosity, thereby reducing water infiltration, air permeability and aggregate  
411 stability, altering elements mobility, and changing N and C cycling (Nawaz et al.  
412 2013; Shah et al. 2017). This can change the niche properties for both soil

413 microorganisms and plant roots. On the other hand, these soil constraints may change  
414 some biotic interactions among microbes and/or plants. For example, legumes and  
415 their rhizobia exhibit diverse tolerances and responses to soil acidity and salinity  
416 (Zahran 2010). In general, strains of *Bradyrhizobium* are more acid tolerant than those  
417 of *Rhizobium* (Castro et al. 2016).

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

### 423 **Modern coexistence theory in agricultural soil-microbe-plant systems**

424 Numerous studies have reported complex interactions between soil microbes and  
425 plants in agroecosystems. Here, we attempt to disentangle the underlying mechanisms  
426 driving these interactions from the perspective of modern coexistence theory (Figure  
427 3). Soil harbors vast numbers of microbes, including bacteria, archaea, fungi, protozoa  
428 and viruses, which participate in many ecological processes in agroecosystems, such  
429 as organic matter decomposition, nutrient cycling, pesticide degradation, soil-borne  
430 pathogen control and abiotic stress tolerance (Sahu et al. 2019). Microbe-microbe  
431 interactions can occur through the transfer of molecular and genetic information, such  
432 as secondary metabolites, siderophores, cellular transduction signaling, quorum  
433 sensing and biofilm formation (Braga et al. 2016). It has even been suggested that the

434 unculturability of many soil bacteria is due to the establishment of intercellular  
435 metabolic networks, which is a form of coexistence that could potentially have major  
436 consequences for microbial functioning (Pande and Kost 2017). Mutualistic  
437 interactions and niche creation, that contribute to coexistence, can occur through  
438 metabolic cross-feeding, where some microorganisms excrete available metabolites to  
439 form new niches that can be occupied by others for their growth (Douglas 2020;  
440 D'Souza et al. 2018; San Roman and Wagner 2018). Antagonistic interactions can  
441 occur through exploitative competition for nutrients, or produce antagonistic  
442 metabolites through interference competition (Ghoul and Mitri 2016; Hibbing et al.  
443 2010). The types and extents of these interactions are largely influenced by various  
444 abiotic and biotic factors, which in turn change the activities of soil microorganisms  
445 and the ecological processes involved (Saleem and Moe 2014).

446 Using multiple microbial consortia consisting of bacteria and fungi that are  
447 beneficial to plants and manipulating rhizosphere microbes to improve crop growth  
448 and resistance is expected to contribute to sustainable agricultural production  
449 (Ahkami et al. 2017). Simple consortia (simple mixtures of plant beneficial bacteria  
450 and/or fungi grown separately before inoculation, or growth of more than one plant  
451 beneficial bacteria and/or fungi together in a medium suitable for each one) and  
452 complex consortia (reconstructing functional metaorganisms based of  
453 microbiomes/metagenomics analyses and/or combined with culture-dependent  
454 approaches) are two known types of consortia formation (Bashan et al. 2020). The

455 various steps involved in designing the ideal artificial microbial consortia include  
456 selecting the origin of the microbes, obtaining and culturing the core microorganisms,  
457 optimizing microbial interactions according to their compatibility, and assessing the  
458 efficacy of these consortia (Kong et al. 2018). One of the main challenges of such  
459 consortia is to explore the interactions between microbial members, as well as specific  
460 interactions within plant holobiont (Bashan et al. 2020). The more species in the  
461 consortia, the more complex the outcomes of interactions as each member of a  
462 consortium can potentially affect the growth and production of metabolites of other  
463 members. It has been shown experimentally that defined microscale spatial structure  
464 is both necessary and sufficient for the stable coexistence of interacting microbial  
465 species in synthetic communities (Kim et al. 2008), thus further complicating the  
466 picture. In addition to the compatibility of multiple microorganisms and plant  
467 holobiont, more practical factors such as initial cell dosages and ratios, physiological  
468 activity, growth conditions of the strains, suitable formulations for survival and shelf-  
469 life of microorganisms, delivery approaches, colonization capacity, interaction with  
470 native microbiota, and potential influence of abiotic and biotic conditions of the  
471 soil/plant environment are bottlenecks for the successful establishment of consortia  
472 (Sessitsch et al. 2019). Nevertheless, some successful consortia have been achieved to  
473 improve crop growth and stress tolerance. For example, a consortium of four bacterial  
474 taxa (*Pseudomonas putida*, *Citrobacter freundii*, *Enterobacter cloacae* and  
475 *Comamonas testosteroni*) has been reported to mobilize soil P and increase crop

476 productivity up to twofold (Baas et al. 2016). A bacterial consortium containing four  
477 compatible and desiccation-tolerant strains (*Pseudomonas putida* KT2440,  
478 *Sphingomonas* sp. OF178, *Azospirillum brasilense* Sp7 and *Acinetobacter* sp.  
479 EMM02) were able to colonize the rhizosphere of plants and enhance desiccation  
480 stress tolerance in maize (Molina-Romero et al. 2017).

481 Soil microbes may have stabilizing or destabilizing effects on plants by generating  
482 negative or positive density-dependent feedbacks, thus facilitating or hindering  
483 coexistence (Bagchi et al. 2014,2010). Plant growth-promoting rhizobacteria such as  
484 N-fixing bacteria (e.g. some species in the genera *Rhizobia*, *Azospirillum*,  
485 *Azotobacter*, *Azoarcus*, and Cyanobacteria) and P-solubilizing bacteria (e.g. some  
486 species in the genera *Azospirillum*, *Azotobacter*, *Pseudomonas*, *Bacillus*, *Rhizobium*,  
487 *Burkholderia*, *Enterobacter*, and *Streptomyces*) may increase the availability of  
488 nutrients and expand the niche partitioning for plants and/or other microorganisms  
489 (Gamalero and Glick 2019). Host specificity in plant-microbe interactions may  
490 contribute to the niche differentiation and nutrient allocation of mycorrhizal plants  
491 and fungi (Tedersoo et al. 2020). Compared with intraspecific competition, it is  
492 expected to reduce interspecific competition and provide a stabilizing mechanism for  
493 promoting coexistence. On the other hand, plant-microbe interactions can provide  
494 different fitness benefits for plants and act as equalizing factors. Root microbiota are  
495 an important factor influencing host plants' performance and competition in response  
496 to biotic and abiotic stressors (Berendsen et al. 2012; Hodge and Fitter 2013).



497 Microbial mediated fitness differences in plants may be due to their different tolerance  
498 to soil borne pathogens or the different benefits they get from interacting soil  
499 microorganisms (Kandlikar et al. 2019). Some plant growth-promoting rhizobacteria  
500 are able to tolerate abiotic stress and maintain plant fitness by regulating hormonal  
501 and nutritional balance and producing plant growth regulators (Kumar and Verma  
502 2018). If host immunity shapes associated microbiota, or if host-microbiota affect  
503 immunity, highly similar root microbiota between host plants may reduce plant  
504 performance due to transfer and coinfection with shared pathogenic bacteria, while  
505 specific microbial taxa in the root may influence competitive interactions among  
506 plants (Castrillo et al. 2017; Fitzpatrick et al. 2018; Hacquard et al. 2017). The plant  
507 associated microbiota are not only depend on host species, but are also largely  
508 affected by soil properties, which then in turn regulate plant performance under biotic  
509 and abiotic stresses. For example, among 30 angiosperm species, 40% of the variation  
510 in endosphere microbial diversity depend on the host species but only 17% in the  
511 rhizosphere soil, and drought shifts the composition of these root microbiomes, with  
512 host-specific changes in the relative abundance of specific bacterial taxa associated  
513 with increased drought tolerance of host plants (Fitzpatrick et al. 2018). In arbuscular  
514 mycorrhizal fungi plant systems, mycorrhizal fungi and hyphal networks tend to  
515 enhance plant intraspecific competition and alleviate interspecific competition by  
516 promoting the performance of inferior competitors and suppressing superior  
517 competitors (Tedersoo et al. 2020). In the context of modern coexistence theory, the

518 extent to which plants coexist or repel is affected by microbial density dependent  
519 feedbacks and niche differentiation, as well as fitness advantages provided by  
520 microbes for plant species (Kandlikar et al. 2019).

521 The rhizosphere is a unique niche for microorganisms that are influenced by plant  
522 root exudates (Pinton et al. 2001). When the rhizosphere microorganisms with  
523 different substrate uptake patterns undergo niche differentiation of metabolic resource  
524 allocation, it leads to stabilizing coexistence (Baran et al. 2015). On the contrary,  
525 competition for the same resource may occur when microorganisms have similar  
526 substrate preferences, leading to competitive exclusion (Freilich et al. 2011). Also, the  
527 substrate concentration is important because microorganisms with low Michaelis-  
528 Menten kinetics constants ( $K_m$ ) values of uptake for the target substrate can prevail at  
529 low concentration and the opposite for microorganisms with high  $K_m$  values. For  
530 example, the slow-growing K-strategic microorganisms with enzymes of high  
531 substrate affinity are better adapted for growth on poorly available substrates, but are  
532 uncompetitive against the r-strategic microorganisms with higher  $K_m$  values in the  
533 rhizosphere (Tian et al. 2020). The kinetic analysis suggested that comammox  
534 *Nitrospira* had higher affinity for ammonia than ammonia oxidizing archaea and  
535 bacteria, and thus might be more competitive under oligotrophic conditions (Kits et al.  
536 2017). Some root exudates, such as phenolics and terpenoids, play an antimicrobial  
537 role in selecting beneficial microbes and resisting soil-borne pathogens (Baetz and  
538 Martinoia 2014). Phenolic compounds can be used as specific substrates or signaling

539 molecules for some bacterial groups and benefit the community by creating specific  
540 chemical niches (Badri et al. 2013). In addition, plants can also indirectly affect soil  
541 microbes by secreting exudates such as organic acids, thus changing soil pH and  
542 nutrient availability (Chen et al. 2016; Dakora and Phillips 2002).

543 Taken together, the effects of microbe-microbe interactions and plant-microbe  
544 interactions on species competitive outcomes in agroecosystem can be understood by  
545 Bever's model of pairwise plant-soil feedback model (Bever 2003; Bever et al. 1997;  
546 Kandlikar et al. 2019; Ke and Wan 2019). Firstly, microbial mutualistic and  
547 antagonistic interactions can affect the niche difference and fitness difference among  
548 competing microbes, which is crucial for maintaining soil microbial diversity and  
549 ecosystem functioning. Second, both beneficial and pathogenic microbes can modify  
550 niche difference and fitness difference between competing plants, thus affecting plant  
551 growth and yield. Thirdly, plants change niche difference and fitness difference  
552 among competing microbes by secreting root exudates that are beneficial or harmful  
553 to soil microbes. By integrating niche competition and interaction between  
554 microorganisms and plants, we can better understand the effects of interactions  
555 between microorganisms and plants on plant fitness. Although these processes are  
556 mainly stabilizing or/and equalizing, their impact on coexistence is integrative rather  
557 than singular and varies with environmental conditions. Therefore, it is difficult to  
558 draw a general conclusion about the influence of soil microorganism on plant  
559 coexistence or the influence of plant on soil microorganism coexistence. However,

560 this framework provides an insight into integrating the roles of multiple soil  
561 microorganisms and determining their contribution to plant coexistence, which can be  
562 applied to the utilization of beneficial microorganisms in plants and the control of soil  
563 borne diseases in crop production. More empirical studies are suggested to test the  
564 framework in mesocosms involving two or more microbial species with and without  
565 plants.

### 566 **Conclusion and future perspectives**

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

581 interactions between species to more complex high-order interactions, even across  
582 multiple scales of space and time.

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

594 When expanding the application of modern coexistence theory in soil microbe-  
595 plant ecosystems, it is necessary to incorporate microbe-microbe interactions and  
596 plant-microbe interactions into the stabilizing and equalizing mechanisms. Both  
597 model and experimental studies should consider more thoroughly the role of plants in  
598 mediating microbial interactions and the effects of microbes on plant niche and  
599 fitness. It has important practical significance and application value for maintaining  
600 microbial and plant diversity and its function in agricultural ecosystems. In plant  
601 microbiome engineering, various microbial strains that promote plant growth are

602 usually screened for under highly artificial conditions. Successful field application  
603 requires further consideration of the coexistence of synthetic microbial communities  
604 and native soil microorganisms, as well as their diversity and ecological functions  
605 under the influence of plant root exudates and other environmental factors. The  
606 application of modern coexistence theory for plant microbiome research can bridge  
607 the gap between laboratory results and field performance.

608

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## 1036 **Authors' contribution**

1037 All authors contributed intellectual input and assistance to this study and manuscript  
1038 preparation. Y.L. developed the original framework. Y.L., N.N. and N.Z. wrote the  
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## 1040 **Declarations**

1041 **Ethics approval** Not applicable.



1042 **Consent to participate** Not applicable.

1043 **Consent for publication** All authors have approved the manuscript in its entirety  
1044 and agreed for its publication.

1045 **Conflict of interest** The authors declare that they have no competing financial  
1046 interests.

### 1047 **Figure legends**

1048 **Figure 1** The conceptual diagram of modern coexistence theory. The competitive  
1049 outcome is determined by the balance between niche difference and fitness difference,  
1050 which can be calculated based on the Lotka-Volterra competition model (Chesson  
1051 2000,2013) or MacArthur's consumer-resource model (Carroll et al. 2011). The dotted  
1052 and solid lines represent the boundaries where  $f_j/f_i$  equals  $1/\rho$  or  $\rho$ , respectively. The  
1053 right area indicates the region where coexistence occurs; the top and bottom areas  
1054 indicate where species  $j$  or  $i$  is dominant, respectively. Figure modified from Ke and  
1055 Letten (2018).

1056 **Figure 2** Graphical presentation of possible effects of biotic and abiotic factors on  
1057 niche and fitness differences. ND: niche difference; FD: fitness difference. Bio: biotic  
1058 interactions; Cli: climate change; Env: environmental stress; Fer: fertilization; Soi:  
1059 soil constraints. Red and blue lines indicate negative and positive relationships,  
1060 respectively. Gray thin arrows indicate indirect impact pathways.

1061 **Figure 3** Schematic illustrating soil microbe-microbe interactions and plant-microbe  
1062 interactions through modern coexistence theory. The conceptual model of microbe-

1063 microbe interactions and plant-microbe interactions is modified after Bever's model  
1064 of pairwise plant-soil feedback and its derived framework (Bever 2003; Bever et al.  
1065 1997; Kandlikar et al. 2019; Ke and Wan 2019). The purple arrows represent mi-  
1066 crobe-microbe interactions, which can be either mutualistic or antagonistic. The up-  
1067 ward red arrows and downward green arrows represent the microbial effects on plants  
1068 and plant effects on microbes, respectively, which both can be either positive or nega-  
1069 tive. Thick arrows indicate stronger interactions/effects than thin arrows.