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1 Extended Plant Metarhizobiome: Understanding Volatile Organic Compounds Signaling in
2 Plant-Microbe Metapopulation Networks

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12 Running Head: VOC-mediated interactions in soil metapopulations

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24 **ABSTRACT**

25 Plant rhizobiomes consist of microbes that are influenced by the physical, chemical and
26 biological properties of the plant root system. While plant-microbe interactions are generally
27 thought to be local, accumulating evidence suggests that topologically disconnected bulk soil
28 microbiomes could be linked with plants and their associated rhizospheric microbes through
29 volatile organic compounds (VOCs). While several studies have focused on the effect of soil
30 physicochemical properties for VOC movement, it is less clear how VOC signaling is affected
31 by microbial communities themselves when VOCs travel across soils. To gain a better
32 understanding of this, we propose that soil microbe-plant communities could be viewed as
33 ‘metarhizobiomes’, where VOC-mediated interactions extend the plant rhizobiome further out
34 through interconnected microbial metapopulation networks. In this minireview, we mainly focus
35 on soil microbial communities and first discuss how microbial interactions within a local
36 population affect VOC signaling, leading to changes in the amount, type and ecological roles of
37 produced VOCs. We then consider how VOCs could connect spatially separated microbial
38 populations into a larger metapopulation network and synthesize how i) VOC effects cascade in
39 soil matrix when moving away from the source of origin and ii) how microbial metapopulation
40 composition and diversity shape VOC-signaling between plants and microbes at the landscape
41 level. Finally, we propose new avenues for experimentally testing VOC movement in plant-
42 microbe metapopulation networks and suggest how VOCs could potentially be used for
43 managing plant health in natural and agricultural soils.

44

45 **Keywords:** Bulk soil microbiome, Microbial metapopulation networks, Long-distance

46 communication, Microbe-plant crosstalk, Rhizosphere microbiome, Volatile organic compounds

47 **INTRODUCTION**

48 Plant-associated microbiomes have received considerable attention from scientists as key
49 components of plant development, growth and immunity (1). In particular, the rhizosphere
50 microbiome (rhizobiome), defined as the microbes that are influenced by the physical, chemical
51 and biological properties of the plant root system, has been demonstrated to play important roles
52 in plant growth, nutrition, pathogen suppression and stress resistance (2-5). Traditionally, these
53 belowground plant-microbiome interactions are considered local, occurring within the immediate
54 vicinity of the plant roots (including root tissues) (5). However, increasing evidence suggests that
55 belowground plant-microbiome interactions extend over longer distances in the soil matrix via
56 volatile organic compounds (VOCs), which could potentially connect plant roots, rhizobiomes
57 and bulk soil microbiomes (6, 7). VOCs are a broad group of small lipophilic compounds (<C15)
58 with low molecular weight (100–500 Da), high vapor pressure and low boiling point (7, 8).
59 These characteristics allow VOCs to diffuse through gas- and water-filled pores, enabling a
60 range of biological functions important for microbe-microbe and plant-microbe interactions (6,
61 8). For example, microbial VOCs can act as nutrient sources (9) and modulate plant vegetative
62 growth, flowering and immune responses (8). They can further trigger both antagonistic and
63 synergistic interactions among plants, pathogen and other soil organisms, such as nematodes and
64 protists (10, 11-13), and are important for competitive (antibiosis) and facilitative (cross-feeding)
65 microbial interactions and microbiome assembly (14-16). Similarly, plant-produced root VOCs
66 can act as antimicrobials, food sources, chemo-attractants or signaling chemicals (17, 18),
67 affecting soil microbe community diversity, composition and functioning (7). Soil VOC effects
68 are thus omnidirectional, complex and shown to take place within and between different trophic
69 levels (6).

70 While several studies have focused on the effect of soil physicochemical properties in
71 governing VOC movement in the soil matrix (16-19), it is less clear how VOC signaling is
72 affected by biotic interactions. Moreover, most of the previous and ongoing work has focused on
73 cataloging the structure and ecological roles of VOCs under laboratory conditions, focusing
74 mainly on interactions between pairs of organisms (7, 19). While this approach allows the
75 controlled study of VOC mechanisms, findings are difficult to extrapolate on more natural and
76 ecologically complex communities. For example, while it is well established that VOC effects
77 can impact distant individuals or even populations (20, 21), it is unclear how VOCs travel
78 through microbial metapopulations. In other words, only a little is known about how VOC
79 signals change when blending with VOCs produced by adjacent populations, which could
80 ultimately determine how VOC effects cascade in space when moving away from the source of
81 origin in the soil. Similarly, while microbial community properties have been shown to drive
82 VOC production locally (22, 23), it is not clear how microbial metapopulation composition and
83 diversity shape VOC-signaling at the landscape level. Given the potential importance of VOCs
84 for soil ecology and agricultural productivity (8, 24), it is important to start considering VOC
85 signaling in plant-microbe communities over larger spatial scales (Fig. 1A). In this minireview,
86 we provide an outlook on the nature and dynamics of VOC-mediated interactions, mainly
87 focusing on soil microbial communities. We also propose a framework on how VOC effects
88 could cascade through microbial metapopulation networks, potentially enabling an extended
89 metarhizobiome by connecting plant roots, rhizobiome and bulk soil into a cohesive underground
90 ecosystem.

91

92 **VOCs ARE PRODUCTS OF LOCAL ENVIRONMENT WITH POTENTIALLY**
93 **GLOBAL EFFECTS**

94 The microbial activity and plant roots are the main sources of VOCs in the soil (14, 19).
95 Additionally, uptake of VOCs from the atmosphere, degradation of organic material and
96 application of organic fertilizers and irrigation contribute to the soil VOC pool (25, 26). Soils can
97 also retain VOCs and the patterns of adsorption and desorption depend on the type of VOCs and
98 soil properties (27, 28). For example, VOC desorption from soils have been shown to increase
99 with decreasing soil particulate size (29) and the number of carbon atoms present in the benzene
100 ring of VOCs (30). Furthermore, VOC desorption tends to peak during periods of high
101 temperatures and low moisture, suggesting that compounds accumulated during the winter may
102 be released later in the summer, even after the sources of VOC emission have long vanished
103 (31). Further, VOCs can escape to the atmosphere (32), bind to organic matter and mineral
104 surfaces (33), undergo biotic and abiotic degradation (25, 26), dissolve in soil water solution (34)
105 and get trapped in macro- and micropores in the soil (35, Fig. 1B). The movement of VOCs in
106 soil results from diffusion and advection; diffusion is driven by concentration gradients and
107 advection can be driven by pressure, density, gravity, or thermal gradients (36, 37). The bulk
108 water flow also plays a significant role in the movement of nutrients, organic waste, microbes
109 and VOCs in the soil (37, 38). Likewise, contiguous and interlocking channels formed in the soil
110 through processes of desiccation, growth and decay of roots and mycelia, and burrowing animals
111 act as superhighways for long distance movement of VOCs (38, 39). Hence, soil
112 physicochemical, environmental and VOCs properties are important in determining the
113 adsorption-desorption dynamics and the effect radius of VOCs in the soil matrix.

114 While the rhizosphere gradient size for most biotic and abiotic processes has been
115 reported 0.5-4 mm and >20 mm for inorganic gases (CO₂ and O₂) (40, 41), there is no study
116 explicitly testing the VOC diffusion dynamics in the soil. However, a few studies have explored
117 the effect of distance on VOC-mediated interactions (7, 42). For example, a study conducted
118 using an olfactometer system demonstrated that plant root VOCs can attract beneficial soil
119 bacteria as far as from 12 cm distance (7). In another field study, it was shown that nematodes
120 can sense a root-produced terpene VOC, (E)- β -caryophyllene, from a 50 cm distance (42).
121 Moreover, diffusion experiments conducted up to 12 cm distances using pure VOC standards
122 suggest that their diffusion capability is specific to given VOC compounds (7, 24). Together
123 these findings suggest that VOCs can extend local microbiome interactions further out,
124 potentially bidirectionally linking bulk and rhizosphere soils into a plant metarhizobiome.
125 However, relatively much less is known about the significance of microbial interactions for the
126 production and movement of VOCs in the soil.

127

128 **MICROBIAL INTERACTIONS WITHIN A POPULATION DETERMINE LOCAL VOC** 129 **PRODUCTION**

130 The production of VOCs is influenced by both abiotic and biotic microenvironmental conditions
131 locally, which include intra- and interspecific microbial interactions (22, 23), substrate
132 composition, temperature and moisture amongst others (43). Recent studies have demonstrated
133 that competition between co-occurring species in a local population can increase the relative
134 proportion of bioactive VOCs (22, 23, 44). For example, the production of antibacterial VOCs
135 peaked at intermediate community richness level in a synthetic 12-species model bacterial
136 community (22). Interestingly, this effect coincided with high bacterial community evenness,

137 which could have allowed more even VOC production by each individual species, and in support
138 of this, the antibacterial activity of communities correlated positively with the number of
139 produced antibacterial VOCs (22). Similarly, VOC effects are also affected by the absence of
140 certain species as shown by another study where the loss of bacterial species was associated with
141 reduced production and activity of anti-fungal VOCs (45). Such effects could be driven by taxa-
142 specific VOC interactions, which have been shown to vary from positive to neutral and negative
143 depending on the specific interacting species pair (22, 23). Moreover, it has been found that
144 bacterial communities can produce ‘emergent’ VOCs that cannot be detected when the VOCs
145 production is measured in bacterial monocultures (22, 23, 44). This could be because the
146 bacterial metabolism is often changed in the presence of other species, which could trigger the
147 upregulation of otherwise silent VOC metabolism-related genes (46). It has also been shown that
148 pairwise VOC responses can be asymmetric. For example, VOCs produced by *Verticillium*
149 *longisporum* fungi upregulated the metabolic activity of *Paenibacillus polymyxa*, while the
150 VOCs of *P. polymyxa* inhibited the cellular metabolism and growth of *V. longisporum* but
151 upregulated genes related to stress responses and the production of antimicrobial VOCs (47).
152 These findings suggest that VOCs could drive and be a result of potential coevolutionary
153 dynamics that warrant further study in the future (24). Microbial VOC interactions are also likely
154 to have indirect effects on other organisms such as plants. Recently, it was demonstrated that
155 bacterial communities that produce high amounts of bacteria-inhibiting VOCs, produce a low
156 amount of plant growth-promoting VOCs (22), which is indicative of a tradeoff between
157 functionally different classes of VOCs. Likewise, VOCs emitted by plant roots could indirectly
158 affect microbial interactions within distantly located microbial populations. For example, insect-
159 damaged maize roots change their VOCs emission, leading to secretion of (E)- β -caryophyllene

160 as the main VOC, which attracts entomopathogenic nematodes (12, 42). Similarly, tomato roots
161 infected with *Fusarium oxysporum* fungal pathogen have been shown to emit several VOCs with
162 known antifungal activity (48), which suggests that plant pathogens could indirectly affect
163 rhizosphere and bulk soil microbiomes by triggering changes in plant root VOC production.
164 Together, the above evidence suggests that local VOC production is highly dependent on the
165 microbial community composition, diversity and the specific interacting species.

166

167 **PREDICTING VOC SIGNALING IN MICROBIAL METAPOPOPULATION NETWORKS**

168 While VOC-mediated interactions are well recognized, it is less clear how VOC effects cascade
169 in space when moving away from the source of origin, and how microbial metapopulation
170 composition and diversity shape VOC-signaling at the landscape level. The VOC effects are
171 likely to decrease as a function of distance in the soil matrix. In support of this, Schulz-Bohm *et*
172 *al.* (7) found a drastic decrease in the detectable amounts of VOCs with sampling distance from
173 the source of origin in the soil. Hence, VOCs are likely to have relatively stronger effects on
174 nearby communities, (Fig. 1C-D), while communities located further away will be less affected
175 due to the natural loss of VOCs over longer distances because of adsorption, trapping,
176 degradation and dissolution (25, 26, 28). Additionally, the original VOC signal could be
177 amplified by adjacent microbial populations when moving away from the site of origin. It is
178 known that different microbial species produce distinct sets of VOCs (44, 49) and their VOC
179 production is affected by local microbial interactions and the surrounding environmental
180 conditions (22, 23, 43). Moreover, airborne VOCs have been reported to alter soil microbial
181 community composition (16), which is strongly correlated with the VOC emission profiles of
182 ‘source’ and ‘target’ populations (50-52). Together, these findings support the concept that an

183 initial VOC signal could blend with the VOCs emitted by adjacent microbial populations,
184 leading to the amplification or complementation of the original signal and a potential increase in
185 the total amount and diversity of emitted VOCs (Fig. 1E). While this could lead to decrease in
186 the relative concentrations of VOCs, the amplification of a specific VOC signal could also occur
187 if the first VOC signal triggers the production of the same VOC by the adjacent community,
188 potentially along with other VOCs, leading to ‘sequential community activation’ via
189 amplification of the original VOC signal. In support of this, it has been shown that VOC profiles
190 are more similar among closely related microbial species (49), and VOCs emission has been
191 found to correlate negatively with soil bacterial diversity (50). While more direct experimental
192 evidence is needed, there is a possibility that taxonomically or functionally similar microbial
193 populations could respond to conspecific signals in a similar way, leading to the amplification of
194 the original VOC signal (Fig. 1F).

195 Current evidence also suggests that the specificity and bioactivity of VOCs is likely to
196 further complicate VOC-signaling outcome in soils (19, 49). For example, schleiferon A VOC is
197 formed via a non-enzymatic reaction, employing precursor VOCs (acetoin and 2-
198 phenylethylamine) that could be emitted by microbes of the same or different species (53). In
199 contrast to such generalist VOCs, microbes also produce specialist VOCs that are specific to
200 certain microbial taxa (49). The taxa-specific VOCs could play a smaller role in spatially
201 heterogenous soil communities if their signal is not received in the absence of specific
202 ‘responder’ species. In contrast, less-specific signals might get amplified more often, having
203 potentially more far-reaching effects across microbial metapopulation networks. As a result,
204 some VOCs could be functionally redundant (19, 28). Moreover, the VOC bioactivity and
205 species VOC-sensitivity will likely be important for VOC outcomes in the soil. For example, the

206 same VOCs produced by bacteria can exert no or little effects on one fungal species (*Fusarium*
207 *solani*), but at the same time showed a very high bioactivity to *Pythium* species (oomycetes) (54).
208 VOC bioactivity could also be affected by the total amount of VOCs produced. In support of
209 this, soil VOC emission has been found to positively correlate with the abundances of
210 prokaryotic *Bacteroidetes* and *Proteobacteria* phyla in one study (50), and with *Firmicutes*,
211 *Proteobacteria*, *Actinobacteria* and *Crenarchaeota* abundances in another study (51). These
212 findings suggest that VOC production could be driven by density-dependent effects, where the
213 most abundant taxa could have the strongest effect (55) on VOC-mediated signaling.
214 Alternatively, VOC responses could be non-linear, where only VOCs exceeding certain response
215 thresholds, or highly bioactive VOCs (19, 22), would be able to influence adjacent microbial
216 populations. In this case, taxa present in low relative abundances could be important contributors
217 as low concentrations of VOCs could mediate response cascades between adjacent microbial
218 populations as has been demonstrated in case of antifungal VOCs produced by rare soil bacterial
219 taxa (45) and relatively rare *Paenibacillus* sp. bacterium that strongly affected the production of
220 VOCs by other much more abundant members of the bacterial community (15). While VOC
221 signaling is further shaped by variation in abiotic microenvironmental conditions of a
222 metapopulation (25), signal cascades might follow natural VOC diffusion in the soil matrix,
223 creating subnetworks and feedback loops between certain ‘source’ and ‘target’ populations. In
224 the future, ideas presented above need to be experimentally tested to better understand the
225 complex chemical interplay of VOCs in the soil matrix. This could be for example achieved by
226 adopting aquatic metapopulation microcosm methods for soil systems (56).

227

228 **METARHIZOBIOME: LINKING MICROBIAL METAPOPOPULATION NETWORKS**
229 **WITH PLANTS**

230 Even though the bulk soil acts as an initial microbial pool for plant rhizobiome, the growth,
231 development and aging of plant cause clear shifts in rhizobiome composition making it distinct
232 from the bulk soil (57). As a result, bulk and rhizosphere soils have very dissimilar community
233 structures, showing clear differences in the relative abundance of different bacterial taxa (58).
234 These relative abundance differences are likely to be correlated with differences in bulk and
235 rhizosphere soils VOC production profiles (50, 51). In further support of this, VOCs belonging
236 to some chemical groups (*i.e.*, alcohols, sulfur compounds, some ketones and aromatic
237 compounds) are predominantly produced by rhizosphere microbes compared to bulk soil
238 microbes (59). Also plant roots release VOCs (*i.e.*, terpenoids, benzenoids, aliphatics, aromatics,
239 fatty acids, etc.) into the rhizosphere (18, 48), making it chemically more diverse to the bulk soil.
240 Rhizosphere soil is thus likely to be a hotspot for VOCs (5, 60), allowing plants to extend their
241 rhizobiome into the bulk soil, while the effects from the bulk soil into the rhizosphere could be
242 relatively weaker. The resulting metarhizobiomes would encompass a far larger space, resulting
243 in a potentially higher number of interactions between a more diverse set of microbial taxa
244 present in both rhizosphere and bulk soils (Fig. 2). Based on the current data on microbial
245 abundance and distance-decay patterns in the soil microbial communities (61), increasing the
246 interaction range from millimeters to centimeters (7) will considerably increase the effective size
247 of plant rhizobiome. This could potentially result in a large range of interactions across generally
248 larger plant-rhizobiome networks. Increasing the interaction network size could also potentially
249 have positive effects on plant rhizobiome stability if metarhizobiomes harbor higher species

250 diversity and functional redundancy (62), being able to act as a source population if soil
251 conditions change significantly for example during crop rotation or tillage (63).

252 The extension of microbial interaction range into the bulk soil via VOCs could promote
253 other long-distance signaling mechanisms, such as ion channel-mediated electrical signaling
254 (64), potentially linking the activity of bulk soil communities with plant growth (Fig. 2). VOC-
255 mediated signaling could also help plants to defend against pathogen attack. For example, in
256 response to VOCs produced by fungal pathogen *Fusarium culmorum*, bacterium *Serratia*
257 *plymuthica* has been shown to upregulate the production of odoriferous VOC (52), which induced
258 the expression of plant defense-related genes in *Arabidopsis thaliana* (65). It is thus plausible
259 that microbes are the first to sense the stress and produce specific metabolites to alert their host
260 plant, as has also been suggested by Rizaludin *et al.* (66). VOC sensing bacteria could thus warn
261 plants from invading pathogens earlier by allowing activation of immune responses (VOCs
262 priming effect) in response to VOCs emitted by distant microbial communities (67), as has also
263 been reported for aboveground VOC-mediated plant to plant warning against insect and disease
264 attack (20). Furthermore, plants have also been reported to sense, integrate and respond to plant-
265 plant cues transmitted through roots (68, 69), which suggests that microbial populations could
266 affect VOC signaling between adjacent plants (59). Similarly, plants could act as mediators and
267 connect microbial metapopulations via VOCs, potentially leading to VOC-mediated inter-
268 dependences and metarhizobiome stability at the landscape level, highlighting the importance of
269 Gamma diversity. For example, Dharanishanthi *et al.* (70) reported that modification of the
270 environmental pH by neighboring bacterial species could be used as a clue of nutrient
271 availability by local bacteria, linking individual bacterial physiology to macroscale collective
272 behavior.

273 Microbes residing in the soil can alter plant VOC profiles as has been reported for faba
274 bean plants treated with arbuscular mycorrhiza fungi (71), and maize plants treated with plant-
275 beneficial bacterium *Pseudomonas putida* (72). Hence, considering long-distance VOCs
276 dispersion (7, 16, 39), it is plausible that VOC-mediated interactions triggered by bulk soil
277 metapopulations could affect plants directly or create conflicts by blurring the boundary of plant
278 control over the rhizobiome. Similarly, plant root VOCs can influence rhizosphere microbial
279 community composition (16, 73) and this effect could extend to bulk soil microbiomes (7) either
280 directly or indirectly via the rhizosphere microbiome. Plant-associated rhizobacteria can induce
281 plant defenses against herbivores, while plants can in turn attract natural enemies of herbivores
282 by emitting herbivore induced plant VOCs (20). Similarly, plants can affect the rhizosphere
283 microbiome of neighboring plants via rhizobacteria-induced aboveground plant VOC production
284 (74). These findings support the concept that VOCs emerging in the bulk soil could also have
285 effects beyond the rhizosphere, affecting the functioning of the whole plant metamicrobiome,
286 including endosphere and phyllosphere (Fig. 2). VOCs could thus potentially be important in
287 linking plant below and aboveground microbiomes.

288

289 **FUTURE PERSPECTIVES**

290 To test our ideas and to develop a predictive theoretical framework on plant metarhizobiome
291 functioning, much more experimental data is required. This could be achieved by developing
292 highly trackable rhizobox and olfactometer systems that allow direct manipulation of VOCs
293 diffusion range, microbial community composition and abiotic environment in plant-microbe
294 metapopulation networks. Moreover, a careful combination of complementary field approaches
295 is needed to study the type and diffusion radius of VOCs of naturally distributed microbial
296 populations in relation to soil physicochemical properties and climatic factors. The VOC-

297 mediated interactions will not increase the total volume of the rhizosphere but will affect the
298 metabolism and physiology of (micro)organisms beyond the rhizosphere environment to at least
299 the centimeter scale as suggested by de la Porte *et al.* (75). This could be especially important in
300 the context of ongoing climatic change, allowing us to better understand how temperature and
301 moisture drive the diffusion range of VOCs in the soil compared to soluble compounds. In
302 addition to quantifying the range of VOC-mediated interactions, it will be important to compare
303 the relative importance of different VOCs, their functional redundancy and diversity in microbial
304 communities. For example, identifying potential keystone microbial species with relatively
305 strong VOC-mediated interactions at the community level that could be used as microbial
306 inoculants could be especially useful during intercropping periods. For example, choosing crop
307 combinations based on VOC signal ‘compatibility’ could be used as selection criteria for
308 increasing agricultural ecosystem productivity. The manipulation of bulk soil microbiome could
309 help to avoid conflicts with the plant and rhizobiome, potentially leading to higher functional
310 stability and redundancy. Several VOCs can also be synthesized, making it potentially possible
311 to apply them as transient and ecologically compatible biological control agents. Further, linking
312 VOC patterns with metagenomic, transcriptomic and metabolomics data could help to elucidate
313 to what extent VOC production patterns can be predicted based on the genetic composition of
314 microbial communities and if the underlying VOC pathways can be identified. A combination of
315 existing and emerging omics and computational technologies could further help to identify
316 chemical pathways underlying VOC production (24, 76). In addition, phenotyping of VOC
317 emissions by using inexpensive small-scale trapping devices, smartphone-based VOC sensitive
318 sensors and portable instruments for real-time measurements could help to better comprehend the
319 dynamics of VOC emissions and discriminating genotype-specific and stress-related VOC

320 profiles and patterns (77). Finally, while VOC-mediated interactions are known to have an
321 important role in microbial ecology, they could also drive microbial evolution by selecting for
322 VOC-resistant bacterial genotypes similar to soluble antimicrobial compounds (78) or facilitate
323 other nutritional or stress-related adaptations. Proposed experimental model systems would allow
324 testing such evolutionary questions and identifying genes and molecular mechanisms that play
325 important roles in VOC interactions.

326

327 **CONCLUSIONS**

328 Here we propose that VOCs could coordinate bulk and rhizosphere soil microbiome functioning
329 as a metarhizobiome, superseding the topological range limitation of contact-dependent microbe-
330 microbe-plant interactions. Such plant metarhizobiomes would include microbes residing in the
331 near physical vicinity of the plants (rhizobiome), as well as the VOC-connected populations
332 located further apart in the bulk soil. Such multidirectional long-distance communication could
333 fundamentally change how we perceive microbial ecology in the spatially structured soil matrix,
334 allowing plant-microbe metapopulations to interact and trade information without restrictions
335 imposed by the proximity and co-occurrence of the same local habitat. The attained knowledge
336 could be potentially further used in the management of plant health in the agricultural context
337 and to understand plant-microbe biodiversity and distribution in the natural environments. The
338 proposed predictions put forward by our conceptual framework should be rigorously tested in the
339 future. This could be achieved by bringing together interdisciplinary scientists working on
340 microbial ecology and evolution, genetics, biochemistry and plant biology, and by taking
341 advantage of bespoke experimental systems that allow direct manipulation and quantification of
342 microbe-plant communities and emitted VOCs.

343

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354

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556 **Figure Legends**

557 **FIGURE 1.** Volatile organic compound (VOC)-mediated interactions can link plants with
558 microbial metapopulation networks. (A) The classical rhizobiome is located in the close vicinity
559 of the plant roots, while VOCs produced by microbes and plant roots disperse over long
560 distances in the soil matrix, being able to connect and mediate multidirectional interactions
561 among physically disconnected metapopulations of rhizosphere and bulk soil and plant (blue
562 arrows). (B) A single microbial metapopulation in the bulk soil. The fate of emitted VOCs
563 depends on the exchange rate and retention properties of VOCs, soil properties and
564 environmental conditions, which ultimately determine VOC movement, binding, evaporation and
565 dissolution. (C) VOC diffusion signal strength (amount of VOCs) from and towards the bulk soil
566 (VOC source) to rhizosphere soil as a function of physical distance: VOCs will have a stronger
567 effect on the rhizosphere and plant roots when in close vicinity (top) and this effect will become
568 weaker with increasing distance (middle and bottom). (D-F) Changes in the signal strength and
569 diversity of VOCs between metapopulations in the bulk and rhizosphere soil. It is possible that

570 both the signal strength and diversity of VOCs decrease as a function of distance from the source
571 of origin (D). Alternatively, the original VOC signal could be strengthened when passing
572 through similar metapopulations through ‘sequential community activation’ (E), which could
573 also further increase the diversity of VOCs as adjacent communities blend in their own VOCs
574 (F). In C-F, the green color shows the VOCs signal strength and the shade of blue arrows shows
575 the diversity of emitted VOCs. The interaction described in C-F could also be initiated by plant
576 root emitted VOCs cascading towards nearby and distant communities in a similar fashion.

577 **FIGURE 2.** Volatile organic compound (VOC)-mediated interactions between bulk soil and
578 rhizosphere could be involved in a range of ecosystem-level functions and link bulk soil
579 microbiome with rhizobiome, endobiome and phyllobiome. Metarhizobiome would allow the
580 plant to connect physically larger space, diversity and abundance of microbes in the soil matrix.
581 Further, VOC effects emerging in the soil could cascade beyond the rhizosphere, affecting
582 microbe-plant interactions inside the plant (endosphere) and on the plant leaves (phyllosphere),
583 linking below and aboveground microbiomes.

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