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1 The underground network: Facilitation in soil bacteria

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8 Our understanding of the fundamental role that soil bacteria play in the structure and functioning
9 of Earth's ecosystems is ever expanding, but insight into the nature of interactions within these
10 bacterial communities remains rudimentary. Bacterial facilitation may enhance the establishment,
11 growth, and succession of eukaryotic biota, elevating the complexity and diversity of the entire
12 soil community and thereby modulating multiple ecosystem functions. Global climate change
13 often alters soil bacterial community composition, which, in turn, impacts other dependent biota.
14 However, the impact of climate change on facilitation within bacterial communities remains poorly
15 understood even though it may have important cascading consequences for entire ecosystems.
16 The wealth of metagenomic data currently being generated gives community ecologists the ability
17 to investigate bacterial facilitation in the natural world and how it affects ecological systems
18 responses to climate change. Here, we review current evidence demonstrating the importance of
19 facilitation in promoting emergent properties such as community diversity, ecosystem functioning,
20 and resilience to climate change in soil bacterial communities. We show that a synthesis is
21 currently missing between the abundant data, newly developed models and a coherent ecological
22 framework that addresses these emergent properties. We highlight that including phylogenetic
23 information, the physicochemical environment, and species-specific ecologies can improve our
24 ability to infer interactions in natural soil communities. Following these recommendations, studies
25 on bacterial facilitation will be an important piece of the puzzle to understand the consequences
26 of global change on ecological communities and a model to advance our understanding of
27 facilitation in complex communities more generally.

28 *Keywords: facilitation, bacteria, climate change, stress-gradient hypothesis, resilience*

29

30 **Introduction**

31 *“Natural, unconscious mutualism is one of the basic principles of biology”*

32 *W.C Allee in ‘Principles of Animal Ecology’, 1949*

33 Soil bacterial communities are integral parts of almost all of earth’s ecosystems, from
34 sediments in the deepest marine trenches to soils on the highest mountains (Takami et
35 al. 1997, Zhang et al. 2009). As fundamental links in the soil-plant interface and chemical
36 pumps for the nitrogen and carbon cycles (Prashar et al. 2014, Naylor et al. 2020,
37 Domeignoz-Horta et al. 2020), the importance of soil bacteria for life on earth is hard to
38 overstate. Mirroring Darwin’s observations on plant communities, repeated evidence has
39 identified soil bacterial diversity as an essential driver of ecosystem functioning (Finlay et
40 al. 1997, Delgado-Baquerizo et al. 2017). Soil bacterial diversity ultimately facilitates
41 many aspects of plant growth (Hayat et al. 2010), survival (Wei et al. 2019) and fertility
42 (Chaparro et al. 2012), and influences atmospheric processes through reducing
43 greenhouse gas emissions and sequestering CO₂ thereby directly impacting human
44 survival and well-being (Paustian et al. 2016). Further, the loss of bacterial diversity can
45 impact large-scale ecosystem processes such as carbon cycling capabilities of soils in a
46 wide range of ecosystems (de Graaff et al. 2015). Our understanding of the relationship
47 between bacterial diversity and soil function continues to improve (Wagg et al. 2019), but
48 studies so far have overlooked the role of biotic interactions in structuring bacterial
49 communities (Horner-Devine et al. 2004, Abdul Rahman et al. 2021).

50 The importance of biotic interactions in specific aspects of microbial ecology has long
51 been recognized, for example, in the formation of biofilms or microbial mats (Davey and

52 O'toole 2000). Microbial ecology has historically focused predominantly on negative
53 interactions in bacterial communities, such as competition for resources (Hibbing et al.
54 2010) or parasitic relationships (Geiman 1964). Over the past decade, these negative
55 interactions and their effects on community functions have continued to be examined in
56 bacterial systems, without taking positive interactions into account (Ghoul and Mitri 2016).
57 The relative importance of positive versus negative interactions has been investigated
58 using culture-based studies (Griffin et al. 2004) and some have argued that, on average,
59 negative interactions are the prevailing drivers of bacterial community structure in
60 experiments while positive interactions would be rare (Palmer and Foster 2022).
61 However, positive interactions have long been known to be an essential component of
62 bacterial communities; decades ago, Hardin (1944) established that some bacterial
63 species cannot exist in mono-culture and require a symbiotic partner for survival. More
64 recent studies have suggested positive interactions are important for community structure
65 and functions, and probably more common than previously thought in bacterial
66 communities (Pacheco et al. 2019, Kehe et al. 2021). As bacterial soil communities are
67 increasingly studied worldwide, in particular because of the tools and data required to do
68 so have increasingly become available, it is important that positive interactions are
69 properly considered in these systems.

70 Interactions can be mutually (+/+) or asymmetrically (+/0) positive, and both types are
71 more broadly referred to as facilitation. The most cited definition of facilitation in
72 community ecology requires a positive effect on a single species' establishment, growth,
73 or recruitment without negatively impacting the other (e.g. Bertness and Callaway 1994,
74 and more specifically in Bronstein 2009). While exploitation or parasitism (+/-) may see

75 one species' growth being facilitated by the presence of another (see e.g. Kehe et al.
76 2021), these interactions are typically grouped outside of ecological facilitation in the
77 literature (see for instance Stachowicz 2001). Facilitation has been shown to have
78 important effects on community structure and functioning in a variety of bacterial
79 communities and can occur both intra- and interspecifically (Miele et al. 2019, Navarro-
80 Cano et al. 2021). Intra-species facilitation, for example in *Myxococcus* strains, can lead
81 to complex emergent effects that provide function and alter community structure in a
82 multicellular community. These populations collectively excrete enzymes to kill 'prey',
83 including larger eukaryotes, a phenomenon referred to as social 'predation' (Contreras-
84 Moreno et al. 2024); and they are also well known for their aggregated fruiting body
85 formation under environmental stress, in which different individuals specialize to facilitate
86 resistant spore development (Reichenbach 1993). Examples of inter-specific facilitation
87 are seen when species defend themselves and other community members against
88 *Myxococcus* predation, by contributing to biofilm formation and through the production of
89 antimicrobial chemicals (Thiery and Kaimer 2020). The bacterial world is full of other
90 examples, where direct, pairwise facilitation benefits growth of bacterial strains (Ferrier et
91 al. 2002, Morris et al. 2008, Pekkonen and Laakso 2012), confers benefits in dealing with
92 environmental stress (Silveira Martins et al. 2016) and structures entire communities and
93 maintains biodiversity (Kaeberlein et al. 2002, Niehaus et al. 2019). Facilitation can also
94 be indirect or context-dependent, and higher order interactions may be important for
95 diversity and resulting ecosystem functions (Bairey et al. 2016). In bacterial soil
96 communities, relatively little is known about the effects of facilitation on community
97 structure, functions and response to global change.

98 Soil bacterial communities are in a time of extensive exploration due to the rapidly
99 increasing availability of genetic data and the development of metagenomic techniques
100 (Riesenfeld et al. 2004, Thompson et al. 2017). As the role of bacteria in driving soil
101 functions in agricultural and natural systems becomes more apparent (Falkowski et al.
102 2008, Astudillo-García et al. 2019), the potential vulnerabilities of soil bacterial
103 communities to climate change has facilitated their inclusion into broader ecological
104 theory (Prosser et al. 2007, Naylor et al. 2020). This makes them an excellent study
105 system for fundamental ecological questions, such as the importance and prevalence of
106 facilitative interactions in complex communities and the relationship of interactions to the
107 environment. However, comprehensive studies of bacterial facilitation in naturally
108 occurring soil communities remain rare in the literature. Recent studies have investigated
109 soil bacterial interactions in a broader ecological framework (Goberna et al. 2019,
110 Hernandez et al. 2021), but many microbial ecology papers only scratch the surface of
111 what interaction networks may explain in regard to facilitation (Goberna and Verdú 2022),
112 and especially how this might be pertinent in relationship to global change.

113 When investigated, facilitation in soil bacteria is often demonstrated to have important
114 consequences for the larger soil community, including eukaryotic structure and function
115 (Rodríguez-Echeverría et al. 2016), and plays a role in the mediation of stressful
116 conditions induced by climate change (David et al. 2020, Yuan et al. 2021). Bacterial soil
117 community interactions are thus intrinsically linked to the functioning and resilience of
118 whole ecosystems. Here, we argue that soil bacterial communities are an underutilized
119 study system for investigating the importance of facilitation in complex natural systems,
120 and we show how their study can help advance our understanding of the way interactions

121 affect the responses of these systems to global change. Specifically, understanding the
122 role of facilitation on emergent properties of soil systems requires adopting a broader
123 ecological framework, which could prove crucial for predicting the effects of global change
124 in both soils and ecosystems more generally.

125

126 **2 - Prevalence of bacterial facilitation in culture and nature**

127 Microcosm studies have provided evidence for the existence of bacterial facilitation since
128 the development of this field of study. The seminal work by Winogradsky on nitrifying
129 organisms first showed how bacteria may depend on the metabolic product produced by
130 another organism (Winogradsky 1890). Later, microcosms continued laying the
131 groundwork of such resource-sharing mechanisms, by which bacteria may grow on
132 otherwise nutrient-deficient media (Winkler et al. 1952). This bacterial ‘cross-feeding’
133 exists in many forms and has long been shown as a requirement for the establishment of
134 some species in microcosm (Yeoh et al. 1968). These examples of cross-feeding are now
135 understood to be more energetically efficient and lead to higher growth rates (Costa et al.
136 2006). Bacterial species that evolve complementary resource-use strategies may make
137 use of available waste products in co-culture, ultimately resulting in higher productivity
138 than in monoculture (Lawrence et al. 2012). It is noteworthy that these studies elucidating
139 the mechanisms underlying facilitation have been limited to the investigation of pairwise
140 bacterial interactions. In complex bacterial communities, facilitative relationships between
141 species are not fixed and consist of a dynamic interplay between different species and
142 genotypes (Velicer 2003). To understand the importance of facilitative interactions in

143 bacterial communities, more studies in the complex conditions of the natural world are
144 needed (Little et al. 2008, Kodera et al. 2022).

145 Natural soil communities consist of bacterial species constantly interacting with each
146 other, and intra- and interspecific relationships are mediated by the abilities of species to
147 communicate with and regulate each other (West et al. 2006). Bacteria that competitively
148 exclude one another in isolated co-culture may instead co-exist in more complex
149 communities (Chang et al. 2023). For example, in natural soils bacteria commonly
150 aggregate in biofilms and thus form intricate ecological and social networks that express
151 many facilitative functions (Watnick and Kolter 2000, Solano et al. 2014). Protection from
152 trophic pressures (Matz and Kjelleberg 2005, Justice et al. 2008), UV-radiation (Córdova-
153 Alcántara et al. 2019) or desiccation (Rosenzweig et al. 2012) are commonly associated
154 with biofilm formation of bacteria, all underlaid by community interactions (Zachar and
155 Boza 2022). Public good production is also required to lay the groundwork for biofilm
156 formation and is further promoted inside closely interacting biofilm communities
157 (Flemming and Wingender 2010, Liu et al. 2015). Biofilms thus represent, essentially, a
158 mediation of the environment, whether resource-based or through other compounds,
159 which is a common way for bacterial organisms to make new niche space available and
160 increase the diversity and productivity of ecosystems (Oña et al. 2021). Biofilms also
161 create a space for rapid bacterial evolution through the facilitation of horizontal gene
162 transfer (Song et al. 2021), and they facilitate the dispersal of biofilm members to novel
163 environments (Kaplan and Fine 2002). Biofilm formation itself is even inherently
164 dependent on facilitative processes such as polymer excretions and metabolic
165 dependencies, but they also form a battleground for bacterial competition (Huang et al.

166 2011, Giaouris et al. 2015). A relevant ecological question thus becomes: how are
167 interaction types influenced by environmental conditions?

168 In the natural world, interactions between bacteria can shift from facilitation to competition
169 depending on environmental conditions (Sun et al. 2022). Shifts from facilitative to
170 competitive relationships may occur as a result of rapid evolution or shifts in community
171 structure when conditions change (Zuñiga et al. 2019, Drew et al. 2021). Indeed, while a
172 large repertoire of metabolic co-dependencies exists in bacterial communities, and many
173 of these codependent interactions occur without significant cost to the facilitator,
174 facilitative strategies may also be costly (Pacheco et al. 2019, Boza et al. 2023). For
175 example, cheaters may exploit such strategies and engage in an 'adaptive race' with the
176 facilitating organisms (Waite and Shou 2012). Potential interactions extend past the
177 metabolic realm to the production and use of specific 'public goods' in bacterial
178 communities, with common examples being the buildup of community-wide antibiotic
179 resistance and other toxicity mediation that improves the environment for other organisms
180 (Lee et al. 2010, Cordero et al. 2012, see Zengler and Zaramela 2018 for a more
181 comprehensive summary). These resource sharing interactions exist on a spectrum from
182 obligate mutualisms to facultative forms of commensalism (Morris et al. 2013), and
183 bacteria can regulate facilitative behaviors through mechanisms like Quorum sensing
184 (O'Brien et al. 2017) and rapid evolution (Drew et al. 2021). Large-scale analysis of
185 natural systems suggests that different types of bacterial communities may emerge as a
186 result, diverging into highly competitive and/or highly facilitative groups (Machado et al.
187 2021). Other evidence demonstrates that many more intermediates exist in nature, with
188 facilitation playing an important role in the functioning of many bacterial communities

189 (Kost et al. 2023). What remains unclear is how the environment drives shifts in
190 interactions in complex natural systems, and how this in turn affects overall bacterial
191 community structure and functioning.

192 **3 - Bacterial facilitation in changing environments**

193 The Stress-Gradient Hypothesis (SGH) is a theoretical framework developed to assess
194 the relationship between the environmental conditions and the frequency and strength of
195 facilitative interactions (Bertness and Callaway 1994). Although the (species- or
196 ecosystem-) specific response of the relationship between environmental stress on the
197 one hand and the direction and strength of interactions in the other hand may differ
198 depending on the type and strength of the stressor (Maestre et al. 2009, Smit et al. 2009),
199 the SGH generally predicts that facilitative interactions should be more common and
200 important under higher environmental stress, such as drought and temperature increases
201 related to climate change (Verwijmeren et al. 2014, Gallien et al. 2018). Depending on
202 the stress type and species-specific responses, facilitative networks have also been
203 shown to collapse entirely under severe stress (Michalet et al. 2014). As conditions
204 change, the overall interaction networks may change in real time as species requirements
205 adapt (Soliveres et al. 2010, Guignabert et al. 2020). While a consensus exists regarding
206 this theory for plant communities, there is only limited evidence for its applicability to other
207 systems such as soil bacterial communities (Adams et al. 2021). The applicability of the
208 SGH in bacterial communities was notably first considered in a mathematical model
209 (Lawrence and Barraclough 2015), and Piccardi et al. (2019) were the first to perform a

210 microcosm study that investigated the interactions type and strength of four bacterial
211 species under changes in available nutrients and heavy metal toxicity.

212 In bacteria, public-goods producers have been used to study the shift in interaction types
213 under resource-based (Hoek et al. 2016) or toxin-based stress gradients (Hesse et al.
214 2018). Indeed, toxicity-remediating bacteria provided the first targeted study system to
215 assess the SGH in bacterial systems (Piccardi et al. 2019), and it presented evidence for
216 the applicability of the SGH in this system (Hammarlund and Harcombe 2019), although
217 earlier studies had already shown similar results without addressing the SGH explicitly
218 (Silveira Martins et al. 2016, Velez et al. 2018). Toxicity gradients and associated public
219 good production remain an important model in SGH research in bacteria, including in
220 naturally occurring bacterial soil communities (Martino et al. 2023), where
221 anthropogenically polluted systems were shown to exhibit a higher proportion of positive
222 interactions in response to copper stress (Hesse et al. 2021) and other heavy metals (Li
223 et al. 2017). These studies have focused mostly on pairwise interactions in co-culture and
224 have provided strong evidence for the utility of the SGH as a framework to investigate
225 bacterial interactions in relationship to soil physicochemistry (Silveira Martins et al. 2016,
226 Weiss et al. 2022), but they are not informative for the broader question of how complex
227 bacterial communities might respond to multi-faceted global change.

228 Naturally occurring soil bacterial communities are increasingly recognized as a model for
229 the study of the SGH, because of their ubiquity (Finlay 2002), large range of potential
230 functions (Finlay et al. 1997), the ease of replication to study evolutionary and ecological
231 time scales (Kayser et al. 2018) and their use as an analog for other biota (Steffan et al.
232 2015). Soil bacterial communities have been used to study interaction networks in the

233 context of environmental stress, pressures, and climate change (see e.g. Yuan et al.
234 2021, Yang et al. 2022). Support for the SGH within soil bacterial communities is found
235 when the effects of holistic stress gradients (Hernandez et al. 2021, Mandakovic et al.
236 2023) or an investigation of different stressors (Zhou et al. 2021) are considered, both
237 mimicking the potential effects of broader global change on soil communities. Narrower
238 environmental gradients such as salinity (Menéndez-Serra et al. 2022) or drought (Gao
239 et al. 2022) may find more conflicting results where different bacterial groups exhibit more
240 variable responses. Collapse of facilitation under high environmental stress is shown in
241 soil bacteria as in other systems (Wang et al. 2018), and drought is frequently reported
242 as a driving environmental control of interaction strengths (de Vries et al. 2018, Gao et al.
243 2022). However, it is not well known how global change may influence soil interaction
244 networks generally, and many studies continue to underreport the interplay between
245 environment and interaction types in soil bacterial communities. Meanwhile, the data and
246 methods are available and often already included in their analyses, yet they fall short in
247 their application within a coherent ecological framework (Ma et al. 2020a, Feng et al.
248 2024).

249 **4 - How to investigate bacterial facilitation in the natural world**

250 The arrival of high-throughput nucleic acid sequencing has offered unique advantages in
251 the study of natural bacterial communities (Hugenholtz et al. 1998, Lozupone and Knight
252 2007) and their relationship to environmental pressures (Fierer and Jackson 2006). 16S
253 rRNA or similar genetic markers enable profiling techniques that are extremely useful for
254 rapidly and comprehensively mapping the structure and diversity of bacterial communities

255 in soils (Thompson et al. 2017). These data readily supply community ecologists with
256 species co-occurrence matrices used to infer the strength and direction of interactions
257 between species using co-occurrence methods (Sfenthourakis et al. 2006, Veech 2013.
258 Such co-occurrence methods may include environmental and spatial data to control for
259 the potential effects of these processes and more accurately reflect real biotic interactions
260 (D'Amen et al. 2018), or indirect interactions between associated species (Morueta-
261 Holme et al. 2016). Compared to other ecological systems, bacterial soil communities
262 have the added benefit of cosmopolitan ranges and high dispersal while simultaneously
263 exhibiting biogeographic species fluctuations (Martiny et al. 2006, Ramette and Tiedje
264 2007, Meyer et al. 2018), allowing for better inference of species' interactions from co-
265 occurrences. Many studies have emerged over the last years inferring interaction
266 networks from soil community metagenomic data with varying degrees of success
267 (Matchado et al. 2021). However, many studies present genetically inferred interaction
268 networks without a clear ecological framework to interpret those results and the
269 drawbacks of using co-occurrence data to infer interaction types is frequently noted
270 (Barner et al. 2018, Blanchet et al. 2020).

271 Marker-gene based co-occurrence network approaches are thus regularly, and justly,
272 criticized for poorly reflecting known species' ecologies (Freilich et al. 2018). However,
273 because metagenomic datasets generate phylogenetically relevant information about
274 investigated bacteria, this information may increase the confidence of inferred interaction
275 types assigned through these co-occurrence methods (Goberna et al. 2019). Closely
276 phylogenetically related bacteria are more likely to exhibit competitive interactions in the
277 same ecosystem (Tan et al. 2012). Therefore, comparing the phylogenetic diversity within

278 ecosystems may help measure the prevalence of competitive interactions in that
279 ecosystem (Stegen et al. 2012). Evidence for this theory, called niche conservatism, has
280 broad application across the tree of life for bacteria and archaea and may increase the
281 confidence of assigning species interactions based on co-occurrence data (Goberna and
282 Verdú 2016).

283 Using phylogenetically informed co-occurrence networks allows researchers to
284 investigate larger conceptual patterns (Goberna and Verdú 2022). Updated frameworks
285 that build on these association methods can further improve detection of interactions by
286 using ecological information about species' traits with better a predictive power than
287 phylogenetic information alone (Kéfi et al. 2016, Alneberg et al. 2020). Studies on bacteria
288 using such trait- (Wang et al. 2023, Metz et al. 2023) and gene-based network methods
289 to infer interaction types (Schaedel et al. 2023) may also help gain information about
290 indirect and non-linear interaction types amongst community members that might not be
291 revealed by a co-occurrence matrix alone (Saiz et al. 2019). Combined methods using
292 these trait-based approaches allow a fuller understanding of the spatial and temporal
293 variation in facilitating relationships (Tumolo et al. 2020), such as joint species distribution
294 models (D'Amen et al. 2018). Network models may also confirm known interactions and
295 reveal previously undiscovered associations between species encompassing both trophic
296 and non-trophic interactions (Thurman et al. 2019). Using models to assess complex
297 interaction webs such as metabolic dependencies and grounding them with empirical data
298 thus confirms underlying relationships (e.g. Liao et al. 2020) even when the microbial
299 species investigated aren't always culturable or their metabolisms known (Lam et al.
300 2020). Promisingly, studies that do consider specific functional groups find a high

301 interaction strength of potential facilitators (Chao et al. 2016) – though these studies, in
302 turn, often refrain from putting such results in a broader ecological framework –
303 hampering our ability to elucidate conclusions applicable to other systems.

304 To investigate the relationship between bacterial facilitation and the environment in a
305 broader ecological framework, networks need to be examined comparatively and
306 incorporate environmental information. Different environments exhibit broader
307 phylogenetic diversity in bacterial communities (Goberna et al. 2014) or may directly
308 influence the prevalence of certain interaction types (Piccardi et al. 2019). Coupled with
309 phylogenetic information, network data may infer the overdispersion of taxonomic
310 diversity and overall richness as a proxy for the strength of facilitative interactions in
311 different environments (Goberna and Verdú 2016). Future research needs to emphasize
312 fine-scale environmental information relevant to the bacterial communities studied to
313 understand its relationship to community interactions and the potential collapse of
314 bacterial networks under environmental stress (Michalet et al. 2014). Alternatively,
315 facilitation may be studied directly in the metagenome of whole communities by looking
316 at cooperative genes (Simonet and McNally 2021). Different approaches may reinforce
317 one another by basing the assumptions on community-level interactions inferred from
318 phylogenetic data on evidence from pairwise-experiments and validating those
319 experiments by assessing natural and heterogeneous communities. These resulting
320 predictions will ultimately be helpful to understand macro-ecological processes and
321 understanding the evolutionary pressures that shape interaction networks (Segar et al.
322 2020, Hall et al. 2020). The relationships between community composition, interaction
323 types and the environment were tested predominantly in plant communities (Carrión et

324 al. 2017, Zhang et al. 2017, Pashirzad et al. 2019) and are also coming to the foreground
325 in research on soil bacteria (Stegen et al. 2012, Pérez-Valera et al. 2017). As these
326 models improve, they need to be used to address such fundamental relationships
327 between community interactions and the environment and can be used to synthesize the
328 role of bacterial communities in whole-system interactions.

329 Moving to a multi-trophic framework remains a pressing challenge for many investigations
330 of community or ecosystem structure (Seibold et al. 2018, Schleuning et al. 2020).
331 Without a doubt, soil bacterial community structure and interactions have immense
332 consequences for other organisms, whether below-ground as pathogens or mutualists in
333 the rhizosphere (Schlatter et al. 2017), above-ground biomass of plants (Saleem et al.
334 2019) and indirect effects on nutrient cycling (Dubey et al. 2019). Bacterial communities
335 may be shaped by the interactions of other microbial trophic levels through parasitism or
336 grazing (Li et al. 2023), while bacterial communities themselves may facilitate plant
337 germination in harsher environments (David et al. 2020). Indirect facilitative effects may
338 arise through inter-trophic interactions and increase both bacterial diversity
339 (Pradeep Ram et al. 2020), as well as that of their predators (Yang et al. 2018, Scheuerl
340 et al. 2019) and plants (Liu et al. 2019) through evolutionary pressures. Plants might
341 benefit from soil bacteria feedbacks under drought (Buchenau et al. 2022), while plant
342 responses to environmental changes further drive bacterial community structure and thus
343 potential interactions (Koyama et al. 2018). Plant-growth-promoting bacteria can mitigate
344 the effects of environmental stress on plants (Yang et al. 2009), but this may also
345 negatively affect resident communities when they favor establishment of invaders (Zhang
346 et al. 2018). A large range of potential mechanisms for facilitation thus exists between

347 these trophic levels, whether nutrient-, water-, immune-mediating- or micro-climate
348 related. A better understanding of the role of interactions in structuring these soil
349 communities can help elucidate ecologically important emergent properties of those
350 systems, such as community functioning, stability, or resilience (van den Berg et al. 2022).

351 **5 – Facilitation’s effect on emergent properties**

352 Mutualisms have long been suggested to be a driving force of ecosystem processes in
353 soil communities (Wall and Moore 1999) and a growing field is studying the emergent
354 properties of interaction networks in both experiments and theoretical models (van den
355 Berg et al. 2022, Chang et al. 2023). Species diversity, specific ecosystem functions and
356 overall system stability or resilience are all emergent properties influenced by species
357 interactions. Stability and resilience are defined in many different ways, but broadly
358 consider the ability of a system to remain in a certain state and the rate at which a system
359 can return to this state following perturbations (van Meerbeek et al. 2021, but see
360 Donohue 2016 for varying definitions). Interaction networks can be evaluated at the taxa
361 level by the number of edges (inferred interactions), the proportions of different inferred
362 edges (e.g. positive versus negative) and other parameters such as centrality or
363 ‘keystoneness’ to determine the role of nodes inside a community (Berry and Widder
364 2014). At the system level, modularity or connectivity may provide hints about a system’s
365 emergent properties, such as stability or resilience (de Vries et al. 2018). Studying how
366 network properties vary under environmental changes allows researchers to assess the
367 vulnerability of soil systems to global change in terms of their functioning, diversity, and
368 resilience.

369 *Productivity and other functions*

370 Productivity may directly be enhanced by facilitative interactions in bacterial communities
371 (Fiegna et al. 2015). Network approaches have identified that cross-feeding interactions
372 may be dominant drivers of bacterial community structure (Germerodt et al. 2016, Hoek
373 et al. 2016). Facilitative interactions in bacterial communities forming biofilms or biocrusts
374 promote bacterial productivity both at the community and species level (Boles et al. 2004,
375 Wu et al. 2019, Li et al. 2020). Horizontal gene transfer may directly increase some
376 community functions by increasing nutrient cycling or stress response in whole
377 communities (Song et al. 2021). In microcosm experiments, environmentally stressed
378 bacterial communities may require higher diversity to perform similar functions (García et
379 al. 2018). Warming may lead to direct losses productivity in microcosms (Bestion et al.
380 2020), but the interplay between environmental changes and species-specific interactions
381 is often more complex (Bestion et al. 2018). Soil functions like nutrient cycling and plant
382 growth promotion may benefit from network complexity, but decrease as networks are
383 stressed by environmental pressures at higher elevations (Chen et al. 2022). Other
384 environmental stressors such as land use may greatly impact the connectivity of bacterial
385 networks and specifically impact important ecosystem functions such as carbon cycling
386 (Xue et al. 2022). How the environment impacts ecosystem functions may be different for
387 subsets of the community, e.g. bacteria within positive interaction networks and those
388 outside (Yang et al. 2022). Different spatial scales also modulate the outcome of
389 interactions between bacterial species, which may be intensely competitive at a very local
390 scale but facilitate co-existence at the community level (Kuhn et al. 2022).

391 *Diversity and stability*

392 Facilitation has been found to be an important driver of biodiversity in plant communities
393 (Navarro-Cano et al. 2021), promoting coexistence both mechanistically and
394 evolutionarily (McIntire and Fajardo 2014). Facilitation in bacterial communities may
395 directly increase species diversity by creating niche space for whole metabolic consortia
396 (Pascual-García et al. 2020) or cheaters (Leinweber et al. 2017) and is often observed
397 specifically in cases such as biofilm formation (Wu et al. 2019). Evidence for increased
398 stability of more diverse bacterial communities may be found when considering their
399 susceptibility to invasions in microcosms (Hodgson et al. 2002, Eisenhauer et al. 2012)
400 and reductions of bacterial diversity can lead to a loss of stability in soil communities
401 (Wagg et al. 2021). For instance, invasions of new bacterial groups can change
402 community dynamics and alter community structure (Amor et al. 2020, Mawarda et al.
403 2020) – an effect to which less biodiverse systems are more susceptible (Xing et al. 2021).
404 Interaction types themselves can influence stability, as stronger competition can decrease
405 stability in bacterial communities (Ratzke et al. 2020). Positive interactions may
406 destabilize bacterial systems by causing dependencies, whereas the negative feedback
407 caused by competitive or exploitative interactions may have a stabilizing effect (Coyte et
408 al. 2015). Theoretical models suggest higher diversity increases community fluctuations
409 but can make facilitating communities more stable depending on the asymmetry and
410 nestedness of their interaction networks – i.e. community structure (Thébault and
411 Fontaine 2010), and experimental studies have confirmed that some of these predictions
412 hold true in microcosms (Hu et al. 2022) and in nature (Liu et al. 2022). Positive
413 correlations between bacterial diversity and ecosystem stability (García-García et al.
414 2019, Xu et al. 2021) and functions (Delgado-Baquerizo et al. 2017, Maron et al. 2018)

415 may be partially explained by interspecies facilitation leading to complementarity (Tilman
416 et al. 2014). The balance of competitive to facilitative interactions is increasingly found to
417 be an important driver of species coexistence and thus of the relationship between whole-
418 community diversity and stability (Gjini and Madec 2021). Importantly, the broader biotic
419 and abiotic environment is thought to drive the relationship between strength of facilitative
420 networks and community stability (De Vries and Shade 2013) and this relationship is not
421 stable under changing environments (Yuan et al. 2021), which makes understanding
422 these relationships ever more relevant in the face of increasing challenges posed by
423 climate change.

424 *Climate resilience*

425 The functional resilience of soil bacterial communities is driven by both the physico-
426 chemical environment and the resulting community structure (Griffiths et al. 2007).
427 Keystone species within interaction networks can contribute significantly to the
428 community's overall resilience to disturbances (Ma et al. 2020b). Predominant interaction
429 types across a whole community may influence their resilience, such as a decreased
430 impact of nutrient stress on highly facilitative communities (Machado et al. 2021).
431 Conversely, highly competitive communities may be less resistant to environmental
432 fluctuations (Ratzke et al. 2020). More phylogenetically and taxonomically diverse
433 communities, implying more potential facilitative links, indeed show higher overall
434 resilience to environmental stress in one study (Xun et al. 2021). Co-occurrence networks
435 may be strengthened under drought stress and thus promote community resilience (Wu
436 et al. 2019), but some bacterial communities show that highly connected co-occurrence
437 networks can break down under drought stress (de Vries et al. 2018). Overall,

438 experimental evidence for the relationship between community interaction types and
439 resilience is rare (Philippot et al. 2021), and increased theoretical modelling efforts may
440 provide better answers (van den Berg et al. 2022). Increased diversity due to facilitation
441 promoting coexistence may have beneficial effects on bacterial community resilience
442 (Yachi and Loreau 1999, Xu et al. 2021), but the direct relationship between bacterial
443 facilitation and resilience in the face of climate change is generally poorly understood
444 (Bardgett and Caruso 2020). Environmental changes can further lead to indirect changes
445 in interaction networks, by influencing other groups such as invasive bacteria (Xing et al.
446 2021) or plants (Pérez Castro et al. 2019) – which may subsequently affect the resilience
447 or other emergent properties of the community.

448 *Resistance to invaders*

449 The increased establishment of invasive species under global warming is a well-known
450 driver of biodiversity loss (Pimentel et al. 2005). In the context of species' interaction
451 networks, new players may drastically alter the existing dynamics of a community and the
452 resulting resistance or resilience of an ecosystem – especially if their traits are different
453 on average (van Kleunen et al. 2010). In soils, bacterial invasions are relatively
454 understudied due to the enormous taxonomic challenges, but microcosm experiments
455 may elucidate some of the general predictions. There is some evidence that highly
456 facilitative communities can be more vulnerable to invaders (Li et al. 2018). Concurrently,
457 higher resident diversity may limit invader success (van Elsas et al. 2012), and tightly
458 interwoven facilitating communities show a higher degree of resistance to invaders (Qian
459 and Akçay 2020, Kurkjian et al. 2021). Interactions with plants and other organisms may
460 further influence the invasibility of bacterial soil communities (Fahey et al. 2020). The

461 relationship of facilitation to community invasion thus depends on a complex interplay
462 between the resident community's existing niche partitions (Wei et al. 2015),
463 environmental conditions (Yang et al. 2017) and species' specific or evolutionary effects
464 (van der Putten et al. 2007, Jousset et al. 2013). The effect of facilitation on such
465 emergent properties has remained a pressing unknown in facilitation research for the last
466 two decades (Richardson et al. 2000, Stachowicz and Byrnes 2006, Li et al. 2018,
467 Piccardi et al. 2022).

468 **6 – Opportunities in bacterial facilitation research**

469 The last decade has seen tremendous progress in the study of bacterial facilitation, from
470 the first experimental evidence for the stress gradient hypothesis in artificial (Piccardi et
471 al. 2019) and natural (Hernandez et al. 2021) settings, to the continuous development of
472 co-occurrence and modeling-based methods (Kodera et al. 2022). The important impacts
473 of environmental change on soil bacteria are now well established and the role of
474 facilitation for soil community climate resilience and resistance remains an important area
475 of future research (Naylor et al. 2020). Both the determinants (Dai et al. 2022) and
476 outcomes (Ratzke et al. 2020) of such emergent properties are increasingly well
477 understood and applied in soil research (Xiang et al. 2023). However, how these
478 emergent properties and complex dynamics emerge from interactions in bacterial
479 communities remains a topic of interest and soil systems are perfectly poised to reveal
480 these associations (Segrè et al. 2023).

481 Microcosm studies have allowed for the study of drivers of selection in shaping
482 community interaction types (Martin et al. 2016, Kayser et al. 2018) and have immense

483 promise to be engineered in a variety of experimental settings, which can help elucidate
484 ecologically meaningful patterns (Friedman et al. 2017, McCarty and Ledesma-Amaro
485 2019). They can also be used to create analogs of natural systems to distinguish
486 interactions between all the different players in a bacterial community and investigate
487 emergent properties in controlled settings (Antoniewicz 2020). Pairwise experiments
488 tracking population growth rates can generate hypotheses and ultimately bring to light the
489 mechanisms by which species might interact (Löder et al. 2014), especially across
490 temporal and environmental variation (Coenen et al. 2020). In nature, modern
491 sequencing technologies make it possible to track both population structure and genetic
492 diversity underlying species interactions on a very fine temporal and spatial scale (Sher
493 et al. 2011, Rodríguez-Verdugo and Ackermann 2021). These experiments can also be
494 especially useful to infer the natural parameters used in constructing models of these
495 populations in artificial space (Boza et al. 2023), while the detailed community-level
496 information can address questions about the effects of facilitation on community assembly
497 or structure (Lin et al. 2018). However, to be useful for predicting the relationship between
498 the environment and species interactions such experiments need to take the complexity
499 of natural systems into account, including accounting for spatial and temporal
500 heterogeneity of communities and the more complex context of field studies (Chamberlain
501 et al. 2014, Xiang et al. 2023). The field is currently perfectly poised to combine both
502 approaches to investigate real-world interaction shifts, based on ground-truthed
503 experimental evidence from microcosms (Gralka et al. 2023).

504 To enable the conceptual understanding of bacterial interaction networks in natural
505 systems, we hope that future research will focus on generating findable, accessible,

506 interoperable, and reusable genetic datasets from culture-based and real-world studies
507 (FAIR, Pacheco et al. 2022). FAIR data will allow microbial ecologists to address
508 ecological hypotheses, including ones related to the prevalence and importance of
509 facilitative interactions, and their role in dealing with challenges posed by global change.
510 Meanwhile, we should not lose sight of the underlying mechanisms that allow bacterial
511 facilitation in a variety of settings, and take great care to study these in detail, both in field
512 and laboratory settings. The genetic pathways underlying cross-feeding (D'Souza et al.
513 2018), immune-mediating (Zélé et al. 2018), or environmental modulation interactions
514 (Madsen et al. 2016) are increasingly mapped to enable the investigation of multiple
515 functions in natural communities (Sun et al. 2022, Wang et al. 2023). Understanding how
516 these interactions influence eventual ecosystem functions remains the challenging task
517 for this field moving forward (Delgado-Baquerizo et al. 2020).

518 By testing ecological predictions (Houlahan et al. 2017) and utilizing the combined
519 methods proposed in this article, we hypothesize that ecosystem functions in soils will be
520 shown to depend on facilitative processes as much as the intensively studied nurse plants
521 – beneficiary systems (Brooker et al. 2008) or the intertidal communities of Bertness
522 (1989). In fact, soil bacteria might be underlying much of the ecology traditionally ascribed
523 to interspecific plant facilitation (Rodríguez-Echeverría et al. 2016), and the role of soil
524 bacteria in ecosystem responses to climate change, including resilience and resistance,
525 will undoubtedly prove crucial in mitigating the climate impacts on ecosystems worldwide
526 (Certini and Scalenghe 2023). Describing and understanding the links between bacterial
527 interactions on the one hand and ecosystem functioning and vulnerability on the other

528 hand will prove to be crucial, particularly in the face of the considerable challenges posed
529 to soil biodiversity by global change (Leal Filho et al. 2023).

530 **Significance statement:**

531 The Oikos special issue “The role of plant facilitation in mediating climate change impact on
532 biodiversity” aims to synthesize the role of plant facilitation on biodiversity in the face of
533 environmental changes. Soil bacteria are of immediate importance to this conversation as their
534 facilitative links underlie function in soil ecosystems that are crucial for plants and other biota, yet
535 are often left out of the discussion altogether. There exists no comprehensive review of the role,
536 structure, and importance of facilitation in bacterial communities in natural soils, and the different
537 fields that do research bacterial facilitation often fall short in investigating those as part of a
538 comprehensive ecological framework. Here, we illustrate that facilitation in soil bacteria is
539 ubiquitous and plays an important role in maintaining diversity, function, and resilience. We
540 provide a synthesis of methodological avenues to improve inference of facilitation in natural soil
541 communities and present an ecological framework to investigate these interactions in regard to
542 global change. We believe that this forum article will help researchers on plant facilitation see
543 their findings in a broader ecological context, help microbial ecologists synthesize their research
544 aims within a broader ecological framework, and will be informative for anyone working in ecology
545 generally to understand the importance of facilitation in bacterial communities and their potential
546 in future study.

547 **Data archiving statement:**

548 No data were used for this paper.

549 **Conflict of interest statement:**

550 The authors declare no conflicts of interest.

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