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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.

552 **References**

- 553 Abdul Rahman, N. S. N., N. W. Abdul Hamid, and K. Nadarajah. 2021. Effects of Abiotic Stress on
554 Soil Microbiome. *International Journal of Molecular Sciences* 22:9036.
- 555 Adams, A. E., E. M. Besozzi, G. Shahrokhi, and M. A. Patten. 2021. A case for associational
556 resistance: Apparent support for the stress gradient hypothesis varies with study system. *Ecology*
557 *Letters* 25:202–217.
- 558 Alneberg, J., C. Bennke, S. Beier, C. Bunse, C. Quince, K. Ininbergs, L. Riemann, M. Ekman, K.
559 Jürgens, M. Labrenz, J. Pinhassi, and A. F. Andersson. 2020. Ecosystem-wide metagenomic binning
560 enables prediction of ecological niches from genomes. *Communications Biology* 3:1–10.
- 561 Amor, D. R., C. Ratzke, and J. Gore. 2020. Transient invaders can induce shifts between alternative
562 stable states of microbial communities. *Science Advances* 6:eaay8676.
- 563 Antoniewicz, M. R. 2020. A guide to deciphering microbial interactions and metabolic fluxes in
564 microbiome communities. *Current Opinion in Biotechnology* 64:230–237.
- 565 Astudillo-García, C., S. M. Hermans, B. Stevenson, H. L. Buckley, and G. Lear. 2019. Microbial
566 assemblages and bioindicators as proxies for ecosystem health status: potential and limitations.
567 *Applied Microbiology and Biotechnology* 103:6407–6421.
- 568 Bairey, E., E. D. Kelsic, and R. Kishony. 2016. High-order species interactions shape ecosystem
569 diversity. *Nature Communications* 7:12285.
- 570 Bardgett, R. D., and T. Caruso. 2020. Soil microbial community responses to climate extremes:
571 resistance, resilience and transitions to alternative states. *Philosophical Transactions of the Royal*
572 *Society B: Biological Sciences* 375:20190112.
- 573 Barner, A. K., K. E. Coblenz, S. D. Hacker, and B. A. Menge. 2018. Fundamental contradictions
574 among observational and experimental estimates of non-trophic species interactions. *Ecology*
575 99:557–566.
- 576 van den Berg, N. I., D. Machado, S. Santos, I. Rocha, J. Chacón, W. Harcombe, S. Mitri, and K. R.
577 Patil. 2022. Ecological modelling approaches for predicting emergent properties in microbial
578 communities. *Nature Ecology & Evolution* 6:855–865.
- 579 Berry, D., and S. Widder. 2014. Deciphering microbial interactions and detecting keystone species
580 with co-occurrence networks. *Frontiers in Microbiology* 5.
- 581 Bertness, M. D. 1989. Intraspecific Competition and Facilitation in a Northern Acorn Barnacle
582 Population. *Ecology* 70:257–268.
- 583 Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology &*
584 *Evolution* 9:191–193.
- 585 Bestion, E., S. Barton, F. C. García, R. Warfield, and G. Yvon-Durocher. 2020. Abrupt declines in
586 marine phytoplankton production driven by warming and biodiversity loss in a microcosm
587 experiment. *Ecology Letters* 23:457–466.

588 Bestion, E., B. García-Carreras, C.-E. Schaum, S. Pawar, and G. Yvon-Durocher. 2018. Metabolic
589 traits predict the effects of warming on phytoplankton competition. *Ecology Letters* 21:655–664.

590 Blanchet, F. G., K. Cazelles, and D. Gravel. 2020. Co-occurrence is not evidence of ecological
591 interactions. *Ecology Letters* 23:1050–1063.

592 Boles, B. R., M. Thoendel, and P. K. Singh. 2004. Self-generated diversity produces “insurance
593 effects” in biofilm communities. *Proceedings of the National Academy of Sciences* 101:16630–
594 16635.

595 Boza, G., G. Barabás, I. Scheuring, and I. Zachar. 2023. Eco-evolutionary modelling of microbial
596 syntrophy indicates the robustness of cross-feeding over cross-facilitation. *Scientific Reports*
597 13:907.

598 Bronstein, J. L. 2009. The evolution of facilitation and mutualism. *Journal of Ecology* 97:1160–1170.

599 Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K.
600 Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J.
601 Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet.
602 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*
603 96:18–34.

604 Buchenau, N., M. van Kleunen, and R. A. Wilschut. 2022. Direct and legacy-mediated drought
605 effects on plant performance are species-specific and depend on soil community composition.
606 *Oikos* 2022:e08959.

607 Carrión, J. F., Gastauer, M, Mota, N M, and Meira-Neto J A A. 2017. Facilitation as a driver of plant
608 assemblages in Caatinga. *Journal of Arid Environments* 142:50–58.

609 Certini, G., and R. Scalenghe. 2023. The crucial interactions between climate and soil. *Science of*
610 *The Total Environment* 856:159169.

611 Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species
612 interactions? *Ecology Letters* 17:881–890.

613 Chang, C.-Y., D. Bajić, J. C. C. Vila, S. Estrela, and A. Sanchez. 2023. Emergent coexistence in
614 multispecies microbial communities. *Science* 381:343–348.

615 Chao, Y., W. Liu, Y. Chen, W. Chen, L. Zhao, Q. Ding, S. Wang, Y.-T. Tang, T. Zhang, and R.-L. Qiu.
616 2016. Structure, Variation, and Co-occurrence of Soil Microbial Communities in Abandoned Sites
617 of a Rare Earth Elements Mine. *Environmental Science & Technology* 50:11481–11490.

618 Chaparro, J. M., A. M. Sheflin, D. K. Manter, and J. M. Vivanco. 2012. Manipulating the soil
619 microbiome to increase soil health and plant fertility. *Biology and Fertility of Soils* 48:489–499.

620 Chen, W., J. Wang, X. Chen, Z. Meng, R. Xu, D. Duoqi, J. Zhang, J. He, Z. Wang, J. Chen, K. Liu, T. Hu,
621 and Y. Zhang. 2022. Soil microbial network complexity predicts ecosystem function along elevation
622 gradients on the Tibetan Plateau. *Soil Biology and Biochemistry* 172:108766.

623 Coenen, A. R., S. K. Hu, E. Luo, D. Muratore, and J. S. Weitz. 2020. A Primer for Microbiome Time-
624 Series Analysis. *Frontiers in Genetics* 11.

625 Contreras-Moreno, F. J., J. Pérez, J. Muñoz-Dorado, A. Moraleda-Muñoz, and F. J. Marcos-Torres.
626 2024. *Myxococcus xanthus* predation: an updated overview. *Frontiers in Microbiology* 15:1339696.

627 Cordero, O. X., L.-A. Ventouras, E. F. DeLong, and M. F. Polz. 2012. Public good dynamics drive
628 evolution of iron acquisition strategies in natural bacterioplankton populations. *Proceedings of the*
629 *National Academy of Sciences* 109:20059–20064.

630 Córdova-Alcántara, I. M., D. L. Venegas-Cortés, M. Á. Martínez-Rivera, N. O. Pérez, and A. V.
631 Rodríguez-Tovar. 2019. Biofilm characterization of *Fusarium solani* keratitis isolate: increased
632 resistance to antifungals and UV light. *Journal of Microbiology* 57:485–497.

633 Costa, E., J. Pérez, and J.-U. Kreft. 2006. Why is metabolic labour divided in nitrification? *Trends in*
634 *Microbiology* 14:213–219.

635 Coyte, K. Z., J. Schluter, and K. R. Foster. 2015. The ecology of the microbiome: Networks,
636 competition, and stability. *Science* 350:663–666.

637 Dai, T., D. Wen, C. T. Bates, L. Wu, X. Guo, S. Liu, Y. Su, J. Lei, J. Zhou, and Y. Yang. 2022. Nutrient
638 supply controls the linkage between species abundance and ecological interactions in marine
639 bacterial communities. *Nature Communications* 13:175.

640 D’Amen, M., H. K. Mod, N. J. Gotelli, and A. Guisan. 2018. Disentangling biotic interactions,
641 environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography*
642 41:1233–1244.

643 Davey, M. E., and G. A. O’toole. 2000. Microbial Biofilms: from Ecology to Molecular Genetics.
644 *Microbiology and Molecular Biology Reviews* 64:847–867.

645 David, A. S., K. B. Thapa-Magar, E. S. Menges, C. A. Searcy, and M. E. Afkhami. 2020. Do plant–
646 microbe interactions support the Stress Gradient Hypothesis? *Ecology* 101:e03081.

647 De Vries, F., and A. Shade. 2013. Controls on soil microbial community stability under climate
648 change. *Frontiers in Microbiology* 4.

649 Delgado-Baquerizo, M., D. J. Eldridge, V. Ochoa, B. Gozalo, B. K. Singh, and F. T. Maestre. 2017. Soil
650 microbial communities drive the resistance of ecosystem multifunctionality to global change in
651 drylands across the globe. *Ecology Letters* 20:1295–1305.

652 Delgado-Baquerizo, M., P. B. Reich, C. Trivedi, D. J. Eldridge, S. Abades, F. D. Alfaro, F. Bastida, A. A.
653 Berhe, N. A. Cutler, A. Gallardo, L. García-Velázquez, S. C. Hart, P. E. Hayes, J.-Z. He, Z.-Y. Hseu, H.-
654 W. Hu, M. Kirchmair, S. Neuhauser, C. A. Pérez, S. C. Reed, F. Santos, B. W. Sullivan, P. Trivedi, J.-T.
655 Wang, L. Weber-Grullon, M. A. Williams, and B. K. Singh. 2020. Multiple elements of soil biodiversity
656 drive ecosystem functions across biomes. *Nature Ecology & Evolution* 4:210–220.

657 Domeignoz-Horta, L. A., G. Pold, X.-J. A. Liu, S. D. Frey, J. M. Melillo, and K. M. DeAngelis. 2020.
658 Microbial diversity drives carbon use efficiency in a model soil. *Nature Communications* 11:3684.

659 Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L.
660 Jackson, M. Lurgi, D. McClean, N. E. O’Connor, E. J. O’Gorman, and Q. Yang. 2016. Navigating the
661 complexity of ecological stability. *Ecology Letters* 19:1172–1185.

662 Drew, G. C., E. J. Stevens, and K. C. King. 2021. Microbial evolution and transitions along the
663 parasite–mutualist continuum. *Nature Reviews Microbiology* 19:623–638.

664 D’Souza, G., S. Shitut, D. Preussger, G. Yousif, S. Waschina, and C. Kost. 2018. Ecology and
665 evolution of metabolic cross-feeding interactions in bacteria. *Natural Product Reports* 35:455–488.

666 Dubey, A., M. A. Malla, F. Khan, K. Chowdhary, S. Yadav, A. Kumar, S. Sharma, P. K. Khare, and M. L.
667 Khan. 2019. Soil microbiome: a key player for conservation of soil health under changing climate.
668 *Biodiversity and Conservation* 28:2405–2429.

669 Eisenhauer, N., S. Scheu, and A. Jousset. 2012. Bacterial Diversity Stabilizes Community
670 Productivity. *PLOS ONE* 7:e34517.

671 van Elsas, J. D., M. Chiurazzi, C. A. Mallon, D. Elhottová, V. Křišťůfek, and J. F. Salles. 2012. Microbial
672 diversity determines the invasion of soil by a bacterial pathogen. *Proceedings of the National*
673 *Academy of Sciences* 109:1159–1164.

674 Fahey, C., A. Koyama, P. M. Antunes, K. Dunfield, and S. L. Flory. 2020. Plant communities mediate
675 the interactive effects of invasion and drought on soil microbial communities. *The ISME Journal*
676 14:1396–1409.

677 Falkowski, P. G., T. Fenchel, and E. F. Delong. 2008. The Microbial Engines That Drive Earth’s
678 Biogeochemical Cycles. *Science* 320:1034–1039.

679 Feng, J., H. Ma, C. Wang, J. Gao, C. Zhai, L. Jiang, and S. Wan. 2024. Water rather than nitrogen
680 availability predominantly modulates soil microbial beta-diversity and co-occurrence networks in a
681 secondary forest. *Science of The Total Environment* 907:167996.

682 Ferrier, M., J. L. Martin, and J. N. Rooney-Varga. 2002. Stimulation of *Alexandrium fundyense* growth
683 by bacterial assemblages from the Bay of Fundy. *Journal of Applied Microbiology* 92:706–716.

684 Fiegna, F., A. Moreno-Letelier, T. Bell, and T. G. Barraclough. 2015. Evolution of species interactions
685 determines microbial community productivity in new environments. *The ISME Journal* 9:1235–1245.

686 Fierer, N., and R. B. Jackson. 2006. The diversity and biogeography of soil bacterial communities.
687 *Proceedings of the National Academy of Sciences* 103:626–631.

688 Finlay, B. J. 2002. Global Dispersal of Free-Living Microbial Eukaryote Species. *Science* 296:1061–
689 1063.

690 Finlay, B. J., S. C. Maberly, and J. I. Cooper. 1997. Microbial Diversity and Ecosystem Function. *Oikos*
691 80:209–213.

692 Flemming, H.-C., and J. Wingender. 2010. The biofilm matrix. *Nature Reviews Microbiology* 8:623–
693 633.

694 Freilich, M. A., E. Wieters, B. R. Broitman, P. A. Marquet, and S. A. Navarrete. 2018. Species co-
695 occurrence networks: Can they reveal trophic and non-trophic interactions in ecological
696 communities? *Ecology* 99:690–699.

697 Friedman, J., L. M. Higgins, and J. Gore. 2017. Community structure follows simple assembly rules
698 in microbial microcosms. *Nature Ecology & Evolution* 1:1–7.

699 Gallien, L., D. Zurell, and N. E. Zimmermann. 2018. Frequency and intensity of facilitation reveal
700 opposing patterns along a stress gradient. *Ecology and Evolution* 8:2171–2181.

701 Gao, C., L. Xu, L. Montoya, M. Madera, J. Hollingsworth, L. Chen, E. Purdom, V. Singan, J. Vogel, R. B.
702 Hutmacher, J. A. Dahlberg, D. Coleman-Derr, P. G. Lemaux, and J. W. Taylor. 2022. Co-occurrence
703 networks reveal more complexity than community composition in resistance and resilience of
704 microbial communities. *Nature Communications* 13:3867.

705 García, F. C., E. Bestion, R. Warfield, and G. Yvon-Durocher. 2018. Changes in temperature alter the
706 relationship between biodiversity and ecosystem functioning. *Proceedings of the National
707 Academy of Sciences* 115:10989–10994.

708 García-García, N., J. Tamames, A. M. Linz, C. Pedrós-Alió, and F. Puente-Sánchez. 2019.
709 Microdiversity ensures the maintenance of functional microbial communities under changing
710 environmental conditions. *The ISME Journal* 13:2969–2983.

711 Geiman, Q. M. 1964. Comparative Physiology: Mutualism, Symbiosis, and Parasitism. *Annual
712 Review of Physiology* 26:75–108.

713 Germerodt, S., K. Bohl, A. Lück, S. Pande, A. Schröter, C. Kaleta, S. Schuster, and C. Kost. 2016.
714 Pervasive Selection for Cooperative Cross-Feeding in Bacterial Communities. *PLOS Computational
715 Biology* 12:e1004986.

716 Ghoul, M., and S. Mitri. 2016. The Ecology and Evolution of Microbial Competition. *Trends in
717 Microbiology* 24:833–845.

718 Giaouris, E., E. Heir, M. Desvaux, M. Hébraud, T. Mørretrø, S. Langsrud, A. Doulgeraki, G.-J. Nychas,
719 M. Kačániová, K. Czaczyk, H. Ölmez, and M. Simões. 2015. Intra- and inter-species interactions
720 within biofilms of important foodborne bacterial pathogens. *Frontiers in Microbiology* 6.

721 Gjini, E., and S. Madec. 2021. The ratio of single to co-colonization is key to complexity in
722 interacting systems with multiple strains. *Ecology and Evolution* 11:8456–8474.

723 Goberna, M., A. Montesinos-Navarro, A. Valiente-Banuet, Y. Colin, A. Gómez-Fernández, S. Donat,
724 J. A. Navarro-Cano, and M. Verdú. 2019. Incorporating phylogenetic metrics to microbial co-
725 occurrence networks based on amplicon sequences to discern community assembly processes.
726 *Molecular Ecology Resources* 19:1552–1564.

727 Goberna, M., J. A. Navarro-Cano, A. Valiente-Banuet, C. García, and M. Verdú. 2014. Abiotic stress
728 tolerance and competition-related traits underlie phylogenetic clustering in soil bacterial
729 communities. *Ecology Letters* 17:1191–1201.

730 Goberna, M., and M. Verdú. 2016. Predicting microbial traits with phylogenies. *The ISME Journal*
731 10:959–967.

732 Goberna, M., and M. Verdú. 2022. Cautionary notes on the use of co-occurrence networks in soil
733 ecology. *Soil Biology and Biochemistry* 166:108534.

734 de Graaff, M.-A., J. Adkins, P. Kardol, and H. L. Throop. 2015. A meta-analysis of soil biodiversity
735 impacts on the carbon cycle. *SOIL* 1:257–271.

736 Gralka, M., S. Pollak, and O. X. Cordero. 2023. Genome content predicts the carbon catabolic
737 preferences of heterotrophic bacteria. *Nature Microbiology* 8:1799–1808.

738 Griffin, A. S., S. A. West, and A. Buckling. 2004. Cooperation and competition in pathogenic
739 bacteria. *Nature* 430:1024–1027.

740 Griffiths, B. S., P. D. Hallett, H. L. Kuan, A. S. Gregory, C. W. Watts, and A. P. Whitmore. 2007.
741 Functional resilience of soil microbial communities depends on both soil structure and microbial
742 community composition. *Biology and Fertility of Soils* 44:745–754.

743 Guignabert, A., L. Augusto, M. Gonzalez, C. Chipeaux, and F. Delerue. 2020. Complex biotic
744 interactions mediated by shrubs: Revisiting the stress-gradient hypothesis and consequences for
745 tree seedling survival. *Journal of Applied Ecology* 57:1341–1350.

746 Hall, A. R., B. Ashby, J. Bascompte, and K. C. King. 2020. Measuring Coevolutionary Dynamics in
747 Species-Rich Communities. *Trends in Ecology & Evolution* 35:539–550.

748 Hammarlund, S. P., and W. R. Harcombe. 2019. Refining the stress gradient hypothesis in a
749 microbial community. *Proceedings of the National Academy of Sciences of the United States of*
750 *America* 116:15760–15762.

751 Hardin, G. 1944. Symbiosis of *Paramecium* and *Oikomonas*. *Ecology* 25:304–311.

752 Hayat, R., S. Ali, U. Amara, R. Khalid, and I. Ahmed. 2010. Soil beneficial bacteria and their role in
753 plant growth promotion: a review. *Annals of Microbiology* 60:579–598.

754 Hernandez, D. J., A. S. David, E. S. Menges, C. A. Searcy, and M. E. Afkhami. 2021. Environmental
755 stress destabilizes microbial networks. *The ISME Journal* 15:1722–1734.

756 Hesse, E., S. O'Brien, A. M. Luján, D. Sanders, F. Bayer, E. M. van Veen, D. J. Hodgson, and A.
757 Buckling. 2021. Stress causes interspecific facilitation within a compost community. *Ecology*
758 *Letters* 24:2169–2177.

759 Hesse, E., S. O'Brien, N. Tromas, F. Bayer, A. M. Luján, E. M. van Veen, D. J. Hodgson, and A.
760 Buckling. 2018. Ecological selection of siderophore-producing microbial taxa in response to heavy
761 metal contamination. *Ecology Letters* 21:117–127.

762 Hibbing, M. E., C. Fuqua, M. R. Parsek, and S. B. Peterson. 2010. Bacterial competition: surviving
763 and thriving in the microbial jungle. *Nature Reviews Microbiology* 8:15–25.

764 Hodgson, D. J., P. B. Rainey, and A. Buckling. 2002. Mechanisms linking diversity, productivity and
765 invasibility in experimental bacterial communities. *Proceedings of the Royal Society of London.*
766 *Series B: Biological Sciences* 269:2277–2283.

767 Hoek, T. A., K. Axelrod, T. Biancalani, E. A. Yurtsev, J. Liu, and J. Gore. 2016. Resource Availability
768 Modulates the Cooperative and Competitive Nature of a Microbial Cross-Feeding Mutualism. *PLOS*
769 *Biology* 14:e1002540.

770 Holling, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and*
771 *Systematics* 4:1–23.

772 Horner-Devine, M. C., K. M. Carney, and B. J. M. Bohannan. 2004. An ecological perspective on
773 bacterial biodiversity. *Proceedings of the Royal Society of London. Series B: Biological Sciences*
774 271:113–122.

775 Houlahan, J. E., S. T. McKinney, T. M. Anderson, and B. J. McGill. 2017. The priority of prediction in
776 ecological understanding. *Oikos* 126:1–7.

777 Hu, J., D. R. Amor, M. Barbier, G. Bunin, and J. Gore. 2022. Emergent phases of ecological diversity
778 and dynamics mapped in microcosms. *Science* 378:85–89.

779 Huang, R., M. Li, and R. L. Gregory. 2011. Bacterial interactions in dental biofilm. *Virulence* 2:435–
780 444.

781 Hugenholtz, P., B. M. Goebel, and N. R. Pace. 1998. Impact of Culture-Independent Studies on the
782 Emerging Phylogenetic View of Bacterial Diversity. *Journal of Bacteriology* 180:4765–4774.

783 Jansson, J. K., and K. S. Hofmockel. 2020. Soil microbiomes and climate change. *Nature Reviews*
784 *Microbiology* 18:35–46.

785 Jousset, A., N. Eisenhauer, E. Materne, and S. Scheu. 2013. Evolutionary history predicts the
786 stability of cooperation in microbial communities. *Nature Communications* 4:2573.

787 Justice, S. S., D. A. Hunstad, L. Cegelski, and S. J. Hultgren. 2008. Morphological plasticity as a
788 bacterial survival strategy. *Nature Reviews Microbiology* 6:162–168.

789 Kaeberlein, T., K. Lewis, and S. S. Epstein. 2002. Isolating “Uncultivable” Microorganisms in Pure
790 Culture in a Simulated Natural Environment. *Science* 296:1127–1129.

791 Kaplan, J. B., and D. H. Fine. 2002. Biofilm Dispersal of *Neisseria subflava* and Other
792 Phylogenetically Diverse Oral Bacteria. *Applied and Environmental Microbiology* 68:4943–4950.

793 Kayser, J., C. F. Schreck, Q. Yu, M. Gralka, and O. Hallatschek. 2018. Emergence of evolutionary
794 driving forces in pattern-forming microbial populations. *Philosophical Transactions of the Royal*
795 *Society B: Biological Sciences* 373:20170106.

796 Kéfi, S., V. Miele, E. A. Wieters, S. A. Navarrete, and E. L. Berlow. 2016. How Structured Is the
797 Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to
798 Increased Persistence and Resilience. *PLOS Biology* 14:e1002527.

799 Kehe, J., A. Ortiz, A. Kulesa, J. Gore, P. C. Blainey, and J. Friedman. 2021. Positive interactions are
800 common among culturable bacteria. *Science Advances* 7:eabi7159.

801 van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between
802 invasive and non-invasive plant species. *Ecology Letters* 13:235–245.

803 Kodera, S. M., P. Das, J. A. Gilbert, and H. L. Lutz. 2022. Conceptual strategies for characterizing
804 interactions in microbial communities. *iScience* 25:103775.

805 Kost, C., K. R. Patil, J. Friedman, S. L. Garcia, and M. Ralser. 2023. Metabolic exchanges are
806 ubiquitous in natural microbial communities. *Nature Microbiology* 8:2244–2252.

807 Koyama, A., J. M. Steinweg, M. L. Haddix, J. S. Dukes, and M. D. Wallenstein. 2018. Soil bacterial
808 community responses to altered precipitation and temperature regimes in an old field grassland are
809 mediated by plants. *FEMS Microbiology Ecology* 94:fix156.

810 Kuhn, T., M. Mamin, S. Bindschedler, R. Bshary, A. Estoppey, D. Gonzalez, F. Palmieri, P. Junier, and
811 X.-Y. L. Richter. 2022. Spatial scales of competition and a growth–motility trade-off interact to
812 determine bacterial coexistence. *Royal Society Open Science* 9:211592.

813 Kurkjian, H. M., M. J. Akbari, and B. Momeni. 2021. The impact of interactions on invasion and
814 colonization resistance in microbial communities. *PLOS Computational Biology* 17:e1008643.

815 Lam, T. J., M. Stamboulian, W. Han, and Y. Ye. 2020. Pathway-based and phylogenetically adjusted
816 quantification of metabolic interaction between microbial species. *bioRxiv*:2020.05.15.097725.

817 Lawrence, D., and T. G. Barraclough. 2015. Evolution of resource use along a gradient of stress
818 leads to increased facilitation. *Oikos* 125:1284–1295.

819 Lawrence, D., F. Fiegna, V. Behrends, J. G. Bundy, A. B. Phillimore, T. Bell, and T. G. Barraclough.
820 2012. Species Interactions Alter Evolutionary Responses to a Novel Environment. *PLoS Biology*
821 10:e1001330.

822 Leal Filho, W., G. J. Nagy, A. F. F. Setti, A. Sharifi, F. K. Donkor, K. Batista, and I. Djekic. 2023.
823 Handling the impacts of climate change on soil biodiversity. *Science of The Total Environment*
824 869:161671.

825 Lee, H. H., M. N. Molla, C. R. Cantor, and J. J. Collins. 2010. Bacterial charity work leads to
826 population-wide resistance. *Nature* 467:82–85.

827 Leinweber, A., R. Fredrik Inglis, and R. Kümmerli. 2017. Cheating fosters species co-existence in
828 well-mixed bacterial communities. *The ISME Journal* 11:1179–1188.

829 Li, G., Y. Wang, H. Li, X. Zhang, and J. Gong. 2023. Quantifying relative contributions of biotic
830 interactions to bacterial diversity and community assembly by using community characteristics of
831 microbial eukaryotes. *Ecological Indicators* 146:109841.

832 Li, H., D. Huo, W. Wang, Y. Chen, X. Cheng, G. Yu, and R. Li. 2020. Multifunctionality of biocrusts is
833 positively predicted by network topologies consistent with interspecies facilitation. *Molecular*
834 *Ecology* 29:1560–1573.

835 Li, M., Z. Wei, J. Wang, A. Jousset, V.-P. Friman, Y. Xu, Q. Shen, and T. Pommier. 2018. Facilitation
836 promotes invasions in plant-associated microbial communities. *Ecology Letters* 22:149–158.

837 Li, X., D. Meng, J. Li, H. Yin, H. Liu, X. Liu, C. Cheng, Y. Xiao, Z. Liu, and M. Yan. 2017. Response of
838 soil microbial communities and microbial interactions to long-term heavy metal contamination.
839 *Environmental Pollution* 231:908–917.

840 Liao, C., T. Wang, S. Maslov, and J. B. Xavier. 2020. Modeling microbial cross-feeding at intermediate
841 scale portrays community dynamics and species coexistence. *bioRxiv*:2020.02.19.956383.

842 Lin, X. B., T. Wang, P. Stothard, J. Corander, J. Wang, J. F. Baines, S. C. L. Knowles, L. Baltrūnaitė, G.
843 Tasseva, R. Schmaltz, S. Tollenaar, L. A. Cody, T. Grenier, W. Wu, A. E. Ramer-Tait, and J. Walter.
844 2018. The evolution of ecological facilitation within mixed-species biofilms in the mouse
845 gastrointestinal tract. *The ISME Journal* 12:2770–2784.

846 Little, A. E. F., C. J. Robinson, S. B. Peterson, K. F. Raffa, and J. Handelsman. 2008. Rules of
847 Engagement: Interspecies Interactions that Regulate Microbial Communities. *Annual Review of*
848 *Microbiology* 62:375–401.

849 Liu, H., C. A. Macdonald, J. Cook, I. C. Anderson, and B. K. Singh. 2019. An Ecological Loop: Host
850 Microbiomes across Multitrophic Interactions. *Trends in Ecology & Evolution* 34:1118–1130.

851 Liu, J., A. Prindle, J. Humphries, M. Gabalda-Sagarra, M. Asally, D. D. Lee, S. Ly, J. Garcia-Ojalvo, and
852 G. M. Süel. 2015. Metabolic co-dependence gives rise to collective oscillations within biofilms.
853 *Nature* 523:550–554.

854 Liu, S., H. Yu, Y. Yu, J. Huang, Z. Zhou, J. Zeng, P. Chen, F. Xiao, Z. He, and Q. Yan. 2022. Ecological
855 stability of microbial communities in Lake Donghu regulated by keystone taxa. *Ecological Indicators*
856 136:108695.

857 Löder, M. G. J., M. Boersma, A. C. Kraberg, N. Aberle, and K. H. Wiltshire. 2014. Microbial predators
858 promote their competitors: commensalism within an intra-guild predation system in
859 microzooplankton. *Ecosphere* 5:art128.

860 Lozupone, C. A., and R. Knight. 2007. Global patterns in bacterial diversity. *Proceedings of the*
861 *National Academy of Sciences* 104:11436–11440.

862 Ma, B., Y. Wang, S. Ye, S. Liu, E. Stirling, J. A. Gilbert, K. Faust, R. Knight, J. K. Jansson, C. Cardona, L.
863 Röttgers, and J. Xu. 2020a. Earth microbial co-occurrence network reveals interconnection pattern
864 across microbiomes. *Microbiome* 8:82.

865 Ma, J., Y. Lu, F. Chen, X. Li, D. Xiao, and H. Wang. 2020b. Molecular Ecological Network Complexity
866 Drives Stand Resilience of Soil Bacteria to Mining Disturbances among Typical Damaged
867 Ecosystems in China. *Microorganisms* 8:433.

868 Machado, D., O. M. Maistrenko, S. Andrejev, Y. Kim, P. Bork, K. R. Patil, and K. R. Patil. 2021.
869 Polarization of microbial communities between competitive and cooperative metabolism. *Nature*
870 *Ecology & Evolution* 5:195–203.

871 Madsen, J. S., H. L. Røder, J. Russel, H. Sørensen, M. Burmølle, and S. J. Sørensen. 2016.
872 Coexistence facilitates interspecific biofilm formation in complex microbial communities.
873 *Environmental Microbiology* 18:2565–2574.

874 Maestre, F. T., I. Martínez, C. Escolar, and A. Escudero. 2009. On the relationship between abiotic
875 stress and co-occurrence patterns: an assessment at the community level using soil lichen
876 communities and multiple stress gradients. *Oikos* 118:1015–1022.

877 Mandakovic, D., C. Aguado-Norese, B. García-Jiménez, C. Hodar, J. E. Maldonado, A. Gaete, M.
878 Latorre, M. D. Wilkinson, R. A. Gutiérrez, L. A. Cavieres, J. Medina, V. Cambiazo, and M. Gonzalez.

879 2023. Testing the stress gradient hypothesis in soil bacterial communities associated with
880 vegetation belts in the Andean Atacama Desert. *Environmental Microbiome* 18:24.

881 Maron, P.-A., A. Sarr, A. Kaisermann, J. Lévêque, O. Mathieu, J. Guigue, B. Karimi, L. Bernard, S.
882 Dequiedt, S. Terrat, A. Chabbi, and L. Ranjard. 2018. High Microbial Diversity Promotes Soil
883 Ecosystem Functioning. *Applied and Environmental Microbiology* 84:e02738-17.

884 Martin, M., T. Hölscher, A. Dragoš, V. S. Cooper, and Á. T. Kovács. 2016. Laboratory Evolution of
885 Microbial Interactions in Bacterial Biofilms. *Journal of Bacteriology* 198:2564–2571.

886 Martino, R. D., A. Picot, and S. Mitri. 2023, May 24. Oxidative stress changes interactions between
887 two bacterial species. *bioRxiv*.

888 Martiny, J. B. H., B. J. M. Bohannan, J. H. Brown, R. K. Colwell, J. A. Fuhrman, J. L. Green, M. C.
889 Horner-Devine, M. Kane, J. A. Krumins, C. R. Kuske, P. J. Morin, S. Naeem, L. Øvreås, A.-L.
890 Reysenbach, V. H. Smith, and J. T. Staley. 2006. Microbial biogeography: putting microorganisms on
891 the map. *Nature Reviews Microbiology* 4:102–112.

892 Matchado, M. S., M. Lauber, S. Reitmeier, T. Kacprowski, J. Baumbach, D. Haller, and M. List. 2021.
893 Network analysis methods for studying microbial communities: A mini review. *Computational and*
894 *Structural Biotechnology Journal* 19:2687–2698.

895 Matz, C., and S. Kjelleberg. 2005. Off the hook – how bacteria survive protozoan grazing. *Trends in*
896 *Microbiology* 13:302–307.

897 Mawarda, P. C., X. Le Roux, J. Dirk van Elsas, and J. F. Salles. 2020. Deliberate introduction of
898 invisible invaders: A critical appraisal of the impact of microbial inoculants on soil microbial
899 communities. *Soil Biology and Biochemistry* 148:107874.

900 McCarty, N. S., and R. Ledesma-Amaro. 2019. Synthetic Biology Tools to Engineer Microbial
901 Communities for Biotechnology. *Trends in Biotechnology* 37:181–197.

902 McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New*
903 *Phytologist* 201:403–416.

904 Menéndez-Serra, M., V. J. Ontiveros, A. Barberán, and E. O. Casamayor. 2022. Absence of stress-
905 promoted facilitation coupled with a competition decrease in the microbiome of ephemeral saline
906 lakes. *Ecology* 103:e3834.

907 Metz, T., N. Blüthgen, and B. Drossel. 2023. Shifts from non-obligate generalists to obligate
908 specialists in simulations of mutualistic network assembly. *Oikos* n/a:e09697.

909 Meyer, K. M., H. Memiaghe, L. Korte, D. Kenfack, A. Alonso, and B. J. M. Bohannan. 2018. Why do
910 microbes exhibit weak biogeographic patterns? *The ISME Journal* 12:1404–1413.

911 Michalet, R., Y. L. Bagousse-Pinguet, J.-P. Maalouf, and C. J. Lortie. 2014. Two alternatives to the
912 stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from
913 facilitation to competition. *Journal of Vegetation Science* 25:609–613.

914 Miele, V., C. Guill, R. Ramos-Jiliberto, and S. Kéfi. 2019. Non-trophic interactions strengthen the
915 diversity—functioning relationship in an ecological bioenergetic network model. *PLOS*
916 *Computational Biology* 15:e1007269.

917 Morris, B. E. L., R. Henneberger, H. Huber, and C. Moissl-Eichinger. 2013. Microbial syntrophy:
918 interaction for the common good. *FEMS Microbiology Reviews* 37:384–406.

919 Morris, J. J., R. Kirkegaard, M. J. Szul, Z. I. Johnson, and E. R. Zinser. 2008. Facilitation of Robust
920 Growth of *Prochlorococcus* Colonies and Dilute Liquid Cultures by “Helper” Heterotrophic
921 Bacteria. *Applied and Environmental Microbiology* 74:4530–4534.

922 Morueta-Holme, N., B. Blonder, B. Sandel, B. J. McGill, R. K. Peet, J. E. Ott, C. Violle, B. J. Enquist, P.
923 M. Jørgensen, and J.-C. Svenning. 2016. A network approach for inferring species associations from
924 co-occurrence data. *Ecography* 39:1139–1150.

925 Navarro-Cano, J. A., M. Goberna, and M. Verdú. 2021. Facilitation enhances ecosystem function
926 with non-random species gains. *Oikos* 130:2093–2099.

927 Naylor, D., N. Sadler, A. Bhattacharjee, E. B. Graham, C. R. Anderton, R. McClure, M. Lipton, K. S.
928 Hofmockel, and J. K. Jansson. 2020. Soil Microbiomes Under Climate Change and Implications for
929 Carbon Cycling. *Annual Review of Environment and Resources* 45:29–59.

930 Niehaus, L., I. Boland, M. Liu, K. Chen, D. Fu, C. Henckel, K. Chaung, S. E. Miranda, S. Dyckman, M.
931 Crum, S. Dedrick, W. Shou, and B. Momeni. 2019. Microbial coexistence through chemical-
932 mediated interactions. *Nature Communications* 10:2052.

933 O’Brien, S., A. M. Luján, S. Paterson, M. A. Cant, and A. Buckling. 2017. Adaptation to public goods
934 cheats in *Pseudomonas aeruginosa*. *Proceedings of the Royal Society B: Biological Sciences*
935 284:20171089.

936 Oña, L., S. Giri, N. Avermann, M. Kreienbaum, K. M. Thormann, and C. Kost. 2021. Obligate cross-
937 feeding expands the metabolic niche of bacteria. *Nature Ecology & Evolution* 5:1224–1232.

938 Pacheco, A. R., M. Moel, and D. Segrè. 2019. Costless metabolic secretions as drivers of
939 interspecies interactions in microbial ecosystems. *Nature Communications* 10:103.

940 Pacheco, A. R., C. Pauvert, D. Kishore, and D. Segrè. 2022. Toward FAIR Representations of
941 Microbial Interactions. *mSystems* 7:e00659-22.

942 Palmer, J. D., and K. R. Foster. 2022. Bacterial species rarely work together. *Science* 376:581–582.

943 Pascual-García, A., S. Bonhoeffer, and T. Bell. 2020. Metabolically cohesive microbial consortia and
944 ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*
945 375:20190245.

946 Pashirzad, M., H. Ejtehadi, J. Vaezi, and R. P. Shefferson. 2019. Plant–plant interactions influence
947 phylogenetic diversity at multiple spatial scales in a semi-arid mountain rangeland. *Oecologia*
948 189:745–755.

949 Paustian, K., J. Lehmann, S. Ogle, D. Reay, G. P. Robertson, and P. Smith. 2016. Climate-smart soils.
950 *Nature* 532:49–57.

951 Pekkonen, M., and J. T. Laakso. 2012. Temporal changes in species interactions in simple aquatic
952 bacterial communities. *BMC Ecology* 12:18.

953 Pérez Castro, S., E. E. Cleland, R. Wagner, R. A. Sawad, and D. A. Lipson. 2019. Soil microbial
954 responses to drought and exotic plants shift carbon metabolism. *The ISME Journal* 13:1776–1787.

955 Pérez-Valera, E., M. Goberna, K. Faust, J. Raes, C. García, and M. Verdú. 2017. Fire modifies the
956 phylogenetic structure of soil bacterial co-occurrence networks. *Environmental Microbiology*
957 19:317–327.

958 Philippot, L., B. S. Griffiths, and S. Langenheder. 2021. Microbial Community Resilience across
959 Ecosystems and Multiple Disturbances. *Microbiology and Molecular Biology Reviews* 85:e00026-
960 20.

961 Piccardi, P., G. Alberti, J. M. Alexander, and S. Mitri. 2022. Microbial invasion of a toxic medium is
962 facilitated by a resident community but inhibited as the community co-evolves. *The ISME Journal*
963 16:2644–2652.

964 Piccardi, P., B. Vessman, and S. Mitri. 2019. Toxicity drives facilitation between 4 bacterial species.
965 *Proceedings of the National Academy of Sciences* 116:15979–15984.

966 Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs
967 associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.

968 Pradeep Ram, A. S., J. Keshri, and T. Sime-Ngando. 2020. Differential impact of top-down and
969 bottom-up forces in structuring freshwater bacterial communities. *FEMS Microbiology Ecology*
970 96:fiaa005.

971 Prashar, P., N. Kapoor, and S. Sachdeva. 2014. Rhizosphere: its structure, bacterial diversity and
972 significance. *Reviews in Environmental Science and Bio/Technology* 13:63–77.

973 Prosser, J. I., B. J. M. Bohannan, T. P. Curtis, R. J. Ellis, M. K. Firestone, R. P. Freckleton, J. L. Green, L.
974 E. Green, K. Killham, J. J. Lennon, A. M. Osborn, M. Solan, C. J. van der Gast, and J. P. W. Young.
975 2007. The role of ecological theory in microbial ecology. *Nature Reviews Microbiology* 5:384–392.

976 van der Putten, W. H., J. N. Klironomos, and D. A. Wardle. 2007. Microbial ecology of biological
977 invasions. *The ISME Journal* 1:28–37.

978 Qian, J. J., and E. Akçay. 2020. The balance of interaction types determines the assembly and
979 stability of ecological communities. *Nature Ecology & Evolution* 4:356–365.

980 Ramette, A., and J. M. Tiedje. 2007. Biogeography: An Emerging Cornerstone for Understanding
981 Prokaryotic Diversity, Ecology, and Evolution. *Microbial Ecology* 53:197–207.

982 Ratzke, C., J. Barrere, and J. Gore. 2020. Strength of species interactions determines biodiversity
983 and stability in microbial communities. *Nature Ecology & Evolution* 4:376–383.

984 Reichenbach, H. 1993. Myxobacteria II. Page (M. Dworkin and D. Kaiser, Eds.). *Am. Soc. Microbiol.*,
985 Washington, DC.

- 986 Richardson, D. M., N. Allsopp, C. M. D'antonio, S. J. Milton, and M. Rejmánek. 2000. Plant invasions
987 – the role of mutualisms. *Biological Reviews* 75:65–93.
- 988 Riesenfeld, C. S., P. D. Schloss, and J. Handelsman. 2004. Metagenomics: Genomic Analysis of
989 Microbial Communities. *Annual Review of Genetics* 38:525–552.
- 990 Rodríguez-Echeverría, S., Y. M. Lozano, and R. D. Bardgett. 2016. Influence of soil microbiota in
991 nurse plant systems. *Functional Ecology* 30:30–40.
- 992 Rodríguez-Verdugo, A., and M. Ackermann. 2021. Rapid evolution destabilizes species interactions
993 in a fluctuating environment. *The ISME Journal* 15:450–460.
- 994 Rosenzweig, R., U. Shavit, and A. Furman. 2012. Water Retention Curves of Biofilm-Affected Soils
995 using Xanthan as an Analogue. *Soil Science Society of America Journal* 76:61–69.
- 996 Saiz, H., Y. L. Bagousse-Pinguet, N. Gross, and F. T. Maestre. 2019. Intransitivity increases plant
997 functional diversity by limiting dominance in drylands worldwide. *Journal of Ecology* 107:240–252.
- 998 Saleem, M., J. Hu, and A. Jousset. 2019. More Than the Sum of Its Parts: Microbiome Biodiversity as
999 a Driver of Plant Growth and Soil Health. *Annual Review of Ecology, Evolution, and Systematics*
1000 50:145–168.
- 1001 Schaedel, M., S. Ishii, H. Wang, R. Venterea, B. Paul, M. Mutimura, and J. Grossman. 2023. Temporal
1002 assessment of N-cycle microbial functions in a tropical agricultural soil using gene co-occurrence
1003 networks. *PLOS ONE* 18:e0281442.
- 1004 Scheuerl, T., J. Cairns, L. Becks, and T. Hiltunen. 2019. Predator coevolution and prey trait variability
1005 determine species coexistence. *Proceedings of the Royal Society B: Biological Sciences*
1006 286:20190245.
- 1007 Schlatter, D., L. Kinkel, L. Thomashow, D. Weller, and T. Paulitz. 2017. Disease Suppressive Soils:
1008 New Insights from the Soil Microbiome. *Phytopathology*® 107:1284–1297.
- 1009 Schleuning, M., E. L. Neuschulz, J. Albrecht, I. M. A. Bender, D. E. Bowler, D. M. Dehling, S. A. Fritz,
1010 C. Hof, T. Mueller, L. Nowak, M. C. Sorensen, K. Böhning-Gaese, and W. D. Kissling. 2020. Trait-
1011 Based Assessments of Climate-Change Impacts on Interacting Species. *Trends in Ecology &*
1012 *Evolution* 35:319–328.
- 1013 Segar, S. T., T. M. Fayle, D. S. Srivastava, T. M. Lewinsohn, O. T. Lewis, V. Novotny, R. L. Kitching, and
1014 S. C. Maunsell. 2020. The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology &*
1015 *Evolution* 35:454–466.
- 1016 Segrè, D., S. Mitri, W. Shou, G. M. Süel, I. Mizrahi, L. Kelly, M. Rebolleda-Gómez, C. Ratzke, C. B.
1017 Ogbunugafor, J. A. Schwartzman, S. Kryazhimskiy, G. E. Leventhal, C. Kost, and T. Bell. 2023. What
1018 do you most want to understand about how collective features emerge in microbial communities?
1019 *Cell Systems* 14:91–97.
- 1020 Seibold, S., M. W. Cadotte, J. S. Maclvor, S. Thorn, and J. Müller. 2018. The Necessity of Multitrophic
1021 Approaches in Community Ecology. *Trends in Ecology & Evolution* 33:754–764.

- 1022 Sfenthourakis, S., E. Tzanatos, and S. Giokas. 2006. Species co-occurrence: the case of congeneric
1023 species and a causal approach to patterns of species association. *Global Ecology and*
1024 *Biogeography* 15:39–49.
- 1025 Sher, D., J. W. Thompson, N. Kashtan, L. Croal, and S. W. Chisholm. 2011. Response of
1026 *Prochlorococcus* ecotypes to co-culture with diverse marine bacteria. *The ISME Journal* 5:1125–
1027 1132.
- 1028 Silveira Martins, S. C., S. T. Santaella, C. M. Martins, and R. P. Martins. 2016. Facilitation as
1029 Attenuating of Environmental Stress among Structured Microbial Populations. *The Scientific World*
1030 *Journal* 2016:e5713939.
- 1031 Simonet, C., and L. McNally. 2021. Kin selection explains the evolution of cooperation in the gut
1032 microbiota. *Proceedings of the National Academy of Sciences* 118.
- 1033 Smit, C., M. Rietkerk, and M. J. Wassen. 2009. Inclusion of biotic stress (consumer pressure) alters
1034 predictions from the stress gradient hypothesis. *Journal of Ecology* 97:1215–1219.
- 1035 Solano, C., M. Echeverez, and I. Lasa. 2014. Biofilm dispersion and quorum sensing. *Current Opinion*
1036 *in Microbiology* 18:96–104.
- 1037 Soliveres, S., L. DeSoto, F. T. Maestre, and J. M. Olano. 2010. Spatio-temporal heterogeneity in
1038 abiotic factors modulate multiple ontogenetic shifts between competition and facilitation.
1039 *Perspectives in Plant Ecology, Evolution and Systematics* 12:227–234.
- 1040 Song, W., B. Wemheuer, P. D. Steinberg, E. M. Marzinelli, and T. Thomas. 2021. Contribution of
1041 horizontal gene transfer to the functionality of microbial biofilm on a macroalgae. *The ISME Journal*
1042 15:807–817.
- 1043 Stachowicz, J. J. 2001. Mutualism, Facilitation, and the Structure of Ecological
1044 Communities Positive interactions play a critical, but underappreciated, role in ecological
1045 communities by reducing physical or biotic stresses in existing habitats and by creating new
1046 habitats on which many species depend. *BioScience* 51:235–246.
- 1047 Stachowicz, J. J., and J. E. Byrnes. 2006. Species diversity, invasion success, and ecosystem
1048 functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors.
1049 *Marine Ecology Progress Series* 311:251–262.
- 1050 Steffan, S. A., Y. Chikaraishi, C. R. Currie, H. Horn, H. R. Gaines-Day, J. N. Pauli, J. E. Zalapa, and N.
1051 Ohkouchi. 2015. Microbes are trophic analogs of animals. *Proceedings of the National Academy of*
1052 *Sciences* 112:15119–15124.
- 1053 Stegen, J. C., X. Lin, A. E. Konopka, and J. K. Fredrickson. 2012. Stochastic and deterministic
1054 assembly processes in subsurface microbial communities. *The ISME Journal* 6:1653–1664.
- 1055 Sun, X., Z. Xu, J. Xie, V. Hesselberg-Thomsen, T. Tan, D. Zheng, M. L. Strube, A. Dragoš, Q. Shen, R.
1056 Zhang, and Á. T. Kovács. 2022. *Bacillus velezensis* stimulates resident rhizosphere *Pseudomonas*
1057 *stutzeri* for plant health through metabolic interactions. *The ISME Journal* 16:774–787.

- 1058 Takami, H., A. Inoue, F. Fuji, and K. Horikoshi. 1997. Microbial flora in the deepest sea mud of the
1059 Mariana Trench. *FEMS Microbiology Letters* 152:279–285.
- 1060 Tan, J., Z. Pu, W. A. Ryberg, and L. Jiang. 2012. Species phylogenetic relatedness, priority effects,
1061 and ecosystem functioning. *Ecology* 93:1164–1172.
- 1062 Thébault, E., and C. Fontaine. 2010. Stability of Ecological Communities and the Architecture of
1063 Mutualistic and Trophic Networks. *Science* 329:853–856.
- 1064 Thiery, S., and C. Kaimer. 2020. The Predation Strategy of *Myxococcus xanthus*. *Frontiers in*
1065 *Microbiology* 11.
- 1066 Thompson, L. R., J. G. Sanders, D. McDonald, A. Amir, J. Ladau, K. J. Locey, R. J. Prill, A. Tripathi, S.
1067 M. Gibbons, G. Ackermann, J. A. Navas-Molina, S. Janssen, E. Kopylova, Y. Vázquez-Baeza, A.
1068 González, J. T. Morton, S. Mirarab, Z. Zech Xu, L. Jiang, M. F. Haroon, J. Kanbar, Q. Zhu, S. Jin Song, T.
1069 Kosciolk, N. A. Bokulich, J. Lefler, C. J. Brislawn, G. Humphrey, S. M. Owens, J. Hampton-Marcell,
1070 D. Berg-Lyons, V. McKenzie, N. Fierer, J. A. Fuhrman, A. Clauset, R. L. Stevens, A. Shade, K. S.
1071 Pollard, K. D. Goodwin, J. K. Jansson, J. A. Gilbert, and R. Knight. 2017. A communal catalogue
1072 reveals Earth’s multiscale microbial diversity. *Nature* 551:457–463.
- 1073 Thurman, L. L., A. K. Barner, T. S. Garcia, and T. Chestnut. 2019. Testing the link between species
1074 interactions and species co-occurrence in a trophic network. *Ecography* 42:1658–1670.
- 1075 Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. *Annual*
1076 *Review of Ecology, Evolution, and Systematics* 45:471–493.
- 1077 Tumolo, B. B., L. Calle, H. E. Anderson, M. A. Briggs, S. Carlson, M. J. MacDonald, J. H. Reinert, and
1078 L. K. Albertson. 2020. Toward spatio-temporal delineation of positive interactions in ecology.
1079 *Ecology and Evolution* 10:9026–9036.
- 1080 Van Meerbeek, K., T. Jucker, and J.-C. Svenning. 2021. Unifying the concepts of stability and
1081 resilience in ecology. *Journal of Ecology* 109:3114–3132.
- 1082 Veech, J. A. 2013. A probabilistic model for analysing species co-occurrence. *Global Ecology and*
1083 *Biogeography* 22:252–260.
- 1084 Velez, P., L. Espinosa-Asuar, M. Figueroa, J. Gasca-Pineda, E. Aguirre-von-Wobeser, L. E. Eguiarte, A.
1085 Hernandez-Monroy, and V. Souza. 2018. Nutrient Dependent Cross-Kingdom Interactions: Fungi
1086 and Bacteria From an Oligotrophic Desert Oasis. *Frontiers in Microbiology* 9.
- 1087 Velicer, G. J. 2003. Social strife in the microbial world. *Trends in Microbiology* 11:330–337.
- 1088 Verwijmeren, M., M. Rietkerk, S. Bautista, A. G. Mayor, M. J. Wassen, and C. Smit. 2014. Drought and
1089 grazing combined: Contrasting shifts in plant interactions at species pair and community level.
1090 *Journal of Arid Environments* 111:53–60.
- 1091 de Vries, F. T., R. I. Griffiths, M. Bailey, H. Craig, M. Girlanda, H. S. Gweon, S. Hallin, A. Kaisermann,
1092 A. M. Keith, M. Kretschmar, P. Lemanceau, E. Lumini, K. E. Mason, A. Oliver, N. Ostle, J. I. Prosser,
1093 C. Thion, B. Thomson, and R. D. Bardgett. 2018. Soil bacterial networks are less stable under
1094 drought than fungal networks. *Nature Communications* 9:3033.

1095 Wagg, C., Y. Hautier, S. Pellkofer, S. Banerjee, B. Schmid, and M. G. van der Heijden. 2021. Diversity
1096 and asynchrony in soil microbial communities stabilizes ecosystem functioning. *eLife* 10:e62813.

1097 Wagg, C., K. Schlaeppli, S. Banerjee, E. E. Kuramae, and M. G. A. van der Heijden. 2019. Fungal-
1098 bacterial diversity and microbiome complexity predict ecosystem functioning. *Nature*
1099 *Communications* 10:4841.

1100 Waite, A. J., and W. Shou. 2012. Adaptation to a new environment allows cooperators to purge
1101 cheaters stochastically. *Proceedings of the National Academy of Sciences* 109:19079–19086.

1102 Wall, D. H., and J. C. Moore. 1999. Interactions Underground: Soil biodiversity, mutualism, and
1103 ecosystem processes. *BioScience* 49:109–117.

1104 Wang, B., X. Wang, Z. Wang, K. Zhu, and W. Wu. 2023. Comparative metagenomic analysis reveals
1105 rhizosphere microbial community composition and functions help protect grapevines against salt
1106 stress. *Frontiers in Microbiology* 14.

1107 Wang, S., X. Wang, X. Han, and Y. Deng. 2018. Higher precipitation strengthens the microbial
1108 interactions in semi-arid grassland soils. *Global Ecology and Biogeography* 27:570–580.

1109 Watnick, P., and R. Kolter. 2000. Biofilm, City of Microbes. *Journal of Bacteriology* 182:2675–2679.

1110 Wei, Z., Y. Gu, V.-P. Friman, G. A. Kowalchuk, Y. Xu, Q. Shen, and A. Jousset. 2019. Initial soil
1111 microbiome composition and functioning predetermine future plant health. *Science Advances*
1112 5:eaaw0759.

1113 Wei, Z., T. Yang, V.-P. Friman, Y. Xu, Q. Shen, and A. Jousset. 2015. Trophic network architecture of
1114 root-associated bacterial communities determines pathogen invasion and plant health. *Nature*
1115 *Communications* 6:8413.

1116 Weiss, A. S., A. G. Burrichter, A. C. Durai Raj, A. von Stempel, C. Meng, K. Kleigrewe, P. C. Münch, L.
1117 Rössler, C. Huber, W. Eisenreich, L. M. Jochum, S. Göing, K. Jung, C. Lincetto, J. Hübner, G. Marinos,
1118 J. Zimmermann, C. Kaleta, A. Sanchez, and B. Stecher. 2022. In vitro interaction network of a
1119 synthetic gut bacterial community. *The ISME Journal* 16:1095–1109.

1120 West, S. A., A. S. Griffin, A. Gardner, and S. P. Diggle. 2006. Social evolution theory for
1121 microorganisms. *Nature Reviews Microbiology* 4:597–607.

1122 Winkler, K. C., A. W. J. van Doorn, and A. F. M. Royers. 1952. Symbiosis of tryptophan-deficient
1123 mutants of *E. coli* B. *Recueil des Travaux Chimiques des Pays-Bas* 71:5–14.

1124 Winogradsky, S. 1890. On the nitrifying organisms. *Sciences* 110:1013–1016.

1125 Wu, G., N. Zhao, C. Zhang, Y. Y. Lam, and L. Zhao. 2021. Guild-based analysis for understanding gut
1126 microbiome in human health and diseases. *Genome Medicine* 13:22.

1127 Wu, Y., P. Cai, X. Jing, X. Niu, D. Ji, N. M. Ashry, C. Gao, and Q. Huang. 2019. Soil biofilm formation
1128 enhances microbial community diversity and metabolic activity. *Environment International*
1129 132:105116.

- 1130 Xiang, Q., D. Zhu, M. Qiao, X.-R. Yang, G. Li, Q.-L. Chen, and Y.-G. Zhu. 2023. Temporal dynamics of
1131 soil bacterial network regulate soil resistomes. *Environmental Microbiology* 25:505–514.
- 1132 Xing, J., X. Jia, H. Wang, B. Ma, J. Falcão Salles, and J. Xu. 2021. The legacy of bacterial invasions on
1133 soil native communities. *Environmental Microbiology* 23:669–681.
- 1134 Xu, M., X. Li, T. W. Kuyper, M. Xu, X. Li, and J. Zhang. 2021. High microbial diversity stabilizes the
1135 responses of soil organic carbon decomposition to warming in the subsoil on the Tibetan Plateau.
1136 *Global Change Biology* 27:2061–2075.
- 1137 Xue, P., B. Minasyan, and A. B. McBratney. 2022. Land-use affects soil microbial co-occurrence
1138 networks and their putative functions. *Applied Soil Ecology* 169:104184.
- 1139 Xun, W., Y. Liu, W. Li, Y. Ren, W. Xiong, Z. Xu, N. Zhang, Y. Miao, Q. Shen, and R. Zhang. 2021.
1140 Specialized metabolic functions of keystone taxa sustain soil microbiome stability. *Microbiome*
1141 9:35.
- 1142 Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating
1143 environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*
1144 96:1463–1468.
- 1145 Yang, D., H. Kato, K. Kawatsu, Y. Osada, T. Azuma, Y. Nagata, and M. Kondoh. 2022. Reconstruction
1146 of a Soil Microbial Network Induced by Stress Temperature. *Microbiology Spectrum* 10:e02748-22.
- 1147 Yang, J., J. W. Kloepper, and C.-M. Ryu. 2009. Rhizosphere bacteria help plants tolerate abiotic
1148 stress. *Trends in Plant Science* 14:1–4.
- 1149 Yang, J. W., W. Wu, C.-C. Chung, K.-P. Chiang, G.-C. Gong, and C. Hsieh. 2018. Predator and prey
1150 biodiversity relationship and its consequences on marine ecosystem functioning—interplay
1151 between nanoflagellates and bacterioplankton. *The ISME Journal* 12:1532–1542.
- 1152 Yang, T., Z. Wei, V.-P. Friman, Y. Xu, Q. Shen, G. A. Kowalchuk, and A. Jousset. 2017. Resource
1153 availability modulates biodiversity-invasion relationships by altering competitive interactions.
1154 *Environmental Microbiology* 19:2984–2991.
- 1155 Yeoh, H. T., H. R. Bungay, and N. R. Krieg. 1968. A microbial interaction involving combined
1156 mutualism and inhibition. *Canadian Journal of Microbiology* 14:491–492.
- 1157 Yuan, M. M., X. Guo, L. Wu, Y. Zhang, N. Xiao, D. Ning, Z. Shi, X. Zhou, L. Wu, Y. Yang, J. M. Tiedje, and
1158 J. Zhou. 2021. Climate warming enhances microbial network complexity and stability. *Nature*
1159 *Climate Change* 11:343–348.
- 1160 Zachar, I., and G. Boza. 2022. The Evolution of Microbial Facilitation: Sociogenesis, Symbiogenesis,
1161 and Transition in Individuality. *Frontiers in Ecology and Evolution* 10.
- 1162 Zélé, F., S. Magalhães, S. Kéfi, and A. B. Duncan. 2018. Ecology and evolution of facilitation among
1163 symbionts. *Nature Communications* 9:1–12.
- 1164 Zengler, K., and L. S. Zaramela. 2018. The social network of microorganisms — how auxotrophies
1165 shape complex communities. *Nature Reviews Microbiology* 16:383–390.

- 1166 Zhang, B., J. Zhang, Y. Liu, P. Shi, and G. Wei. 2018. Co-occurrence patterns of soybean rhizosphere
1167 microbiome at a continental scale. *Soil Biology and Biochemistry* 118:178–186.
- 1168 Zhang, L., B. Wang, and L. Qi. 2017. Phylogenetic relatedness, ecological strategy, and stress
1169 determine interspecific interactions within a salt marsh community. *Aquatic Sciences* 79:587–595.
- 1170 Zhang, L.-M., M. Wang, J. I. Prosser, Y.-M. Zheng, and J.-Z. He. 2009. Altitude ammonia-oxidizing
1171 bacteria and archaea in soils of Mount Everest. *FEMS Microbiology Ecology* 70:208–217.
- 1172 Zhou, X., M. F. A. Leite, Z. Zhang, L. Tian, J. Chang, L. Ma, X. Li, J. A. van Veen, C. Tian, and E. E.
1173 Kuramae. 2021. Facilitation in the soil microbiome does not necessarily lead to niche expansion.
1174 *Environmental Microbiome* 16:4.
- 1175 Zuñiga, C., C.-T. Li, G. Yu, M. M. Al-Bassam, T. Li, L. Jiang, L. S. Zaramela, M. Guarnieri, M. J.
1176 Betenbaugh, and K. Zengler. 2019. Environmental stimuli drive a transition from cooperation to
1177 competition in synthetic phototrophic communities. *Nature Microbiology* 4:2184–2191.
- 1178