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Forum

The underground network: facilitation in soil bacteria

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

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

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Introduction

'Natural, unconscious mutualism is one of the basic principles of biology'.

W. C. Allee in 'Principles of animal ecology', 1949.

Soil bacterial communities are integral parts of almost all of earth's ecosystems, from sediments in the deepest marine trenches to soils on the highest mountains (Takami et al. 1997, Zhang et al. 2009). As fundamental links in the soil–plant interface and chemical pumps for the nitrogen and carbon cycles (Prashar et al. 2014, Naylor et al. 2020, Domeignoz-Horta et al. 2020), the importance of soil bacteria for life on earth is hard to overstate. Mirroring Darwin's observations on plant communities, repeated evidence has identified soil bacterial diversity as an essential driver of ecosystem functioning (Finlay et al. 1997, Delgado-Baquerizo et al. 2017). Soil bacterial diversity ultimately facilitates many aspects of plant growth (Hayat et al. 2010), survival (Wei et al. 2019) and fertility (Chaparro et al. 2012), and influences atmospheric processes through reducing greenhouse gas emissions and sequestering CO_2 thereby directly impacting human survival and well-being (Paustian et al. 2016). Further, the loss of bacterial diversity can impact large-scale ecosystem processes such as carbon cycling capabilities of soils in a wide range of ecosystems (de Graaff et al. 2015). Our understanding of the relationship between bacterial diversity and soil function continues to improve (Wagg et al. 2019), but studies so far have overlooked the role of biotic interactions in structuring bacterial communities (Horner-Devine et al. 2004, Abdul Rahman et al. 2021).

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

Interactions can be mutually (+/+) or asymmetrically (+/0) positive, and both types are more broadly referred to as facilitation. The most cited definition of facilitation in community ecology requires a positive effect on a single species' establishment, growth, or recruitment without negatively impacting the other (e.g. Bertness and Callaway 1994, and more specifically in Bronstein 2009). While exploitation or parasitism (+/−) may see one species' growth being facilitated by the presence of another (Kehe et al. 2021), these interactions are typically grouped outside of ecological facilitation in the literature (Stachowicz 2001). Facilitation has been shown to have important effects on community structure and functioning in a variety of bacterial communities and can occur both intra- and interspecifically (Miele et al. 2019, Navarro-Cano et al. 2021). Intra-species facilitation, for example in *Myxococcus* strains, can lead to complex emergent effects that provide function and alter community structure in a multicellular community. These populations collectively excrete enzymes to kill 'prey', including larger eukaryotes, a phenomenon referred to as social 'predation' (Contreras-Moreno et al. 2024); and they are also well known for their aggregated fruiting body formation under environmental stress, in which different individuals specialize to facilitate resistant spore development (Reichenbach 1993). Examples of interspecific facilitation are seen when species defend themselves and other community members against *Myxococcus* predation, by contributing to biofilm formation and through the production of antimicrobial chemicals (Thiery and Kaimer 2020). The bacterial world is full of other examples, where direct, pairwise facilitation benefits growth of bacterial strains (Ferrier et al. 2002, Morris et al. 2008, Pekkonen and Laakso 2012), confers benefits in dealing with environmental stress (Silveira Martins et al. 2016) and structures entire communities and maintains biodiversity (Kaeberlein et al. 2002, Niehaus et al. 2019). Facilitation can also be indirect or context-dependent, and higher order interactions may be important for diversity and resulting ecosystem functions (Bairey et al. 2016). In bacterial soil communities, relatively little is known about the effects of facilitation on community structure, functions and response to global change.

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

When investigated, facilitation in soil bacteria is often demonstrated to have important consequences for the larger soil community, including eukaryotic structure and function (Rodríguez-Echeverría et al. 2016), and plays a role in the mediation of stressful conditions induced by climate change (David et al. 2020, Yuan et al. 2021). Bacterial soil community interactions are thus intrinsically linked to the functioning and resilience of whole ecosystems. Here, we argue that soil bacterial communities are an underutilized study system for investigating the importance of facilitation in complex natural systems, and we show how their study can help advance our understanding of the way interactions affect the responses of these systems to global change. Specifically, understanding the role of facilitation on emergent properties of soil systems requires adopting a broader ecological framework, which could prove crucial for predicting the effects of global change in both soils and ecosystems more generally.

Prevalence of bacterial facilitation in culture and nature

Microcosm studies have provided evidence for the existence of bacterial facilitation since the development of this field of study. The seminal work by Winogradsky (1890) on nitrifying organisms first showed how bacteria may depend on the metabolic product produced by another organism. Later, microcosms continued laying the groundwork of such resource-sharing mechanisms, by which bacteria may grow on otherwise nutrient-deficient media (Winkler et al. 1952). This bacterial ‘cross-feeding’ exists in many forms and has long been shown as a requirement for the establishment of some species in microcosm (Yeoh et al. 1968). These examples of cross-feeding are now understood to be more energetically efficient and lead to higher growth rates (Costa et al. 2006). Bacterial species that evolve complementary resource-use strategies may make use of available waste products in co-culture, ultimately resulting in higher productivity than in monoculture (Lawrence et al. 2012). It is noteworthy that these studies elucidating the mechanisms underlying facilitation have been limited to the investigation of pairwise bacterial interactions. In complex bacterial communities, facilitative relationships between species are not fixed and consist of a dynamic interplay between different species and genotypes (Velicer 2003). To understand the importance of facilitative interactions in bacterial communities, more studies in the complex conditions of the natural world are needed (Little et al. 2008, Kodera et al. 2022).

Natural soil communities consist of bacterial species constantly interacting with each other, and intra- and interspecific relationships are mediated by the abilities of species to communicate with and regulate each other (West et al. 2006). Bacteria that competitively exclude one another in isolated co-culture may instead co-exist in more complex communities (Chang et al. 2023). For example, in natural soils bacteria commonly aggregate in biofilms and thus form intricate ecological and social networks that express many facilitative functions (Watnick and Kolter 2000, Solano et al. 2014). Protection from trophic pressures (Matz and Kjelleberg 2005, Justice et al. 2008), UV-radiation (Córdova-Alcántara et al. 2019) or desiccation (Rosenzweig et al. 2012) are commonly associated with biofilm formation of bacteria, all underlaid by community interactions (Zachar and Boza 2022). Public good production is also required to lay the groundwork for biofilm formation and is further promoted inside closely interacting biofilm communities (Flemming and Wingender 2010, Liu et al. 2015). Biofilms thus represent, essentially, a mediation of the environment, whether resource-based or through other compounds, which is a common way for bacterial organisms to make new niche space available and increase the diversity and productivity of ecosystems (Oña et al. 2021). Biofilms also create a space for rapid bacterial evolution through the facilitation of horizontal gene transfer (Song et al. 2021), and they facilitate the dispersal of biofilm members to novel environments (Kaplan and Fine 2002). Biofilm formation itself is even inherently dependent on facilitative processes such as polymer excretions and metabolic dependencies, but they also form a battleground for bacterial competition (Huang et al. 2011, Giaouris et al. 2015). A relevant ecological question thus becomes: how are interaction types influenced by environmental conditions?

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

Bacterial facilitation in changing environments

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

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

Naturally occurring soil bacterial communities are increasingly recognized as a model for the study of the SGH, because of their ubiquity (Finlay 2002), large range of potential functions (Finlay et al. 1997), the ease of replication to study evolutionary and ecological time scales (Kayser et al. 2018) and their use as an analog for other biota (Steffan et al. 2015). Soil bacterial communities have been used to study interaction networks in the context of environmental stress, pressures, and climate change (Yuan et al. 2021, Yang et al. 2022). Support for the SGH within soil bacterial communities is found when the effects of holistic stress gradients (Hernandez et al. 2021, Mandakovic et al. 2023) or an investigation of different stressors (Zhou et al. 2021) are considered, both mimicking the potential effects of broader global change on soil communities. Narrower environmental gradients such as salinity (Menéndez-Serra et al. 2022) or drought (Gao et al. 2022) may find more conflicting results where different bacterial groups exhibit more variable responses. Collapse of facilitation under high environmental stress is shown in soil bacteria as in other systems (Wang et al. 2018), and drought is frequently reported as a driving environmental control of interaction strengths (de Vries et al. 2018, Gao et al. 2022). However, it is not well known how global change may influence soil interaction networks generally, and many studies continue to underreport the interplay between environment and interaction types in soil bacterial communities. Meanwhile, the data and methods are available and often already included in their analyses, yet they fall short in their application within a coherent ecological framework (Ma et al. 2020a, Feng et al. 2024).

How to investigate bacterial facilitation in the natural world

The arrival of high-throughput nucleic acid sequencing has offered unique advantages in the study of natural bacterial communities (Hugenholtz et al. 1998, Lozupone and Knight 2007) and their relationship to environmental pressures (Fierer and Jackson 2006). 16S rRNA or similar genetic markers enable profiling techniques that are extremely useful for rapidly and comprehensively mapping the structure and diversity of bacterial communities in soils (Thompson et al. 2017). These data readily supply community ecologists with species co-occurrence matrices used to infer the strength and direction of interactions between species using co-occurrence methods (Sfenthourakis et al. 2006, Veech 2013. Such co-occurrence methods may include environmental and spatial data to control for the potential effects of these processes and more accurately reflect real biotic interactions (D'Amen et al. 2018), or indirect interactions between associated species (Morueta-Holme et al. 2016). Compared to other ecological systems, bacterial soil communities have the added benefit of cosmopolitan ranges and high dispersal while simultaneously exhibiting biogeographic species fluctuations (Martiny et al. 2006, Ramette and Tiedje 2007, Meyer et al. 2018), allowing for better inference of species' interactions from co-occurrences. Many studies have emerged over the last years inferring interaction networks from soil community metagenomic data with varying degrees of success (Matchado et al. 2021). However, many studies present genetically inferred interaction networks without a clear ecological framework to interpret those results and the drawbacks of using co-occurrence data to infer interaction types is frequently noted (Barner et al. 2018, Blanchet et al. 2020).

Marker-gene based co-occurrence network approaches are thus regularly, and justly, criticized for poorly reflecting known species' ecologies (Freilich et al. 2018). However, because metagenomic datasets generate phylogenetically relevant information about investigated bacteria, this information may increase the confidence of inferred interaction types assigned through these co-occurence methods (Goberna et al. 2019). Closely phylogenetically related bacteria are more likely to exhibit competitive interactions in the same ecosystem (Tan et al. 2012). Therefore, comparing the phylogenetic diversity within ecosystems may help measure the prevalence of competitive interactions in that ecosystem (Stegen et al. 2012). Evidence for this theory, called niche conservatism, has broad application across the tree of life for bacteria and archaea and may increase the confidence of assigning species interactions based on co-occurrence data (Goberna and Verdú 2016).

Using phylogenetically informed co-occurrence networks allows researchers to investigate larger conceptual patterns (Goberna and Verdú 2022). Updated frameworks that build on these association methods can further improve detection of interactions by using ecological information about species' traits with better a predictive power than phylogenetic information alone (Kéfi et al. 2016, Alneberg et al. 2020). Studies on bacteria using such trait- (Metz et al. 2023, Wang et al. 2023) and gene-based network methods to infer interaction types (Schaedel et al. 2023) may also help gain information about indirect and non-linear interaction types amongst community members that might not be revealed by a co-occurrence matrix alone (Saiz et al. 2019). Combined methods using these trait-based approaches allow a fuller understanding of the spatial and temporal variation in facilitating relationships (Tumolo et al. 2020), such as joint species distribution models (D'Amen et al. 2018). Network models may also confirm known interactions and reveal previously undiscovered associations between species encompassing both trophic and non-trophic interactions (Thurman et al. 2019). Using models to assess complex interaction webs such as metabolic dependencies and grounding them with empirical data thus confirms underlying relationships (Liao et al. 2020) even when the microbial species investigated aren't always culturable or their metabolisms known (Lam et al. 2020). Promisingly, studies that do consider specific functional groups find a high interaction strength of potential facilitators (Chao et al. 2016) – though these studies, in turn, often refrain from putting such results in a broader ecological framework – hampering our ability to elucidate conclusions applicable to other systems.

To investigate the relationship between bacterial facilitation and the environment in a broader ecological framework, networks need to be examined comparatively and incorporate environmental information. Different environments exhibit broader phylogenetic diversity in bacterial communities (Goberna et al. 2014) or may directly influence the prevalence of certain interaction types (Piccardi et al. 2019). Coupled with phylogenetic information, network data may infer the overdispersion of taxonomic diversity and overall richness as a proxy for the strength of facilitative interactions in different environments (Goberna and Verdú 2016). Future research needs to emphasize fine-scale environmental information relevant to the bacterial communities studied to understand its relationship to community interactions and the potential collapse of bacterial networks under environmental stress (Michalet et al. 2014). Alternatively, facilitation may be studied directly in the metagenome of whole communities by looking at cooperative genes (Simonet and McNally 2021). Different approaches may reinforce one another by basing the assumptions on community-level interactions inferred from phylogenetic data on evidence from pairwise-experiments and validating those experiments by assessing natural and heterogeneous communities. These resulting predictions will ultimately be helpful to understand macroecological processes and understanding the evolutionary pressures that shape interaction networks (Segar et al. 2020, Hall et al. 2020). The relationships between community composition, interaction types and the environment were tested predominantly in plant communities (Carrión et al. 2017, Zhang et al. 2017, Pashirzad et al. 2019) and are also coming to the foreground in research on soil bacteria (Stegen et al. 2012, Pérez-Valera et al. 2017). As these models improve, they need to be used to address such fundamental relationships between community interactions and the environment and can be used to synthesize the role of bacterial communities in whole-system interactions.

Moving to a multi-trophic framework remains a pressing challenge for many investigations of community or ecosystem structure (Seibold et al. 2018, Schleuning et al. 2020). Without a doubt, soil bacterial community structure and interactions have immense consequences for other organisms, whether below-ground as pathogens or mutualists in the rhizosphere (Schlatter et al. 2017), above-ground biomass of plants (Saleem et al. 2019) and indirect effects on nutrient cycling (Dubey et al. 2019). Bacterial communities may be shaped by the interactions of other microbial trophic levels through parasitism or grazing (Li et al. 2023), while bacterial communities themselves may facilitate plant germination in harsher environments (David et al. 2020). Indirect facilitative effects may arise through intertrophic interactions and increase both bacterial diversity (Pradeep Ram et al. 2020), as well as that of their predators (Yang et al. 2018, Scheuerl et al. 2019) and plants (Liu et al. 2019) through evolutionary pressures. Plants might benefit from soil bacteria feedbacks under drought (Buchenau et al. 2022), while plant responses to environmental changes further drive bacterial community structure and thus potential interactions (Koyama et al. 2018). Plant-growth-promoting bacteria can mitigate the effects of environmental stress on plants (Yang et al. 2009), but this may also negatively affect resident communities when they favor establishment of invaders (Zhang et al. 2018). A large range of potential mechanisms for facilitation thus exists between these trophic levels, whether nutrient-, water-, immune-mediating- or micro-climate related. A better understanding of the role of interactions in structuring these soil communities can help elucidate ecologically important emergent properties of those systems, such as community functioning, stability or resilience (van den Berg et al. 2022).

Facilitation's effect on emergent properties

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

Productivity and other functions

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

Diversity and stability

Facilitation has been found to be an important driver of biodiversity in plant communities (Navarro-Cano et al. 2021), promoting coexistence both mechanistically and evolutionarily (McIntire and Fajardo 2014). Facilitation in bacterial communities may directly increase species diversity by creating niche space for whole metabolic consortia (Pascual-García et al. 2020) or cheaters (Leinweber et al. 2017) and is often observed specifically in cases such as biofilm formation (Wu et al. 2019). Evidence for increased stability of more diverse bacterial communities may be found when considering their susceptibility to invasions in microcosms (Hodgson et al. 2002, Eisenhauer et al. 2012) and reductions of bacterial diversity can lead to a loss of stability in soil communities (Wagg et al. 2021). For instance, invasions of new bacterial groups can change community dynamics and alter community structure (Amor et al. 2020, Mawarda et al. 2020) – an effect to which less biodiverse systems are more susceptible (Xing et al. 2021). Interaction types themselves can influence stability, as stronger competition can decrease stability in bacterial communities (Ratzke et al. 2020). Positive interactions may destabilize bacterial systems by causing dependencies, whereas the negative feedback caused by competitive or exploitative interactions may have a stabilizing effect (Coyte et al. 2015). Theoretical models suggest higher diversity increases community fluctuations but can make facilitating communities more stable depending on the asymmetry and nestedness of their interaction networks – i.e. community structure (Thébault and Fontaine 2010), and experimental studies have confirmed that some of these predictions hold true in microcosms (Hu et al. 2022) and in nature (Liu et al. 2022). Positive correlations between bacterial diversity and ecosystem stability (García-García et al. 2019, Xu et al. 2021) and functions (Delgado-Baquerizo et al. 2017, Maron et al. 2018) may be partially explained by interspecies facilitation leading to complementarity (Tilman et al. 2014). The balance of competitive to facilitative interactions is increasingly found to be an important driver of species coexistence and thus of the relationship between whole-community diversity and stability (Gjini and Madec 2021). Importantly, the broader biotic and abiotic environment is thought to drive the relationship between strength of facilitative networks and community stability (De Vries and Shade 2013) and this relationship is not stable under changing environments (Yuan et al. 2021), which makes understanding these relationships ever more relevant in the face of increasing challenges posed by climate change.

Climate resilience

The functional resilience of soil bacterial communities is driven by both the physico-chemical environment and the resulting community structure (Griffiths et al. 2007). Keystone species within interaction networks can contribute significantly to the community's overall resilience to disturbances (Ma et al. 2020b). Predominant interaction types across a whole community may influence their resilience, such as a decreased impact of nutrient stress on highly facilitative communities (Machado et al. 2021). Conversely, highly competitive communities may be less resistant to environmental fluctuations (Ratzke et al. 2020). More phylogenetically and taxonomically diverse communities, implying more potential facilitative links, indeed show higher overall resilience to environmental stress in one study (Xun et al. 2021). Co-occurrence networks may be strengthened under drought stress and thus promote community resilience (Wu et al. 2019), but some bacterial communities show that highly connected co-occurrence networks can break down under drought stress (de Vries et al. 2018). Overall, experimental evidence for the relationship between community interaction types and resilience is rare (Philippot et al. 2021), and increased theoretical modelling efforts may provide better answers (van den Berg et al. 2022). Increased diversity due to facilitation promoting coexistence may have beneficial effects on bacterial community resilience (Yachi and Loreau 1999, Xu et al. 2021), but the direct relationship between bacterial facilitation and resilience in the face of climate change is generally poorly understood (Bardgett and Caruso 2020). Environmental changes can further lead to indirect changes in interaction networks, by influencing other groups such as invasive bacteria (Xing et al. 2021) or plants (Pérez Castro et al. 2019) – which may subsequently affect the resilience or other emergent properties of the community.

Resistance to invaders

The increased establishment of invasive species under global warming is a well-known driver of biodiversity loss (Pimentel et al. 2005). In the context of species' interaction networks, new players may drastically alter the existing dynamics of a community and the resulting resistance or resilience of an ecosystem – especially if their traits are different on average (van Kleunen et al. 2010). In soils, bacterial invasions are relatively understudied due to the enormous taxonomic challenges, but microcosm experiments may elucidate some of the general predictions. There is some evidence that highly facilitative communities can be more vulnerable to invaders (Li et al. 2018). Concurrently, higher resident diversity may limit invader success (van Elsas et al. 2012), and tightly interwoven facilitating communities show a higher degree of resistance to invaders (Qian and Akçay 2020, Kurkjian et al. 2021). Interactions with plants and other organisms may further influence the invasibility of bacterial soil communities (Fahey et al. 2020). The relationship of facilitation to community invasion thus depends on a complex interplay between the resident community's existing niche partitions (Wei et al. 2015), environmental conditions (Yang et al. 2017) and species' specific or evolutionary effects (van der Putten et al. 2007, Jousset et al. 2013). The effect of facilitation on such emergent properties has remained a pressing unknown in facilitation research for the last two decades (Richardson et al. 2000, Stachowicz and Byrnes 2006, Li et al. 2018, Piccardi et al. 2022).

Opportunities in bacterial facilitation research

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

Microcosm studies have allowed for the study of drivers of selection in shaping community interaction types (Martin et al. 2016, Kayser et al. 2018) and have immense promise to be engineered in a variety of experimental settings, which can help elucidate ecologically meaningful patterns (Friedman et al. 2017, McCarty and Ledesma-Amaro 2019). They can also be used to create analogs of natural systems to distinguish interactions between all the different players in a bacterial community and investigate emergent properties in controlled settings (Antoniewicz 2020). Pairwise experiments tracking population growth rates can generate hypotheses and ultimately bring to light the mechanisms by which species might interact (Löder et al. 2014), especially across temporal and environmental variation (Coenen et al. 2020). In nature, modern sequencing technologies make it possible to track both population structure and genetic diversity underlying species interactions on a very fine temporal and spatial scale (Sher et al. 2011, Rodríguez-Verdugo and Ackermann 2021). These experiments can also be especially useful to infer the natural parameters used in constructing models of these populations in artificial space (Boza et al. 2023), while the detailed community-level information can address questions about the effects of facilitation on community assembly or structure (Lin et al. 2018). However, to be useful for predicting the relationship between the environment and species interactions such experiments need to take the complexity of natural systems into account, including accounting for spatial and temporal heterogeneity of communities and the more complex context of field studies (Chamberlain et al. 2014, Xiang et al. 2023). The field is currently perfectly poised to combine both approaches to investigate real-world interaction shifts, based on ground-truthed experimental evidence from microcosms (Gralka et al. 2023).

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

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

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Author contributions

Jesse Jorna: Conceptualization (lead); Writing – original draft (lead); Writing – review and editing (lead); **Byron Adams:** Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting); **Zachary Aanderud:** Writing – review and editing (supporting); **Paul Frandsen:** Writing – review and editing (supporting); **Cristina Takacs-Vesbach**: Writing – review and editing (supporting); **Sonia Kéfi:** Conceptualization (equal); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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