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Yang, Pu; van Elsas, Jan Dirk

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Review

Mechanisms and ecological implications of the movement of bacteria in soil

Pu Yang^{a,b}, Jan Dirk van Elsas^{a,*}^a Microbial Ecology Cluster, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands^b College of Life Sciences, Shanxi University, Wucheng Lu No. 92, 030006 Taiyuan, Shanxi Province, China

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ABSTRACT

The extent of translocation of bacteria through soil strongly affects parameters of bacterially-mediated bioremediation and biocontrol. Here, we discuss the main strategies that bacteria use for their dispersal through the soil matrix. Cell dispersal mechanisms are scale-dependent and may be either growth- or cell organelle-driven (active, small scale) or water/wind/vector-organism-driven (passive, large scale). The active modes of dispersal (growth, swimming, swarming and twitching motility) are limited to the scale of (connected) soil pores or aggregates. In contrast, water- or wind-driven transport dominates large-distance bacterial dispersal. Remarkably, the association of bacteria with other (vector) organisms, in particular plant roots, fungal hyphae and moving organisms like earthworms, assists them in the crossing of soil matrix discontinuities. We posit that a dynamic “underground transport web” exists in soil, which is organism- (plant-, fungal- and/or soil animal-) driven. In particular, we examine the role of fungal hyphae as facilitators of short- or long-distance bacterial migration through soil. The transport web thus has strong implications for the occupancy of novel ecological niches and nutrient cycling dynamics. The effects of this underground transport web are examined.

1. Introduction – The importance of bacterial dispersal for differentiation processes and soil functioning

Numerous studies have demonstrated that soil constitutes a key reservoir of biological entities that – together – exhibit enormous diversity. Next to plants and larger soil (in)vertebrates, this reservoir includes populations of bacteria, fungi, protozoa, nematodes, earthworms and arthropods (Bardgett and van der Putten, 2014; Bender et al., 2016). Across this complex biota, bacteria – in the light of their extremely high numbers – stand out as key soil inhabitants. Bacteria are the prime players in the soil biogeochemical cycles, such as those of carbon, nitrogen, sulfur and phosphorus (Long et al., 2016). These cycles are crucial for soil fertility, as they recycle materials and provide nutrients for plant growth. Bacteria are also involved in bioremediation processes in cases of soil pollution. However, due to their small cell sizes, bacteria act within very small spheres of influence (Kuzakov and Blagodatskaya, 2015), requiring dispersal mechanism(s) to broaden their zones of influence across the soil. The nature of the soil matrix clearly places strong limits to bacterial spread (Griffin and Quail, 1968; Vanapalli et al., 1999). We here examine how such bacterial dispersal through soil can take place, i.e. via either active or passive processes, or by a combination of these two.

Depending on nutrient supply (Banitz et al., 2012) and predation pressure (Otto et al., 2017a), active bacterial movement along surfaces

can occur in a variety of ways (Henrichsen, 1972; Jarrell and McBride, 2008). Thus, under proper conditions of nutrient supply, bacteria can actively reach remote sites by: (i) flagellum-driven swimming motility (over a surface with a sufficiently thick fluid film), and/or (ii) swarming motility (at a surface with a limited fluid layer). Often, chemotaxis is involved, determining directional movement (Furuno et al., 2010; Haq et al., 2016). In addition, so-called twitching motility driven by type four pili (T4P) may take place. Twitching is highly localized, as driven by the extension and retraction of T4 pilus proteins. Another type of (pilus/flagellum-independent) movement, called gliding motility, can occur on specific surfaces in the soil matrix. Gliding motility relies on the presence of a focal adhesion complex which allows bacterial cells to glide over a relatively dry, hard surface (Nan and Zusman, 2011). Lastly, researchers have recently found (Park et al., 2015; Shrout, 2015), in experiments on agar surfaces, that bacterial cells can be “pushed” forward by expansive force in a growing colony. In the process, cells delay their timing of septum formation and division, with the concomitant action of surfactants. This type of motility has been denominated sliding motility. Here, one should notice that the active migration processes are energy-expensive, and so particular “nutrient-rich” or “nutrient-sufficient” conditions need to exist in the soil to make active migration successful. Additionally, low levels of predation pressure have been found to promote bacterial translocation along dispersal networks (Otto et al., 2017a). However, it is not yet understood to what

* Corresponding author.

E-mail address: j.d.van.elsas@rug.nl (J.D. van Elsas).

extent and under which conditions this process operates in soil settings; very likely, it is important in short-distance movement.

In addition to the afore-discussed active modes of bacterial cell spread along surfaces, cells can be moved passively in soil, e.g. along with water flowing through soil (Hekman et al., 1995) or even by blowing wind [in dry top soils] (Kellogg and Griffin, 2006). A suite of previous studies and reviews have addressed the translocation of bacterial cells with water flow through soil (Breitenbeck et al., 1988; Hekman et al., 1995; Stevik et al., 2004), and hence this type of movement will not be extensively discussed in this paper. Rather, we will place a focus on organism-driven transport modes, as discussed in the following.

Several recent studies have revealed that specific bacterial types possess capacities to “hitchhike” along with other (vector) organisms through the soil. Such vector organisms range from protozoa, nematodes and earthworms to soil fungi and plant root systems (Daane et al., 1996; Kohlmeier et al., 2005; Warmink and van Elsas, 2009; Glaeser et al., 2016), and soil physicochemical parameters are important determinants of the movement.

We here first examine the conditions in soil that critically affect the motility of bacterial cells in soil. Then, we address the prevailing types of bacterial motility as related to soil conditions. We examine to what extent these, depending on the soil ecological context, drive bacterial dispersal. Moreover, we propose a revision of the classical theory that posits that bacteria are largely confined to their microhabitats in soil and will only travel longer distances when driven by water, wind and moving soil organisms like earthworms (Hekman et al., 1995; Daane et al., 1996; Kellogg and Griffin, 2006). In the revision, fungal hyphae are also key actors in bacterial transportation, as they provide “highways” along which bacterial cells may travel, passively and/or actively. An “underground transport web” is thus proposed to exist, which is dynamic and includes fungal hyphal networks, plant roots and earthworms, and interconnections between these. This transport web is perceived to broaden the translocation possibilities of particular bacteria through the soil matrix, which may directly affect soil processes in cases where establishment of such migrated bacterial cells in novel soil microhabitats is possible. Finally, we examine the potential ecological effects of bacterial dispersal in soil. On the basis of these analyses, a novel framework for bacterial movement through soil is proposed.

2. Bacterial dispersal is affected by the soil pore network and water properties

Moisture content is an essential factor that mediates bacterial cell motility in soil, with bacterial cells having greater possibilities to migrate with increasing soil water content. For instance, *Pseudomonas aeruginosa* Migula was shown to move 20 mm in 24 h in soil under relatively wet, but not under dry conditions (Griffin and Quail, 1968). The level of connectivity of the water-filled (versus air-filled) pores in the soil has been invoked as an explanatory factor influencing cell motility, with the liquid phase being discontinuous in water-unsaturated soil (Vanapalli et al., 1999). Thus, the air-filled pores between soil particles represent structural discontinuities that impair cell motility, while the ones that are filled with water bridge the gaps. With respect to what they do for the 0.5–2 μm soil bacteria, the pores in the soil matrix have been classified on the basis of the pore size (defined as equivalent cylindrical diameter, ECD, which is computed from the cylindrical capillary rise), into transmission pores ($60 < \text{ECD} < 600 \mu\text{m}$), coarse storage pores ($6 < \text{ECD} < 60 \mu\text{m}$), fine storage pores ($0.2 < \text{ECD} < 6 \mu\text{m}$) and residual pores ($\text{ECD} < 0.2 \mu\text{m}$) (Hayashi et al., 2006). In this depiction, transmission and coarse storage pores have dimensions that greatly exceed those of the majority of bacterial cells. If not water-filled, these effectively impair cell passage. Bacterial cells may largely find shelter inside the so-called storage pores. Clearly, the soil pore size distribution exerts a critical overall influence on (active and passive) bacterial motility in soil. In contrast to actual pore

median size, pore neck sizes are important; pores with necks equal to, or lower than, bacterial cell sizes, are likely to restrict the rate of bacterial movement (Andreoglou et al., 2003).

The pore size distribution is intrinsically linked to the soil textural type, with a coarser (sandy) soil having a larger proportion of large pores when compared to a finer (clay) soil. Thus, soil texture directly affects bacterial motility in soil, first on the basis of the soil pore network characteristics and secondly due to the forces of attraction exerted by the soil surfaces that bacterial cells are exposed to (MacDonald and Duniway, 1978). In order to translocate in soil, bacterial cells have to resist the attractive forces exerted by soil surfaces. Additionally, soil density (linked to soil compaction) is an important factor that influences bacterial motility in soil. That is, higher soil bulk densities clearly limit the movement of bacterial cells with percolating water (van Elsas et al., 1991). Another issue is the degree of hydrophobicity of soil, which affects its infiltration capacity and subsequently the three-dimensional distribution and dynamics of soil moisture (Doerr et al., 2000). This also influences the formation of water films in soil, as well as the water connectivity (Goebel et al., 2011) and bacterial dispersal.

3. Bacterial movement through soil

3.1. Active movement

In the presence of water that increases the connectivity of soil micro-aggregates, bacterial cells can move actively via flagellar motility, in addition to their passive translocation as a result of Brownian movement (Griffin and Quail, 1968). In cases flagella are present, the latter type of movement is often overruled (Abu-Ashour et al., 1994). Thus, flagellum-driven chemotaxis was described early-on for the plant growth promoters *Azospirillum brasilense* and *Pseudomonas fluorescens*, which both migrated up to 80 mm in soil towards wheat seedlings and synthetic attractants (Bashan, 1986). Conversely, a recent study (in which chemotaxis did not occur) showed that *Bradyrhizobium japonicum* was able to move randomly up to 7 mm away from its inoculation site in water-saturated soil via flagellar activity (Covelli et al., 2013). Interestingly, much like soil fungi, some bacterial types can form multicellular chain structures, which also support their migration, by sliding motility, through soil. Next to the well-known actinomycetes and *Bacillus mycoides*, a recent example is given by experiments with *Bacillus cereus* (strain ATCC14597). Growing cells of this organism can switch to a multicellular phenotype, forming chains and then clumps. These forms can span a considerable distance in soil (tens of micrometers), which results in the overcoming of structural gaps in the soil matrix (Vilain et al., 2006).

3.2. Passive movement

Passive movement through soil can occur due to water flow, wind blows or in connection with organismal vectors. First, water flow through the soil pore network can act as an important mechanism for bacterial cell movement. In several experiments, percolating water has been found to facilitate large-scale/-distance (up to 400 mm) bacterial translocation in soil. Models based on soil physical parameters have been able to describe bacterial cell movement through soil, with bacterial density distributions matching exponential curves depicting cell density decreases with increasing soil depths (Breitenbeck et al., 1988; Hekman et al., 1995). The rate of translocation was thus determined by parameters of the soil pore network, the water flow rate and the number of times the soil was flushed (Trevors et al., 1990; Stevik et al., 2004; Unc and Goss, 2004). Moreover, the contextual soil properties, the initial moisture content and the soil bulk density are also key aspects that drive cell translocations (van Elsas et al., 1991). Intricate models describing water-flow-induced transport are described in several key studies (Beven and Germann, 1982; Hagedorn et al., 2000; Ma et al., 2010), and will not be further discussed here. For the purpose of

this review, it suffices to state that the soil textural type, the presence of different clay types and the soil conditions (pH, types of ions present, temperature) are key determinants of adsorption/desorption processes, which affects the degree to which a moving bacterial population can migrate through soil. In nature, rainfall and irrigation provide water flows through soil, albeit irregularly; the extent of water-carried transport is driven by the rules set by the models.

Wind blowing over a relatively dry soil surface also constitutes a driver of microbial translocation over distances that may be in the kilometer range (Kellogg and Griffin, 2006). Microbial cells attached to particular soil dusts (which are lifted high by the wind) can disperse over distances that reach up to 5,000 km (Kellogg and Griffin, 2006), with particles uplifts to 8,000 m (Meloni et al., 2007). Thus, only those bacteria that are able to survive under the harsh atmospheric conditions (due to UV radiation, desiccation and freezing) have been found to be detectable at sites where such dust settled (Kellogg and Griffin, 2006; Peter et al., 2014). Spore-forming bacteria (such as *Bacillus* species) stood out as the key organisms that are able to survive such long-distance dispersal by wind (Prospero et al., 2005). Clearly, the success of long-distance dispersal depends on the successful establishment of the incoming population in the recipient environment. As such, it depends on local soil conditions, such as water content, pH, temperature and the invader-suppressive nature of the resident community (Meola et al., 2015).

3.3. Soil organisms mediating movement

In the light of the fact that, generally, a top soil is in water-unsaturated condition (denoted as “field capacity”), bacterial movement over longer distances will be critically dependent on the chances bacteria have to cross air gaps between soil microhabitats. A key role for “vector” organisms is thus envisioned. Hence, the movement of bacterial cells in soil is to some extent driven externally, i.e. bacterial cells can “hitchhike” along with other (moving or growing) soil organisms. This hitchhiking effect constitutes a mechanism that has been relatively understudied. For example, earthworms, nematodes, protozoa, soil fungi and even plant roots constitute major vectors that promote the dispersal of their associated bacterial cells. They may act either as “trucks” (earthworms, nematodes, protozoa) or as “networks” (fungi, plant roots). Hereunder, we examine the mechanisms behind, and potential impact of, these two modes of bacterial translocation.

3.3.1. “Trucks”

Nematodes, earthworms, protozoa, next to other soil animals (encompassing many soil arthropods), can be regarded as “trucks” that move through the soil, i.e. these organisms constitute individual transport units that can take on “bacterial cargo”. Either pulsed or gradual shedding of the bacterial cell cargo, followed by bacterial cell establishment, will lead to a particular defined dispersal trajectory of the cargo along the “truck” path. Bacterial cells may hitchhike along with such vector organisms by adhering to the available surfaces, being external (skin) or internal (e.g. intestines) (Hekman et al., 1995; Daane et al., 1996). Previous studies have shown that nematode and earthworm intestines represent complex microbial systems that enable cargo loading followed by casting-related bacterial spread through soil. Earthworms (*Lumbricus terrestris*, *L. rubellus* and *Aporrhectodia trapezoides*) indeed enhanced the movement of *Pseudomonas fluorescens* C5t (pJP4) through soil. The bacterial cell population, of 10^8 CFU/g soil at day 0, decreased to $10^{6.72}$ CFU/g soil at day 14 in top soil, and was not detected in deeper soil in the absence of earthworms (Daane et al., 1996). On the other hand, the presence of the earthworms moved bacteria to deeper soil parts, in dependency of the depth the earthworm could reach (up to 40 cm depth for *L. terrestris*). The bacterial cell density decreased with increasing soil depth ($10^{6.51}$ CFU/g soil in the top soil and $10^{2.96}$ CFU/g soil in 35–40 cm soil, in the presence of *L. terrestris*) (Daane et al., 1996). Earthworm guts are known to harbor

microorganisms that are acquired from the soil and subsequently selected by the host (Hekman et al., 1995; Byzov et al., 2007; Singh et al., 2015). Thus, movement of earthworms through soil promotes the dispersal of bacterial types via casting (next to shedding). Three key processes, i.e. bacterial cell uptake/adherence, survival and release to establishment, determine the rate of dispersal of bacterial cells along with the moving earthworm. In a similar way, soil nematodes (Berg et al., 2016) and arthropods also contain specialized microbiomes in their guts and on their skins that are shaped by similar processes. The potato cyst nematode *Caenorhabditis elegans* was found to strongly select members of the *Enterobacteriaceae*, *Burkholderiaceae*, *Propionibacteriaceae*, *Xanthomonadaceae* and *Pseudomonadaceae* (Berg et al., 2016), whereas *Microbacteriaceae*, *Xanthomonadaceae*, *Enterobacteriaceae*, *Chitinophagaceae* were dominant in the gut of the microarthropod *Folsomia candida* (Agamennone et al., 2015). These findings indicated that the soil microbiome can be strongly modulated at local sites of casting and/or shedding (Thimm et al., 1998; Agamennone et al., 2015). Moreover, death of these vector organisms will incite a decomposition process with specialized bacterial cells locally increasing in abundance. Thus a hotspot for decomposer bacterial outgrowth emerges, fostering the “net” movement within the soil.

3.3.2. Networks

Plant roots and fungal hyphae both form network structures consisting of interconnected biological surfaces in soil. Such interconnected surfaces, although often ephemeral, can be colonized by particular bacteria (as well as other microbes) and constitute “highways” along which bacterial cells may be able to move.

Plant root networks – a hallmark study on the effects of plant roots showed that, mediated by type I and type III fimbriae, *Klebsiella* strains can effectively attach to root cap cells and to the root elongation zone of *Poa pratensis*, thus migrating along with growing roots (Hahtela et al., 1986). The presence of the inoculant *Klebsiella* on the roots stimulated root growth and branching, and hence some degree of mutualism was noticed. Similarly, Kamilova and colleagues showed that several bacteria, including *Pseudomonas fluorescens*, *Pseudomonas putida*, *Aeromonas hydrophila* and *Pantoea agglomerans*, in association with tomato roots, can act as biocontrol agents, taking profit of the extension of the roots to migrate. All bacteria were motile, showing higher colonization ability of the root than the model tomato root tip colonizer *Pseudomonas fluorescens* WCS365 (Kamilova et al., 2005). In a very recent study, *Rhizobium radiobacter* F4 was found to first colonize the primary roots (1 cm in length) of barley at 5 days post-inoculation (5 dpi), after which it spreads to the secondary roots and covers the primary and secondary roots subsequently at 30 dpi (Glaeser et al., 2016). The ability to attach to the plant root may have been the key factor that determined the successful bacterial colonization of the root. In particular, the ability to hold on to the root tips, thus, migration along with developing roots, was primordial. In contrast, flagellar dispersion and/or chemotaxis are likely crucial for microbial transport processes on mature roots, where tissues are immobile (Dupuy and Silk, 2016).

Hyphal networks – There is an increasing body of literature highlighting fungal growth as a key mechanism promoting bacterial movement through soil (Kohlmeier et al., 2005; Warmink and van Elsas, 2009; Furuno et al., 2012; Worrlich et al., 2016a; Yang et al., 2016). Kohlmeier et al. first clearly highlighted the importance of a “fungal highway” as a transport network for particular bacteria through soil (Kohlmeier et al., 2005). This revealing finding actually was a reconfirmation of much earlier findings on fungi spurring the movement of bacteria through soil (Wong and Griffin, 1976). In our own studies, we found that the growing hyphae of the soil saprotroph *Lyophyllum* sp. strain Karsten can act as a “fungal highway” that facilitates the translocation of cells of a suite of *Burkholderia* (now *Paraburkholderia*) strains (Warmink and van Elsas, 2009; Nazir et al., 2012). One of these strains, *P. terrae* BS001, was shown to disperse along with several (basidiomycetous and actinomycetous) fungi, which characterizes it as a broad-

Table 1

Proposed model describing the development of plant root (rhizosphere) versus mycelium (mycosphere) associated bacterial populations (after Scott et al.¹). The model was based on the assumption that both gross translocation with extending cells and growth influence bacterial dispersal in the rhizosphere and mycosphere. Parameters that feed the model are key soil, rhizosphere/mycosphere and bacterial parameters.

Rhizosphere ¹		Mycosphere ²	
Symbol	Explanation	Symbol	Explanation
<i>Soil characteristics</i>			
D _s	Diffusion coefficient of substrate in free solution	D _s	Diffusion coefficient of substrate in free solution
f	Impedance factor that is related to the tortuous pathway through the soil pores	f	Impedance factor that is related to the tortuous pathway through the soil pores
w	Soil moisture content	w	Soil moisture content
		pH	pH of the soil ³
<i>Rhizosphere/mycosphere characteristics</i>			
Hf _{int}	Rate of exudation of substrate from root into rhizosphere	Hf _{int}	Rate of exudation of substrate from fungal hyphae into mycosphere
Hf _{out}	Rate of substrate diffusion from the rhizosphere into the bulk soil	Hf _{out}	Rate of substrate diffusion from the mycosphere into the bulk soil
d _r	Width of rhizosphere	d _m	Width of mycosphere
d _z	Depth of the layer	d _z	Distance between original site and sampling site
K _s	Nutrient saturation constant	K _s	Nutrient saturation constant
A _{rh}	Horizontal areas of the rhizosphere over which the diffusion of substrate will take place	A _{mh}	Horizontal areas of the mycosphere over which the diffusion of substrate will take place
A _{rv}	Vertical areas of the rhizosphere over which the diffusion of substrate will take place	A _{mv}	Vertical areas of the mycosphere over which the diffusion of substrate will take place
V _r	Volume of the rhizosphere	V _m	Volume of the mycosphere
		θ	Fungal hyphal hydrophobicity (contact angle of hyphae) ⁴
<i>Microbial characteristics</i>			
μ _{md}	Maximum specific growth rate in dry habitat	μ _{mw}	Maximum specific growth rate in soil with moisture content at “w” ⁵
μ _{mw}	Maximum specific growth rate in wet habitat		
k _d	Death rate in dry habitat	k _{dw}	Death rate in soil with moisture content at “w” ⁵
K _w	Death rate in wet habitat		
Y	Growth yield	Y	Growth yield in soil with moisture content at “w”
<i>Variable parameters</i>			
G _d	Bacterial concentration in dry habitat	G _w	Bacterial concentration in soil with moisture content at “w” ⁶
G _w	Bacterial concentration in wet habitat		
S _r	Substrate concentration in rhizosphere	S _m	Substrate concentration in mycosphere
S _b	Substrate concentration in bulk soil	S _b	Substrate concentration in bulk soil
		t	Time after bacterial inoculation ⁷

¹ Scott et al. (1995).

² Proposed in this paper.

³ Low soil pH strongly restricts bacterial survival and dispersal in mycosphere (Yang et al., 2018).

⁴ Bacterial cells disperse along with hydrophilic fungal hyphae, not with hydrophobic hyphae (Vila et al., 2016).

⁵ Bacterial growth/death is associated with water availability (water activity).

⁶ The highest cell density that bacteria can reach might be related to soil moisture.

⁷ It takes longer time for bacterial cells to reach new habitats in the mycosphere with low-pH soil (Yang et al., 2018).

spectrum co-migrator (Warmink and van Elsas, 2009; Nazir et al., 2014). Interestingly, strain BS001 was even able to mediate the dispersion of another soil bacterium, *Dyella japonica* BS013 (an organism not able to migrate alone with the fungal hyphae), with *Lyophyllum* sp. strain Karsten (Warmink et al., 2011). A later in situ study showed that several *Fusarium* strains were able to facilitate the spread of *Stenotrophomonas maltophilia* and *Ochrobactrum pectoris*, 40 mm away from their original site in soil (Simon et al., 2015). Moreover, spread of particular naphthalene-degrading bacterial strains over air gaps, mediated by the soil oomycete *Pythium ultimum*, was also reported (Furuno et al., 2012). Importantly, the dispersal of bacterial cells along fungal hyphae improved their access to natural or anthropogenic compounds in soil, spurring the bacterial turnover of these (Banitz et al., 2016).

In recent work, we found that progressively lowered soil pH restricted the survival and migration of *P. terrae* along fungal hyphae in soil. Remarkably, migration in the non-hyphal-extension direction was found, which showed a weak correlation with the newly-formed hyphae in this soil area (Yang et al., 2018). Very convincing evidence was found for the contention that flagella play a key role in the migration of *P. terrae* BS001 along with *Lyophyllum* sp. strain Karsten hyphae, whereas the type three secretion system (T3SS) and type four pili (T4P) had minor influences (Yang et al., 2016; 2017). Thus, fungal hyphae in soil forming mycelial networks promote the motility of particular bacteria, like *P. terrae*. We further found that only soil-dwelling hyphae,

which were hydrophilic, can support bacterial migration. In contrast, aerial hyphae, which are more hydrophobic, did not allow efficient migration (Vila et al., 2016). Overall, on the basis of our findings, and in line with findings by Furuno et al. (2010), we posit that a water film formed around the soil-borne fungal hyphae is critical for the occurrence of bacterial swimming motility driven co-migration along the fungal highway.

3.3.3. Processes involved in bacterial cell movement at, and colonization of, fungal hyphae in soil

Several models have been proposed for bacterial migration along with fungal networks. Based on all studies, including those of our own group, we propose the process of bacterial migration along with fungal hyphae to proceed in soil as follows:

- (1) **Approach:** soil-borne bacterial cells get closer to an emergent or existing fungal surface, using chemotaxis-mediated short-distance movement. The approach may also be incited as a result of fungal hyphal elongation, which places the fungal surface in close vicinity of the bacterial cells. Bacterial cells may also move to fungal surfaces mediated by other soil organisms (such as other fungal hyphae, plant roots or earthworms).
- (2) **Attachment:** some (but not all) bacterial cells bind to the fungal surface. Key drivers are fungal nutrient-rich surface areas, such as found at the apical tip. In this step, anchoring “devices” such as

T3SS and type-four pili may assist or mediate the process.

- (3) **Growth:** attached bacterial cells start to utilize nutrients secreted by the fungal hyphae and grow on the fungal surface.
- (4) **Spread:** some (specialized) cells may spread (movement) as driven by chemotaxis. Within-population competition is a factor of importance here. Along with the bacterial density increases by growth, the locally-available nutrient levels decrease, and so competition between the cells augments. Some cells may leave the origin microsite and disperse along with the fungal hyphae. Sensing and moving towards enhanced fungal exudates (chemotaxis) may play a role. In this step, the presence of a water film around fungal hyphae is critical.
- (5) **Establishment and formation of a new niche:** following the migration, the specialized bacterial cells reach new microsites at the fungal surface, establish there, and repeat the former steps 1–4.
- (6) **Biofilm formation:** following cycles of steps 1–5, eventually large populations of bacterial cells occupy the hyphal surface. At enhanced cell densities, biofilms are formed around the cell populations.
- (7) **Unloading:** bacterial cells are unloaded from the fungal surfaces either via dislodgement or following decay of the fungal cells. This potentially results in novel bacterial hotspots in soil, that are available for subsequent transport by any of the mechanisms/actors discussed here.

3.3.4. Model describing bacterial dispersal through networks in soil

A model that describes the bacterial movement along with wheat plant roots was constructed by Scott et al. (Scott et al., 1995). According to the model, the movement is determined by a set of at least 22 key parameters (Table 1). These include: soil water potential, time, soil properties [diffusion coefficient of substrate in solution (D_s), impedance factor (f) that mimicks the tortuous pathway through the soil pores, soil water content (θ)], root zone characteristics [rate of exudation of substrate from root into rhizosphere ($Hf_{x_{int}}$), rate of substrate diffusion from the rhizosphere into the bulk soil ($Hf_{x_{out}}$), width of rhizosphere (d_r), depth of the layer (d_z), nutrient saturation constant (K_s), horizontal (A_{rh}) and vertical (A_{rv}) areas of the rhizosphere over which the diffusion of substrate will take place, volume of the rhizosphere (V_r)], next to microbial characteristics [maximum specific growth rate in dry (μ_{md}) and wet (μ_{mw}) habitat, death rate in dry (k_d) and wet (k_w) habitat, growth yield (Y)], variable parameters [bacterial concentration in dry (G_d) and wet habitat (G_w), substrate concentration in rhizosphere (S_r) and in bulk soil (S_b)]. This model matched experimental data obtained with a *Pseudomonas fluorescens* strain introduced into the rhizosphere of wheat fairly well (Scott et al., 1995). Thus, for *P. fluorescens*, movement in the rhizosphere can be depicted as a process of bacterial dispersal along extending plant roots, with key roles for movement, the utilization of nutrients and local reproduction. The length reached by the plant roots determined how far the bacterial cells can move away from the original site and the nutrient availability in the rhizosphere was critical to local bacterial cell densities that can be reached.

Given the similarity of the root and hyphal extension systems (and in the current absence of a dedicated model), we here propose that bacterial movement in the mycosphere is subjected to similar rules as given by the Scott et al model: the hyphae of saprotrophic as well as mycorrhizal fungi grow in soil by hyphal extension, to explore novel nutritive sites. Upon growth, they release small carbonaceous molecules, like glycerol and oxalate, which may serve to feed accompanying bacteria. Thus, mycosphere-adapted bacterial cells will accompany the hyphal extension in accordance with their migration and growth capacities, allowing the reaching of novel ground. To describe this, we propose the use of a modified model (Table 1) with parameters that describe the events in the mycosphere to describe the movement of bacteria along fungal hyphae. The model should be based on the concept of bacterial cell density at each specific site in the mycosphere being the result of bacterial dispersal and growth. Fungal hyphae

extending over time, coupled to local nutrient levels, determine the dispersal distance of bacteria. The growth of fungal hyphae might be arrested in harsh conditions (such as in nutrient-scarce sites or at low temperatures like in winter), and may be recovered in favorable conditions. Thus, broad bacterial dispersal is subjected to the vagaries of the soil habitat and might be discontinuous. Also, properties of the mycosphere, such as its width, and its water potential (Worrich et al., 2016a) and substrate availability, are important. Finally, based on recent data (Yang et al., 2018), soil pH is a key factor to be considered in this proposed model.

4. An “underground transport web” that drives the migration of bacteria through soil

In line with the concept of major bacterial spread through soil by “truck-like” or “network” vector organisms, we posit that these two transport systems can lead to strongly divergent ecological outcomes. Whereas the soil trucks, particularly earthworms, protozoa and nematodes, drive *pulsed cargo transport* that may result in stochastic and spatially idiosyncratic delivery, the networks provided by plant roots and fungal hyphae constitute a connected “*underground transport web*” that facilitates, over a considerable time span, a rather continuous (and homogeneous) bacterial dispersion along the defined biological highway. Moreover, as shown in Fig. 1, plant roots, fungal hyphae and soil animals may be in contact with other transport vectors in soil, resulting in overall complex patterns of bacterial dispersal.

4.1. Trucks support pulsed cargo delivery

The organisms, e.g. earthworms and/or nematodes, that constitute the “truck-like” cargo system in soil facilitate temporally- and spatially-explicit bacterial movement and delivery. Depending on their typical life modus, some specific earthworms are known to either move up/down, horizontally or erratically in soil. Upon transporting bacterial cargo, they haphazardly release cells, or do so along with casts. In their behavior in soil, they have ample opportunities to interact with plant roots or fungal hyphae, which may result in either idiosyncratic or organized patterns of bacterial dispersal (Fig. 1). For instance, one key outcome of such “truck-like” transport was found to be the movement of *Sinorhizobium meliloti* from bulk soil onto the roots of the legume *Medicago truncatula* by the soil nematode *Caenorhabditis elegans*. The bacterium was stably carried by the vector organism which was attracted to the plant roots (by plant-released volatiles), where the bacterial cargo was unloaded (Horiuchi et al., 2005). Additionally, earthworms utilize plant roots and fungi as food (Curry and Schmidt, 2007). Thus, the bacterial cells attached to the latter are taken up by earthworms, being converted into bacterial cargo. The earthworm *L. terrestris* moves vertically, from the surface to a depth exceeding 2 m (Joergensen et al., 1998), providing an extended pathway for pulsed vertical bacterial transport in soil.

4.2. Networks yield highways for continuous cargo delivery

In previous work, the mycosphere dweller *P. terrae* BS001 was translocated over 40 mm in soil, along with several fungal species, including the saprotroph *Lyophyllum* sp. strain Karsten, the phytopathogens *Rhizoctonia solani* AG3 and *Fusarium oxysporum* Fo47, and the biocontrol agent *Trichoderma asperellum* 302 (Nazir et al., 2014). Use of the Scott et al. theory allowed us to estimate the movement of strain BS001 over larger distances and time spans (using theoretical conditions of no competition, like in the laboratory experiments). The result of such simulations indicated that, given transport-favorable parameter settings, the networks that form by these fungi in soil can facilitate the spread of BS001, from tens of centimeter to meter distances over periods of months. As an example, the soil saprotroph *Lyophyllum* sp. strain Karsten, accompanied by *P. terrae* BS001, was found to extend 2.6 mm/

Fig. 1. Underground transport web in soil that facilitates bacterial motility in soil. (a) earthworm “trucks”; (b) plant root network; (c) fungal hyphal network; (d) earthworm surface (blue) or intestine (dark green) associated bacteria; (e) plant root associated bacteria; (f) fungal hypha associated bacteria; (g) soil organisms connected with each other and bacterial cells can move from one organism to another. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

day (resulting in 45 cm – 6 months; 1.8 m – 2 years) in soil sampled from Droevendaal (Wageningen, Netherlands; Nazir et al., 2012). Although not proven, we expect the soil fungus *Armillaria ostoyae* to constitute a major soil transportation network. This fungus has been described as the largest organism on Earth, being able to occupy $\sim 10 \text{ km}^2$ belowground as a single organism (Ferguson et al., 2003). Given the potential function of this very extensive belowground hyphal network, highly revealing experiments may be cogitated with respect to the movement of cells of bacteria that associate with it.

On top of the fungal-driven bacterial spread through soil, connections with other fungal hyphae and/or plant roots form in a dynamic manner. For instance, common mycorrhizal networks play a critical role in long-distance transport of nutrients through the soil ecosystem (Bücking et al., 2016). Thus, a picture emerges of an often large (semi) continuous fungal-mediated connected belowground network, along which specific bacteria are able to migrate in accordance with the local factors affecting this migration. Additionally, some roots of trees reach deep soil layers (up to tens of meters), and distribute widely in top soil, facilitating vertical as well as horizontal bacterial dispersal. Thus, next

to the afore-described water- and wind-driven dispersal, a complex transport web formed by earthworms, plant roots and fungal hyphae in top soil may grossly mediate bacterial dispersal (Fig. 1).

5. Ecological and evolutionary effects of bacterial dispersal through soil

The nutrients (sources of carbon and energy) that support the survival and growth of bacteria in soil are often distributed in a very discontinuous way. Thus, in most soils, bacteria occur in nutrient-exhausted microhabitats, whereas several hotspots of enhanced nutritional status may exist only millimeters away. In these, a suite of energy-rich nutrients is – although often ephemerally – available. Such hotspots can be found in specific soil sites such as the mycosphere, the mycorrhizosphere, the rhizosphere, the drillosphere and the detritosphere (Kuzakov and Blagodatskaya, 2015). By moving in the soil matrix, bacterial cells are able to explore newly-available soil areas and thus utilize the locally available nutrients from which they had previously been separated. Thus, next to water-driven transport, the

presence of either an *underground transportation network* or a “*truck delivery*” system, or both, are key assets that greatly foster net bacterial dispersal rates in unsaturated soils.

Extracellular DNA (eDNA) that enters soil as a result of cell death and lysis has also been considered to play a key role in soil. First, it can be utilized as a source of C, N and P by heterotrophic microorganisms (Levy-Booth et al., 2007). Secondly, it may have a role in biofilm formation (Pietramellara et al., 2009). Finally, it may be (horizontally) transferred into bacterial cells, spurring adaptive processes (Nielsen et al., 2007). Motile bacterial cells in soil may acquire eDNA and either use it as a nutrient source, or as a source of novel information. Conversely, they may also serve as providers of eDNA in the local bacterial communities. Thus, bacterial dispersal clearly plays a key role in bacterial community evolution in soil.

Bacterial dispersal may be a *conditio-sine-qua-non* for the efficient remediation of polluted soil that needs bacterially-mediated degradation activity. An important early finding was that fungi (Kohlmeier et al., 2005; Furuno et al., 2012) and/or earthworms (Li et al., 2015) are able to mediate the movement of pollutant-degrading bacteria to key sites in soil, thus spurring the degradation of the toxic compounds. The fungal-mediated physical “highway” was posited to mediate bacterial access to the pollutants (Banitz et al., 2012; 2016; Knudsen et al., 2013; Worrich et al., 2016a, 2016b; Otto et al., 2017a). Presumably, this included positive chemotaxis towards the pollutants (Furuno et al., 2010), the overall outcome being fungal-mediated stimulation of bacterial survival and growth. Clearly, the mechanism enhanced the ecological opportunities for the bacteria, as described (Warmink and van Elsas, 2009; Yang et al., 2018). Here, one should take into account that also non-single-strain migrator bacteria may move along with the fungal hyphae, by a hitchhiking effect (Warmink et al., 2011). Finally, fungal mycelia were also found to facilitate predators (*Bdellovibrio bacteriovorus* 109J) to catch their prey bacteria *Pseudomonas fluorescens* LP6a (Otto et al., 2017b). This process enhanced the fitness of the predator as well as the prey, affecting ecosystem function.

On another notice, some phytopathogens (Leben, 1984) or human pathogens (Williams et al., 2006) were found to disperse in soil, thus reaching vegetable crops, which is an undesirable process that may threaten plant and human health. One solution to control such pathogens may be the use of highly mobile antagonistic bacteria, that can efficiently translocate along vector organisms, and thus chase and reach the pathogens to exert antagonistic effects.

With respect to ecological effects, some fungal-associated bacteria can exert beneficial effects to the host. For instance, *P. terrae* BS001 was found to protect its fungal host, *Lyophyllum* sp. strain Karsten, against the antifungal agent cycloheximide present in the soil (Nazir et al., 2014). Similarly, the hypermotile *P. fluorescens* F113 strain showed higher competitive colonization ability on alfalfa root surfaces than other strains, thus replacing other strains at the root surface. This improved biocontrol activity (Barahona et al., 2011). Moreover, other plant growth promoting rhizobacteria, such as bacteria belonging to the genera *Burkholderia* and *Pseudomonas*, can enhance plant growth (Pii et al., 2015) and undefined gut-associated bacteria have been reported to provide essential amino acids for earthworms (Larsen et al., 2016). Dispersal extends the living area of these bacteria, and enhances the beneficial effects exerted on their hosts. Thus, the interactions between bacterial cells and their hosts can be regarded as mutualistic if dispersal facilitation is included in our considerations.

6. Conclusions

Bacterial dispersal through soil occurs in diverse ways and is affected by several environmental factors. A key emerging concept is that of an underground transport network, in which both (temporally-restricted) continuous transport (plant root and fungal networks) and pulsed transport (“truck-like” agents) are taking place. Dispersal is key to applications in environmental management, such as in polluted soil.

Use of bacterial-dispersal-enhancing soil organisms, combined with pollutant-degrading bacteria, may improve in situ degradation efficiencies. Also, the use of combined biological agents can facilitate bacterial cells in colonizing plant roots and exert plant-beneficial effects on these. Additionally, bacterial dispersal agents may play an important role in the spread of phytopathogens between plant roots. Thus, it is critical to avoid dispersal of the latter organisms via these avenues, along with enhanced combatting of these. Moreover, human pathogens can be carried by similar migration avenues through the soil. In cases of massive transport, this may enhance the incidence of disease incited from edible crops. Thus, bacterial dispersal in soil is an important environmental issue. In specific cases, the diverse modes of translocation should be scrutinized in order to assess the chances of success of application (bioremediation) or the risks associated with pathogens. Finally, this paper has focused on the dispersal of bacteria, where we know that Archaea do occur in considerable numbers in soil, and have key specialized roles (for instance, in ammonia oxidation and methane formation) in there. Moreover, motility in Archaea has been reported widely (Kinosita et al., 2016; Legerme et al., 2016; Albers and Jarrell, 2018). Thus, we here argue that – although data are scarce – it is likely that also archaeal cells disperse along with vector organisms and extend their range of ecological action to microhabitats away from their original sites in soil.

7. Declarations of interest

None.

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