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Understanding the joint impacts of soil architecture and microbial dynamics on soil functions: Insights derived from microscale models

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Abstract

Over the last decades, a new generation of microscale models have been developed to simulate soil microbial activity. An earlier article (Pot et al., 2021) presented a detailed review of the description of soil architecture and microbial dynamics in these models . In the present article, we summarize the main results obtained by these models according to six model outputs: growth and spatial organization of microbial colonies, soil hydraulic conductivity, coexistence and trophic interactions of microorganisms, temporal dynamics of the amount of solid and dissolved organic matter in soil and, microbial production of CO_2. For each of these outputs, we draw particular attention to the respective roles of soil architecture and microbial dynamics, and we report how microscale models allow for disentangling and quantifying them. We finally discuss limitations and future directions of microscale models in combination with the on-going development of high-performance imaging tools revealing the spatial heterogeneity of the actors of soil microbial activity.

Highlights

- We review the insights on soil functions derived from microscale models of soil microbial processes
- Microscale models disentangle the complex interactions between soil architecture and microbial dynamics
- Spatial accessibility of resources to microbes, growth and ecological interactions are key factors in soil functions

● Translation of knowledge of interactions at the microscopic scale into larger scales is still in its infancy

Keywords: bacteria models, fungi models, spatial accessibility, ecological interactions, soil organic matter

1. Introduction

In the last two decades, a new generation of microscale models of soil microbial activity has been developed (e.g., Baveye et al., 2018 ; König et al., 2020 ; Pot et al., 2021). These models describe soil architecture at a small scale (from a few μm^3 to a few cm^3), as well as the heterogeneous distribution in it of trophic resources and microorganisms, and they account for soil-borne processes at the scale of soil microhabitats (Pot et al., 2021). In so doing, microscale models make it possible for users, through modelling scenarios, to explore the role of physico-chemical gradients and spatial accessibility of trophic resources to decomposers on soil microbial activity.

In Pot et al. (2021), we reviewed in detail how microbial dynamics and soil architecture are described in microscale models. Microscale models are defined by a computing grid of node size ranging between 1 μm^3 to 1 mm^3 where the physico-chemical environment, microorganisms, trophic resources and microbial products are spatialized. Box 1 visually depicts and explains how such models are used while Box 2 details an example of the use of the microscale model of Portell et al. (2018). In a nutshell, microscale models generally consider an explicit representation of microbial growth instead of a black-box approach that is widely adopted in the broader soil-related literature (e.g., Wieder et al., 2015). Measurable soil organic pools representing plant residues based on their degree of polymerization (non-labile polymers, labile monomers), biomass, and biomass by-products (metabolites, enzymes, glue agents, exo-polymeric substances) are described (e.g., Gras et al., 2011) rather than lumped organic matter (OM) pools based on their different degree of chemical recalcitrance to degradation. Most of the microscale models consider a depolymerization step before the dissolved OM can be taken up (e.g., Allison, 2005; Pagel et al., 2020; Zech et al., 2022), and this step can be controlled by the production of enzymes by microbes (e.g., Wang & Allison, 2019). Other models also include complex ecological interactions like commensalism, competition, mutualism (e.g., Folse & Allison, 2012; Wang & Or, 2014), fungal deadlock, intermingling, or replacement (e.g., Falconer et al., 2008), or bacterial dispersion through “fungal highway” (e.g., Banitz et al., 2011, 2016). Three-

dimensional images of soil architecture (mostly obtained from cutting-edge non-invasive imaging tools), informing on the geometry of the pore space and the spatial localisation of air-water interfaces, can be direct inputs for microscale models (e.g., Falconer et al., 2012). To decrease the amount of information needed in this detailed description of soil architecture, diverse strategies of simplification are used. Morphological models (e.g., Monga et al., 2014) and irregular pore-network models (e.g., Perez-Reche et al., 2012) reconstruct simplified pore spaces by extracting the median axes of the imaged pores and filling the pores with well-defined geometrical forms (e.g., balls, cylinders, angular pores). Simpler (regular) pore-network models (e.g., Ebrahimi et al., 2014; Laudone et al., 2011, 2013) make use of statistical properties of pore connectivity and size defined according to values found in natural soil systems in order to reconstruct a simplified pore space. In these simplifications of the pore geometry, the exact spatial heterogeneity of the clustering of pores is lost. Finally, in contrast to these explicit approaches, another class of micromodels describes soil architecture in an implicit way by attributing lumped values of bulk porosity, water content and/or diffusion coefficient to the computational nodes of spatial grids (e.g., Folse & Allison, 2012). Whatever the level of detail of the soil architecture description contained in microscale models, different scenarios of spatial distribution of solid OM fragments, dissolved OM, physico-chemical gradients and microbes (bacteria and fungi, mostly) are proposed (e.g., Falconer et al., 2015; Ebrahimi & Or, 2015). Some of them are based on experimental data (e.g., Babey et al., 2017, Centler et al., 2011) whereas others use statistical models of the spatial distribution of bacteria (e.g. Pagel et al., 2020; Mbé et al., 2021).

Microscale models can thus lead to modelling scenarios where spatial interactions encompass optimal or low accessibility of OM to microbes, and thus can tackle how soil microbial activity is related to soil heterogeneity. However, these models face a number of limitations in describing the complexity of soil architecture and microbial life. Most of them describe a static soil architecture although innovative studies have attempted to investigate the feedback loops between architecture and microbes (Crawford et al., 2012 ; Ray et al., 2017) or roots (Aravena et al., 2014 ; Kolb et al., 2017) and physico-chemical processes (Rupp et al., 2019). Regarding ecological interactions, a number of simplifications have been undertaken, such as, among others, a simplification of soil biodiversity and an omission of the role of living roots (Pot et al., 2021). Although the research on the role of trophic regulation in soils has made important progress (Erktan et al., 2020), predation has not been explicitly included in microscale models, except for the model of Pagel et al. (2020).

Box 1: Space is at the heart of microscale models of soil functions. Soil architecture is accounted for mainly following two types of spatial description: explicit and implicit (Figure 1). The explicit description relies on a representative image of soil architecture (for example a CT image) from which the solid phase and the pore space is extracted. Other phases such as water and organic matter can also be imaged to some extend. Pore space is either directly implemented at the nodes of the model grid – using a regular mesh or finite element (FE) or finite volume (FV) meshing – or simplified by using geometrical approaches (for example Maximal Inscribed Balls) or pore network models (PNM). The spatial distribution of air/water interfaces, microorganisms, and OM (solid or dissolved) are added to the explicit description of the pore space. In some circumstances, these distributions can be measured using imaging tools (µCT, neutron CT, synchrotron µCT, 2D microscopy, …) but, more often, they are computed. For example, the Young-Laplace law can be used to water fill or empty pores and statistical models can be used to distribute microorganisms in the pore space, or meaningful scenarios can be used. Alternatively to the explicit approach, an implicit description of soil architecture can also be adopted. In this implicit approach, the bulk values of porosity, water content and effective molecular diffusion coefficient – measured on the considered soil samples or calculated from semi-empirical laws – are distributed at the grid nodes made of a regular mesh. Spatial heterogeneity of these variables can be generated by statistical models or scenarios.

In microscale models, microbial activity is accounted for explicitly (Figure 1). Solid OM pools are depolymerized in labile components (DOC) to be taken up by microorganisms. Ecological interactions, including competition for resources, mutualism or commensalism can be this way easily implemented by establishing relationships between different OM pools.

Coupling between the soil architecture and microbial dynamics (purple arrows in Figure 1) is achieved through the transport of the soluble and gaseous components (DOC, enzymes, emitted gases) and the microorganisms in pore space (via processes of diffusion, advection, colonization of fungal hyphae and bacterial chemotaxis or random movement).

Finally, the outputs of microscopic models can generally be divided at two levels (Figure 1): (i) spatialized output variables at different output times of the models, and (ii) temporal evolutions of these output variables averaged over the entire simulated domain.

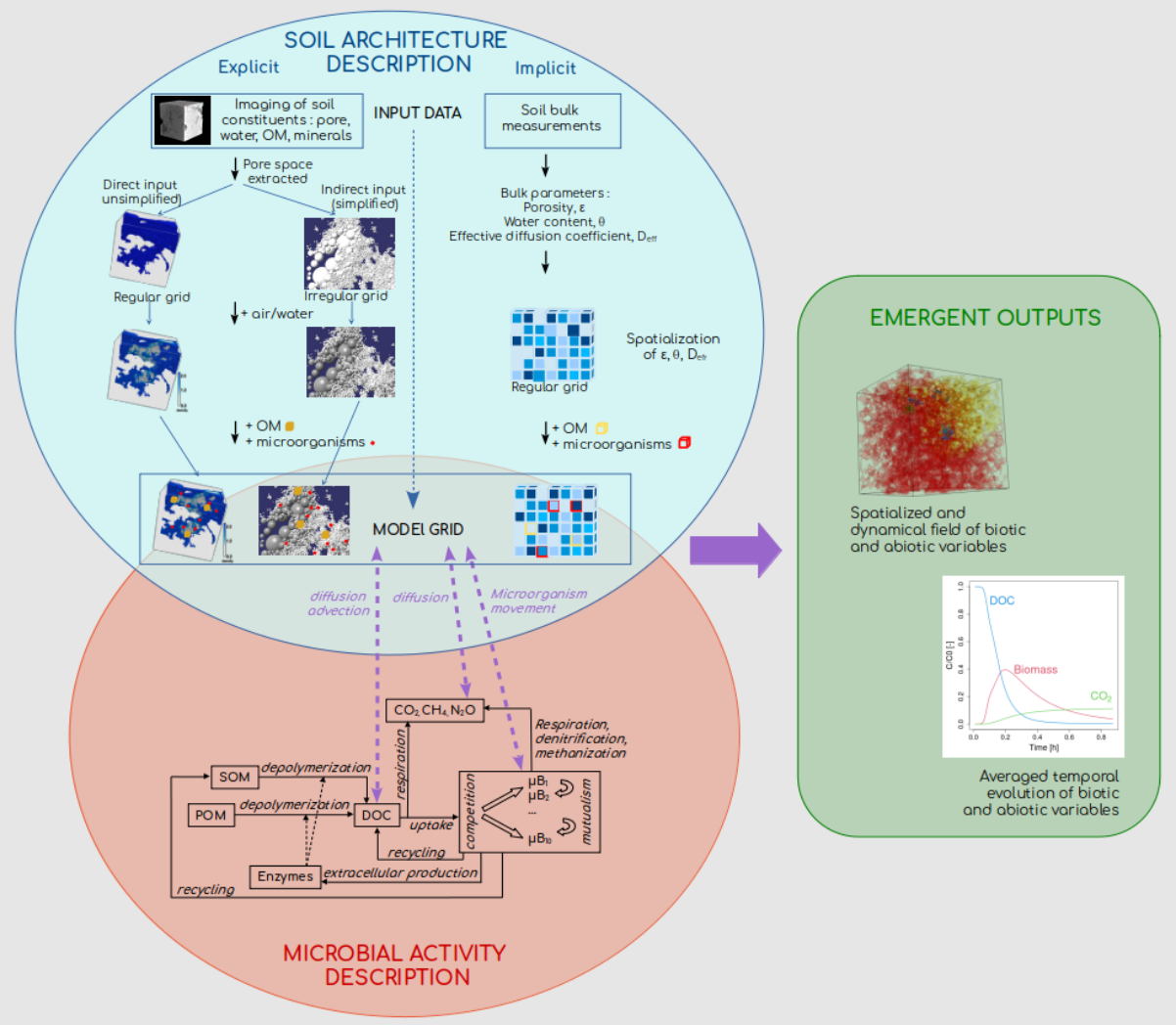

Figure1: Main set-up characteristics of microscale models of soil functions.

In that general context and to complement the review of Pot et al. (2021), we summarize in the present review the main insights gained by this new generation of microscale models on the understanding of soil functions. These new insights relate to the emergence of a spatial organization of microbial (bacteria and fungi) colonies (Section 2.1), its consequence on the hydraulic conductivity in idealized porous media (Section 2.2), coexistence and trophic interactions (Section 2.3), and finally, the decomposition of solid and dissolved OM and the emission of CO_2 (Section 2.4). We then describe how microscale models can disentangle the role of soil architecture and microbial dynamics (Section 3) and we finally discuss issues related to the assessment of these models and upscaling and advocate for future directions (Section 4).

Box 2: Example of microscale modelling study tackling bacterial diversity. The IbLBioS microscale model of Portell et al. (2018) couples a lattice-Boltzmann approach – to describe the diffusion of dissolved organic carbon hydrolyzing from particulate organic matter (POM) – with an individual-based model – to describe bacterial dynamics (Figure 2A). It assumes an explicit description of soil architecture using X-ray µCT images describing the solid phase and pore space. The water distribution is computed using a two-phase lattice-Boltzmann model for three levels of water saturation (Sw=100 %, 50% and 25%). 690 initial bacteria having parameter combinations representative of competitive, poorly competitive and versatile Arthrobacter Sp. Strains are randomly distributed in the water phase (Figure 2B). The role of spatial accessibility of OM to bacteria is accounted for with three scenarios initializing a fixed amount of carbon distributed in one chunk of POM, four chunks of POM and already available as DOC (Figure 2C). The main outputs studied by the authors were the time evolutions of the averaged POM and DOC amount, CO_2 production, biomass of the bacterial strains and the growth observed in the bacterial microcolonies (Figure 2D). In addition, they computed the geodesic distance between these microcolonies and the POM chunks.

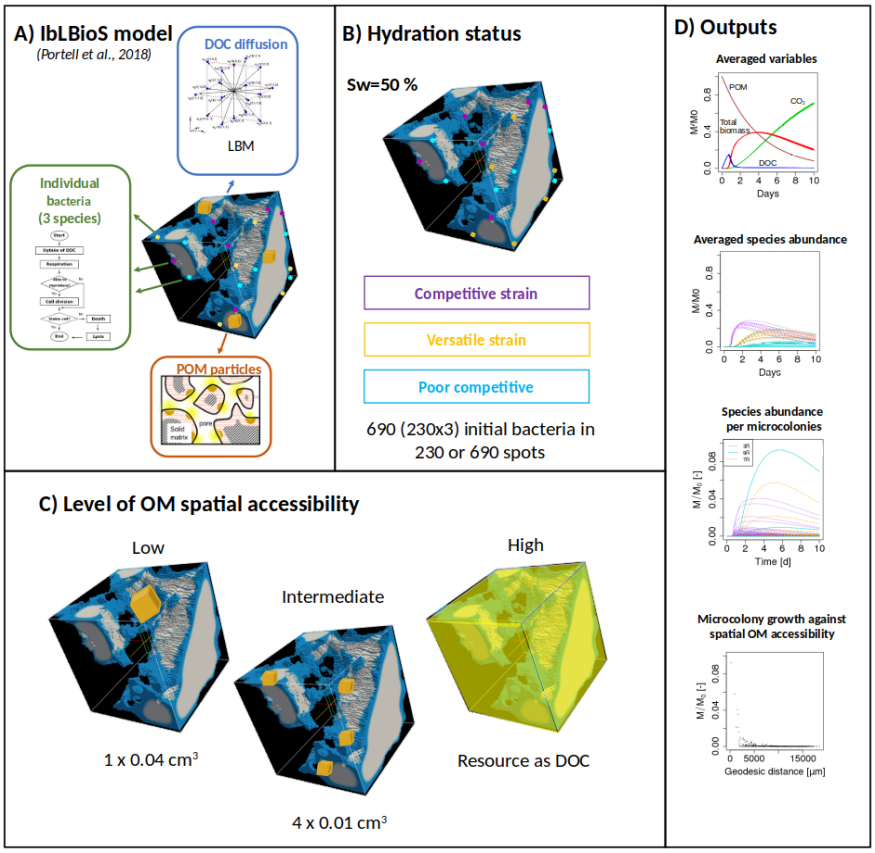

Figure 2: Overview of the main steps of modelling scenarios with a microscale model.

2. Main insights derived from microscale models

2.1 Spatial organization of soil microbial colonies

2.1.1 Case of bacteria

In modelling scenarios based on an implicit approach to describe soil architecture, Folse & Allison, (2012) developed an individual-based model that considers competition, coalition, and cooperation between different genotypes of a bacterial species. The microbes feed on carbon-, nitrogen- and phosphorous-containing substrates that are distributed on a 2D grid. These substrates need to be hydrolyzed by substrate-specific enzymes in order to be available. Bacteria that produce extracellular enzymes and opportunists or cheaters that do not produce such enzymes are initially randomly distributed on the 2D grid. Unlike the enzymes and the bacteria, the C, N, and P substrates do not diffuse on the grid. The heterogeneity of soil architecture is not investigated and an effective diffusion coefficient is assigned to the enzymes. Given these assumptions, Folse and Allison, (2012) found that the spatial organization of bacteria varies with enzyme diffusion and production rates. Following the same approach, König et al. (2017, 2018, 2019) located disturbance events at random microsites on the computational grid. These events, consisting of a decrease in biomass, modify the spatial structure of the bacterial communities and lead to habitat fragmentation. The spatial characteristics of the disturbances (size and degree of fragmentation) influence the resilience of the system by affecting the ability of bacteria located in undisturbed areas to recolonize disturbed areas. In these modeling scenarios, an effective diffusion coefficient is attributed to bacteria. The dynamic of the spatial structure of bacterial colonies is controlled by threshold effects and high growth rate is identified as an asset for recovery in the case of medium intensity disturbances

Using an explicit but simplified 3D description of soil architecture, Resat et al. (2012) involved enzyme producers and cheaters that feed on two cellulose patches placed in distinct zones of the computational grid. They came to the same overall conclusions as Folse and Allison (2012). The bacterial growth dynamics relies on a balance between the degradation kinetics of the substrate (in this case cellulose), the dynamics of enzyme production, and the mixing in pores by diffusion. The model predicts that bacteria preferentially grow near cellulose spots. Surprisingly, Resat et al. (2012) found similar growth dynamics, except for a shift in time, from those obtained in single cylindrical micropores. Growth remains also insensitive to modification of the porosity of the porous medium, although it is varied over a significant range (20% to 50%). One explanation is that the artificial and

highly connected pore network of the simulated domains may have prevented critical cases of diffusion limitation.

The role of chemotaxis on the emergence of different spatial patterns is explored by Gharasoo et al. (2014) who compared 2D simplified soil architectures considering pore networks made of cylindrical bonds of either constant radius or variable radius. When the supply of substrate is constant and homogeneous, bacterial distribution remains uniform in the presence of chemotaxis toward the substrate (Gharasoo et al., 2014). When bacteria are further attracted by the presence of fellow bacteria, spatial organization emerges. Increasing the strength of chemotaxis towards bacteria triggers non-trivial populations in a homogeneous porous medium. In the heterogeneous porous media, a distribution of pluri-millimeter size patches emerges when attraction to nutrient is low and bacteria tend to migrate from larger pores toward smaller pores. The authors conclude that the distribution of bacteria in soil is strongly related to the chemotactic behavior of the bacteria.

The additional role of water hydration status of pores in the emergence of distinct spatial organizations of bacteria is evidenced in different levels of description of soil architecture. Using pore networks made of angular bonds to describe 2D and 3D analogs of soil aggregates, Ebrahimi and Or (2014) showed that when the water content is high enough to ensure a high connectivity, chemotaxis toward substrate makes it possible to favor the shortest paths to the source of nutrients, and avoid tortuous paths associated with random displacements. In the case of many isolated clusters, chemotaxis has the opposite effect, as it can guide bacteria to dead-end pores, and travel times can become longer than required for random movements (Ebrahimi & Or, 2014). In the case of an explicit description of an idealized 2D soil architecture representing porous rough surfaces (Long & Or, 2007), microscale models predict a larger annular expansion of a bacterial colony under wet conditions (matric potential of -0.01 kPa) compared to drier conditions (matric potential of -1 to -2 kPa). These spatial patterns are the result of an interplay between nutrient diffusion limitation and motility of the bacteria. The inner center becomes rapidly depleted in nutrients because of the local consumption by bacteria therein but also because of the interception of the nutrients by bacteria located at the periphery of the colony. The different patterns observed between the saturation conditions are accounted for by a decrease of the connectivity of the water phase due to the fragmentation of the liquid phase and to the slowing down of the diffusion of nutrients (Wang & Or, 2010). Using a 2D implicit description of the porous rough surfaces, Kim and Or (2016) found that the spatial structure of two bacterial colonies is modified by the water hydration status and ecological interactions. In the case of competitive trophic interactions, the

two species segregate along circular “travelling bands”. Species 1 follows species 2 and consumes the nutrients left by species 2. Under dry conditions, the double bands disappear and form a unique band made of several small sectors of the same species. In this case, diffusion of the nutrients is reduced and the species need to compete to remain at the front line. In the case of mutualistic interactions, under wet conditions, species 1 grows better than species 2, which consumes the by-product of species 1, whereas the reverse is observed for dry conditions.

The role of the spatial distribution of carbon substrate also appears to be key to account for the spatial organization of aerobic and anaerobic species in 3D analogs of soil aggregates. In modelling scenarios carried out by Ebrahimi and Or (2015), the same number of aerobic and anaerobic bacterial cells are inoculated in the center of the aggregate. A constant O_2 concentration is supplied at the periphery of the aggregate, while the carbon source is located either at the center of the aggregate or at the periphery. A spatial organization with physical separation of the two species occurs between the anoxic center of the aggregate and the oxygenated periphery (Ebrahimi & Or, 2015). Borer and Or (2018) further confirmed, in simulated domains mimicking experimental micrometric pore networks etched in glass, that the absence of counter-gradients of oxygen and carbon resulted in a uniform distribution of aerobes and anaerobes. However, the distribution is conditioned by the presence of a carbon source internal to the aggregate. In the absence of this source, the anaerobic species does not survive (Ebrahimi & Or, 2015). The size of the aggregate is also a key factor in the distribution and maintenance of the two species (Ebrahimi & Or, 2016). Using a simplified 2D description of soil analogs, Borer et al. (2019) introduced a metabolic flexibility where the anaerobes can grow in both aerobic and anaerobic environments by adapting their metabolism. This adaptation permits the spatial segregation of the facultative anaerobes into an aerobic population growing close to the oxygen peripheral source and an anaerobic population close to the internal carbon source.

In conclusion, the reported modelling studies show that the spatial distribution of bacterial colonies can differ strongly, depending on the interplay between factors related to spatial accessibility of OM and O_2 to bacteria, and factors related to microbial dynamics. The former factors are the heterogeneity of soil architecture, water content, substrate spatial distribution and chemotactic behavior of bacteria. The latter factors are the growth rate of bacteria, their enzyme production rate, and ecological interactions which are directly related to the efficiency of bacteria to consume OM.

2.2.2 Case of fungi

The role of soil architecture in the invasion of fungi-like microbes is highlighted by a series of modelling scenarios (Perez-Reche et al., 2012) where the pore space is described using an irregular pore-network model made of nodes and links (pores) distributed in a way that preserves the spatial distribution and width of the pore arrangement. Invasion of microbe analogs is carried out through a generic probabilistic model that could resemble fungal invasion (Bailey et al., 2000) and growth is not considered. The probability for a microbe to invade a new pore is constrained by the length but also by the width of the links. Perez-Reche et al. (2012) demonstrated that the inclusion, in their pore-network model, of the extra complexity of the width of the links has a significant impact on the ability of microbe to invade the soil sample. The invasion distance is underestimated when the lengths and width of the links but also the number of nodes are not sufficiently considered in the invasion probability. Bailey et al. (2000) and Otten et al. (2001) showed how fungal colony morphology can be linked to such probabilities and tested the approach in experimental 2D systems with localized C sources (Otten et al., 2004a) on a lattice as well as for spread of a pathogen through a population of plants (Cook et al., 2007).

Assuming an idealized soil architecture made of different proportions of solid and porous nodes and addressing the complexity of fungal processes, i.e., by including substrate uptake, hyphal tip growth, branching, Boswell (2008) showed that the simulated biomass length and the total number of hyphal tips decrease as the density of soil increases. The hyphal growth unit, which is the total mycelial length divided by the number of branches in the mycelium, is the greatest in dense soils. These results agree with the visual observations made by Harris et al. (2003) in soil thin sections (Otten et al., 2006). One explanation would be that the fungus has less opportunity to branch when the pore space is reduced as observed by Otten et al. (1999) and Soufan et al. (2018). In another set of modelling scenarios where detailed soil architecture is considered through the use of CT images of sandy soil samples repacked at different densities, Pajor et al. (2010) also found that the colonization rate of the fungus is highest for the repacked sandy soils with the lowest density. Indeed, fungal biomass spreads faster and further in better-connected soil (Otten et al., 2006). The model of Pajor et al. (2010), which is derived from that of Falconer et al. (2007), describes the invasion of fungal hyphae according to a diffusion process and this explains the fact that a well-connected pore space is ultimately colonized. The total porosity of the domain is then the key factor explaining the spatial expansion of the fungus. However, if the pore connectivity decreases, the fraction of pores colonized with distance declines more rapidly than in a

well-connected pore space. In this case, it is the connectivity of the pore space that becomes the key factor explaining the spatial expansion of the fungus. The results of Pajor et al. (2010) agree with the experimental results of Harris et al. (2003) who showed that the hyphae initially colonize the largest-sized pores, followed by colonization of smaller pores. Nevertheless, the model overestimates the spread of hyphae in the small pores compared to the experimental results of Otten et al. (2004b). A more heterogeneous distribution of carbon or the result of blockage of small pores by the presence of water in the experiments may explain these differences. Indeed, in the scenarios of Pajor et al. (2010), all pores are assumed to be filled with air. Kravchenko et al. (2011) modelled fungal colonization in detailed soil architecture obtained from CT images of undisturbed soil samples. They also showed that the fragmented pore space disadvantages fungal invasion whereas large connected pores promote invasion.

The spread of fungal hyphae is also directly dependent on the initial distribution of the substrate since the complex arrangement of pores imposes constraints on the accessibility of resources to the fungus. This relationship is further influenced by the complexity of fungal processes, as demonstrated in modelling scenarios describing either idealized (Boswell et al., 2007) or detailed soil architecture obtained by CT images of soil samples (Cazelles et al., 2013). When carbon is co-located with the inoculum, the fungus consumes the local resource resulting in an increase in its biomass there and a smaller spatial expansion in the soil than for a homogeneous distribution of the resource (Cazelles et al., 2013). Biomass recycling, which reallocates biomass through the mycelium and favors faster growth and an exploratory behavior of the fungus, is an effective strategy to compensate for heterogeneous distributions of the substrate in a complex porous medium (Boswell et al., 2003; Boswell et al., 2007; Cazelles et al., 2013; Falconer et al., 2007).

A significant decrease in the growth of the fungus is observed in relation to water unsaturated conditions (Falconer et al., 2012). The spatial expansion is prevented by the presence of pores filled with water, which strongly alters the connectivity of the air phase. Simulations of fungal growth in two soil samples of contrasted pore space geometry interestingly shows that it is not the sample with the largest water content that inhibits the most the fungal colonization. More important than the water content is the location of the water filled pores that disconnect the gas phase. Water films that contain nutrients can also guide fungi to colonize pore space and find new resources (Boswell et al., 2007). The macroscopic water content of soil samples is therefore not a sufficient measure to predict the growth and spatial expansion of the fungus. Knowledge of the heterogeneity of the soil microhabitats and in

this case of the distribution of water and air in the pores and the connectivity of the air phase, is therefore essential (Falconer et al., 2012). This role of unsaturated pores has been observed in microfluidic devices by Soufan et al. (2018).

The role of soil architecture combined with ecological interactions is evinced in the spatial distribution of two fungal colonies (Falconer et al., 2008). The model simulates complex fungal deadlock (inhibited invasion of one species into the territory of the other species), intermingling (fusion of fungal colonies) and replacement (autophagy) processes. In agreement with the experimental results of Stahl and Christensen (1992), the deadlock and intermingling processes occur for environments with high and low trophic resources respectively in absence of soil architecture. When simplified soil architecture is described, the two colonies inoculated at the opposite edges of the simulated domain only manage to cross the domain for a defined porosity interval (0.31-0.55) because connected paths between opposite edges are numerous enough for individuals to cross while avoiding each other. It is important to notice that these simulations were in a 2D space where fungal colonies spreading from opposite directions are always going to meet. This in contrast for soil where, for soils with low pore connectivity, colonies can grow past each other in different sections of the 3D pore volume.

Like for bacteria, spatial colonization by fungi is explained by a balance between the accessibility of trophic resources (which depends on the connectivity, size and water saturation of pores), and the physiological characteristics of fungi, such as their biomass recycling and ecological interactions .

2.2. Modification of hydraulic conductivity in idealized porous media

Biofilms, i.e., a continuous layer of accumulated biomass and its metabolic by-products along the pore-solid interfaces, can be found in artificial porous media during industrial processes of filtration. Most of the reported modelling studies simulating this process carry out scenarios in idealized porous media usually consisting of packings of cylinders or glass beads. A reduction of global permeability of these idealized porous media is observed during growth of these biofilms together with the creation of preferential water flow paths (e.g., Graf von der Schulenburg et al., 2009 ; Kapellos et al., 2007 ; Tartakovsky et al., 2009). The shear forces prevent the development of biomass in the pores oriented in the transverse flow direction even if the local concentrations of the trophic resources in these pores would allow bacterial development (Knutson et al., 2005). Feedback loops emphasize this pattern since bacteria that are more concentrated close to preferential flow paths consume more food than in the case of more homogeneous flow fields and thus leave less food for the bacteria cells located farther,

reducing transverse expansion (Tang et al., 2013). Bioclogging of pores differently affects water flow reduction and is controlled by the water saturation of pores (Rosenzweig et al., 2013).

Inclusion of more complex processes in microscale models changes the picture one gets of the spatial proliferation of bacteria. When detachment processes of bacterial cells from biofilms are considered in microscale models, the spatial expansion of bacteria downstream of the water flow increases (Kapellos et al., 2007). In this case, detached cells are transported by advection and are redeposited farther downstream, forming new colonies. When motility of bacteria occurs via diffusion against local solute concentration gradients, localized accumulations of bacterial cells are reported in regions of more stagnant flow (Peszynska et al., 2016). When permeability in biofilms is introduced, the shear forces at the biofilm-water interface are reduced and cell re-attachment to the biofilm surface is enhanced (Kapellos et al., 2007).

Whereas the above examples are all dealing with artificial porous media and have applications that do not directly involve soils (for more details, see the recent review by Sadeghnejad et al. (2021)), they address important interactions that occur as well within soil environments but have yet to be captured by microscale models designed to describe and predict soil functions. Local accumulation of biomass and its metabolic by-products in soils, although not in the form of continuous biofilms (Baveye, 2020; Flemming et al., 2021), can contribute to preferential flow paths. Feedback loops emerge that alter pore geometry, which in-turn alters physical processes that impact biomass growth. The extent to which this phenomenon, referred to by Crawford et al. (2012) as self-organization of soil systems, is implemented in soil microscale models remains limited at this stage (Crawford et al., 2012; Ray et al., 2017), but it seems fair to consider that much can be learned from the studies referred to above.

2.3. Coexistence and trophic interactions of microorganisms

Soils are known to be characterized by an enormous biodiversity (e.g., Baveye et al., 2016). Because of computational limitations and especially of a fundamental lack of relevant input data, microscale models cannot reflect that biodiversity. However, they are able to capture key factors controlling the survival and/or coexistence of a limited number of meaningful functional groups of microbial species. When soil architecture is not explicitly described and a single value of effective diffusion coefficient is used throughout the simulated domain, survival and coexistence of simulated species is mainly attributed to a balance between the rates of production of enzymes by communities experiencing different ecological interactions (competition, coalition, and cooperation) and the rates of enzyme

diffusion (Folse & Allison, 2012). When considering local spatial heterogeneity in porosity and water content in their simulated domain, Long and Or (2005) identified the key role of local microenvironments conditions on survival and coexistence of two bacterial species (one more competitive than the other) for the same trophic resource. The coexistence of the species is made possible for low water contents, whereas the less competitive species becomes extinct under conditions when diffusion is not limiting. The fragmentation of aquatic habitats shelters less competitive species and sustains nutrient gradients. When the least competitive bacterial colonies are located near active diffusion paths, they can survive and thus compensate for their disadvantage in terms of competition with respect to the most competitive species (Long & Or, 2005). Under wet conditions, the motility of bacteria accelerates extinction due to a higher local expansion of the most competitive species that intercepts the available nutrients (Wang & Or, 2013). However, drier conditions reduce the role of motility, which decreases sharply even for the most competitive species (Long & Or, 2009). Variably water-saturated conditions can counterbalance negative effects on the survival of the least competitive species and thus promote biodiversity (Wang & Or, 2013). In modelling scenarios of wetting and drying cycles, Wang and Or (2013) found similar growth dynamics for both species. These results are consistent with experimental results on bacterial diversity that is not affected by wetting and drying cycles in soils regularly subjected to these cycles (Fierer et al., 2003).

Using a detailed description of soil architecture obtained from CT images of undisturbed soil, Portell et al. (2018) found that the spatial distribution of OM residues has an important role in shaping bacterial diversity in the case of three bacterial strains, a competitive, a generalist, and a poorly competitive one, for the same trophic resource. Whereas at the scale of the whole simulated domain, the evolution of the total biomass is not affected by the location of OM, the evolution of the biomass of each strain is strongly modified. When the residues are gathered in a unique location, the less competitive strain can grow as much as the generalist strain. In these rare cases, the probability of being near the unique carbon source is lower but, when this happens, the large amount of dissolved organic carbon produced by the aggregated residues can provide an advantage and promotes the growth of the less competitive strain. These results confirm those of Long and Or (2005) on the critical role of spatial location of colonies near active diffusion pathways. In addition, Portell et al. (2018) also found that the least competitive strain cannot grow if it is co-located with a competitive strain even when they are located near the resource. The proximity of bacteria to residues is thus not sufficient to maintain biodiversity, the less competitive strain must also not be co-located with a competitive strain.

Microscale models, in exploring the labyrinth of pores, have provided valuable insight into key factors maintaining soil bacterial biodiversity. While ecological interactions are crucial, the occurrence of transient water saturated conditions in soils, by fragmenting the complex aquatic habitats of bacteria, and the heterogeneous spatial distribution of trophic resources, offer sufficiently diverse ecological niches where less competitive species can survive.

2.4. SOM decomposition and CO_2 emission

2.4.1 Role of soil architecture, spatial distribution of OM and microbes

Respiration rates are highly influenced by the connectivity of pores. Using a detailed description of soil architecture obtained from CT images of soil columns, Yan et al. (2016) simulated lower respiration rates in denser soils. In their microscale model, the role of oxygen is considered in bacterial growth together with diffusion of O_2 in liquid and gaseous phases. In denser soil with poorer connectivity, OM is less accessible to bacteria, O_2 is limited by gaseous diffusion and this explains the lower respiration rates (Yan et al., 2016). This is in agreement with the experimental results of Franzluebbers (1999) who showed that carbon and nitrogen mineralization is generally lower in compressed soils compared to natural soils. However, pore connectivity does not alone explain the SOM decomposition and respiration rates that were found. There are complex relationships depending on the spatial distribution of OM and bacteria within soil architecture. For example, in the case of the modelling scenarios of Mbé et al. (2021), mineralization of OM decreases when soil bulk density increases in the case of aggregated bacteria distribution whereas it is similar when bacteria are homogeneously distributed.

A convenient feature of microscale models is their ability to control the distribution of OM and microbes in the simulated soil architecture. Different modelling scenarios have been proposed to test how spatial accessibility of OM to bacteria influence SOM decomposition and CO_2 production at the scale of the entire simulated domain. Modelling scenarios can be established based on experimental results relating the distribution of OM and bacteria to the size of pores. For example, Strong et al. (2004) found that the most active and largest bacterial population is found in the pores of class 15-60 µm and Lugato et al. (2009) found that the organic carbon of the soil is positively correlated with pores of size 0.1-5 µm and negatively correlated with pores of size 30-75 µm. Following these experimental findings, Ngom et al. (2011) carried out modelling scenarios where OM is placed in pores smaller than 20 µm and bacteria are distributed in larger pores because they are the most aerated. Up to a two-fold

amount of OM is mineralized in grass land soil aggregates that exhibit much less small, isolated pores than in cultivated plowed soil aggregates, because OM is then more accessible to bacteria.

Other scenarios do not relate the spatial distribution of OM and bacteria to the size of pores but compare dispersed (random) versus aggregated spatial distributions of OM residues and/or bacterial cells. A reduction in CO_2 production in the long term is observed in the case of an increase in the aggregation of bacterial spots (Masse et al. 2007). In these scenarios, decomposition takes place only when there is a physical contact between the bacterial spots and the OM patches that are placed in a minimalist 3D space where pore geometry and diffusion processes are ignored. The number of bacterial spots no longer having access to OM increases sharply and this is enough to reduce the overall carbon mineralization. Similar results are obtained with a more accurate description of soil architecture. Mbé et al. (2021) used a morphological approach to describe the pore space of repacked sandy loam soil samples obtained from CT images. Their microscale model considers diffusion of dissolved carbon in the liquid phase. For a homogeneous distribution of dissolved OM, Mbé et al. (2021) found lower mineralization when bacteria are aggregated compared to scenarios where bacteria are homogeneously distributed. In the latter case, there is a greater accessibility of bacteria to the trophic resource. In a simplified 1D geometry representing an experimental micromodel, Centler et al., (2011) also found that degradation efficiency is the highest for homogeneous bacteria distribution and decreases as pattern formation of bacteria sets up. Aggregation of bacteria stems from the introduction of flagellated movement and chemotaxis toward nutrient and toward chemo-attractant produced by the bacteria. Increasing the chemotaxis strength toward substrate or fellow bacteria reduces further the total biomass and degradation activity in the case of aggregated distributions of bacteria (Gharasoo et al., 2014). All these modelling results agree with the experimental data of Dechesne et al. (2010) who showed lower substrate mineralization rates for aggregated bacterial distributions.

For random distributions of bacterial spots, an increase in the aggregation of OM patches increases mineralization (Mbé et al., 2021) but also the variability among repetitions (Masse et al., 2007; Nunan et al., 2020). Although access to the trophic resource becomes increasingly limited, the amount of OM to which some bacteria have access remains sufficient to produce greater mineralization in the long term. When both spatial distribution of bacteria and OM are aggregated, mineralization is not ranked against the degree of clustering of OM or bacteria (Mbé et al., 2021). Results are highly influenced by the occurrence of co-localization of bacterial hot-spot with large plant residues containing a high amount of OM which can even surpass mineralization of a random distribution of OM (Mbé et al.,

2021). All these modelling results agree with the experimental measurements of Bending and Turner (1999) who showed a greater emission of CO_2 in the presence of large chunks of plant residues. However, they are in apparent contradiction with experimental results that have shown that large plant residues, having a high C/N ratio, cause less mineralization than smaller residues. In these experiments, the soil N bioavailability is probably increased by a more even distribution of residues in the soil and a higher contact surface for smaller residues (e.g., Angers & Recous, 1997; Tarafdar et al., 2001). In the scenarios of Portell et al. (2018), where N is unlimited, the OM residues are positioned in such a way that the contact surface is always identical whatever their aggregation. The production of dissolved organic carbon (DOC) by hydrolysis of these residues is a constant rate per unit surface that leads to similar global CO_2 emissions and DOC consumption. In the scenarios of Masse et al. (2007) the contact surface decreases when the degree of aggregation increases. However, aggregation also causes an increase in the amount of carbon available for bacterial spots and results in a higher available amount of OM explaining the highest CO_2 emissions. However, using the same model of Masse et al. (2007), mineralization decreases when the size of the plant residue increases in the case of N limitation (Garnier et al., 2008).

The emission of CO_2 through fungal activity is also directly related to nutrient access, itself controlled by pore connectivity. Higher CO_2 emissions are simulated for scenarios where carbon is co-located with the inoculum (Cazelles et al., 2013). On the contrary, in the homogeneous distribution of carbon throughout the pore space, the fungus must expand to have total access. This results in a lower assimilation of biomass and a lower respiration. A non-linear relationship between respiration of fungi and amount of solid OM residues has been found (Falconer et al., 2015). In these scenarios, the impact of the distribution of OM but also their size and amount of carbon is considered. For small amounts of carbon in the OM residues, the fungus biomass decreases and the amount of accumulated CO_2 stabilizes. Above critical thresholds of the amount and size of OM residues (3% of carbon and 60% coverage of the solid-pore interface by OM, respectively), the cumulative CO_2 follows an exponential growth over time. In addition, Falconer et al. (2015) observed a difference between replicated samples up to a factor of 100 between the amounts of cumulative CO_2 for different sizes of OM. Respiration is the largest but also the most variable for the largest sizes of OM residues in line with the results of Masse et al. (2007) and Nunan et al. (2020). A better assimilation of biomass in the presence of small OM residues can be promoted by modifying the physiological parameters of fungal growth (Falconer et al., 2015). When increasing the carbon diffusion rates in the hyphae and lowering the associated

metabolic costs, the fungus develops an exploratory behavior and more easily finds the dispersed OM residues. These authors pointed out that bulk measurements of OM residues in soil samples are not sufficient to predict CO_2 production and that it is vital to describe spatial heterogeneity of soils at the microhabitat scale. They also advocated that macroscopic models should abandon the linear description of the response of soil microorganisms to nutrients on the basis of the bulk concentration of nutrients (Falconer et al., 2015).

2.4.2 Role of water saturation

It has been long evinced that bacterial respiration depends on soil water saturation (e.g., Skopp et al., 1990). Water content, as well as the geometry and connectivity of pores control nutrient diffusion, soil aeration and accessibility of nutrients to bacteria. In agreement with experimental results, OM decomposition decreases in modelling scenarios involving decreasing water saturation levels (e.g., Borer et al., 2019; Monga et al., 2008; Vogel et al., 2015; Yan et al., 2016). This effect is enhanced in the case of a heterogeneous distribution of OM residues. When OM is placed in large pores, the decomposition decreases when soil becomes drier because the large pores are first emptied of water and become isolated and are not accessible to bacteria (Monga et al., 2008). This is in line with the experimental results of Dechesne et al. (2010) where the decrease of substrate mineralization under heterogeneous distribution of bacteria accentuated with the decrease of matric potentials (from -1 kPa to -50 kPa).

Calibrating their microscale model on the growth of six bacterial strains in sand under saturated conditions, Monga et al. (2014) obtained longer lag times for respiration rates under drier conditions, compared to experimental data. This suggests that their micromodel underestimates the diffusion of fructose. One hypothesis put forward by the authors is an overestimation of the fragmentation of the liquid phase as wetting films are not considered in their morphological approach of pore space description. The fact that pores smaller than the resolution of the tomographic images (in this case 5 µm) are ignored could also explain lower OM decomposition rates. When considering water films preserving connectivity for water saturation of 50 % in soil microaggregates, Zech et al. (2022) observed no difference in the total OM consumption and CO_2 production compared to the saturated case. However, differences arise locally with the onset of hot-spots of microbial activity depending on the geodesic distance of bacteria to OM source.

Other modelling scenarios have shown contrasting impact of water saturation on decomposition rates of soluble OM (Vogel et al., 2015; Mbé et al., 2021). This is related to the spatial accessibility of trophic resource to the decomposers, and to the amount of OM. Increase or decrease of fructose degradation are found when water saturation decreases (Vogel et al., 2015). Degradation decreases when bacterial colonies are located far from the initial fructose pulse and experience limiting diffusion conditions. However, when accessibility is optimal, degradation increases for low water saturation. In this latter case, the increase of fructose concentration in the remaining liquid phase stimulates bacterial growth. This stimulation can be so high that one bacterial spot can be as efficient in consuming DOC than ten of them (Vogel et al., 2015). In the case of homogeneous distribution of bacteria and DOC (Mbé et al., 2021), mineralization always increases, although to a small extent, when water saturation decreases. This effect is less pronounced in soil with higher bulk density, suggesting that the increase of DOC concentration in the remaining liquid phase explains this trend (Mbé et al. 2021). When the distribution of bacteria is aggregated in a small region, the amount of produced CO_2 is not anymore ranked according to water saturation, suggesting that stimulation of biomass growth by higher DOC concentrations can surpass diffusion constraints.

A heterogeneous microscale distribution of water-saturated regions in soils affects the intensity and location of reactive hotspots. Considering only aerobic respiration, Yan et al., (2018) showed how a balance between OM accessibility and O_2 diffusion can drive microbial respiration. Hotspots of OM decomposition are simulated under high water saturation conditions, which promotes OM bioavailability, whereas hotspots nearly disappear when water saturation further increases because this limits the gaseous diffusion of O_2.

Most of the reported modelling studies have dealt with different water saturations but have ignored water advection and its complex role in influencing microbial response. In modelling scenarios describing an idealized straight pore and water saturated conditions, Schmidt et al. (2018) showed that in the presence of water flow, the aggregation of bacterial colonies can lead to a significant reduction in degradation rates. When bacteria are gathered in spots, they do not have the same access to the substrate as when they are distributed homogeneously along the pore. Consequently, due to advection, part of the substrate is evacuated from the pore without having been consumed. In a more complex description of soil architecture, Gharasoo et al. (2012) observed that an increase in the heterogeneity of the pore-size distribution leads to a decrease of substrate bioavailability because it increases

preferential flow paths. However, in their scenarios, heterogeneous distributions of biomass have a minor effect on substrate availability in the case of homogeneous pore-size distributions.

2.4.3 Role of ecological interactions

The role of ecological interactions combined with environmental conditions at the microhabitat scale is complex. Using an implicit description of soil architecture, Kaiser et al. (2014) showed how the spatio-temporal dynamics of interacting functional groups can alleviate microbial N limitation in the decomposition of litter of low C:N ratios. Ecological interactions can also maintain the rates of OM decomposition in the case of low spatial accessibility to nutrients . For instance, Portell et al. (2018) found unchanged overall carbon turnover for random or aggregated spatial distributions of OM, and Pagel et al. (2020) found that only a strong spatial clustering of decomposer communities can reduce the rate of decomposition of carbon compounds. In both studies three functional groups defined according to their capacity to consume the resources are considered. Redundancy of the three functional groups is suggested to compensate to some extent the diffusion limitations of nutrients (Pagel et al., 2020). However, when the diffusion limitations are too severe, compensation cannot be achieved.

The modelling scenarios of Nunan el al. (2020) explore different acquisition strategies of the resources ranging from generalists (bacterial taxa can consume the same resources) to specialists (bacterial taxa can consume only one resource), In the absence of functional redundancy (specialists), the proportion of resources consumed is increased when bacterial diversity increases, i.e., more taxa with fewer individuals consume more than few taxa with a higher number of individuals (Nunan et al., 2020). The aggregation of the resources increases only the variability of the consumption. When up to ten different resources are submitted to different acquisition strategies (generalists and/or specialists), the aggregation of OM gives a competitive advantage on generalists over specialists and the resource is more consumed (Nunan et al., 2020). There is a higher probability of co-location of generalist bacterial cells on one of the resources they can consume than for specialists. In these modelling scenarios, soil architecture is not described explicitly, and circular patches of OM are randomly distributed within a 2D space, following the approach of Masse et al. (2007). A different picture emerges in scenarios where specialists are given an advantage on getting their food. In this microscale model, bacteria are singular spots and acquire resource within a disc whose radius can be modified (Nunan et al., 2020). When

increasing the size of the area where specialists can take up the resource, a disadvantage for generalists compared to specialists is found and leads to an overall low resource consumption.

A different result can be obtained, namely a decrease of OM decomposition, when bacterial diversity is high (Evans et al., 2016; Folse & Allison, 2012; Kaiser et al., 2015). In this case, ecological interactions are based on complementary resources acquisition in communities of producers and cheaters. When diffusion limitations are high, nutrient enzymatic depolymerization is increased in the presence of competitive interactions between different types of bacteria, from enzyme-producers to cheaters (Folse & Allison, 2012). Low diffusion limits the development of cheaters that rely on enzyme diffusion to survive. By contrast, in high diffusion situations, biodiversity is increased and the cheaters and coalitions of intermediate types in competition with the generalist producers reduce enzyme production and thus nutrient depolymerization (Folse & Allison, 2012). In the modelling scenarios of Kaiser et al. (2015), the decay rates of litter can be reduced by up to 90% in the presence of cheaters, depending on their maximum growth rate. This effect is further enhanced when ecological interactions are combined with variable water content as simulated in dry-rewetting cycles by Evans et al. (2016). During drought, a critical limitation by diffusion can locally create hotspots of dissolved OM due to the continuous enzymatic depolymerization. During re-wetting, diffusion of soluble compounds is increased and this additional amount of available OM triggers high increase of CO_2 production (e.g., Barnard et al., 2020). This effect, known as the Birch effect, is dampened in presence of cheaters (Evans et al., 2016). Whereas cheaters are sensitive to drought, they out-compete enzyme-producers under rewetting. The fast response of cheaters when diffusion limitations are relieved upon rewetting, confers them an advantage over the producers and leads to an overall decrease of OM decomposition.

2.5 Summary of main insights

The many modelling scenarios investigated and the sometimes contradictory results obtained show the complexity arising from processes interacting at the microbial habitats. However, if we summarize these results in the light of the role of OM spatial accessibility to microorganisms, tendencies can be found (Table 1). In general, when spatial accessibility is optimal, it promotes SOM decomposition, CO_2 production and fungal expansion whereas soil biodiversity is reduced. Opposite results are found in the case of a low OM spatial accessibility. We could not extract clear trends for the bacterial spatial organization. However, we identified several parameters or processes that control the strength of these

microbial activities. These factors can relieve constraints imposed by low OM spatial accessibility and reframe microbial activity to some extent (Table 1).

Table 1: Main effects of optimal and low OM spatial accessibility on microscale model outputs and main sensible parameters and processes controlling or modifying (indicated in this case by blue symbols in parentheses) these effects.

	optimal OM spatial accessibility	low OM spatial accessibility
Bacterial spatial organization	+/-	+/-
Fungal expansion	+	- (+)
Bacterial biodiversity	--	++ (+)
OM decomposition	++	-- (-)
CO2 production	++	-- (-)
Sensible parameters or processes	Maximum bacterial growth rate Enzyme production rate Ecological interactions Fungal biomass recycling	High bacterial growth rate High fungal biomass recycling Ecological ineractions Chemotactic behaviour

3. Disentangling the role of soil architecture and microbial dynamics

In microscale models, one can decouple the respective roles of soil architecture and microbial dynamics on soil functions by considering interactions at the microscopic scale and feedback loops, as illustrated in Figure 3, which emphasizes the main links between the inputs and outputs of the models. We can classify model inputs into six groups of different nature: 1) soil architecture, which describes the spatial arrangement of soil particles, the geometry of pores and pore-solid interfaces; 2) water content, which describes the amount of water and the distribution of air-water interfaces within the pores; 3) the initial spatial distribution of solid OM; 4) the initial spatial distribution of dissolved chemical species (including OM, O_2, enzymes); 5) the initial spatial distribution of microbes, either in suspension in the water phase and/or attached to the pore-solid interfaces (for bacteria), and in the air-filled pore space (in the case of fungi); and 6) the initial species. The first five inputs are directly related to the spatial accessibility of trophic resources to microbes. The six outputs are those reported in the previous sections. Table S1 lists each reported microscale model according to this classification.

System properties or processes that directly influence spatial accessibility of the trophic resources to microbes are displayed by red arrows. The green arrows correspond to ecological interactions and processes that control the efficiency of microbes to depolymerize and uptake OM, emit gases and grow.

The black arrows correspond to other system properties or processes not linked to spatial accessibility or microbial dynamics. Feedback loops are displayed by thick arrows in Figure 3.

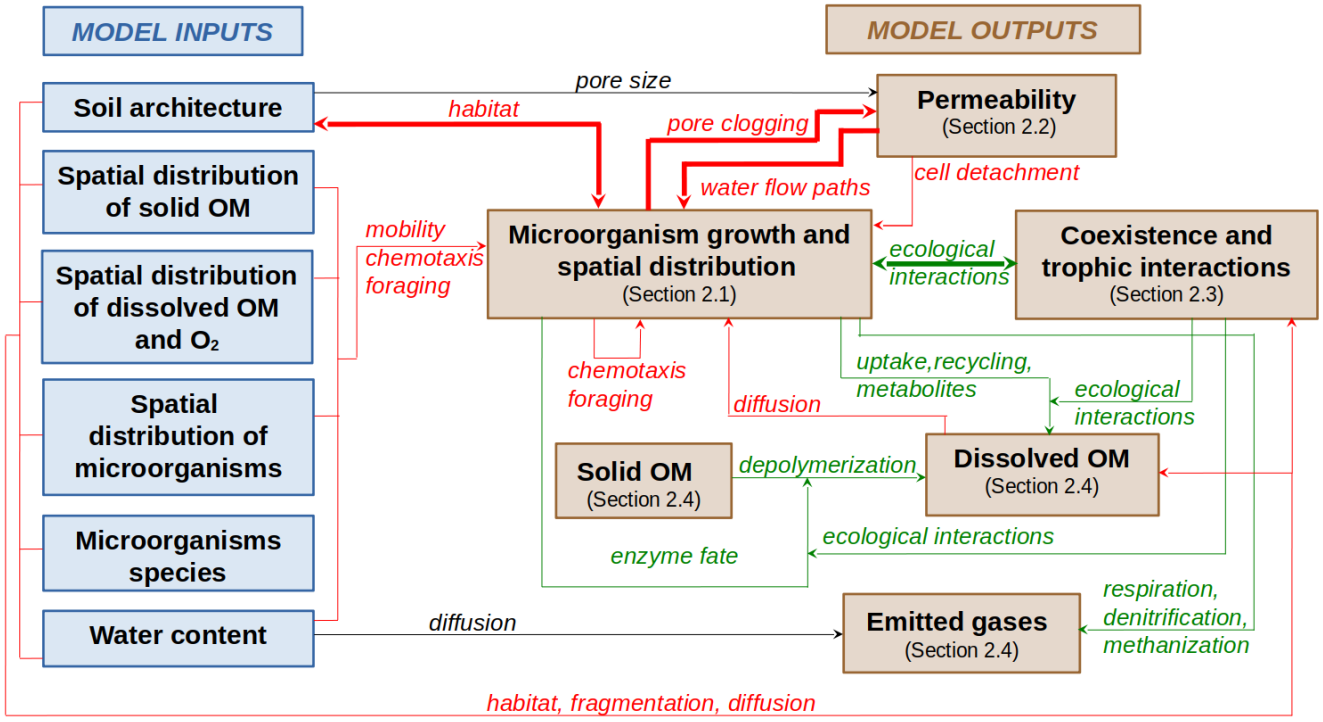

Figure 3: Schematic overview of the main inputs and outputs of microscale models highlighting the spatial and ecological interactions at the microhabitat scale. Red arrows correspond to interactions between inputs and outputs that control spatial accessibility of the trophic resource to microbes. These links are associated to system properties and processes. Green arrows correspond to the links that control the efficiency of microbes to depolymerize and uptake OM and to emit gases. These links are associated to processes. Thick red and green arrows correspond to feedback loops linked to spatial accessibility and ecological interactions respectively. Black arrows correspond to other links that don't control spatial accessibility or efficiency of microbial activity.

From Figure 3, it can be seen that, in microscale models, soil architecture provides an initial stage of spatial accessibility and promotes interactions between the actors of OM decomposition (red arrows between inputs). This accessibility is a key factor explaining most of the model outputs, from a direct influence on hydraulic properties (pore size, black arrow) to indirect influences on the decomposition of OM, emission of gases and soil biodiversity maintenance through its role in shaping the spatial accessibility (red arrows between inputs and outputs). The temporal dynamics of most of the outputs (the spatial distribution of microbial colonies, dissolved OM, soil hydraulic properties, soil

biodiversity) makes spatial accessibility a highly dynamic variable and contributes thus to feedback loops. We identified three feedback loops: (i) soil architecture provides an habitat for microorganisms growth and distribution and in turn microorganisms modify soil architecture (through fungal enmeshment, aggregation) (thick red arrow); (ii) water flow paths can alter the spatial distribution of microorganisms which in turn can alter the pore geometry (until pore clogging) that modifies permeability and water flow paths (two thick red arrows); (iii) biodiversity creates ecological interactions that have an impact on the microorganism growth and distribution which in turn can modify the biodiversity by sustaining or extinguishing species (thick green arrow). Finally, microbial dynamics and ecological interactions can relieve constraints imposed by low spatial accessibility (green arrows).

Microscale models are thus a useful tool to help disentangle these complex interactions between soil architecture and microbial dynamics and rank their contributions. In a few studies they have been used to quantify and rank these complex interactions. In a sensitivity analysis performed on a factorial design where geometry of the pore space, water saturation, spatial distribution of bacteria and physiological trait (bacterial dormancy) are the factors, Vogel et al. (2015) found, for their modelling scenarios, that bacterial spatial distribution alone explains about 30% of the total variance of fructose decrease. About half of the variance of fructose decrease is explained by two-factor interactions between water saturation and bacterial spatial distribution, between geometry of pore space and water saturation, and between geometry of pore space and bacterial spatial distribution. Interestingly, under optimal accessibility, physiological parameters can generate greater variability in fructose decrease, CO_2 production and biomass growth (Vogel et al., 2018). When accessibility is low, the consumption of fructose remains very limited regardless of the efficiency of microbial uptake. This is in line with Pagel et al. (2020) who reported that maximum growth rate can have a higher influence than the spatial heterogeneity of the microbes on the resource consumption. In another sensitivity analysis of a fungal growth microscale model, Cazelles et al. (2013) also showed that parameters related to biomass recycling processes, and in particular the biomass yield efficiency, strongly impact total biomass and respiration. These parameter sensitivities are further dependent on the microenvironment contexts. For example, variability in spatial colonization of pores by a fungus is affected by the parameter describing immobilisation of mobile biomass in the mycelium in scenarios where the carbon resource is homogeneously distributed in the pore space. By contrast, it is the parameter describing the reverse

process, mobilization of the insulated biomass, that is sensitive in scenarios where carbon resource is initially co-located with the fungal inoculum (Cazelles et al., 2013).

Vogel et al. (2018) pointed out that measuring the time evolution of bulk DOC concentration is the best proxy to identify the role of soil architecture and micro-environments on microbial activity. Although easier to measure, the time evolution of CO_2 is less informative because CO_2 is a more integrative variable and its dynamics is also strongly influenced by the physiology of bacteria (Vogel et al., 2018).

4. Discussion

4.1 Assessment of microscale models

Most of the reported microscale models play with “what-if” scenarios to understand the interactions between the actors that control the soil microbial activity. Then, the trends observed are generally compared to experimental findings. The majority of studies that have tried to reproduce experimental conditions consider idealized geometries such as micromodels (e.g., Borer et al., 2018, 2019; Centler et al., 2011), packs of spherical grains (e.g., Gharasoo et al., 2012; Peszynska et al., 2016) and in a few cases repacked soils (e.g., Babey et al., 2017, Monga et al., 2014). Assessment of microscale models on experimental microfluidic devices, as advocated by Smercina et al. (2021), appears promising since biodiversity and the movement of microbes can be easily controlled and monitored (e.g., Long & Hilpert, 2008). For example, Borer et al. (2019) were able to reconcile contradictory results between their microscale model and experiments carried out on microfluidic devices by introducing more complex metabolic pathways in their biological module.

Due to the simplification of the biodiversity contained in microscale models and the still unreachable description of the whole span of pore size of soil architecture, assessing microscale models against experiments in intact soil samples seems unrealistic. Comparison of microscale models to controlled experiments in soils that have attempted to simplify biodiversity also faces a number of difficulties. Sterilization of soils and inoculation of specific micro-organisms have unwanted consequences, such as an unrealistic increase of necromass. Inoculation of the targeted species also poses the question on where to localize the microorganisms in the pores (e.g., Juarez et al., 2013; Pinheiro et al. 2015). Maintaining sterile conditions throughout incubation experiments also makes the experimental protocols considerably more cumbersome. Several attempts have considered instead the injection of labeled dissolved OM into different pore sizes to activate microorganisms located in these

pores (e.g., Ruamps et al., 2011; Kravchenko et al., 2020). However, as pointed out by Baveye et al. (2018) there is still a lack of experimental data to better characterize soil heterogeneity at the microscale habitat and this also contributes to hindering attempts to accurately assess microscale models.

4.2 How to upscale the information given by microscale models

Another difficult challenge is how to translate the knowledge gained on interactions at the microscopic scale into larger scales (König et al., 2020). Upscaling differential equations of reactive transport including non-linear reaction rates, such as Monod-type reaction rates, is complex because it leads to a concentration-dependent transition between reaction-limited and diffusion-limited regimes which is not observed for first-order reaction rates (Heße et al., 2009). This results in an upscaling behavior depending on the substrate concentration. In a simple pore geometry, Heße et al., (2009) succeeded in finding two concentration-independent effective parameters in situations of biomass continuoulsy covering pore walls. These effective parameters were successfully applied to heterogeneous bacterial colonies distribution within a straight pore (Schmidt et al., 2018). However, it is expected that additional scaling factors that are functionals of pore geometry should be considered to improve the upscaled rate estimates in complex soil architecture (Jung & Meile, 2019). Chakrawal et al. (2020) advocated for the use of the scale transition theory, which upscales population dynamic functions (such as Monod dynamics) instead of the partial differential equations of fluxes, as performed in predator-prey ecology models (e.g., Bergström et al., 2006). In this theory, the spatial heterogeneity of substrate and microorganisms at the microscale is considered by keeping the second-order spatial moments when spatially averaging the functions. However analytical expression of these second-order moments have yet to be developed for non-linear reaction rates. Using another approach, Ebrahimi and Or (2016, 2017, 2018) proposed an upscaling procedure to compute the flux of biogeochemical gases at the soil profile scale by using a microscale model that calculates the gases produced in single aggregates of different sizes. Then, the fluxes are summed up to represent those resulting from an assembly of soil aggregates. However, this approach assumes that the aggregates are surrounded by air-filled pores which is not necessarily the case (Baveye et al., 2022; Vogel et al., 2021; Kravchenko et al., 2019).

Alternatively, microscale models can be used to search for a suitable formulation of the effective reaction rate in macroscopic soil carbon models or to improve multiplicative functions used to weight

762 the effective reaction rate. For instance, Wang & Allison (2019) found that enzymatic degradation rates
763 based on the equilibrium chemistry approximation (ECA, Tang & Riley, 2013), which is a more general
764 formulation of “reverse” and “forward” Michaelis-Menten kinetics, could be used to fit outputs from
765 the DEMENT microscale model (Allison, 2012), which uses “forward” Michaelis-Menten kinetics.
766 Ruiz et al. (2020) could fit a simple macroscopic nitrogen model to predictions of a microscale model
767 carried out in complex soil architecture provided that two parameters linked to surface to volume ratios
768 of fertilizer pellets and soil surfaces respectively are considered in the formulation of the dissolved
769 organic nitrogen rates. These results are in line with those of Garnier et al. (2008) and Iqbal et al.
770 (2014) who could fit the macroscopic OM decomposition model CANTIS (Garnier et al., 2003) with
771 measured data of incubation of plant residues, provided that a parameter linearly linked with the
772 specific surface of residues is included in the effective decomposition rate. Thus, rate modifiers that
773 take into account the role of spatial accessibility of OM to the soil decomposers could be found.
774 Indeed, by ignoring spatial information, macroscopic models of OM turnover assume optimal spatial
775 accessibility and may overestimate CO_2 production.

776 Rather than mathematically upscaling to larger spatial scales, a few modelling studies have
777 attempted to finding spatial descriptors of soil architecture that could encompass these microscopic
778 interactions and statistically correlate with the model outputs. Most of these descriptors are based on
779 the spatial accessibility of microbes to the trophic resources. Wang & Or (2012) proposed a bacterial
780 coexistence index equal to the ratio of a characteristic distance traversed by a bacterial cell generation
781 to the effective radius of water clusters. This index aims to quantify the role of soil architecture and
782 hydration status of pores on the coexistence of two competitive species. Portell et al. (2018) calculated
783 the geodesic distance from bacterial colonies to OM residues and compared them to growth of these
784 colonies. They showed that none of the colonies are able to develop for a geodesic distance greater than
785 around 5 mm, which is consistent with experimental data (Gaillard et al., 1999; Védère et al., 2020).
786 The most active microbial habitats are those with the shortest geodesic distance, however some habitats
787 do not develop although they are at a short geodesic distance from the residues. This suggests that other
788 variables such as the local soluble carbon concentration reaching the microhabitats may play a role.
789 This was considered in the accessibility coefficient of Mbé et al. (2021), which is calculated as the
790 average of the shortest geodesic distance between bacterial colonies and OM residues, multiplied by
791 the amount of OM in each residue. Satisfactory statistical correlations (linear regression coefficient R^2
792 of 0.7) between simulated CO_2 and this microscale descriptor is found for different modelling

scenarios. Although these results are encouraging, these latter two descriptors do not consider other processes such as the protection of OM by mineral-associations (e.g., Basile-Doelsch et al., 2020), the translocation of carbon by fungi that can dynamically alter the accessibility of OM in intact soils (e.g., Boswell et al., 2003, 2007; Védère et al., 2020; Vidal et al., 2021), the spatial invasion of fungi and to a lesser extent the motility of bacteria by chemotaxis or using fungal highways (e.g., Banitz et al., 2011). Banitz et al. (2016) found that the combination of two metrics describing the spatial configuration of fungal highways for bacteria was best suited to explain the biodegradation of glucose. The advantage of spatial descriptors based on accessibility of OM is that they can be calculated in soil CT images, provided that accurate segmentation of air, water and organic matter phases are achieved (e.g., Rawlins et al., 2016; Ortega-Ramirez et al., 2021; Rohe et al., 2021). Development of complementary 2D imaging tools such as microscopy and nanoSIMS which provide spatial distribution of chemicals and microorganisms (e.g., Eickhorst & Tippkötter, 2008; Vidal et al., 2021) and whose integration with CT images has begun (Hapca et al. 2011; Schlüter et al., 2019) will certainly help to give accurate information on the relative distributions of OM and microorganisms.

4.3 Overall limitations and future directions of microscale modelling

Describing spatialized microbial activity in 3D and at the microhabitat scale asks for intense computational resources. Obviously, microscale models are not designed to describe soil biodiversity in detailing the many species and complex food webs, which should be better left for ecological models. Nonetheless, the latter may identify main functional groups to be included in microscale models.

We advocate for introducing a dynamical soil architecture in microscale models. Environmental factors such as drying-rewetting cycles and feedbacks of microbial activity on modifying transport pathways and microbial habitats change the spatial OM accessibility. Microscale models would be good candidates to test the hypotheses explaining the still poorly understood Birch effect (Schimel, 2018) that can result in large amounts of emitted CO_2 (e.g., Barnard et al., 2020). Incentive works are those of Ebrahimi & Or (2018), Evans et al. (2016), Šťovíček et al., (2017), Wang & Or (2013) and Zech et al. (2022) who evolved water content at the grid nodes to simulate drying-rewetting cycles. In addition, based on experimental data obtained with X-ray CT imaging tools such as the ones by Bottinelli et al. (2016) one could draw statistical rules to modify the size and connectivity of pores.

Another research gap is the role of meso and macro fauna that, to our knowledge, has been ignored in microscale modelling. Worms (e.g., earthworms, enchytraeids) play an important role in soil carbon

and nitrogen mineralization. Their casts are hotspots for microbial activity, and they modify the pore space morphology through their burrowing activity thereby impacting gas exchanges and transfer in the active microsites. As a result, enhanced CO_2 and N_2O emissions were reported in the presence of worms (e.g., Lubbers et al., 2010; Porre et al., 2016). Including experimental imaging data of burrow systems such as enchytraeids in microscale models would be a good start, as their size fits the microscale models better than earthworm.

We also advocate for including rhizosphere in microscale models. Indeed, most of the reported studies have dealt with detritusphere. However, rhizosphere constitutes hotspots of soil microbial activity and rhizodeposition has a role in priming effect and soil aggregation (e.g., Baumert et al., 2018). Current advances in modelling and experimental methods offer now opportunities to quantify the rhizosphere at microscopic scales and advance new insights how these microscopic processes impact across scales, and current challenges in the rhizosphere (Schnepf et al., 2022). Microscale models could help in quantifying the respective role of detritusphere and rhizosphere in SOM decomposition and greenhouse gases production. To do so, microscale models could benefit from 3D models of root water and nutrients uptake that include soil-root interactions and high-performance imaging tools that reveal root architecture (e.g., Keyes et al., 2013) .

5. Conclusions

Microscale models provide valuable “what-if” scenarios to test hypotheses about the role of soil architecture and microbial dynamics to explain non-linear responses of soil microorganisms. The reported modelling scenarios highlight how microbial activity relies on a balance between the physical and biological processes taking place in the complex soil architecture and reveal threshold effects. They confirm that soil architecture does matter. For example, it contributes to the emergence of a spatial organization of the microbial communities which in turn can modify significantly soil OM decomposition and soil gaseous emissions. They highlight the role of spatial accessibility of trophic resources to microbes, which when combined with ecological interactions, can shape different pictures regarding the amount of OM decomposed in soil. Indeed, microbial dynamics and ecological interactions can counterbalance limitations imposed by low spatial accessibility of OM to decomposers. When spatial accessibility is optimal, they become the major drivers of soil OM decomposition. Local accumulation of biomass can also alter hydraulic properties of soil and influence water flow field. Microscale models also demonstrate that using bulk measures such as bulk water content or bulk soil

density is clearly insufficient to predict soil microbial activity. An accurate description of both the soil microhabitats and microbial dynamics in models is thus crucial to understand soil functions.

Even though the assessment of microscale models is still limited, due to a scarcity of relevant experimental data on soils, these models are useful tools to search for spatial descriptors of the soil micro-environments explaining soil microbial activity. Another key function of these microscale models at this early stage is to guide experimentation by generating new and testable hypotheses based upon our current knowledge, which is encapsulated in the models. Modelling also helps to integrate new knowledge we gain from improved technology, which unravels novel information at microscopic/nano scales.

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7. Data availability statement

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

8. References

Allison, S. D. (2005). Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters*, 8, 626–635. https://doi.org/10.1111/j.1461-0248.2005.00756.x

Allison, S.D. (2012). A trait-based approach for modelling microbial litter decomposition. *Ecology Letters* 15, 1058–1070. doi:10.1111/j.1461-0248.2012.01807.x

Angers D.A., Recous S. (1997). Decomposition of wheat straw and rye residues as affected by particle size. *Plant and Soil* 189, 197-203. doi:https://doi.org/10.1023/A:1004207219678

884 Aravena J.E., Berli M., Ruiz S., Suarez F., Ghezzehei T.A., Tyler S.W. (2014). Quantifying coupled
885 deformation and water flow in the rhizosphere using X-ray microtomography and numerical
886 simulations. *Plant Soil* 376, 95–110. doi:10.1007/s11104-013-1946-z
887 Babey, T., Vieublé-Gonod, L., Rapaport, A., Pinheiro, M., Garnier, P. & de Dreuzy, J.R. (2017).
888 Spatiotemporal simulations of 2,4-D pesticide degradation by microorganisms in 3D soil-core
889 experiments. Ecological Modelling 344, 48-61. DOI: 10.1016/j.ecolmodel.2016.11.006
890 Bailey D.J., Otten W., Gillican C.A. (2000). Saprotrophic invasion by the soil-borne fungal plant
891 pathogen Rhizoctonia solani and percolation thresholds. *New Phytologist* 146, 535-544.
892 doi:10.1046/j.1469-8137.2000.00660.x
893 Banitz, T., Fetzer, I., Johst, K., Wick, L. Y., Harms, H., & Frank, K. (2011). Assessing biodegradation
894 benefits from dispersal networks. *Ecological Modelling*, 222, 2552–2560.
895 https://doi.org/10.1016/j.ecolmodel.2010.07.005
896 Banitz, T., Frank, K., Wick, L. Y., Harms, H., & Johst, K. (2016). Spatial metrics as indicators of
897 biodegradation benefits from bacterial dispersal networks. *Ecological Indicators*, 60, 54–63.
898 https://doi.org/10.1016/j.ecolind.2015.06.021
899 Barnard R.L., Blazewicz S.J., Firestone M.K. (2020) Rewetting of soil: Revisiting the origin of soil
900 CO_2 emissions. *Soil Biology and Biochemistry* 147, 107819. doi:10.1016/j.soilbio.2020.107819
901 Basile-Doelsch I., Balesdent J., Pellerin S. (2020). Reviews and syntheses: The mechanisms underlying
902 carbon storage in soil. *Biogeosciences* 17, 5223-5242. doi:10.5194/bg-17-5223-2020
903 Baumert VL, Vasilyeva NA, Vladimirov AA, Meier IC, Kögel-Knabner I and Mueller CW (2018).
904 Root Exudates Induce Soil Macroaggregation Facilitated by Fungi in Subsoil. Frontiers in
905 Environmental Science 6, 140. doi: 10.3389/fenvs.2018.00140
906 Baveye P.C. (2020). “Soil biofilms”: Misleading description of the spatial distribution of microbial
907 biomass in soils. *Soil Ecology Letters* 2, 2-5. doi:10.1007/s42832-020-0024-8
908 Baveye, P. C., Balseiro-Romero, M., Bottinelli, N., Briones, M., Capowiez, Y., Garnier, P., Kravchenko,
909 A., Otten, W., Pot, V., Schlüter, S., Vogel, H.J., (2022). Lessons from a landmark 1991 article on soil
910 structure: distinct precedence of non-destructive assessment and benefits of fresh perspectives in soil
911 research. Soil Research. In press. doi: 10.1071/SR21268
912 Baveye, P. C., Berthelin, J., & Munch, J. C. (2016). Too much or not enough: reflection on two
913 contrasting perspectives on soil biodiversity. Soil Biology and Biochemistry, 103, 320-326. doi:
914 10...1016/j.soilbio.2016.09.008

915 Baveye P.C., Otten W., Kravchenko A., Balseiro-Romero M., Beckers E., Chalhoub M., Darnault C.,
916 Eickhorst T., Garnier P., Hapca S., Kiranyaz S., Monga O., Mueller C.W., Nunan N., Pot V., Schlüter
917 S., Schmidt H., Vogel H.J. (2018). Emergent properties of microbial activity in heterogeneous soil
918 microenvironments: Different research approaches are slowly converging, yet major challenges
919 remain. *Frontiers in Microbiology* 9, 1929. doi: 10.3389/fmicb.2018.01929
920 Bending G.D., Turner M.K. (1999). Interaction of biochemical quality and particle size of crop residues
921 and its effect on the microbial biomass and nitrogen dynamics following incorporation into soil.
922 *Biology and Fertility of Soils* 29, 319-327. doi:10.1007/s003740050559
923 Bergström, U., Englund, G., and Leonardsson, K. (2006). Plugging space into predator-prey models: an
924 empirical approach., *The American Naturalist* 167, 246–259. doi:10.1086/499372, 2006.
925 Borer B., Ataman M., Hatzimanikatis V., Or D. (2019). Modeling metabolic networks of individual
926 bacterial agents in heterogeneous and dynamic soil habitats (IndiMeSH). *PLoS Computational*
927 *Biology* 15, e1007127. doi:10.1371/10.1371/journal.pcbi.1007127
928 Borer B., Tecon R., Or D. (2018). Spatial organization of bacterial populations in response to oxygen
929 and carbon counter-gradients in pore networks. *Nature communications* 9, 769. doi:10.1038/s41467-
930 018-03187-y
931 Boswell G.P. (2008). Modelling mycelial networks in structured environments. *Mycological Research*
932 112, 1015-1025. doi:10.1016/j.mycres.2008.02.006
933 Boswell, G., Jacobs, H., Davidson, F. A., Gadd, G. M., & Ritz, K. (2003). Growth and function of
934 fungal mycelia in heterogeneous environments. *Bulletin of Mathematical Biology*, 65, 447–477.
935 https://doi.org/10.1016/S0092-8240(03)00003-X
936 Boswell, G. P., Jacobs, H., Ritz, K., Gadd, G. M., & Davidson, F. A. (2007). The development of fungal
937 networks in complex environments. *Bulletin of Mathematical Biology*, 69, 605–634.
938 doi:10.1007/s11538-005-9056-6
939 Bottinelli N, Zhou H, Boivin P, Zhang ZB, Jouquet P, Hartmann C, Peng X (2016). Macropores
940 generated during shrinkage in two paddy soils using X-ray micro-computed tomography. *Geoderma*
941 265, 78-86. doi:10.1016/j.geoderma.2015.11.011
942 Cazelles K., Otten W., Baveye P.C., Falconer R.E. (2013). Soil fungal dynamics: Parameterisation and
943 sensitivity analysis of modelled physiological processes, soil architecture and carbon distribution.
944 *Ecological Modelling* 248, 165-173. doi:10.1016/j.ecolmodel.2012.08.008

945 Centler , F., Fetzer, I., & Thullner, M. (2011). Modeling population patterns of chemotactic bacteria in
946 homogeneous porous media. *Journal of Theoretical Biology*, 287, 82–91.
947 https://doi.org/10.1016/j.jtbi.2011.07.024
948 Chakrawal A., Herrmann A.M., Koestel J., Jarsjö J., Nunan N., Kátterer T., Manzoni S. (2020).
949 Dynamic upscaling of decomposition kinetics for carbon cycling models. *Geoscientific Model*
950 *Development* 13, 1399-1429. doi:10.5194/gmd-13-1399-2020
951 Cook A.R., Otten W., Marion G., Gibson G., Gilligan C.A. (2007). Estimation of multiple transmission
952 rates for epidemics in heterogeneous populations. *Proceedings of the National Academy of Sciences*
953 104, 20392-7. doi:10.1073/pnas.0706461104
954 Crawford J.W., Deacon L., Grinev D., Harris J.A., Ritz K., Singh B.K., Young I. (2012). Microbial
955 diversity affects self-organization of the soil –microbe system with consequences for function
956 *Journal of the Royal Society of Interface* 9, 1302–1310. doi:10.1098/rsif.2011.0679
957 Dechesne A., Owsianiak W., Bazire A., Grundmann G.L., Binning P.J., Smets B.F. (2010).
958 Biodegradation in a Partially Saturated Sand Matrix : Compounding Effects of Water Content,
959 Bacterial Spatial Distribution, and Motility. *Environmental Science & Technology* 44, 2386-2392.
960 doi:10.1021/es902760y.
961 Ebrahimi A., Or D. (2014). Microbial dispersal in unsaturated porous media: Characteristics of motile
962 bacterial cell motions in unsaturated angular pore networks. *Water Resources Research* 50, 7406-
963 7429. doi:10.1002/2014WR015897
964 Ebrahimi A.N., Or D. (2015). Hydration and diffusion processes shape microbial community
965 organization and function in model soil aggregates. *Water Resources Research* 51, 9804-9827.
966 doi:10.1002/2015WR017565
967 Ebrahimi A., Or D. (2016). Microbial community dynamics in soil aggregates shape biogeochemical
968 gas fluxes from soil profiles – upscaling an aggregate biophysical model. *Global Change Biology*
969 22, 3141-3156. doi:10.1111/gcb.13345
970 Ebrahimi, A., & Or, D. (2017). Mechanistic modeling of microbial interactions at pore to profile scale
971 resolve methane emission dynamics from permafrost soil. *Biogeosciences* 122, 1216–1238.
972 doi:10.1002/2016JG003674
973 Ebrahimi, A., & Or, D. (2018). Dynamics of soil biogeochemical gas emissions shaped by remolded
974 aggregate sizes and carbon configurations under hydration cycles. *Global Change Biology* 24, e378–
975 e392. doi:10.1111/gcb.13938

Eickhorst, T., Tippkötter, R. (2008). Improved detection of soil microorganisms using fluorescence in situ hybridization (FISH) and catalyzed reporter deposition (CARD-FISH). *Soil Biology and Biochemistry*, 40, 1883–1891. doi:10.1016/j.soilbio.2008.03.024

Erktan A., Or D., Scheu S. (2020). The physical structure of soil: Determinant and consequence of trophic interactions. Soil Biology and Biochemistry 148, 107876. doi:10.1016/j.soilbio.2020.107876

Evans S., Dieckmann U., Franklin O., Kaiser C. (2016). Synergistic effects of diffusion and microbial physiology reproduce the Birch effect in a micro-scale model. *Soil Biology and Biochemistry* 93, 28-37. doi:10.1016/j.soilbio.2015.10.020

Falconer R.E., Bown J.K., White N.A., Crawford J.W. (2005). Biomass recycling and the origin of phenotype in fungal mycelia. *Proceedings of the Royal Society B* 272, 1727-1734. doi:10.1098/rspb.2005.3150

Falconer R.E., Battaia G., Schmidt S., Baveye P., Chenu C., Otten W. (2015). Microscale Heterogeneity Explains Experimental Variability and Non-Linearity in Soil Organic Matter Mineralisation. *PLOS One* 10, e0123774. doi:10.1371/journal.pone.0123774

Falconer R.E., Brown J.L., White N.A., Crawford J.W. (2007). Biomass recycling : a key to efficient foraging by fungal colonies. *Oikos* 116, 1558-1568. doi:10.1111/j.2007.0030-1299.15885.x

Falconer R.E., Bown J.L., White N.A., Crawford J.W. (2008). Modelling interactions in fungi. *Journal of the Royal Society Interface* 5, 603–615. doi:10.1098/rsif.2007.1210

Falconer R., Houston A.N., Otten W., Baveye P.C. (2012). Emergent Behavior of Soil Fungal Dynamics : Influence of Soil Architecture and Water Distribution. *Soil Science* 177, 111-119. doi:10.1097/SS.0b013e318241133a

Fierer N., Schimel J.P., Holden P.A. (2003). Influence of Drying-Rewetting Frequency on Soil Bacterial Community Structure. Microb Ecol 45, 63–71 doi:10.1007/s00248-002-1007-2

Flemming, H. C., Baveye, P., Neu, T. R., Stoodley, P., Szewzyk, U., Wingender, J., & Wuertz, S. (2021). Who put the film in biofilm? The migration of a term from wastewater engineering to medicine and beyond. npj Biofilms and Microbiomes, 7(1), 1-5. Doi: 10.1038/s41522-020-00183-3.

Folse III H.J., Allison S.D. (2012). Cooperation, competition, and coalitions in enzyme-producing microbes: Social evolution and nutrient depolymerisation rates. *Frontiers in Microbiology* 3, 338. doi:10.3389/fmicb.2012.00338

Franzluebbers A.J. (1999). Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils. Applied Soil Ecology 11, 91-101. doi:10.1016/S0929-1393(98)00128-0

Gaillard, V., Chenu, C., Recous, S., Richard, G. (1999). Carbon, nitrogen and microbial gradients induced by plant residues decomposing in soil. *European Journal of Soil Science* 50, 567–578. doi:10.1046/J.1365-2389.1999.00266.X

Garnier P., Cambier C., Bousso M., Masse D., Chenu C., Recous S. (2008). Modeling the influence of soil-plant residue contact on carbon mineralization: Comparison of a compartmental approach and a 3D spatial approach. *Soil Biology and Biochemistry* 40, 2754-2761. doi:10.1016/j.soilbio.2008.07.032

Garnier P., Neel C., Aita C., Recous S., Lafolie F., Mary B. (2003). Modelling carbon and nitrogen dynamics in soil with and without straw incorporation. European Journal of Soil Science, 54:555–568. doi:10.1046/j.1365-2389.2003.00499.x

Gharasoo M., Centler F., Fetzer I., Thullner M. (2014). How the chemotactic characteristics of bacteria can determine their population patterns. *Soil Biology and Biochemistry* 69, 346-358. doi:10.1016/j.soilbio.2013.11.019

Gharasoo, M., Centler, F., Regnier, P., Harms, H., & Thullner, M. (2012). A reactive transport modeling approach to simulate biogeochemical processes in pore structures with pore-scale heterogeneities. *Environmental Modelling & Software*, 30, 102–114. doi:10.1016/j.envsoft.2011.10.010

Graf von der Schulenburg D.A., Pintelon T.R.R., Picioreanu C., Van Loosdrecht M.C.M., Johns M.L. (2009). Three-Dimensional Simulations of Biofilm Growth in Porous Media. *AIChe Journal* 55, 494-504. doi:10.1002/aic.11674

Gras, A., M. Ginovart, J. Valls and P. C. Baveye (2011). Individual-based modelling of carbon and nitrogen dynamics in soils: parameterization and sensitivity analysis of microbial components. *Ecological Modelling* 222, 1998–2010. doi:10.1016/j.ecolmodel.2011.03.009

Hapca, S. M., Wang, Z. X., Otten, W., Wilson, C., & Baveye, P. C.

(2011). Automated statistical method to align 2D chemical maps with 3D X-ray computed micro-tomographic images of soils. *Geoderma*, 164(3–4), 146–154. https://doi.org/10.1016/j.geoderma.2011.05.018

Harris K., Young I.M., Gilligan C.A., Otten W., Ritz K. (2003). Effect of bulk density on the spatial organisation of the fungus Rhizobacteria solani in soil. *FEMS Microbiology Ecology* 44, 45-56. doi:10.1111/j.1574-6941.2003.tb01089.x

Heße F., Radu F.A., Thullner M., Attinger S. (2009). Upscaling of the advection–diffusion–reaction equation with Monod reaction. *Advances in Water Resources* 32, 1336-1351. doi:10.1016/j.advwatres.2009.05.009

Iqbal A., Garnier P., Lashermes G., Recous S. (2014). A new equation to simulate the contact between soil and maize residues of different sizes during their decomposition. *Biology and Fertility of Soils* (2014) 50:645–655. doi:10.1007/s00374-013-0876-5

Juarez S. Nunan N., Duday A-C., Pouteau V., Chenu C. (2013). Soil carbon mineralisation responses to alterations of microbial diversity and soil structure. *Biology and Fertility of Soils* 49, 939-948. doi:10.1007/s00374-013-0784-8

Jung H., Meile C. (2019). Upscaling of microbially driven first-order reactions in heterogeneous porous media. J*ournal of Contaminant Hydrology* 224, 103483. doi:/10.1016/j.jconhyd.2019.04.006

Kaiser, C., Franklin, O., Dieckmann, U., & Richter, A. (2014). Microbial community dynamics alleviate stoichiometric constraints during litter decay. Ecology Letters, 17, 680–690. doi:10.1111/ele.12269

Kaiser C., Franklin O., Richter A., Dieckmann U. (2015). Social dynamics within decomposer communities lead to nitrogen retention and organic matter build-up in soils. *Nature Communications* 6:8960. doi: 10.1038/ncomms9960

Kapellos G.E., Alexiou T.S., Payatakes A.C. (2007). Hierarchical simulator of biofilm growth and dynamics in granular porous materials. *Advances in Water Resources* 30, 1648-1667. doi:10.1016/j.advwatres.2006.05.030

Keyes SD, Daly KR, Gostling NJ, Jones DL, Talboys P, Pinzer BR, Boardman R, Sinclair I, Marchant A, Roose T (2013) High resolution synchrotron imaging of wheat root hairs growing in soil and image based modelling of phosphate uptake. *New Phytologist* 198, 1023–1029. doi:10.1111/nph.12294

Kim, M., & Or, D. (2016). Individual-based model of microbial life on hydrated rough soil surfaces. PLoS One, 11, e0147394. doi:10.1371/journal.pone.0147394

Knutson C.E., Werth C.J., Valocchi A.J. (2005). Pore-scale simulation of biomass growth along the transverse mixing zone of a model two-dimensional porous medium. *Water Resources Research* 41, W07007. doi:10.1029/2004WR003459

König S., Worrich A., Centler F., Wick L.Y., Miltner A., Kästner M., Thullner M., Frank K., Banitz T. (2017). Modelling functional resilience of microbial ecosystems : Analysis of governing processes. *Environmental Modelling & Software* 89, 31-39. doi:10.1016/j.envsoft.2016.11.025

König S., Worrich A., Banitz T., Centler F., Harms H., Kästner M., Miltner A., Wick L.Y., Thullner M., Frank K. (2018). Spatiotemporal disturbance characteristics determine functional stability and collapse risk of simulated microbial exosystems. *Scientific Reports* 8, 9488. doi:10.1038/s41598-018-27785-4

König S., Köhnke M.C., Firie A-L., Banitz T., Centler F., Frank K., Thullner M. (2019). Disturbance Size Can Be Compensated for by Spatial Fragmentation in Soil Microbial Ecosystems. *Frontiers in Ecology and Evolution* 7, 290. doi:10.3389/fevo.2019.00290

König S., Vogel H.J., Harms H., Worrich A. (2020). Physical, Chemical and Biological Effects on Soil Bacterial Dynamics in Microscale Models. *Frontiers in Ecology and Evolution* 8, 53. doi: 10.3389/fevo.2020.00053

Kravchenko A., Falconer R.E., Grinev D., Otten W. (2011). Fungal colonization in soils with different management histories: modeling growth in three-dimensional pore volumes. *Ecological Applications* 21, 1202-1210. doi:10.2307/23022990

Kravchenko A., Guber A., Gunina A., Dippold M., Kuzyakov Y. (2020). Pore-scale view of microbial turnover: Combining 14 C imaging, μCT and zymography after adding soluble carbon to soil pores of specific sizes. *European Journal of Soil Science*, 1-15. doi:10.1111/ejss.13001

Kravchenko, A., Otten, W., Garnier, P., Pot, V., & Baveye, P. C. (2019). Soil aggregates as biogeochemical reactors: Not a way forward in the research on soil–atmosphere exchange of greenhouse gases. *Global Change Biology* 25, 2205–2208. doi:10.1111/gcb.14640

Laudone, G. M., Matthews, G. P., Bird, N. R. A., Whalley, W. R., Cardenas, L. M., Gregory, A. S. (2011). A model to predict the effects of soil structure on denitrification and N_2O emission. *Journal of Hydrology*, 409, 283–290. doi:10.1016/j.jhydrol.2011.08.026

Laudone, G. M., Matthews, G. P., Gregory, A. S., Bird, N. R. A., Whalley, W. R. (2013). A dual-porous, inverse model of water retention to study biological and hydrological interactions in soil. *European Journal of Soil Science*, 64, 345–356. doi:10.1111/ejss.12055

Long T., Or D. (2005). Aquatic habitats and diffusion constraints affecting microbial coexistence in unsaturated porous media. *Water Resources Research* 41, W08408. doi:10.1029/2004WR003796

Long, T., & Or, D. (2007). Microbial growth on partially saturated rough surfaces: Simulations in idealized roughness networks. *Water Resources Research* 43, W02409. doi:10.1029/2005WR004781

Long T., Or D. (2009). Dynamics of Microbial Growth and Coexistence on Variably Saturated Rough Surfaces. *Environmental Microbiology* 58, 262-275 doi:10.1007/s00248-009-9510-3

Long W., Hilpert M. (2008). Lattice-Boltzmann modeling of contaminant degradation by chemotactic bacteria: Exploring the formation and movement of bacterial bands. *Water Resources Research* 44, W09415. doi:10.1029/2007WR006129

Lubbers IM, Pulleman MM, van Groenigen JW (2010). Can earthworms simultaneously enhance decomposition and stabilization of plant residue carbon? *Soil Biology and Biochemistry* 105, 12-24. doi:10.1016/j.soilbio.2016.11.008

Lugato, E., Morari, F., Nardi, S., Berti, A., Giardini, L. (2009). Relationship between aggregate pore size distribution and organic–humic carbon in contrasting soils. *Soil & Tillage Research* 103, 153–157. doi:10.1016/j.still.2008.10.013

Masse D., Cambier C., Brauman A., Sall S., Assiggbetse K., Chotte J.L. (2007). MIOR : an individual-based model for simulating the spatial patterns of soil organic matter microbial decomposition. *European Journal of Soil Science* 58, 1127-1135. doi:10.1111/j.1365-2389.2007.00900.x

Mbé B., Monga O., Pot V., Otten W., Hecht F., Raynaud X., Nunan N., Chenu C., Baveye P.C., Garnier P. (2021). Scenario modelling of carbon mineralization in 3D soil architecture at the microscale: Toward an accessibility coefficient of organic matter for bacteria. *European Journal of Soil Science*. doi:10.1111/ejss.13144

Monga O., Bousso M., Garnier P., Pot V. (2008). 3D geometric structures and biological activity: Application to microbial soil organic matter decomposition in pore space. *Ecological Modelling* 216, 291-302. doi:10.1016/j.ecolmodel.2008.04.015

Monga O., Garnier P., Pot V., Coucheney E., Nunan N., Otten W., Chenu C. (2014). Simulating microbial degradation of organic matter in a simple porous system using the 3-D diffusion-based model MOSAIC. *Biogeosciences* 11, 2201-2209. doi:10.5194/bg-11-2201-2014

Ngom N.F., Garnier P., Monga O., Peth S. (2011). Extraction of three-dimensional soil pore space from microtomography images using a geometrical approach. *Geoderma* 163, 127–134. doi:10.1016/j.geoderma.2011.04.013

Nunan N., Schmidt H., Raynaud X. (2020). The ecology of heterogeneity: soil bacterial communities and C dynamics. *Philosophical Transactions of the Royal Society B* 375: 20190249. doi:10.1098/rstb.2019.0249

Ortega-Ramirez P., Pot V., Laville P., Schlüter S., Hadjar D., Basile-Doelsch I., Henault C., Caurel C., Mazurier A., Lacoste M.; Garnier P. (2021). Role of soil microstructure on the emission of N_2O in intact small soil columns. EGU21-12438, EGU General Assembly 2021. doi:10.5194/egusphere-egu21-12438

Otten W., Gilligan C.A., Watts C.W., Dexter A.R., Hall D. (1999). Continuity of air-filled pores and invasion thresholds for a soil-borne fungal plant pathogen, Rhizoctonia solani. *Soil Biology and Biochemistry* 31, 1803-1810. doi:10.1016/S0038-0717(99)00099-1

Otten W., Hall D., Harris K., Ritz K., Young I.M., Gilligan C.A. (2001). Soil physics, fungal epidemiology and the spread of Rhizoctonia solani. *New Phytologist* 151, 459-468. doi:10.1046/j.0028-646x.2001.00190.x

Otten W., Bailey D.J., Gilligan C.A. (2004a). Empirical evidence of spatial thresholds to control invasion of fungal parasites and saprotrophs. *New Phytologist* 163, 125-132. doi:10.1111/j.1469-8137.2004.01086.x

Otten W., Harris K., Young I.M., Ritz K., Gilligan C.A. (2004b). Preferential spread of the pathogenic fungus Rhizoctonia solani through structured soil. *Soil Biology and Biogeochemistry* 36, 203-210. doi:10.1016/j.soilbio.2003.09.006

Otten W. Gilligan C.A. (2006). Soil structure and soil-borne diseases: using epidemiological concepts to scale from fungal spread to plant epidemics. *European Journal of Soil Science* 57, 26–37. doi:10.1111/j.1365-2389.2005.00766.x

Pagel H., Kriesche B., Uksa M., Poll C., Kandeler E., Schmidt V., Streck T. (2020). Spatial Control of Carbon Dynamics in Soil by Microbial Decomposer Communities. *Frontiers in Environmental Science* 8, 2. doi: 10.3389/fenvs.2020.00002

Pajor R., Falconer R., Hapca S., Otten W. (2010). Modelling and quantifying the effect of heterogeneity in soil physical condictions on fungal growth. *Biogeosciences*, 7, 3731–3740. doi:10.5194/bg-7-3731-2010

Perez-Reche F.J., Taraskin S.N., Otten W., Viana M.P., Costa L. da F., Gilligan C.A. (2012). Prominent effect of soil network heterogeneity on microbial invasion. *Physical Review Letters* 109, 098102. doi:10.1103/PhysRevLett.109.098102

Peszynska M., Trykozko A., Iltis G., Schlueter S., Wildenschild W. (2016). Biofilm growth in porous media: Experiments, computational modeling at the porescale, and upscaling. *Advances in Water Resources* 95, 288-301, doi: 10.1016/j.advwatres.205.07.008

Pinheiro M., Garnier P., Beguet J., Martin Laurent F., Vieublé Gonod L. (2015). The millimetre-scale distribution of 2,4-D and its degraders drives the fate of 2,4-D at the soil core scale. *Soil Biology and Biochemistry* 88, 90-100. doi:10.1016/j.advwatres.2015.07.008

Porre RJ, van Groenigen JW, de Deyn GB, de Goede RGM, Lubbers IM (2016). Exploring the relationship between soil mesofauna, soil structure and N_2O emissions. *Soil Biology and Biochemistry* 96, 55-64. doi:10.1016/j.soilbio.2016.01.018

Portell X., Pot V., Garnier P., Otten W., Baveye P.C. (2018). Microscale Heterogeneity of the Spatial Distribution of Organic Matter Can Promote Bacterial Biodiversity in Soils: Insights From Computer Simulations. *Frontiers in Microbiology* 9, 1583. doi:10.3389/fmicb.2018.01583

Pot V., Portell X., Otten W., Garnier P., Monga O., Baveye P.C. (2021). Accounting for soil architecture and microbial dynamics in microscale models: Current practices in soil science and the path ahead. *European Journal of Soil Science*. doi:10.1111/ejss.13142

Quigley M.Y., Rivers M.L. and Kravchenko A.N. (2018). Patterns and Sources of Spatial Heterogeneity in Soil Matrix From Contrasting Long Term Management Practices. Front. Environ. Sci. 6, 28. doi: 10.3389/fenvs.2018.00028

Rawlins, B. G., Wragg, J., Reinhard, C., Atwood, R. C., Houston, A., Lark, R. M., & Rudolph, S. (2016). Three-dimensional soil organic matter distribution, accessibility and microbial respiration in macroaggregates using osmium staining and synchrotron X-ray computed tomography. *The Soil* 2, 659–671. doi:10.5194/soil-2-659-2016

Ray N., Rupp A., Prechtel A. (2017). Discrete-continuum multiscale model for transport, biomass development and solid restructuring in porous media. *Advances in Water Resources* 107, 393-404. doi:10.1016/j.advwatres.2017.04.001

Resat H., Bailey V., McCue L.A., Konpka A. (2012). Modeling Microbial Dynamics in Heterogeneous Environments : Growth on Soil Carbon Sources. *Microbial Ecology* 63, 883-897. doi:10.1007/s00248-011-9965-x

Rohe L., Apelt B., Vogel H-J., Well R., WU G-M., Schlüter S. (2021). Denitrification in soil as a function of oxygen availability at the microscale. *Biogeosciences* 18, 1185–1201. doi:10.5194/bg-18-1185-2021

Rosenzweig D., Furman A., Shavit U. (2013). A Channel Network Model as a Framework for Characterizing Variably Saturated Flow in Biofi lm-Affected Soils. *Vadose Zone Journal* doi:10.2136/vzj2012.0079

Ruamps L.S., Nunan N., Chenu C. (2011). Microbial biogeography at the soil pore scale. *Soil Biology and Biochemistry* 43, 280-286. doi:10.1016/j.soilbio.2010.10.010

Ruiz S.A., McKay Fletcher D.M., Boghi A., Williams K.A., Duncan S.J., Scotson C.P., Petroselli C., Dias T.G.S., Chadwick D.R., Jones D.L., Roose T. (2020). Image-based quantification of soil microbial dead zones induced by nitrogen fertilization. *Science of the Total Environment* 727, 138197. doi:10.1016/j.scitotenv.2020.138197

Rupp A., Guhra T., Meier A., Prechtel A., Ritschel T., Ray N. and Totsche K.U. (2019). Application of a Cellular Automaton Method to Model the Structure Formation in Soils Under Saturated Conditions: A Mechanistic Approach. *Frontiers in Environmental Science* 7, 170. doi: 10.3389/fenvs.2019.00170

Sadeghnejad S., Enzmann F., Kersten M. (2021). Digital rock physics, chemistry, and biology: challenges and prospects of pore-scale modelling approach. *Applied Geochemistry* 131, 105028. doi:10.1016/j.apgeochem.2021.105028

Schlüter S., Eickhorst T., Mueller C.W. (2019). Correlative Imaging Reveals Holistic View of Soil Microenvironments. *Environmental Science & Technology* 53, 829−837. doi:10.1021/acs.est.8b05245

Schimel JP (2018). Life in dry soils; Effect of drought on soil microbial communities and processes. The Annual Review of Ecology, Evolution, and Systematics 49, 409-432. doi:10.1146/annurev-ecolsys-110617-062614

Schmidt S.I., Kreft J.H., Mackay R., Picioreanu C., Thullner M. (2018). Elucidating the impact of micro-scale heterogeneous bacterial distribution on biodegradation. *Advances in Water Resources* 116, 67–76. doi:10.1016/j.advwatres.2018.01.013

Skopp J., Jawson M.D., Doran J.W. (1990). Steady-State Aerobic Microbial Activity as a Function of Soil Water Content. *Soil Science Society of America Journal* 54, 1619-1625. doi:10.2136/sssaj1990.03615995005400060018x

Smercina D.N., Bailey V.L., Hofmockel S. (2021). Micro on a macroscale: relating microbial-scale soil processes to global ecosystem function. *FEMS Microbiology Ecology* 97, fiab091. doi:10.1093/femsec/fiab091

Schnepf A, Carminati A, Ahmed MA, Benard P, Bentz J, Bonkowski M, Knott M, Diehl D, Duddek P, Kröner E, et al. (2022). Linking rhizosphere processes across scales: Opinion. *Plant and Soil*. doi:10.1007/s11104-022-05306-7

Soufan, R., Delaunay, Y., Gonod, L. V., Shor, L. M., Garnier, P., Otten, W., Baveye P.C. (2018). Pore-scale monitoring of the effect of microarchitecture on fungal growth in a two-dimensional soil-like micromodel. Front. Environ. Sci. 6:68. doi: 10.3389/fenvs.2018.00068.

Stahl, P. D. & Christensen, M. (1992). In vitro interactions among members of a soil microfungal community. *Soil Biology and Biochemistry* 24, 309–316. doi:10.1016/0038-0717(92)90190-9

Šťovíček A., Kim M., Or D., Gillor O. (2017). Microbial community response to hydration-desiccation cycles in desert soil. Scientific Reports 7, 45735. doi:10.1038/srep45735

Strong D.T., de Wever, H., Merckx, R., Recous S. (2004). Spatial location of carbon decomposition in the soil pore system. *European Journal of Soil Science* 55, 739–750. doi:10.1111/j.1365-2389.2004.00639.x

Tang Y., Valocchi A.J., WerthC.J., Liu H. (2013). An improved pore-scale biofilm model and comparison with a microfluidic flow cell experiment. *Water Resources Research* 49, 8370-8382. doi:10.1002/2013WR013843

Tang, J.Y., Riley, W.J., 2013. A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial litter decomposition. *Biogeosciences* 10, 8329–8351. doi:10.5194/bg-10-8329-2013

Tartakovsky A.M., Scheibe T.D., Meakin P. (2009). Pore-Scale Model for Reactive Transport and Biomass Growth. *Journal of Porous Media* 12, 417-434. doi:10.1615/JPorMedia.v12.i5.30

Védère C., Vieublé-Gonod L., Pouteu V., Girardin C., Chenu C. (2020). Spatial and temporal evolution of detritusphere hotspots at different soil moistures. *Soil Biology and Biochemistry* 150, 107975. doi:10.1016/j.soilbio.2020.107975

Vidal A., Klöffel T., Guigue J., Angst G., Steffens M., Hoeschen C., Mueller C.W. (2021). Visualizing the transfer of organic matter from decaying plant residues to soil mineral surfaces controlled by microorganisms. *Soil Biology and Biochemistry*, 160, 108347. doi: 10.1016/j.soilbio.2021.108347

Vogel H-J., Balseiro-Romero M., Kravchenko A., Otten W., Pot V., Schlüter S., Weller U., Baveye P.C. (2021). A holistic perspective on soil architecture is needed as a key to soil functions. European Journal of Soil Science. doi:10.1111/ejss.13152

Vogel L., Makowski D., Garnier P., Vieublé-Gonod L., Coquet Y., Raynaud X., Nunan N., Chenu C., Falconer R., Pot V. (2015). Modeling the effect of soil meso- and macropores topology on the biodegradation of a soluble carbon substrate. *Advances in Water Resources* 83, 123-126. doi:10.1016/j.advwatres.2015.05.020

Vogel L.E., Pot V., Makowski D., Garnier P., Baveye P.C. (2018). To what extent do uncertainty and sensitivity analyses help unravel the influence of microscale physical and biological drivers in soil carbon dynamics models? *Ecological Modelling* 383, 10-22. doi:10.1016/j.ecolmodel.2018.05.007

Wang B., Allison S.D (2019). Emergent properties of organic matter decomposition by soil enzymes. *Soil Biology and Biochemistry* 136, 107522. doi:10.1016/j.soilbio.2019.107522

Wang, G., & Or, D. (2010). Aqueous films limit bacterial cell motility and colony expansion on partially saturated rough surfaces. *Environmental Microbiology*, 12, 1363–1373. https://doi.org/10.1111/j.1462-2920.2010.02180.x

Wang G., Or D. (2012). A Hydration-Based Biophysical Index for the Onset of Soil Microbial Coexistence. *Scientific Reports* 2, 881. doi:10.1038/srep00881

Wang G., Or D. (2013). Hydration dynamics promote bacterial coexistence on rough surfaces. *ISME Journal* 7, 395-404. doi:10.1038/ismej.2012.115

Wang G., Or D. (2014). Trophic interactions induce spatial self-organization of microbial consortia on rough surfaces. *Scientific Reports* 4, 6757. doi:10.1038/srep06757

Wieder W.R., Allison S.D., Davidson E.A., Georgiou K., Hararuk O., He Y., Hopkins F., Luo Y., Smith M.J., Sulman B., Todd-Brown K., Wang Y-P., Xia J., Xu X. (2015). Explicitly representing soil microbial processes in Earth system models. *Global Biogeochemical Cycles* 29, 1782-1800. doi:10.1002/2015GB005188.

Yan Z., Liu C., Todd-Brown K.E., Liu Y., Bond-Lamberty B., Bailey V.L. (2016). Pore-scale investigation on the response of heterotrophic respiration to moisture conditions in heteregeneous soils. *Biogeochemistry* 131, 121-134. doi:10.1007/s10533-016-0270-0

Yan Z., Wang T., Wang L., Yang X., Smith P., Hilpert M., Li S., Shang J., Bailey V., Liu C. (2018). Microscale water distribution and its effects on organic carbon decomposition in unsaturated soils. *Science of the Total Environment* 644, 1036-1043. doi:10.1016/j.scitotenv.2018.06.365

Zech S., Ritschel T., Ray N., Totsche K.U., Prechtel A. (2022). How water connectivity and substrate supply shape the turnover of organic matter – Insights from simulations at the scale of microaggregates. *Geoderma* 405, 115394. doi:10.1016/j.geoderma.2021.115394

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