

Review Paper

The unexplored role of preferential flow in soil carbon dynamics

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ABSTRACT

Water is a crucial factor controlling the fate and processing of soil organics. Water commonly flows through the vadose zone via preferential flow pathways, resulting in nonuniform and rapid infiltration. Hence, a large portion of the soil matrix is bypassed. Preferential flow paths, often associated with well-connected macropore networks (>300 μm Ø), offer a unique balance between water availability, nutrient delivery, and re-oxygenation upon drainage. The heightened concentrations of moisture, nutrients, and oxygen make these locations optimal for high rates of microbial activity. Flow paths often display temporal stability. This stability results in repeated wetting and biogeochemical reactivation through time creating a lasting impact on micro-environmental conditions relevant to microbial functioning and carbon cycling in soil. Despite decades of research on preferential flow, there is still a need to link flow paths and the resultant heterogeneous moisture distributions to soil function. In this review, we discuss how preferential flow can serve as a framework of reference for the spatially and temporally heterogeneous biogeochemical cycling of soil carbon. We highlight the importance of combining current knowledge of pore-scale carbon dynamics with an appreciation of connected networks of hydraulically active pores/paths within the soil profile. Such combination opens new possibilities for upscaling pore-scale processes with the inclusion of resource heterogeneity at the macroscale. Working within this hydraulically connected framework can provide insight for the mechanistic representation of hot moments, which are temporally isolated large pulses of CO₂ after rewetting or thawing events. We conclude with suggestions on knowledge gaps and stress the critical need of linking soil physics with biology to mechanistically understand soil functions.

1. Introduction

1.1. Emerging biophysical relationships

In their landmark review, Beven and Germann (1982) posed the question, “How do macropores operate hydrologically?” highlighting the need to incorporate spatial heterogeneity into theoretical approaches to model water flow and contaminant transport in soil. Macropores are pores >300 μm Ø (Jarvis, 2007) that arise biotically from roots and worm burrows, or abiotically from shrink-swell processes and erosive subsurface flow. Even when constituting less than 1% of the soil matrix, macropores are capable of transmitting more than 90% of infiltrating water (Sanders et al., 2012; Watson and Luxmoore, 1986). The outcome of this non-equilibrium phenomenon, termed preferential flow, is that portions of the soil matrix are bypassed (Flury et al., 1994). In the years following Beven and Germann

(1982), research on macropores rapidly grew, generating important insights into their physical properties and associated hydrology (Luxmoore et al., 1990; McDonnell, 1990; Nielsen et al., 1986; Richard and Steenhuis, 1988). Interest in predicting and modeling preferential flow as a soil physical process has continued (Jury, 1999; Šimůnek et al., 2003; Guo and Lin, 2018; Nimmo, 2012; Beven, 2018; Gerke et al., 2010; Jarvis, 2016), but the role of preferential flow phenomena in soil biogeochemical cycling has so far received little attention (Baveye and Laba, 2015). We argue that despite decades of research on preferential flow, there is a need to link flow paths and the resultant heterogeneous soil moisture distributions to soil functions, especially, to biogeochemical processes.

One may ask, why does preferential flow need to be accounted for in studies of soil biogeochemical processes? After all, soil biology and biochemistry have already been making meaningful strides in understanding soil functioning without considering preferential flow. The

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short answer is – upscaling. Accurate upscaling of non-linear microscale biogeochemical processes that drive soil heterogeneity and their conversion into relevant predictions of macroscale functions has remained a “holy grail” of soil science (Baveye et al., 2018; Clark et al., 2015; Falconer et al., 2015). Translating the knowledge of key drivers of biochemical processes into whole soil profile predictions requires information on the spatial distribution patterns of such drivers. We highlight that preferential flow fundamentally affects the whole profile distribution of the most important of such drivers, soil moisture, and substantially influences carbon distribution and microbial activity as well.

While the role of soil moisture for individual biogeochemical phenomena such as soil oxygenation (Jost et al., 2015; Schlüter et al., 2018), microbial activity and motility (Skopp et al., 1990; Manzoni et al., 2012; Kleyer et al., 2020; Wang and Or, 2013), or soil respiration (Leon et al., 2014; Sponseller, 2007; Moore and Dalva, 1993) has been researched at length, a general understanding of the interplay between soil physical and biological processes remains fragmented and incomplete. The culprit is the prevalence of narrow intra-discipline foci. For example, soil physicists study soil moisture in terms of amount, flow speed, and the related transport processes (Nielsen et al., 2010; Wang et al., 2013; Villholth et al., 2000). Soil microbiologists are interested in how moisture affects microbial ecology (Wilpiszeski et al., 2019; Zhao et al., 2019), and soil biogeochemists examine how soil moisture controls greenhouse gas efflux (Kim et al., 2012; Leitner et al., 2017; Warner et al., 2018). As we will discuss, the influence of preferential flow on soil functioning is a complex outcome of interacting physics, hydrology, geochemistry, and biology. Thus, further progress in studying them will require interdisciplinary efforts.

Water is crucial for the processing and mineralization of soil carbon. Thus, following the water as it preferentially travels through the soil profile may offer explanations for carbon dynamics that have otherwise been challenging to describe. Such an approach requires soil to be viewed as an interconnected 3-dimensional space (Smith et al., 2017) where individual pores combine to form larger connected hydraulic networks (Sidle et al., 2001) that control the overall fluxes of nutrients and elemental budgets in catchments (Liu and Lin, 2015). Taking a 3D structural approach with a focus on hydraulic connectivity is of great importance as efforts to link biodiversity and microbial activity to soil function are “doomed to failure” without taking into consideration the physical habitat that controls resource delivery (Young and Bengough, 2018). Recognition of the importance of soil structure and connectivity of the liquid phase for carbon cycling is ubiquitous. However, efforts to integrate knowledge from various disciplines and across scales are not (Baveye et al., 2018).

1.2. Biogeochemical heterogeneity in the soil matrix

The majority of ecologically relevant biogeochemical processes are thought to occur within microbial hotspots, which are small volumes of soil where carbon turnover rates can be 10–100 times greater than the bulk soil (Kuzakov and Blagodatskaya, 2015). Thus, processes occurring in very active spatially defined locations within the soil matrix should be of primary interest when investigating biogeochemical processes. Heterogeneity in resource supply, including fresh organic inputs from plant and animal sources, is the main cause of hotspot formation, making it the main driver of micro-scale spatial heterogeneity in biogeochemical processes. The other cause is the heterogeneity of the physical micro-environments where the processes take place, which is largely dictated by the size and connectivity of soil pores. Recent attempts in identifying structure-function relationships at the pore-scale have attributed functional soil properties such as carbon mineralization to specific features of soil structure (Young and Crawford, 2004; Crawford et al., 2012; Nunan et al., 2017; Rabot et al., 2018). Bridging the analyses of hotspot activities with characteristics of the pores that surround them (e.g., Kravchenko et al., 2017) and elucidating microbial

interactions with soil structure and the aqueous phase (Tecon and Or, 2017) are important steps in deciphering the drivers of soil biogeochemical heterogeneity. Unfortunately, it remains unclear how these relationships can be translated into meaningful predictions of macroscale soil function. While technical difficulties such as coarse model resolution play a role, we suggest that the lack of accounting for perhaps the most dominant factor controlling moisture and resource distributions in soil – preferential flow – is a conceptual drawback halting progress for mechanistic models.

1.3. Preferential flow paths and carbon cycling: a baseline for new hypotheses

We postulate that the following features make preferential flow paths crucial components of soil functioning: 1) substantial inputs of water and nutrients that likely stimulate microbial activity (Bundt et al., 2001a; Franklin et al., 2019); 2) temporal stability enabling reactivation for long periods, providing a defined network of pores where carbon cycling will most readily occur (Ritsema and Dekker, 2000; Hagedorn and Bundt, 2002; Leinemann et al., 2016; Kapetas et al., 2014); 3) sizeable spatial extent, often spanning the entire depth of the soil profile (Chabbi et al., 2009; Bak et al., 2019); and 4) pore architecture beneficial for enhanced microbial activity as well as for soil carbon protection by means of increased aggregation and chemical bonding of microbially processed organic matter (Anthony et al., 2020; Cotrufo et al., 2013). Preferential flow paths are, in essence, spatially well-connected and highly active hotspots continuously operating within the soil profile (Bundt et al., 2001a). Furthermore, they offer links to subsoil regions resulting in horizontal stratification of the age and concentration of carbon distributions at depths (Chabbi et al., 2009; Fontaine et al., 2007; Rumpel and Kögel-Knabner, 2011).

Examination of preferential flow's impact on soil carbon cycling is becoming increasingly important. In the coming years, prolonged periods of drought caused by global environmental change are expected in many regions worldwide (IPCC, 2021). Drought conditions can induce increases in soil macroporosity and will likely contribute to an intensified hydrologic cycle (Hirmas et al., 2018). Increased macroporosity, in turn, can promote the occurrence of preferential flow. But how preferential flow will affect the hydrologic and carbon cycle remains difficult to predict. Therefore, addressing biogeochemical heterogeneity and potential climatic feedback loops linked with increased macroporosity and preferential flow will be an important step forward. In this review, we specifically focus on the role of preferential flow in soil carbon cycling as a biogeochemical cycle of major importance for the Earth System (Falkowski et al., 2000) with pertinent policy implications (Clothier et al., 2008).

2. Preferential flow

2.1. Types of preferential flow and associated moisture conditions

Preferential flow refers to the uneven and rapid infiltration of water, which bypasses portions of the soil matrix. This phenomenon is omnipresent; a soil that does not exhibit preferential flow would be considered an outlier (Flury et al., 1994). Up to fifteen different types of preferential flow have been identified (Lin, 2010), but generally, by its origin and properties, preferential flow can be classified into three main categories: macropore flow, unstable flow, and funnel flow (Fig. 1). *Macropore flow* primarily occurs along root channels, worm burrows, cracks, and fissures. Macropore flow can also occur through voids created by termites (Chen et al., 2019; Jouquet et al., 2016), ants (Li et al., 2019), crabs (Xiao et al., 2019), and soil-dwelling mammals (Wilson and Smith, 2015), but for simplicity, we have chosen not to represent them in Fig. 1. *Unstable flow*, often referred to as fingered flow or fingering, occurs through paths that have formed when a uniform horizontal (stable) wetting front breaks into individual fingers. Unlike

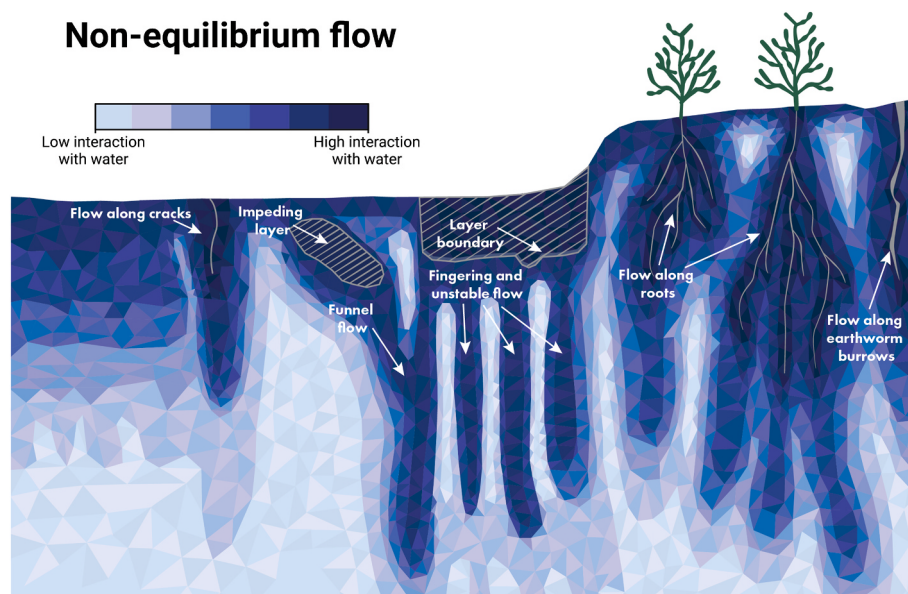


Fig. 1. Heterogeneous moisture distributions caused by different types of preferential flow: macropore flow along cracks, roots and worm burrows, fingering and unstable flow, and funnel flow. Regions that have high interaction with water are dark blue, while regions with little interaction are light blue. Adapted from Hendrickx and Flury (2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

macropore flow, fingered flow is not directly dependent on soil structural properties and has even been shown to occur in homogeneously packed media (Wang et al., 2003a). Fingers arise due to flow-inhibiting interfaces such as pressure gradients, air entrapment, or regions of water repellency (Nimmo, 2020). *Funnel flow* is driven by the redirection of water into distinct pathways due to sporadic textural heterogeneities and inclusions such as lenses (Kung, 1990). The occurrence, spatial patterns, and volumes of preferential flow depend on soil properties such as soil type, soil structure, antecedent moisture, soil water repellency, and others including rainfall intensity. Thus, the effects of preferential flow on soil biogeochemistry will vary depending on the flow regime and characteristics of the soil profile.

Preferential flow paths can represent small percentages of the soil matrix but account for the transmission of considerable portions of infiltrating water (Watson and Luxmoore, 1986). Thus, preferential flow is a key mechanism controlling moisture and nutrient distributions in soil and should be expected to play a substantial role in shaping microbial ecology both locally and across the landscape (Bak et al., 2019; Tecon and Or, 2016; Wang et al., 2013; Young and Bengough, 2018). The moisture conditions a microbe may experience are quite diverse depending on its location in the soil profile and on the size (Nunan et al., 2003) and connectivity (Lee and Kang, 2020) of the pore space it inhabits. For example, hydrologic studies showed that ~80% of rainfall traveled through <25% of the soil matrix (Quisenberry et al., 1993). Another study employing X-ray computed tomography on intact soil cores revealed that the hydrologically active macropore network accounted for less than 10% of the total porosity (Sammartino et al., 2015), and others showed that only ~30% of macropores significantly contributed to the infiltration process (Mori et al., 1999). This is noteworthy as the primary mode of nutrient acquisition for bacteria is often determined by the arrival of resources rather than motility (Nunan et al., 2020; Lehmann et al., 2020). The question remains, however, how do these small volumes of soil that transmit the majority of water and solutes shape the soil microbiome and overall soil function? We refer readers who have further interest in the physical and hydrological characteristics of preferential flow to other published reviews (Gerke, 2006; Beven and Germann, 2013; Jarvis, 2007; Nimmo, 2020). Additionally, a review of the methods commonly used to study preferential flow can be found in Allaire et al. (2009).

2.2. Flow path stability

In undisturbed soils, preferential flow paths often exhibit temporal stability, meaning that flow repeatedly takes place through the same pore networks (Quisenberry et al., 1994). This observation has been reported in field studies (Leinemann et al., 2016) and across scales (Lin, 2006). Despite temporal changes in pore size distributions, the overall structure of soil has a much longer “memory” (Targulian and Bronnikova, 2019). Layers of cutans (finely textured deposits) and mottling (redoximorphic features) coating macropore walls in well-structured soil are further evidence of the longevity and active functioning of flow paths (Beven and Germann, 1982; Quisenberry et al., 1993). The persistence of flow paths certainly depends on soil characteristics, structural development, and the presence of management disturbances, but as demonstrated via isotopic analysis, preferential flow paths in undisturbed soils can exist for decades (Hagedorn and Bundt, 2002).

Another cause for flow path stability is hysteresis in the soil moisture characteristic (SMC) curve where at the same matric potential the water content in the drying limb of SMC is higher than that in the wetting limb. The effect of hysteresis is evident in the physical evolution of fingered flow paths. A finger can be thought of as having two components, the finger core where the majority of flow takes place, and the finger fringe, which is a small wetting zone that surrounds the finger core (Glass et al., 1989). Initially, the finger core and finger fringe have the same moisture content, but as the fingertip infiltrates downward, the pores in the finger core empty. At this moment, the finger core and the finger fringe have equivalent matric potentials. However, the finger core coincides with the drying portion of the SMC, whereas the finger fringe remains on the wetting curve (DiCarlo et al., 1999; Glass et al., 1989). This induces sustained lateral movement of water from the finger fringe back into the finger core, and thus the fingers remain narrow (Jury et al., 2003; Wang et al., 2003b). In addition to hysteresis, fingers have been shown to initiate where water repellency was the lowest (Ritsema and Dekker, 1994). Hydrophobic compounds may create near impermeable coatings around soil aggregates (Capriel, 1997) that reinforce the locations of flow paths. Furthermore, if the matrix soil outside of the fingers remains dry, reactivation of the fingers is expected to occur during subsequent rewetting events due to higher hydraulic conductivities offered by the

previously wetted finger regions.

A third mechanism that may create flow path stability is microbial engineering through the excretion of extracellular polymeric substances (EPS) (Morales et al., 2010). For example, Rubol et al. (2014) observed the development of a preferential flow path due to bioclogging of the surrounding matrix. The reduction in porosity caused by cell proliferation resulted in the rapid preferential movement of water at 1.4 times the velocity of the matrix. The high flow velocity impeded microbial growth in the path itself, creating a positive feedback cycle where oxygen and nutrients were channeled along the path, thereby further increasing microbial growth and activity at the periphery of the flow path. The presence of EPS helps maintain optimal conditions for microbial activity (Guo et al., 2018) and can create micro-hydrological niches by bridging multiple pores and creating continuity of the liquid phase upon soil drying (Benard et al., 2019). EPS increases soil water retention (Zheng et al., 2018; Benard et al., 2019; Guo et al., 2018) resulting in local micro-sites with higher water content. The increased water content combined with redirections of water from bioclogging and wetting instabilities (hydrophobicity) created by EPS, may generate a similar wetting effect (Morales et al., 2010) as previously discussed - the wetter, and more conductive, regions offer a path of least resistance for the next flow event.

The stability of macropores of biological origin can have seasonal (Schneider et al., 2018) and species dependencies (Capowiez et al., 2015; Felten and Emmerling, 2009). For example, anecic earthworms eat their way through the soil and eject surface casts creating compacted burrows (Lavelle, 1988), while endogeic earthworms are more likely to refill their burrows with their casts (Capowiez et al., 2014). The differences in life strategy impact the hydrology of the burrows (Whalen et al., 2015), but burrows of the compacted variety are expected to invoke an influence on hydrology and carbon dynamics as long as decades (Brown et al., 2000). Even plant roots can create stable macropores that last for years (Hoang et al., 2016). Despite documentation of flow path stability and multiple ascribed mechanisms, the persistence of flow paths and moisture distributions is poorly documented. Perhaps, this is because the traditional belief has largely been that preferential flow is simply unpredictable (Jarvis et al., 2012). However, emerging evidence and theory suggest that due to the widespread occurrence of preferential flow across all soils, the existence of a persistent network of fast flow pathways is likely (Jarvis et al., 2016). Even in tilled fields, flow paths can form and remain stable for the length of a growing season or until physically altered (Ritsema and Dekker, 2000). The persistence of flow patterns and their interconnectivity remains challenging to describe (Wessolek et al., 2009), but there are important modeling implications that should be taken into consideration as quasi-stable states of oxygen saturation, nutrient gradients, bacterial organization, and others can result (Franklin et al., 2019; Kuzyakov and Razavi, 2019). Such stability supports the idea that soils behave in a self-organizing fashion, where order arises out of a seemingly random system (Borer et al., 2018; Crawford et al., 2012; Young and Crawford, 2004; Sidle et al., 2001; Beven and Germann, 2013).

2.3. Biogeochemical properties of preferential flow paths

The stability of flow paths and their recurring activation can lead to local accumulation of nutrients within the flow path domains, ultimately influencing soil biogeochemistry and carbon cycling. Preferential flow paths often contain significantly greater concentrations of carbon and nitrogen as compared to non-flow path regions. This occurs in both managed and natural soils, with carbon concentrations in flow paths as much as 70% greater than the matrix soil in some cases (Bundt et al., 2001a; Chabbi et al., 2009; Fuhrmann et al., 2019; Bogner et al., 2012). Moreover, the carbon and nitrogen associated with flow paths tends to be of recent age while those located within the surrounding soil matrix are several millennia older (Bundt et al., 2001b; Chabbi et al., 2009; Marin-Spiotta et al., 2011). Continuous inputs of new labile carbon into

flow path domains (Leinemann et al., 2016) combined with the lack of physical protection of the added inputs due to high pore connectivity, offer conditions suitable for enhanced microbial activity, development of biofilms, and associated accretion of EPS (Yan et al., 2017).

Biofilms are hydrated dense clusters of cells composed of organisms having various geno- and phenotypes (Stewart and Franklin, 2008). While biofilms embedded in an EPS matrix play a role in soil hydrology and perhaps even flow path stability as discussed earlier, they also operate as key drivers of biogeochemical cycling (Stewart and Franklin, 2008). High levels of microbial activity and high rates of carbon mineralization within preferential flow paths (Hagedorn et al., 2015; Fuhrmann et al., 2019) ensure that they often function as microbial hotspots (Bundt et al., 2001a). As demonstrated experimentally, localized high rates of microbial activity can develop very quickly after preferential flow path establishment (Franklin et al., 2019). Modeling work has further demonstrated that biofilm growth and activity are maximal along preferential flow paths (Yan et al., 2017). Preferential flow paths can also turn into localities with high rates of pesticide mineralization (Mallawatantri et al., 1996; Pivetz et al., 1996; Vinther et al., 2001; Dechesne et al., 2014; Monard et al., 2008; Liu et al., 2011). The latter is likely due to high organic carbon concentrations allowing for increased sorption of pesticides in combination with exceptionally high microbial activity (Bundt et al., 2001b). Moreover, microbial communities have been shown to adapt to the prevailing conditions (Lüneberg et al., 2018), thus flow paths can become enriched in pesticides degraders (Monard et al., 2008).

Variations in microbial habitat characteristics within a flow path itself can be as large as those between the flow path and the adjacent soil matrix. Franklin et al. (2019) demonstrated using oxygen-sensitive planar optodes, that micro-environmental conditions within preferential flow paths can exhibit high degrees of heterogeneity not only in nutrient and carbon inputs but also in oxygenation. To simulate preferential flow, coarse (595–841 μm) and fine (210–297 μm) sands were used as proxies for macropore channels and the pores that surround them, respectively. After a single flow event containing glucose and a soil slurry (to introduce microorganisms), oxygen depletion resulting from microbial utilization was found at the textural interfaces, or “linings,” of the macropore channels (Fig. 2A and C). When flow occurred through coarse sand on both sides of the fine sand, oxygen consumption outpaced oxygen diffusion resulting in an anaerobic center in the fine sand (Fig. 2B), similar to oxygen depletion patterns found in soil aggregates (Sextstone et al., 1985). As soil drains a “big gulp” occurs, which describes the downward suction of oxygen (Jarecke et al., 2016). Water flow through macropores often occurs in films, meaning the pore space is not entirely full of water (Nimmo, 2020), allowing for quick gaseous exchange. In addition, macropores cannot hold water against gravitational forces (Soil Science Society of America, 2008) so they and the pores nearby are the first to become oxygenated upon drainage. Thus, macropore networks that have just experienced a nutrient-laden water flux will have the first opportunity to mineralize carbon upon drainage. Further exploration of the spatial patterns in microbial activity and oxygen gradients caused by soil structure and resource delivery may help in understanding community organization and the formation of anaerobic microsites (Keiluweit et al., 2018; Owens et al., 2017).

The formation of microbial activity gradients in flow paths of non-biological origin is highly dependent on flow velocity (Rubol et al., 2014) and the delivery of nutrients. As a result, not the entire body of the flow path functions as a microbial hotspot. Rather, the smaller pores adjacent to the main flow path that allow for the accumulation of nutrients and protection from high flow velocities (Nunan et al., 2003) become the locations where microbial activities are the highest (Franklin et al., 2019). In macropores of biological origin, such as earthworm burrows, the intra-path heterogeneity begins with deposition of organic residues on the pore walls, and then likely continues to develop with the formation of the above-mentioned heterogeneity of flow and nutrient delivery. Different sources of organic materials

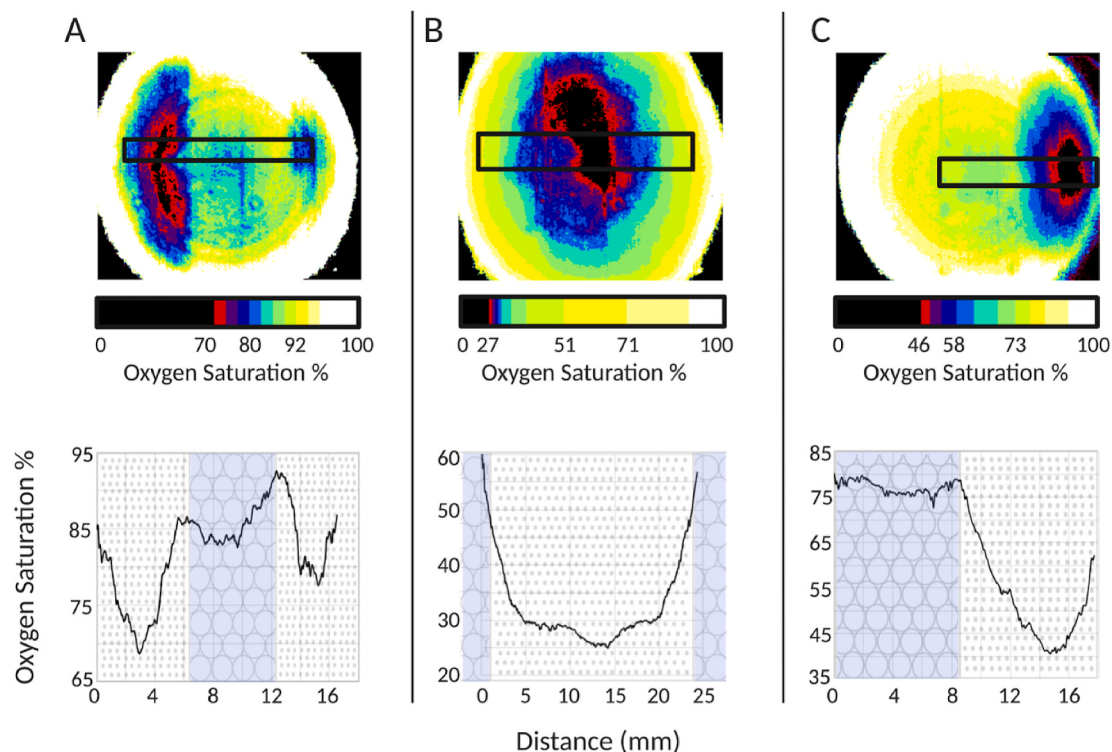


Fig. 2. The top row of images shows averaged oxygen depletion over time and highlights the creation of unique and dynamic micro-environmental niches. Color scales were made separately to emphasize the averaged differences in oxygen saturation in each case. The black rectangles in the top images are the regions of interest that are plotted in the graphs below that express spatial oxygen saturation in the two sand types. Panel A shows coarse sand (circles) surrounded by fine sand (dots) on both sides. Panel B shows fine sand surrounded by coarse sand on both sides. Panel C shows half coarse and fine sand. Flow (shaded blue) primarily took place in coarse sand. Adapted from Franklin et al. (2019). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

involved in pore formation can affect subsequent flow path functioning and contribution to biochemical processes within the soil profile (Leue et al., 2017, 2018). Organic coatings along worm burrows are more hydrophobic than coatings along cracks of non-biological origin (Ellerbrock et al., 2016), and the type of organics present along the walls can have significant effects on wettability and flow regime (Gerke, 2006; Haas et al., 2018; Leue et al., 2019; Larsbo et al., 2016). Recent work has begun to explore the composition and processing of organic matter in earthworm and root biopores further (Banfield et al., 2018; Hoang et al., 2016, 2017), but it must be noted that studies on biopores and their associated carbon compositions and biological processes are being viewed largely under discipline-specific lenses, rather than holistically.

Macropores originated by earthworms or root-originated macropores that have been subsequently populated by earthworms can have very different characteristics from macropores solely populated by plant roots (Hoang et al., 2016). Earthworm-populated macropores have a considerable amount of coating of earthworm origin on their walls. The coating layer closes pore openings into the macropore reducing lateral connectivity between the macropore and the remaining soil matrix (Pagenkemper et al., 2015). These coatings can be further compacted after subsequent earthworm passage (Binet and Curmi, 1992) leading to substantial increases in the bulk density of the soil surrounding macropores of earthworm origin (Schrader et al., 2007). Thus, preferential flow paths of earthworm origin might have the least influence on the surrounding soil as there is less water exchange with the surrounding matrix (Bastardie et al., 2005). But they can have a great influence on the carbon processes of the entire soil profile by serving as a direct route for dissolved organic carbon movement to deeper soil horizons (Kodešová et al., 2012). Different carbon contents and microbial activities observed in earthworm burrows as opposed to pores created by roots further increase variability in the contribution of biological

macropores to soil carbon processing - the walls of earthworm burrows have higher carbon levels and greater microbial activity than the walls of biopores generated solely by plant roots (Hoang et al., 2016).

Sustained contrasts in micro-environmental conditions within preferential flow paths might lead to the formation of contrasting microbial communities characterized by different ecological functions and carbon use efficiencies. Recently, Bak et al. (2019) sampled flow paths (biopores, fractures, and sand lenses) and the associated soil matrix to depths of 6 m to compare bacterial community structure. They found that flow paths contained greater bacterial abundance and diversity in comparison to the matrix soil. Moreover, they reported that aerobic processes could take place in flow paths at depths of over 5 m, highlighting the need to include this information when modeling nutrient turnover in well-structured clayey tills. In related work, the active dispersing potential of bacterial communities coming from flow path regions and the matrix soil was evaluated using porous surface models (Krüger et al., 2019). The models allow the assessment of distances traveled by bacteria by controlling water film thickness on a soil-like surface. Results showed that bacteria from flow path regions expressed greater dispersive potential when compared to bacteria from the matrix soil. The greater dispersive potential expressed by bacteria in flow path regions may be used to colonize new habitats (Krüger et al., 2019) perhaps reflecting a necessary survival strategy needed to endure repeated and rapid changes in moisture conditions.

3. Pores: the building blocks of flow paths and their contribution to carbon dynamics

Macropore flow has varied levels of interaction with surrounding pores, involving volumes much greater than just a few pores (Weiler and Flühler, 2004). The same is true for unstable and funnel flow where many pores are involved in the infiltration process. Thus, complex pore

networks of varying size and connectivity are working in conjunction to maximize infiltration through the soil profile, often converging to form larger preferential flow systems across the landscape (Sidle et al., 2001). The best way to conceptualize this comes from recent work by van der Linden et al. (2019) that describes a self-organized group of primary pathways that have inter- and intra-connections with secondary and tertiary pathways. Here we denote primary pathways as large macropores $>300\ \mu\text{m}$ $\varnothing$ (Jarvis, 2007), secondary pathways as $30\text{--}300\ \mu\text{m}$ $\varnothing$ pores (Kravchenko et al., 2019), and tertiary pathways as $<30\ \mu\text{m}$ $\varnothing$ pores (Yao et al., 2011). This classification accounts both for a pore's ability to transmit water and the living space it provides for microorganisms (Fig. 3). It is likely representative of pore systems in many soil types, although in some cases where permeability is very low, pores as small as $30\ \mu\text{m}$ $\varnothing$ can function as the main flow channels (Tokunaga and Wan, 2001). Poiseuille's Law stipulates that laminar fluid transmission through a narrow tube is dependent on the radius of the tube raised to the fourth power. Thus, a $300\ \mu\text{m}$ $\varnothing$ pore could transmit 16 times more water than a $150\ \mu\text{m}$ $\varnothing$ pore, resulting in preferential flow at the pore scale (Bottero et al., 2013; Sanders et al., 2012). Although applying Poiseuille's Law to soil water flow is overly simplistic, it nevertheless clearly demonstrates the significant influence that even a small change in pore size can have on flow velocity and associated nutrient delivery, thus their effects on microbial habitat and function.

From a microbial perspective, primary pathways such as larger macropores ($>300\ \mu\text{m}$ $\varnothing$) offer less than favorable conditions for communities to thrive due to extreme wetting and drying regimes and little protection from predators (Nunan et al., 2003; Kravchenko et al., 2019). Additionally, nutrients are easily lost from these pores through leaching. Work from soil aggregates and intact cores suggests that $\sim 30\text{--}300\ \mu\text{m}$ $\varnothing$ pores generate the most substantial influence on the decomposition of organics and soil respiration (Kravchenko and Guber, 2017; Quigley et al., 2018; Kravchenko et al., 2019) indicating that secondary pathways ($30\text{--}300\ \mu\text{m}$ $\varnothing$) are of main importance for microbial carbon processing (Fig. 3). Secondary pathways experience reduced flow velocities in comparison to primary pathways, offer moderate water retention, allow for ready oxygen influx, provide sufficient space for biofilm building (Nunan et al., 2003; Bouckaert et al., 2013), and thus, for active functioning of the resident microorganisms. That contrasts with tertiary pathways (i.e., small $<30\ \mu\text{m}$ $\varnothing$ pores), which are not of sufficient size to accommodate a large microbial community, and further, may remain anaerobic due to water retention and limited oxygen diffusion. Tertiary paths would be more suitable for entombment and protective storage of the organic inputs arriving via the primary and

secondary pathways, especially, the decomposition products from the organisms inhabiting secondary pathways. Observations of more labile carbon coming from larger pores than from smaller pores (Smith et al., 2017; Bailey et al., 2017) support this suggestion. Thus, preferential flow paths present a unique spatial arrangement of tightly knit micro-environments where: 1) the primary paths ($>300\ \mu\text{m}$ $\varnothing$) supply new inputs, including organic substrates; 2) secondary paths ($30\text{--}300\ \mu\text{m}$ $\varnothing$) offer inter- and intra-connections that host microbial communities benefiting from the inputs; and 3) tertiary paths ($<30\ \mu\text{m}$ $\varnothing$) serve as localities for carbon storage and protection (Fig. 3).

The microbial communities populating preferential flow path regions likely differ in their composition depending on the distance from the primary path and on the prevailing properties of the pore spaces that they inhabit. However, what effect such variations in microbial community composition might have on carbon processing is unclear. There has been considerable interest in whether pore characteristics or microbial community composition has a greater effect on carbon mineralization in soil pores. To address this, Nunan et al. (2017) performed a reciprocal transplant experiment showing that connectivity and diffusion pathways were greater determinants of carbon mineralization than was microbial community structure. X-ray tomography has revealed that atmospherically connected pores exhibit decomposition rates up to 15 times higher than those that are not atmospherically connected (Rabbi et al., 2016; Kravchenko et al., 2015). In addition, while there is evidence that microbial communities in differently sized pores are unique, the structural properties of the pore architecture and connectivity of water (Treves et al., 2003) tend to have a greater influence on carbon mineralization (Negassa et al., 2015; Kravchenko et al., 2014; Ruamps et al., 2011). The findings from pore-scale studies have greatly improved our understanding of soil functionality. Arguably, they can provide insight as we consider heterogeneous carbon and moisture distributions resulting from preferential flow to more accurately assess carbon (and others) dynamics at the catchment and continental scales (Crowther et al., 2019).

4. Upscaling biogeochemical heterogeneity

Processes of ecological relevance occur in hotspots heterogeneously located in the soil profile, which are often formed and activated by the presence of water (Kuzakov and Blagodatskaya, 2015; Krause et al., 2017; McClain et al., 2003; Lee and Kang, 2020). Preferential flow serves as an important local scale phenomenon that affects field-scale processes (Vervoort et al., 1999) making further study of the topic an

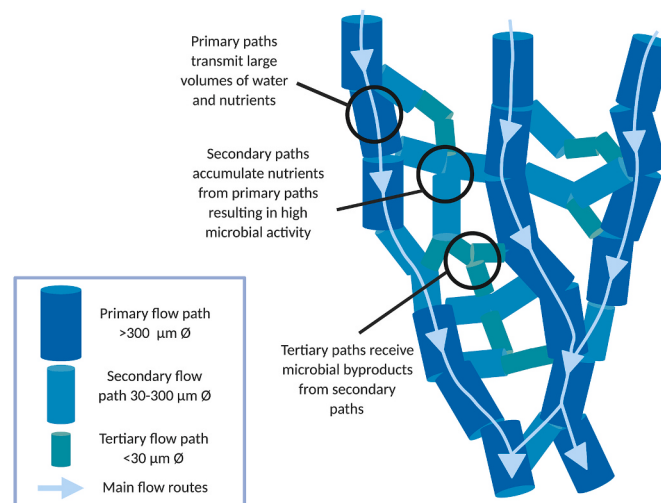


Fig. 3. Conceptual model showing the relationship between pore size, water flow, and carbon dynamics within preferential flow paths. Primary paths transmit large volumes of water at high flow velocities. The nutrients carried in primary pathways are deposited in secondary pathways and processed microbially. Microbial byproducts from secondary pathways are introduced to tertiary pathways where they may be protected and stored. Adapted from van der Linden et al. (2019).

appealing course of action to combine efforts for the accurate upscaling and representation of pore-scale processes in Earth System Models (ESMs) (Band et al., 2014; Cotrufo et al., 2013). ESMs are guided by pedotransfer functions (PTFs), which are estimations of soil processes based on easy-to-measure soil properties such as texture (Bouma, 1981, 1989; Van Looy et al., 2017). However, current PTFs lack the inclusion of soil structure (Lin, 2003) leaving ESMs unable to extrapolate the climatic impacts of small-scale soil hydrology to the global scale (Fatichi et al., 2020; Vereecken et al., 2019). Thus, to achieve more representative PTFs, they must reflect our knowledge of the soil structural influence on soil hydrology and preferential flow (Castellano et al., 2012; Lin, 2012; Lin et al., 2005; Pachepsky et al., 2006).

Generation of PTFs and ESMs with consideration given to soil structure has been executed with promising results (Quisenberry et al., 1993; Shaw et al., 2000; Fatichi et al., 2020; Rahman and Rosolem, 2017), but an overall lack of studies of this kind highlight the need for additional development. To generate and assess the performance of new PTFs, innovation is necessary to get past the bottlenecks associated with the study of preferential flow (Guo and Lin, 2018). Some improvement could be achieved by long-term monitoring using grid lysimeters *in situ*, allowing for the high spatial and temporal sampling of effluent during rewetting events (Andreini and Steenhuis, 1990; Bowman et al., 1994; De Rooij and Stagnitti, 2002; Mohanty et al., 2016; Quisenberry et al., 1994). Determining the isotopic signature of water at high temporal and spatial frequency with grid lysimeters offers insight into residence times and will provide benchmark information for testing and developing models (Dwivedi et al., 2020; Eriksson, 1971). This will allow a mechanistic understanding that avoids highly parameterized equations that can only fit, as opposed to validate, data (Kirchner, 2006). Modeling efforts using Maximum Flow, Minimum Cost algorithms to complement imaging techniques such as X-ray tomography (van der Linden et al., 2019) may be a promising way forward in determining spatial arrangement and connectivity of active flow paths. Similarly, ESMs that incorporate mechanistic microscale processes in the development of macroscopic heterotrophic respiration models (Yan et al., 2018; Yan et al., 2016) could provide important insight into heterogeneous biogeochemical processes, though continued experimental validation for model development and benchmarking is needed.

Rabot et al. (2018) express there is a need for a soil structure library and suggest compiling standardized X-ray tomography data from undisturbed soil cores from which structure-function relationships could be assigned. We believe there is value to this. However, we must note potential limitations related to representative elementary volumes (REV) for different soils (Koestel et al., 2020) and the tradeoff between scale and resolution, i.e., larger samples result in lower resolution images. Recent work has performed scale fusion, where large soil cores (~7.5 cm Ø) are imaged and then subsampled and scanned at finer resolutions to uncover the full pore size distribution (Köhne et al., 2011; Lucas et al., 2020; Schlüter et al., 2011; Vogel et al., 2010); however, this seems daunting to include in such a soil structure library. At larger scales, the use of electrical resistivity tomography (ERT) to monitor soil moisture and guide spatial analysis (Calamita et al., 2017) is promising, along with ongoing advancements in remote sensing (Mohanty, 2013).

It is unlikely that all of the intricacies of soil biology could be fully encompassed by PTFs, so it is likely necessary to represent biophysical interactions explicitly in ESMs (Wieder et al., 2013, 2015). As shown in Fig. 3, the microbiological and physical properties of soil are intimately tied. Therefore, our knowledge of pore-scale carbon dynamics can be used by placing it in macroscopically defined moisture networks with emphasis on connectivity and preferential flow. This may provide a new theoretical modeling framework to work from or aid in further development of pre-existing models such as CIPS (Kuka et al., 2007), PROMISE (Waring et al., 2020) or the dynamic interaction model proposed by Meurer et al. (2020). We hope this will allow for better quantification of the spatial distribution and volumes of active micro-habitats and provide greater insight into their overall influence on

soil function (Smercina et al., 2021). In addition, the conceptualization presented in Fig. 3, can be used to guide experimental designs and sampling schemes to verify theoretical predictions. There are exciting opportunities to examine soil ecology *in situ* using microfluidic chips with controlled pore sizes and geometries (Harvey et al., 2020; Mafla-Endara et al., 2021). Furthermore, evaluation of the active fraction of microorganisms will aid in relating microbial diversity to soil function (Blagodatskaya and Kuzyakov, 2013; Couradeau et al., 2019; Heitkötter and Marschner, 2018). There is increasing awareness that long-term soil carbon persistence is due to connectivity constraints (Smith et al., 2017) and physical protection (Lehmann and Kleber, 2015; Lehmann et al., 2020) as opposed to chemical recalcitrance. Comparably, connectivity constraints have been expressed in dual-porosity models that assume the existence of mobile and immobile domains of water (Gerke and van Genuchten, 1993; Šimůnek et al., 2003). Ultimately, to progress, there must be coordinated efforts in terms of techniques and data availability (i.e., technical aspects), conceptual developments (i.e., how to do it), and organizational aspects (i.e., who will do it) to increase interoperability (Vargas et al., 2017) and move towards an integration of preferential flow in soil carbon science.

5. Preferential flow and CO₂ emissions

5.1. Hot moments

Of particular importance for an accurate representation of preferential flow and the associated biogeochemical responses in ESMs is the prediction of hot moments. After dry soils are rewet, they often experience a sudden burst, or hot moment, of CO₂ emissions known as the “The Birch Effect” (Birch, 1958). The underlying mechanisms driving these large pulses of CO₂ have been recently reviewed by Barnard et al. (2020). The five predominant mechanisms are: 1) microbial cells accumulate solutes during drying to remain hydrated, which are then released as easily degradable compounds upon rewetting to avoid rupturing (Fierer and Schimel, 2003), 2) dead microbial cells are mobilized (Blazewicz et al., 2014), 3) mobilization of desorbed organic compounds (Blankinship and Schimel, 2018; Deneff et al., 2001), 4) increased connectivity of the liquid phase allows microbes to access substrate (Smith et al., 2017) and 5) infiltrating water causes degasification whereby CO₂ is pushed out of pore spaces where it has been previously accumulated (Marañón-Jiménez et al., 2011). Hot moments driven by water pulses contribute substantially to total annual CO₂ budgets. In drylands, hot moments can result in increases of CO₂ efflux upwards of 15,000% (Groffman et al., 2009; Kim et al., 2012), and >200% even in temperate wetlands (Petrakis et al., 2017). The magnitude of CO₂ efflux after rewetting is less pronounced in wetter ecosystems, but even in a mesic temperate deciduous forest, pulses of CO₂ after rainfall have been shown to account for 16–21% of the annual efflux (Lee et al., 2002). Hot moments are often missed due to a lack of continuous measurements *in situ* or misrepresented by models due to the use of semi-empirical functions based on overly simplistic relationships between averaged values of soil temperature and soil moisture (Vargas et al., 2018). We suggest that given the challenges in predicting ecosystem response to rewetting, taking into consideration preferential flow might contribute to a better mechanistic understanding of hot moments of CO₂ emissions.

5.2. Effects of heterogeneous moisture and rainfall variability on CO₂ efflux

In ecosystems undergoing prolonged periods of drought soils will often display hydrophobic characteristics (Doerr and Ritsema, 2005). Hydrophobicity can result in the development of unstable preferential flow patterns (Dekker and Ritsema, 1994; Ritsema and Dekker, 1994). It has been suggested that a reduction of CO₂ efflux could occur as a result of incomplete rewetting due to preferential flow caused by

hydrophobicity (Muhr and Borken, 2009). This appears to be true during the rewetting period as infiltrating water degasses fewer soil pores when channeled through smaller soil volumes (i.e., preferential flow paths) (Sánchez-García et al., 2020a). However, the effect of preferential flow on the 24–48 h post wetting efflux (Rey et al., 2017; Wang et al., 2016) when hydraulic redistribution is occurring remains unclear. High rainfall intensities often lead to the increased occurrence of preferential flow (Buckingham et al., 2008; Jarvis, 2007), and larger rainfall events commonly result in larger CO₂ effluxes (Barnard et al., 2020; Chen et al., 2009; Sponseller, 2007). These observations leave us with paradoxical conclusions on the effects of preferential flow on CO₂ efflux. While preferential flow may cause an initial reduction in total CO₂ efflux, the preferentially wetted regions will likely constitute the most biologically active locations (Franklin et al., 2019).

As research on this topic remains in its infancy, considerable uncertainty remains as to how soil water repellency and preferential flow affects carbon dynamics in various soil types and under different precipitation patterns (Sánchez-García et al., 2020b). As an example, we present a scenario where CO₂ efflux is not proportional to rainfall intensity (Fig. 4; Vargas et al., 2018). In Case I and II, the ecosystem response to rewetting after the long dry season is shown. While the day of the year is the same and both represent the first rainfall after a long drought, there are large differences in the responses of CO₂ efflux. In Case I, the precipitation event was 25 mm at a rate of 5 mm/h, whereas in Case II the precipitation event was 5 mm at a rate of 1 mm/h but resulted in greater CO₂ efflux. These results support the hypothesis that preferential flow will cause a reduction in CO₂ efflux (Muhr and Borken, 2009). In Case II, lower rainfall intensity resulted in more uniform wetting and greater CO₂ efflux in comparison to Case I. Also, note that in Case II, bare soil resulted in greater CO₂ efflux when compared to vegetated soil. This was likely due to the increased occurrence of preferential flow along plant roots causing incomplete wetting, thus less degassing.

To overcome the apparent paradox and inconsistent relationships between CO₂ efflux and rainfall intensity, rather than simply reporting event size as total rainfall, complementary analyses are needed. Information on antecedent soil conditions, storm composition, and the type of flow events that will be brought on by a specific storm should aid in this effort. This type of information can help predict the extent and timing of preferential flow onset, which has been shown to affect the concentrations of mobilized solutes (McGrath et al., 2008). Taking measures such as these into account will offer a more comprehensive and accurate determination of how precipitation events influence soil CO₂ production and efflux. General moisture metrics such as the water status index (Yan et al., 2014), volumetric water content (Leon et al., 2014), water-filled pore space (Franzuebbers, 1999), matric potential

(Castellano et al., 2011), relative extractable soil water (Vargas et al., 2013), soil moisture characteristic curve (Ghezzehei et al., 2019), and mean precipitation within a season (Warner et al., 2019) have been used with moderate success in predicting CO₂ efflux at different spatial and temporal scales. Nevertheless, uncertainty remains as none of these metrics can fully account for the heterogeneity of water movement and its effects on carbon cycling in soils.

Even though the influence of preferential flow on CO₂ efflux remains unknown, it certainly plays a role. In an infiltration experiment, ¹⁴C-labeled dissolved organic matter (DOM) was used to track how much DOM was leached, how much was retained, and how much was mineralized to CO₂. The results showed that 80% of the labeled DOM was bound to mineral surfaces, and on average, only 2–9% was mineralized to CO₂ (Hagedorn et al., 2015). Due to the increased presence of labeled DOM found along flow path regions, Hagedorn et al. (2015) determined that DOM accumulation over time would result in flow paths functioning as hotspots of organic matter degradation, though the majority of the carbon being processed may be of older age. Their results are in agreement with the “DOM cycling downward” conceptual model proposed by Kaiser and Kalbitz (2012), in which they assume DOM is temporarily immobilized on mineral surfaces, processed microbially, and then released by desorption and dissolution, and finally leached deeper into the soil profile (Afsar, 2020).

6. Conclusions

The works outlined in this review highlight the role of preferential flow in the carbon cycle. Preferential flow paths exhibit temporal stability, which allows for their repeated activation over periods as long as decades. Recurrence of flow results in heightened concentrations of carbon and microbial biomass. Flow paths often self-organize, forming large hydraulic networks across the landscape. These macroscopic networks can be viewed as assemblages of well-connected pores rather than large singular units. These assemblages of pores harbor highly active and diverse microbial communities. A conceptual model (Fig. 3) was developed describing a hierarchical classification of pores based on their hydrology and contribution to soil carbon processing. The conceptual model categorizes 1) primary paths as large macropores >300 µm Ø; 2) secondary paths as pores 30–300 µm Ø; and 3) tertiary paths as pores <30 µm Ø. Primary paths function as the main flow channels, supplying water and nutrients. Secondary paths provide protection from high flow velocities, ample levels of oxygen, and accumulate inputs from the primary paths. These factors allow secondary paths to host active microbial communities that play a significant role in carbon processing. Tertiary paths are too small for significant growth of biomass and may serve as anaerobic microsites due to oxygen limitations. This makes tertiary

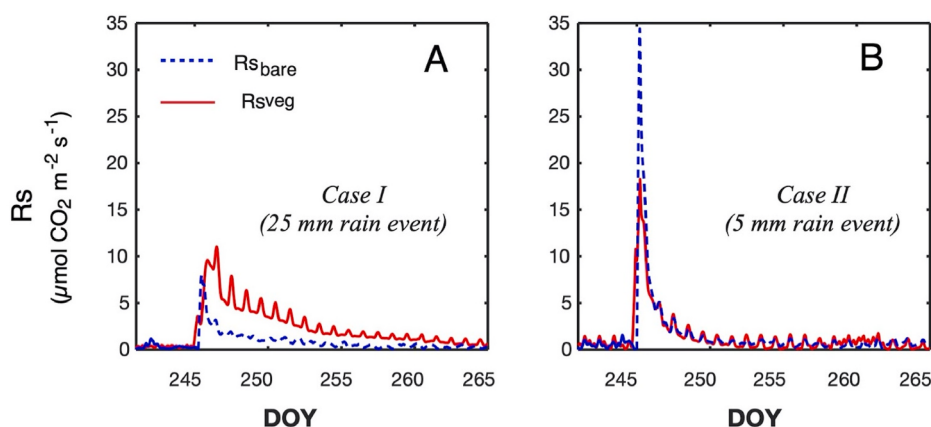


Fig. 4. Pulse responses of soil CO₂ efflux (Rs) under vegetation (Rsveg) or in bare soil (Rs_{bare}) following the first rainfall after a long drought in a water-limited grassland. Solid lines represent Rs measured under vegetation (Rsveg) and dashed lines represent Rs measured in bare soil (Rs_{bare}). The numbers in the x-axis represent the day of the year (DOY) for years 2011 (a) and 2012 (b) for each panel. Adapted from Vargas et al. (2018).

paths viable localities for carbon storage and protection.

Micro-habitat is significantly shaped by pore size, pore arrangement, pore connectivity, and the associated moisture conditions. This information can be used to develop new experimental and modeling frameworks that will offer improved quantification of the volumes of active micro-sites. Elucidating such biophysical interactions will be crucial to increase ESM accuracy. The importance of preferential flow has been implicitly recognized in soil and biogeochemical research for years, but almost no work explicitly accounts for its role in microbial ecology and overall soil function. This has likely stemmed from narrow disciplinary foci and the difficulty of studying both preferential flow and microbiology *in situ*. However, with theoretical and technological advancements there are now ways to achieve this. There is undeniable synergy between soil physics and biology that has been largely unexplored. We conclude that the use of preferential flow networks as a framework of interest for the study of microbial ecology and biogeochemical processes will reveal new insights into soil functionality.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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