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Review paper

Microbial hotspots and hot moments in soil: Concept & review

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ABSTRACT

Soils are the most heterogeneous parts of the biosphere, with an extremely high differentiation of properties and processes within nano- to macroscales. The spatial and temporal heterogeneity of input of labile organics by plants creates microbial hotspots over short periods of time – the hot moments. We define microbial hotspots as small soil volumes with much faster process rates and much more intensive interactions compared to the average soil conditions. Such hotspots are found in the rhizosphere, detritusphere, biopores (including drilosphere) and on aggregate surfaces, but hotspots are frequently of mixed origin. Hot moments are short-term events or sequences of events inducing accelerated process rates as compared to the average rates. Thus, *hotspots and hot moments are defined by dynamic characteristics, i.e. by process rates*.

For this hotspot concept we extensively reviewed and examined the localization and size of hotspots, spatial distribution and visualization approaches, transport of labile C to and from hotspots, lifetime and process intensities, with a special focus on process rates and microbial activities. The fraction of active microorganisms in hotspots is 2–20 times higher than in the bulk soil, and their specific activities (i.e. respiration, microbial growth, mineralization potential, enzyme activities, RNA/DNA ratio) may also be much higher. The duration of hot moments in the rhizosphere is limited and is controlled by the length of the input of labile organics. It can last a few hours up to a few days. In the detritusphere, however, the duration of hot moments is regulated by the output – by decomposition rates of litter – and lasts for weeks and months. Hot moments induce succession in microbial communities and intense intra- and interspecific competition affecting C use efficiency, microbial growth and turnover. The faster turnover and lower C use efficiency in hotspots counterbalances the high C inputs, leading to the absence of strong increases in C stocks. Consequently, the *intensification of fluxes is much stronger than the increase of pools*. Maintenance of stoichiometric ratios by accelerated microbial growth in hotspots requires additional nutrients (e.g. N and P), causing their microbial mining from soil organic matter, i.e. priming effects. Consequently, *priming effects are localized in microbial hotspots and are consequences of hot moments*. We estimated the contribution of the hotspots to the whole soil profile and suggested that, irrespective of their volume, the hotspots are mainly responsible for the ecologically relevant processes in soil. By this review, we raised the importance of concepts and ecological theory of distribution and functioning of microorganisms in soil.

1. Introduction: definitions and the most important hotspots

1.1. Definitions and concept

The most ecologically relevant biogeochemical processes in soils are microbially mediated. Despite the enormous amount of microbial cells, i.e. 10^7–10^{12} in one gram soil (Watt et al., 2006), their localization is restricted to very small microhabitats comprising much less than 1% of total soil volume (Young et al., 2008) and globally covering merely 10^{-6} % of the soil surface area (Young and Crawford, 2004). Many soil microorganisms tend to form colonies and biofilms and tend to aggregate (Hodge et al., 1998; Ekschmitt et al., 2005), forming microbial hotspots. Consequently, ecologically relevant biogeochemical processes mainly occur in the small volume of soil **hotspots**. We define microbial **hotspots** as small soil volumes with much faster process rates and

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much more intensive interactions (between pools) compared to the average soil conditions (Fig. 1) (Kuzyakov, 2009, 2010). As microbial activity is limited by various environmental factors and especially by carbon (C) availability (Hodge et al., 2000), microorganisms in soil are mainly in a dormant state (Blagodatskaya and Kuzyakov, 2013). They become active during short hot moments after the limitations are removed. Accordingly, we define microbial **hot moments** as short-term events or sequences of events that accelerate microbial processes as compared to the average rates. Thus, hot moments occur in or lead to the formation of hotspots, but the hotspots do not necessarily disappear at the end of hot moments and may maintain some microbial activity parameters at high level over lengthier periods even after substrate is degraded (Blagodatskaya and Kuzyakov, 2013). *We therefore define the hotspots and hot moments based on dynamic properties, specifically the intensity of processes, i.e. by process rates*, not by the concentration of the substances or any other static properties. Such definitions underline the *dynamic nature of hotspots and hot moments*. These definitions consider the heterogeneity in distribution of locations and the periods of maximal activity of microorganisms in space and time.

Note that previous definitions of hotspots and hot moments were focused mainly on abiotic fluxes (rainfall or erosion events) on much larger scales, e.g. landscape (McClain et al., 2003; Vidon et al., 2010; Leon et al., 2014). The heterogeneity of soil properties on the meso- and macroscales have been frequently described and analyzed statistically earlier (Parkin, 1993; Webster, 2000; Heuvelink and Webster, 2001). However, meso- and macroscales and the related previous definitions of hotspots and hot moments were not focused on microbial processes and were not applicable on the scales from μm to m - the scales relevant for microbial activities and functions at the level of aggregates up to soil profile. Therefore, new concept and definition of hotspots and hot moments relevant for microbial processes is necessary. This review is focused on the spatial and temporal scales comparable with the size and life periods of microorganisms in soil.

The hotspots and hot moments are relevant not only from the perspective of organic matter availability and C limitation, but also from the perspective of other specific factors limiting microbial activity or process rates under particular conditions, including soil moisture, oxygen availability, N excess. This affects many processes such as denitrification, methanogenesis (see below), nitrification, or weathering. Localized input of high N excess (e.g. fertilizer grains or urine of animals) triggers N turnover including strong nitrification (Strong et al., 1997) and denitrification. Therefore, the hotspots and hot moments are not confined to the input of labile C (described below) but have a much bigger impact and broader perspective involving the removal of any limitations of microbial processes.

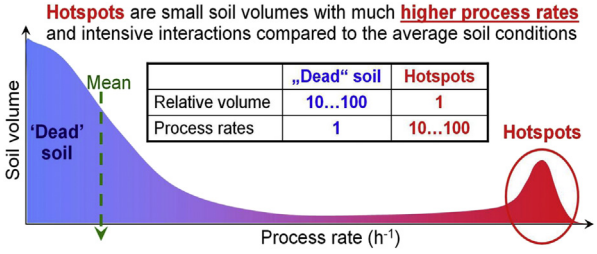

Fig. 1. Concept of microbial hotspots in soil: Hotspots are small soil volumes with much higher process rates and intensive interactions compared to the average soil conditions. The Table inset represents the relative volume and process rates in the hotspots and bulk soil. "Mean" represents the weighted average process rates by soil mixing.

The simultaneous occurrence of numerous hotspots in microhabitats cumulatively affects the dynamics of pools and fluxes and is therefore relevant at higher scales, including the ecosystem scale. The importance of microbial hotspots at the micro-scale level is therefore determined by their relevance to the functions at the higher scales (Blagodatsky and Smith, 2012). Thus, abundant hotspots within a soil volume transforms the environment and extends the hotspots to the hotspheres (Beare et al., 1995) such as rhizosphere or detritusphere, with a high impact at the macroscale. The mechanistic understanding of soil functioning at profile, ecosystem and landscape levels is impossible without quantifying and localizing the hotspots, as well as identifying their origin and formation, their spatial and temporal organization, processes and interactions, along with critical thresholds of intensities necessary for functions at higher scales.

1.2. The most important microbial hotspots in soil

Microbial activity in all soils is limited by labile C (easily available organics) and energy (Blagodatsky et al., 1998; Hodge et al., 2000; Schimel and Weintraub, 2003). Consequently, removing this limitation – the input of labile C – boosts the abundance and activity of microorganisms in soil and produces microbial hotspots. Based on the sources of high input (not the content!) of labile organics and their localization in soil, we emphasize the following hotspot groups (Fig. 2, Table 1):

- Rhizosphere: input of labile root exudates and other less decomposable rhizodeposits at various soil depths (Jones et al., 2004; Hinsinger et al., 2009).
- Detritusphere: input of mainly recalcitrant highly polymeric (Kogel-Knabner, 2002) (but also some labile, low molecular weight) organics as litter, mainly on the mineral soil surface, and upon root death at various depths.
- Biopores: a) input of labile and recalcitrant organics passed through and processed within the hindgut of earthworms (drilosphere) and other soil organisms (mainly invertebrates) at various depths or/and b) formed by deep-growing roots and maintained by roots and burrowing animals (Tiunov and Scheu, 1999, 2004; Brown et al., 2000; Schrader et al., 2007). Also animal feces in soil with the input of labile and recalcitrant organics can be grouped to the biopores.
- Aggregate surfaces: input of organics leached from the detritusphere (e.g. O horizon), from the C rich Ah horizon and partly from the rhizosphere (Kaiser and Kalbitz, 2012). This hotspot group is especially important in deep soil horizons (Fig. 2).

Other locations in the soil have sometimes been mentioned as spots of microbial activities: biochar-sphere (Lehmann et al., 2011), porosphere, drilosphere, guts of soil animals (Mohr and Tebbe, 2006) etc. These locations, however, can be included in one of the above-mentioned hotspots (porosphere consists of biopores and aggregate surfaces, biochar-sphere is partly related to the detritusphere), are of secondary importance and will not be reviewed here separately.

The distribution and importance of the four hotspot groups depend on the ecosystem and soil depth (Fig. 2). Above the mineral soil surface, the detritusphere is the most important hotspot. The density of the rhizosphere is especially high in the top of the Ah (or Ap) horizon. The relevance of biopores and aggregate surfaces for C input in topsoil is marginal compared to the effects of the detritusphere and rhizosphere, but their importance strongly increases with depth (Kautz et al., 2014). The three first hotspots – detritusphere, rhizosphere and biopores – have a *biotic origin*. Only aggregate surfaces have a mainly *abiotic origin*, especially in the

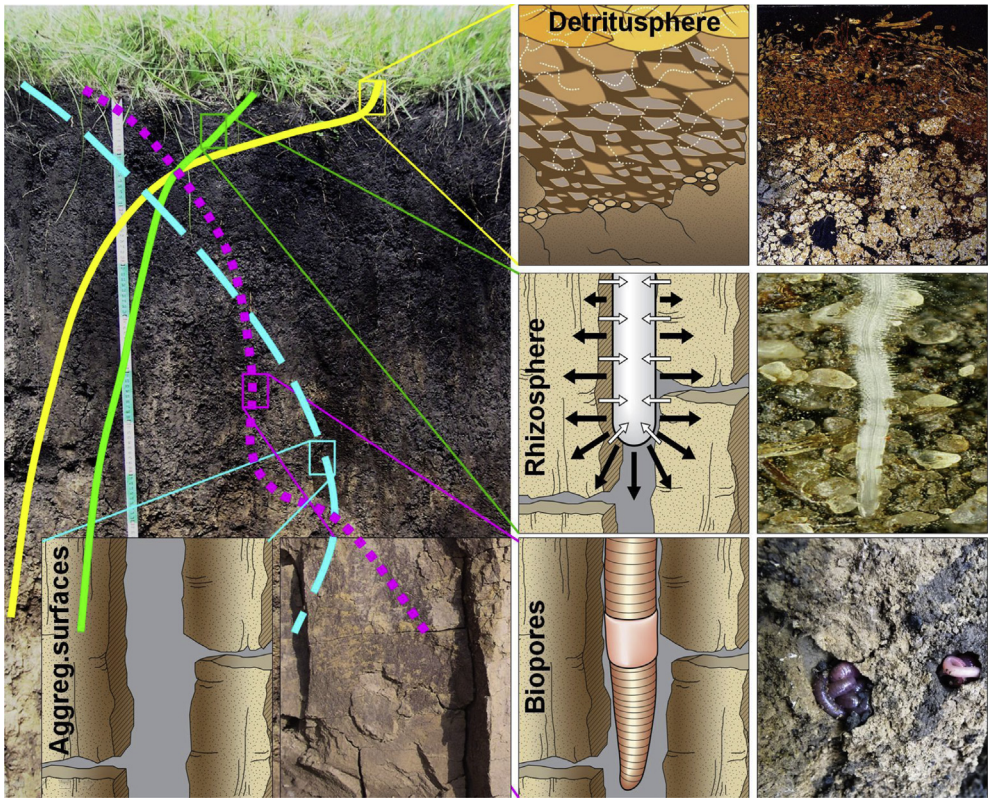

Fig. 2. Schemas and examples of four microbial hotspot groups in soil: Detritusphere (top right), Rhizosphere (middle right), Biopores (bottom right) and Aggregate surfaces (bottom left) and their relative importance up to 1 m depth along a soil profile (Voronic Chernozem). The relative importance of hotspots along the depth may strongly differ between soils under grasslands, forests or crops, and strongly depends on soil parent material and climatic conditions. The thin section example of detritusphere is kindly provided by Dr. Otto Ehrmann (Bildarchiv Boden, http://www.bildarchiv-boden.de). The rhizosphere example is from Yaalon (2000).

subsoil. Therefore, aggregate surfaces have been disregarded or even neglected in most studies of microbial hotspots in soil.

1.3. The role of abiotic and biotic factors in hotspot formation

The occurrence of hotspots in soil, which is the most heterogeneous and complex component of the biosphere (Young and Crawford, 2004), is a result of soil development. The increasing variability of soil properties is a key characteristic of soil formation, structuring the environment. Such properties include local density and pore volume, soil acidity and redox potential, organic matter and nutrient contents, microbial biomass and composition of microbial communities, and enzyme activities. Remarkably, the variation of all these properties in parent material is much less than in developed soil. The heterogeneity of the soil environment is responsible for huge diversity not only of microorganisms but also of various processes ongoing at close distances that would be not possible in a homogeneous system (Focht, 1992). Consequently, *increasing variability is a prerequisite for hotspot formation*. Many properties and especially process rates in soil surrounding hotspots vary by orders of magnitude within very short distances and within very short periods. This is especially the case at scales comparable with the size of microbial cells and their colonies, i.e. distances ranging from μm to mm. Examples of soil structuring (vertical profile differentiation, formation of aggregates and various concretions) reflect that processes are ongoing in specific locations with (much) higher intensity compared to surrounding soil. Thus, the formation of hotspots by differentiation of morphological and biochemical soil properties is a consequence of contrasting process rates.

Soil structuring starts by an oscillation of abiotic factors: freezing/thawing, drying/rewetting, water percolation events, varying oxic/anoxic conditions (Oades, 1993) that alter the physical environment by redistributing water, dissolved nutrients and labile organics. This increases the local concentrations of substances necessary for biotic activity (Rasa et al., 2012). Biotic factors further strongly modify the surrounding physicochemical environment, leading to the development of specific microbial communities (Feeney et al., 2006). Thus, physicochemical structuring of soil by abiotic and biotic factors and the subsequent local removal of limitation are prerequisites for the formation of microbial hotspots – e.g. for a *concentration of life in locations with less limitation*.

The input of **labile substrate** to the hotspots removes limitation, triggers microbial activity and thus **drives the hot moments**. The duration and intensity of the input of labile organics stimulating microbial activities are specific for the hotspot groups (Tables 1 and 2). Depending on the factors responsible for substrate input/redistribution, the hot moments can be of biotic or abiotic nature. The main drivers of biotic hot moments are root exudation, litter fall and root death, root ingrowth in a new soil volume, and activities of burrowing animals (Table 1). These hot moments are directly linked with the input of labile organic C into the soil. Therefore, the *biotically induced hot moments always lead to formation or maintenance of hotspots*.

Abiotic processes also change the soil environment because labile organics i) are released and become accessible for microorganisms, or ii) are redistributed to new locations and thus produce hotspots. Freezing/thawing and drying/rewetting disrupt soil aggregates and release encapsulated particulate and dissolved organics (Borken and Matzner, 2009). Such hotspots induced by

Table 1
Properties of the most common hotspot groups in soil.

Hotspots	Rhizosphere	Detritusphere	Biopores	Aggregate surface
Origin	Primary biotic; roots	Primary biotic; litter	Secondary biotic; burrowing animals, roots	Secondary (mainly) abiotic; swelling/shrinking
Volume range in soil, %	0 … 100	0 … 100	0 … 10	0 … 10
Common volume in Ah/Ap, %	5 … 10	0 … 100	1 … 5	1 … 3
Common volume below Ah/Ap - in subsoil, %	<5	0 … < 1	1 … 2	1 … 5
Boundary, mm	2 … 10	5 … 20	1 … 3	0.1 … 1
Relative C availability	High	High … medium	Medium … low	Low
C/N ratio	~10	>20	? … .	10 … 20
Relevance	Whole soil profile	Above mineral soil surface, Topsoil	Below Ah/Ap, subsoil	Below Ah/Ap, subsoil
Regularity	Occasional + regular	Regular + occasional	Occasional	Occasional
Duration of hot moments[a]	Days (weeks)	Weeks - months	Days - weeks	Days

[a] This means only the duration of active processes after the C input (not the existence of the property themselves). E.g. the life time of the aggregates in subsoil in Bt can be decades or even centuries, but the microbial activity on the aggregate surface increases only for few days (to weeks) after the C input from the topsoil by rain.

abiotic drivers are randomly distributed in soil. They persist over much shorter periods and are much less active compared to biotically induced hotspots (Table 2). Heavy rains produce two groups of hotspots: i) on aggregate surfaces and in biopores by leaching of soluble organics from the detritusphere into deeper soil (Kaiser and Kalbitz, 2012), and ii) on the landscape level[1] due to erosion, i.e. runoff of particulate and dissolved organics. Snow melting is an important factor interacting with the detritusphere. Because microbial processes remain active at temperatures below zero (Panikov et al., 2006), the litter will be partly decomposed and accumulate in the detritusphere over the winter. During the short snow melting period, the partly decomposed organics will be removed and leached into the biopores and cracks (if the soil is not frozen) or moved to lower landscape positions, producing hotspots there. Generally, the abiotic processes redistribute the available C already present in soil (and partly preprocessed by microorganisms). Therefore, the *intensity of processes induced by abiotic drivers is generally less and shorter than that induced biotically.*

1.4. Transport into and from hotspots

Initiation and formation of hotspots requires either delivery of labile C or other limiting substances to the microbial cells or, less frequently, transport of the microorganisms to the substrate. Generally, there are three potential mechanisms for the transport of labile and soluble C to microorganisms: 1) direct release of organics at an already existing hotspot. This is very common in all three hotspots of biotic origin. 2) Transport of organics dissolved in water by advection – mass flow. This is common in all four hotspot groups. 3) Transport by diffusion. Because the diffusion coefficients of labile organics are very low and range from (10^{-7}–10^{-5} cm^2 s^{-1}) (Kuzyakov et al., 2003; Raynaud, 2010), microbial utilization is much faster than the C delivery by diffusion. Therefore, the transport by diffusion can be disregarded for hotspot production. This makes the direct input and advection with water flow the main ways of C transport to hotspots.

The second mechanism – the transport of microorganisms to the substrate – is relevant mainly for branch- and filament-forming microorganisms, mainly fungi, some cyanobacteria, streptomycetes and other actinobacteria. Proliferation of fungal hyphae enables reaching the substrate allocated many cm and even dm from the mother cells very fast. Fungi have a huge advantage over bacteria to reach distant locations with excess labile C: the ability of hyphae to penetrate water films in soil pores because hyphae release hydrophobin strongly decreasing surface tension (Talbot, 1999). Therefore, hyphae commonly show ingrowths into the detritusphere (Wardle et al., 2002), rhizosphere (Thorn, 2002) (Rillig, 2004) and biopores (Athmann et al., 2013). The transport of cells in soil by advection or by soil animals (Thorpe et al., 1996) is generally possible, but does not play a significant role for the origin or triggering of the four hotspot groups under aerobic conditions. This transport by advection as well as other transport mechanisms (chemotaxis-induced flagellar motility, spinning, flexing, gliding over surfaces etc.) are sufficient to bring individual microorganisms to the C source and may be relevant to start new colonies at spots of excess labile C.

The hotspots under anaerobic conditions (see below) exhibit the reverse situation: the consumption of oxygen is faster than its replacement by diffusion. This makes the origin of anaerobic hotspots dependent on slow diffusion of O_2 through pores filled by water.

The removal of microbial metabolites – the transport of transformation products out of the hotspots – has never been investigated. Some metabolites may be toxic for microorganisms at hotspots during hot moments. The common examples are the production of organic acids such as acetate or propionate, or the release of excess H^+ strongly decreasing the pH. In our opinion, the transport of these products out of hotspots is mainly driven by diffusion (a slow process). Consequently, hot moments in some cases may terminate due not only to exhaustion of labile C, but also to accumulation of toxic products.

2. Spatial and temporal characteristics of hotspots and hot moments

2.1. The size of microbial hotspots

Estimating the size of hotspots and the proportion of the total soil volume that they represent is a major challenge in soil ecology.

Table 2
Connection between hotspots and hot moments.

Hot moments	Hotspots			
	Rhizosphere	Detritusphere	Biopores	Aggregate surfaces
Biotic				
- Litter fall		XXX	X	X
- Root ingrowth	XXX		XX	X
- Root death	X	XXX	X	
- Animal activities			XXX	
Abiotic				
- Heavy rains		X	XX	XXX
- Snow melting		XXX	X	XX
- Freezing/thawing		XX		X
- Drying/rewetting	X	XX	X	XX
- Erosion events		XX		XX

The number of "X" presents the intensity of the effect: X - small effect, XXX - very strong effect. This assessment was done based on 'expert knowledge'.

[1] The hotspots on the landscape scale are not the focus of this review. See (McClain et al., 2003; Vidon et al., 2010).

Correct estimation is essential 1) to relate process intensities to the real volume in which the processes are ongoing instead of total soil volume (see Figs. 1), 2) to clarify the regulation of microbial density, 3) to analyze the communication between microbial colonies in hotspots (Gantner et al., 2006) and 4) to consider competitive and synergic interactions between key microbial groups in hotspots (Kaiser et al., 2014). Hotspot visualization studies showed that the areas with the highest activities of various enzymes cover: <5% (Spohn and Kuzyakov, 2013; Spohn et al., 2013), <5% (^{15}N uptake by microbial cells in the rhizosphere (Clode et al., 2009), ~5% based on O_2 release and ~1% based on pH changes in the rhizosphere (Blossfeld et al., 2011; Rudolph et al., 2013), ~1% for locations with intensive rhizodeposition (Pausch and Kuzyakov, 2011). Nannipieri et al. (2003) concluded that less than 5% of the available soil space is occupied by microorganisms in hotspots. The space occupied by bacteria in subsoil is about one order of magnitude lower and amounts to <0.2% (Nunan et al., 2003). This confirms that soil is a 'desert' in which life is discretely distributed, especially considering that even unicellular microorganisms perform their functions in colonies (Hinsinger et al., 2009) that represent hotspots of activity. This assessment, however, requires refinement and specification for hotspot groups developed under specific conditions.

The range of hotspot sizes is very broad and the uncertainties are very high (Fig. 3, note logarithmic scale of both axes). Individual microbial cells are insufficient to be accepted as hotspots because they functions are not relevant on the higher scales. Therefore, the (micro)colonies, biofilms and other cell assemblages should be considered as relevant microbial hotspots in soil (Panikov, 2010). Consequently, the size of microbial hotspots is at least a few μm (Grundmann et al., 2001; Dechesne et al., 2003; Eickhorst and Tippkotter, 2008b; Raynaud and Nunan, 2014). The soil volumes in which labile C is released in the rhizosphere or detritusphere are much larger than this minimal size. Accordingly, the size of microbial hotspots reaches up to a few mm (Fig. 3). Visualization of exudate allocation at root tips showed that the respective microbial hotspots are about 2–3 mm in diameter and up to 10 mm long (Pausch and Kuzyakov, 2011). Similar sizes were obtained by visualizing oxygen consumption, pH and redox changes in the rhizosphere (Blossfeld et al., 2011; Schmidt et al., 2011; Rudolph et al., 2013), or enzyme activities in the rhizosphere and detritusphere (Spohn and Kuzyakov, 2013). H_2-oxidizing bacteria and their activity were logarithmically distributed in the few mm proximity to the rhizobia nodule surface (Lafavre and Focht, 1983). Microbial abundance changes within 1–2 mm from the root and detritus surface (Marschner et al., 2012) or up to several mm in the detritusphere (Moritsuka et al., 2004; Ha et al., 2007). This corresponds roughly to the estimations based on destructive cutting approaches in both the rhizosphere (Kandeler et al., 2002; Kuzyakov et al., 2003; Sauer et al., 2006; Marschner et al., 2012) and detritusphere (Kandeler et al., 2002; Marschner et al., 2012). Simulating the rhizosphere extension by the rates of root exudation revealed exudate diffusion and decay rates (Raynaud, 2010) extending from 0.5 up to ~10 mm. Based on the studies reviewed here, we conclude that *the size of microbial hotspots ranges over 3-4 orders of magnitude: from a few μm up to several mm* (Fig. 3).

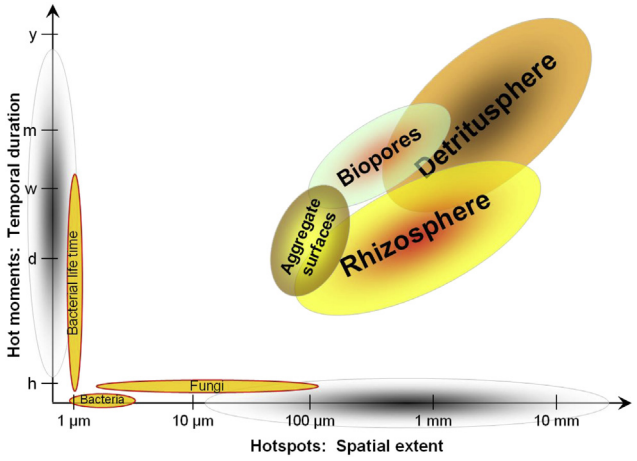

Fig. 3. Spatial and temporal scales of microbial hotspots in soil. Note that the allocation of the areas corresponds to the size and duration of microbial hotspots and hot moments, but not to the size of the properties themselves (e.g. aggregate surfaces may exist years and decades, but the duration of hotspots on the aggregate surfaces is limited by days). Logarithmic Y scale corresponds to h: hours, d: days, w: weeks, m: months, y: years. The intensity of gray on shaded areas on X and Y axis represents schematically the spatial and temporal probability of microbial hotspots.

This very broad range of 3-4 orders of magnitude reflects not only the variation and uncertainties in the spatial distribution of properties but especially of the processes. Because we define the hotspots by process rates (Fig. 1), *the size of hotspots can also be viewed as governed by metabolism and not by arbitrary distance* (Focht, 1992). The microbial metabolic pathways strongly depend on the amounts of substrate (Dippold and Kuzyakov, 2013). This is why *the C utilization pattern and its stabilization in hotspots are also different from that in bulk soil.*

The distribution of microhabitats (the mean distance between patches) strongly depends on microbial groups, substrate input and pore distribution and range from 50 μm to a few mm (Dechesne et al., 2003). A strong increase of the input rate of substrates, e.g. by increasing root density in grassland, may lead to overlapping individual hotspots. The result is that hotspots affect the entire soil (Raynaud, 2010). Only very few studies are available on this issue, and we expect that broad ranges will be presented in the near future.

2.2. Duration of hot moments

The process rates in most hotspots are not constant, but vary with time. The hot moments can be occasional or regular as part of periodic processes (Table 1). The regularity of hot moments depends on natural vegetation cycles such as annual litter fall in autumn or intensive root growth in spring (Philippot et al., 2009), or even diurnal cycles of photosynthesis (Herron et al., 2013).

The importance of hot moments is raised especially by the short lifetime of many hotspots. It is challenging to estimate experimentally the lifetime of hotspots and thus to draw conclusions about the duration of hot moments. The duration of hot moments depends on: i) duration of the input of labile C, and ii) rates of microbial utilization of the labile C. The input of labile organics in soil, e.g. as exudates by roots or release of soluble organics from decomposing litter or from earthworm coprolites, is not very fast and usually takes at least a few days (Poll et al., 2010; Pausch et al., 2013). Microbial uptake and the utilization period of organics depend on their quality and are usually very short for labile substances. As reviewed from 155 soils, the half lifetime ($T_{½}$) of amino acids is about 2.9 h (Jones et al., 2005) with almost immediate uptake by microorganisms within a few minutes (Rousk and Nadkarni, 2009; Glanville et al., 2012; Hobbie and Hobbie, 2012). This is (much) shorter than the duration of the input and, consequently, *the duration of hot moments in the rhizosphere depends mainly on the input.*

After the input into the hotspot stops, the rates of microbial utilization become significant. Assuming that $T_{½}$ of other low molecular weight organic substances (e.g. carboxylic acids, sugars) is similar to that of amino acids (Jones et al., 2005), hotspot lifetime is

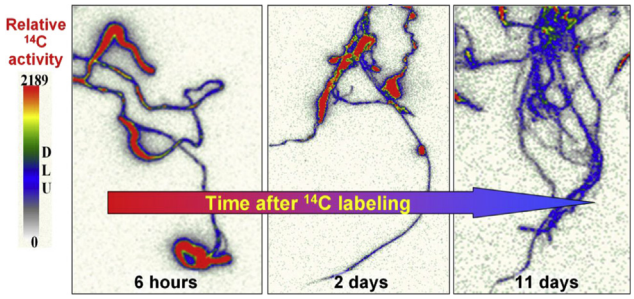

Fig. 4. ^{14}C imaging of relative ^{14}C activity at the root tips at increasing time after labeling of *Lolium perenne* in $^{14}CO_2$ atmosphere: 6 h, 2 d, and 11 d after the ^{14}C labeling. The color scale presents the ^{14}C activity as digital light units (DLU) (from Pausch and Kuzyakov, 2011, changed).

restricted to 10–20 h after input of labile C ceases. Considering the dynamic nature of C inputs (e.g. diurnal dynamics of root exudation) it is challenging to determine this lifetime. The time-resolved ^{14}C imaging after $^{14}CO_2$ pulse labeling of *Lolium perenne* enabled determining the lifetime (1–3 days) of hotspots at root tips (Fig. 4) (Pausch and Kuzyakov, 2011). Such hotspots, however, exist longer if substrate input is continuous. Root development and death transforms the rhizosphere to a detritusphere hotspot (see below) with much longer lifetime. The lifetime of detritusphere hotspots at dying roots (screened by zymography of cellulase, chitinase and phosphatase activities) was 10–30 days (Spohn and Kuzyakov, 2014). Longer hot moments in the detritusphere vs. rhizosphere are explained by prolonged release of labile organics from decaying litter (Bastian et al., 2009; Poll et al., 2010) and their relative recalcitrance (Table 1). We conclude that *the duration of hot moments in the rhizosphere is limited by the input of labile organics, but in the detritusphere by the output, namely by the decomposition rate of litter.*

2.3. Transition between the hotspots of multiple origins

The hotspots described above (Fig. 2, Table 1) *frequently have mixed origin*. Various processes and C sources contributed to their development simultaneously or successively. In the subsoil (because of high bulk density), roots commonly grow in cracks (Rasa et al., 2012) and develop their rhizosphere between the aggregates, i.e. on their surface (Fig. 5). When the mature rhizosphere is established (Jones et al., 2004), the roots die, developing the detritusphere (Fig. 5). After microbial utilization of detritus, the remaining root-originated biopores may be used by burrowing animals (and develop drilosphere) because of: i) better aeration and more moisture compared with the surrounding soil (Tiunov and Scheu, 1999; Uteau et al., 2013), ii) richness in nutrients and labile C (Athmann et al., 2013; Kautz et al., 2013), and iii) easier possibility to move down- and upwards because of lower bulk density (Bengough et al., 2011) and higher porosity (Feeney et al., 2006). Such biopores may be reused repeatedly by newly growing roots (Fig. 5). Consequently, the transition from aggregate surfaces to rhizosphere through detritusphere and further to biopores – between all four hotspot groups – may undergo cycles. Many hotspots, especially in subsoil, have not only a mixed origin and mixed use, but also a *mixed age* – they are reutilized because of their preferred habitat conditions for roots and (micro)organisms. So, life repeatedly concentrates at the locations with beneficial conditions compared with bulk soil. This is one of the ecosystem self-engineering properties resulting in soil structuring and ecological development of (micro)habitats.

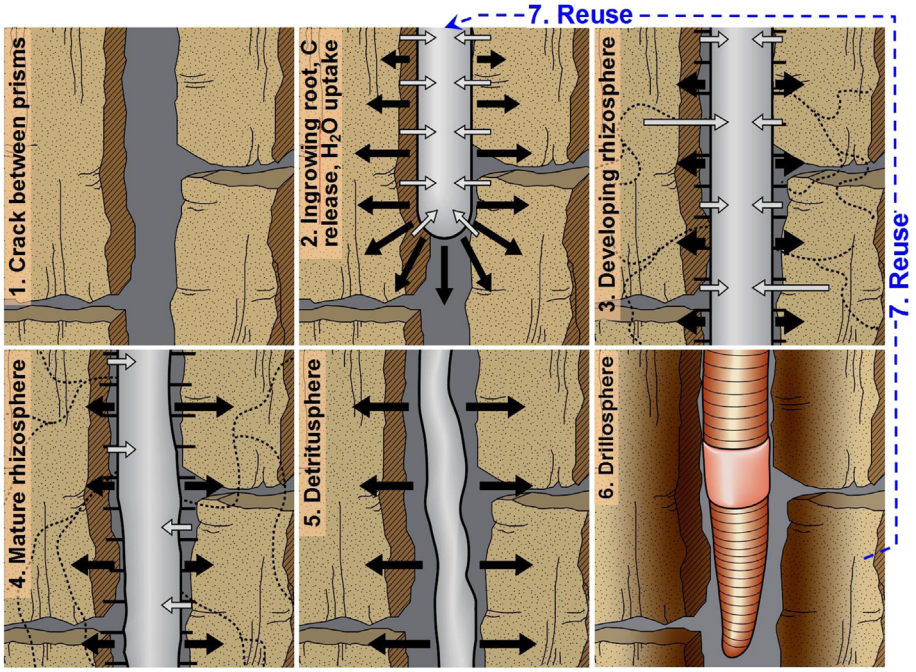

Fig. 5. Transition between the hotspots of multiple origins: 1) Crack between aggregates, 2) Juvenile rhizosphere: root ingrowing in the crack between aggregates, 3) Developing rhizosphere, 4) Mature rhizosphere, 5) Detritusphere: dying root, 6) Biopore: occupation of rhizosphere-detritusphere environment by earthworms, 7) Reuse of the existing hotspots: → back to ingrowing root and the rhizosphere. Black arrows show the C release by rhizodeposition; weight arrows present the uptake of water and nutrients; black dotted lines reflect mycorrhizal hyphae.

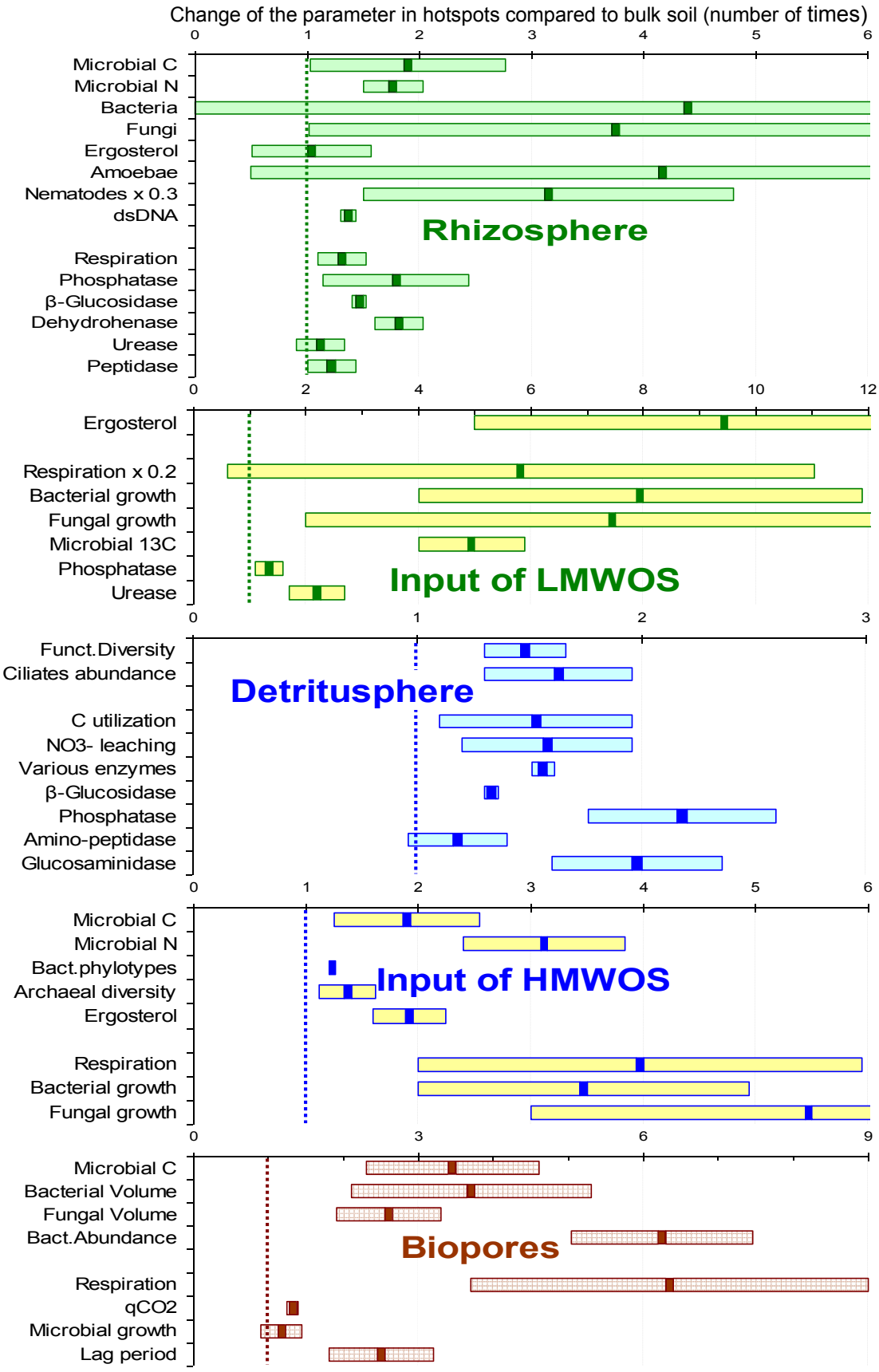

Fig. 6. Changes of microbial parameters (means ± SD) in various hotspots: in the Rhizosphere (top), after the input of Low Molecular Weight Organic Substances (LMWOS) in soil (2nd from top), in the Detritusphere (middle), after the input of High Molecular Weight Organic Substances (HMWOS) in soil (2nd from bottom), and in Biopores (bottom) compared to bulk untreated soil. The X axes show the changes in number of times compared to bulk soil. Straight vertical dotted line (X = 1.0) corresponds to the absence of changes. For each

Table 3
Relative changes of PLFA content by activation/de-activation of soil microbial community during hot moments.

Effect of	Relative changes in PLFA content				Source
	Total	Fungal	Bacterial		
			Gram +	Gram −	
Hotspots in comparison to bulk soil					
Plant roots (rhizosphere)	↑ 1.5–1.7	↓ 1.1–1.3	↑↓ 1.1	↑ 1.1–1.3	Denef et al., 2009
	↑ 1.8–3.4				Rajaniemi et al., 2009
	↑ 1.3-↓ 1.2	↑ 1.0–1.6	↑↓ 1.3		Marschner et al., 2012.
Plant growth	↑ 1.7		↑ 1.8	↑ 2	Lu et al., 2004
Plant species	↑ 1–1.7	↑ 1.4–2	↑ 1–1.2	↑ 1–1.3	Hamer and Makeschin, 2009
Detritusphere	↑ 1.8–5.1	↑ 11–68	↑ 2.1-↓ 1.6		Baldrian et al., 2010
Detritusphere	↑ 1.1–1.4	↑ 2–2.3	↑ 1.5-↓ 1.3		Marschner et al., 2012.
Detritusphere	↑ 1.2	↑ 2.5–4	↑ 1.1–1.3		Rousk and Baath, 2007.
Activation during hot moments					
Rewetting	↑ 1.4–1.6				McIntyre et al., 2009
Available nutrients	↑ 2.4	↑ 50	↑ 1.2		Ehlers et al., 2010
Wheat straw & fertilizer	↑ 1.7	1.1	↑ 1.7	↑ 5.5	Aciego Pietri and Brookes, 2009
	↑ 1.9	↑ 1.4	↑ 1.5	↑ 2.2	
	↑ 1.3	1.0	↑ 1.2	↑ 1.2	
Barley straw		↑ 4	↑ 1.3		Rousk and Baath, 2007.
Leaf litter	↑ 1.5–4.7				McIntyre et al., 2009
Sorghum residues	↑ 1.7–2	↑ 2.3–3	↑ 1.5	↑ 2	White and Rice, 2009
Change in competition	↑ 2.3	↑ 1.4–2	↓		Demoling et al., 2009
Hotspots expiration - end of hot moments					
One year incubation	↓ 3.5–3.6	↓ 6–10	↓ 2.7–5	↓ 2.9–6	Feng and Simpson, 2009
Soil depth	↓ 3	↓ 3.5	↓ 1.5	↓ 2.7	White and Rice, 2009
	↓ 7.5–26				Schutz et al., 2009
Decreasing pH	↓ 2.1	↑ 1.3	↓ 1.7		Djukik et al., 2010
	↓ 2.2	↓ 1.5	↓ 2.1	↓ 4.5	Aciego Pietri and Brookes, 2009
Grazing		↓ 2	↑ 2		Klumpp et al., 2009

↑ means increase and ↓ means decrease of PLFA content for number of times.
The part: *Hotspots in comparison to bulk soil* - shows just the comparison of PLFAs between hotspot and bulk soil. The second part: *Activation during hot moments* - shows the changes of PLFAs at the increase start of the hot moment. The part: *Hotspots expiration - end of hot moments* - shows the decrease of PLFAs at the end of the hot moment.

3. Microbial activity as a driver of hotspot functioning

3.1. Microbial abundance and activity as related to process rates in hotspots

Hotspots are characterized by higher microbial abundance, resulting in 2–3 times greater total biomass compared with bulk soil (Marschner et al., 2012). The total biomass, however, represents mainly dormant microorganisms, whereas active microorganisms perform most biochemical processes. The fraction of active microorganisms is up to 2 times greater in the rhizosphere than in bulk soil (Blagodatskaya et al., 2014a). In the detritusphere, however, where C delivery is longer and microbial competition with roots is weaker (see below) than in the rhizosphere, the active biomass is 4–20 times greater than in bulk soil (Blagodatskaya et al., 2009). The portion of active microorganisms remaining in a physiologically alert stage (De Nobili et al., 2001) is much higher in hotspots with high substrate availability and longer hot moments. This results in much faster microbial responses to C input in the rhizosphere and detritusphere compared to bulk soil (Patterson et al., 2008; Poll et al., 2008). Higher microbial activity (and abundance) in hotspots led to litter decomposition at rates up to three times those of bulk soil, resulting in 2–10 times higher concentrations of soluble products (Blagodatskaya et al., 2009). The activity of hydrolytic enzymes in the rhizosphere was 3–5 times higher (Marschner et al., 2012; Spohn and Kuzyakov, 2013; Lee et al., 2013b) and the N_2O emissions in the detritusphere were 2–9 times more intensive (Blagodatskaya et al., 2010) than in bulk soil. Consequently, not only total microbial biomass, but especially the portion of active microorganisms, is higher in hotspots. This leads to much faster process rates than in bulk soil (see Fig. 1).

In Fig. 6 we summarized several studies on the changes of microbial parameters in hotspots and during hot moments induced by addition of low or high molecular weight organics to soil (Fig. 6). The most intensive hot moments were induced by adding low molecular weight organics. Furthermore, some activity parameters, e.g. respiration and microbial growth rates, increased more than the content parameters, e.g. microbial C and ergosterol (Fig. 6).

3.2. Microbial diversity and community structure in hotspots

Hotspots are characterized by higher microbial diversity compared to individually scattered microbial cells in mineral soil (Marschner et al., 2012; Lee et al., 2013b). Higher substrate availability stimulates microbial growth and shapes community structure specific to the hotspot groups. The abundance of fungal and bacterial species compared to bulk soil increases more in the detritusphere than in the rhizosphere (Table 3). The higher increase in fungal than in bacterial PLFAs in the rhizosphere (by the factor 1.4) and especially in the detritusphere (by the factor 4.7) resulted in higher fungal-to-bacterial ratios in both hotspots compared with bulk soil (Marschner et al., 2012; Turner et al., 2013) (Table 3). Nonetheless, the increase of individual fungal (up to 50 times, Ehlers et al., 2010) and Gram(−) bacterial (up to 5.5 times, Aciego

subfigure: the parameters above the free line correspond to changes of pools, and the parameters below the free line reflect the changes of fluxes or of microbial activities. V_{max} values are presented for changes of enzyme activities. Note different X scales for the 5 subfigures. The X scales for 1st, 2nd and 4th subfigures were cut for better presentation of the average values. Note that the high increase of Nematode density (top) and Respiration intensity (2nd from top) were multiplied by 0.3 and 0.2, respectively, to bring the values on the scale convenient for other parameters. The results were collected from the following studies: For Rhizosphere: (Norton and Firestone, 1991; Appuhn and Joergensen, 2006; Renella et al., 2006; Berg and Steinberger, 2008; Marschner et al., 2012; Troxler et al., 2012; Turner et al., 2013); For LMWOS: (Renella et al., 2006; Lemanski and Scheu, 2014; Leon et al., 2014; Reischke et al., 2014); For Detritusphere: (Bonkowski et al., 2000b; Berg and Steinberger, 2008; Marschner et al., 2012; Lee et al., 2013a; Xiao, 2014); For HMWOS: (Rousk and Baath, 2007); For Biopores: (Tiunov and Scheu, 1999; Troxler et al., 2012).

Pietri and Brookes, 2009) PLFAs in the detritusphere can strongly exceed the total PLFA increase (Table 3). Thus, microbial community structure in hotspots specifically depends on substrate composition and input duration.

Microbial community structure within a particular hotspot group is affected by substrate quality. Microbial diversity differs in the rhizosphere of plant species (Kowalchuk et al., 2002; Turner et al., 2013) or even along the roots (Schmidt and Eickhorst, 2014) and it changes during root development (Remenant et al., 2009; Schmidt and Eickhorst, 2014). Similarly, microbial communities in the detritusphere are affected by litter quality and decomposition stage (Bastian et al., 2009; Esperschutz et al., 2013). Fungi dominate more strongly in the detritusphere under coniferous vs. deciduous litter (Blagodatskaya and Anderson, 1998). The decline of the fungal-to-bacterial ratio in the detritusphere with depth is more pronounced under coniferous vs. deciduous forest (Baldrian, 2009). Also, the contribution of archaea to the structure and functioning of hotspots is important (Lee et al., 2013b). The higher activity of hydrolytic enzymes in the detritusphere vs. mineral soil depends mainly on the diversity of bacteria and archaea, but is less affected by fungi (Lee et al., 2013b).

Despite differences in microbial community structure between and within hotspots at the micro-scale, microbial functioning at the higher scales, i.e. at the soil profile or ecosystem levels, remains similar (Parkin, 1993). Functional redundancy and the excessive microbial pool principle[2] (Morris, 2007; Young et al., 2008; Kuzyakov et al., 2009; Ruamps et al., 2013) lead to high similarities in the functions of hotspots differing in microbial community structure. In soil under diverse plant communities such as grasslands, microbial functioning (e.g. utilization of organic C, assimilation of root exudates, enzyme activity) remains rather stable unless the plant diversity drops below a threshold of 4 species (Loranger-Merciris et al., 2006; Sanaullah et al., 2011). Thus, microbial functioning at the ecosystem level is much more stable than the microbial community structure.

3.3. Microbial strategies in hotspots

Microbial functions in the hotspots depend strongly on the dominance of the ecological groups such as *r*- and *K*-strategists (Fontaine and Barot, 2005; Nottingham et al., 2009). This dominance, however, is not directly related to phylogenic structure of microbial community because both *r*- and *K*-strategists are abundant within bacterial and fungal phyla as well as within Gram+ and Gram-bacteria groups (Fierer et al., 2007). The dominant strategy can be determined by the kinetics and efficiency of microbial growth (Panikov, 1995; Stenström, 1998; Nocentini et al., 2010). According to the kinetic parameters of microbial communities (carbon use efficiency, CUE is the amount of C in microbial biomass compared to the C in the substrate; K_m: Michaelis constant; μ: microbial growth rates, etc.), the input of small amounts of labile substrates activates fast-growing *r*-strategists (Blagodatskaya et al., 2009, 2010). This is common in the rhizosphere (Philippot et al., 2013), where the utilization of substrate is at least 2 times less efficient (CUE ~0.2) than in bulk soil (Blagodatskaya et al., 2007, 2009). Domination of slow-growing *K*-strategists is attributed to microbial communities decomposing plant residues (Blagodatskaya et al., 2009), i.e. in the detritusphere, which was confirmed by a high CUE of ~0.6 (Thiet et al., 2006).

Microbial functioning in hotspots can be distinguished by the dynamics of catabolic and anabolic processes during growth. High substrate availability in the rhizosphere leads to a simultaneous increase of catabolic (detected by respiration) and anabolic (detected by DNA increase) activities (Blagodatskaya et al., 2014a). In the detritusphere, however, the increase of cell component contents (ergosterol, bacterial and fungal PLFAs) was delayed for 10 days compared to the rise in respiration (Rousk and Baath, 2007).

Functional differences in the microbial communities in hotspots can be assessed by the affinity of enzymes to substrates (K_m): it is lower for *r*-strategists (the K_m is higher). In accordance with ecological principles, the K_m increased in the rhizosphere but decreased in the detritusphere compared to bulk soil (Blagodatskaya et al., 2009). This demonstrates the differences in functional traits of microorganisms in hotspots of various origins.

Specific microbial growth rates – the intrinsic feature of the dominant population (Birgander et al., 2013) – are useful to distinguish hotspots. Microbial growth rates were 1.5 slower in the detritusphere than in the rhizosphere (Blagodatskaya et al., 2009). Slow growth rates, however, do not mean low activity. The active biomass was ca. 10 times greater in detritusphere than in the rhizosphere. This illustrates the higher input of labile C in the latter, but longer duration in the former. Therefore, *the increase of microbial activity in the rhizosphere is much higher, but the lifetime of the rhizosphere hotspots is much shorter than that in the detritusphere* (Fig. 3).

3.4. Competition in hotspots

The high microbial activity (and abundance) in the rhizosphere (Lynch and Whipps, 1990), detritusphere (Kandeler et al., 1999; Poll et al., 2008; Marschner et al., 2012) and biopores (Tiunov and Scheu, 1999, 2000; Tiunov and Dobrovolskaya, 2002) is well demonstrated, but little attention has been paid to the competition between organisms in the hotspots (Alphei et al., 1996; Bonkowski et al., 2000a; Marschner et al., 2012). Excess labile C in hotspots leads to nutrient limitation (Marschner et al., 2012). Rhizosphere and detritusphere differ in their competition structure. While competition in the detritusphere occurs within or between microbial species, in the rhizosphere it occurs mainly between plants and microorganisms (Kuzyakov and Xu, 2013). The latter is strongly affected by nutrient uptake by roots and can reduce microbial growth, especially if the plant is a strong competitor for N (Bonkowski et al., 2000a). Furthermore, protozoan grazing can delay microbial decomposition of organics in the detritusphere (Bonkowski et al., 2000b; Blagodatskaya et al., 2014b). This results in fluctuations of process rates – accelerated activity in hotspots may be followed by retardation of microbial growth (Zelenev et al., 2006; van Bruggen et al., 2008) and enzyme activities (Lavrent'eva et al., 2009).

In all hotspots, C availability commonly decreases after the input is finished (Bastian et al., 2009; Poll et al., 2010). This is because the most labile substrates are preferentially utilized at the start of hot moments and less labile recalcitrant organics remain (Theuerl and Buscot, 2010). Therefore, the decline in activity within the hotspots is prolonged because of the declining substrate quality (and quantity). This boosts competition at the end of hot moments. This is confirmed by a 3.5–26 fold decrease in the PLFA content in the rhizosphere and detritusphere at the end of hot moments (Feng and Simpson, 2009; Schutz et al., 2009, Table 3). The PLFAs of fungi and Gram(−) bacteria decrease more strongly than do Gram(+) bacteria (Aciego Pietri and Brookes, 2009), probably because of the latter's higher competitive abilities when hot

[2] Excessive pool principle (or 'storage effect', Morris and Blackwood, 2007): soils have an excessive pool of total microbial biomass. Only a small portion of microorganisms is active, but a very large dormant pool with a broad spectrum of potential metabolic activities provides a quick growth response after input of any labile substrate.

moments terminate. The exhaustion of substrates and boosted competition at the end of hot moments frequently trigger priming effects (Fontaine et al., 2003).

3.5. Signaling pathways at hot moments

The ability to rapidly switch physiological states (i.e. from activity to dormancy and *vice versa*) depending on substrate availability is an important microbial adaptation to dynamic environmental conditions in the hotspots. Besides physico-chemical drivers (e.g. moisture and temperature) that induce a shift from dormancy to activity and back, the activation/deactivation mechanisms based on signaling molecules are particularly important. The transition of active cells to dormancy as an outcome of quorum sensing, i.e. by secretion of molecules inducing reduction of population density, is relatively well studied (Gray and Smith, 2005). Little, however, is known about biochemical pathways of the inverse process – activation of dormant cells in hotspots. The origin of inducers – substances or events initiating microbial activation – regulates the differences between the two inverse signalings. In hotspots, quorum sensing serves to autoregulate population density by secreting signaling molecules that induce the expression of genes responsible for producing antimicrobial substances and for cell mortality (Winson et al., 1995; Redfield, 2002; Ekschmitt et al., 2005). Thus, the switch from activity to dormancy is regulated by *internal* signals: autoinducer molecules (e.g. γ-butyrolactones, gomoseryllacton) secreted by the microbial population (Raffa et al., 2005). In contrast, *external* signals are often required to wake microbes up from dormancy to activity. Such external triggering signals occur at the start of hot moments, when low amounts of labile C such as glucose, amino acids or yeast extract serve as external inducers activating microorganisms (De Nobili et al., 2001). The general patterns of such signaling are described for plant-growth-promoting bacteria, whereas the roles of internal and external signals in the activation/deactivation mechanisms of specific microbial groups in the hotspots remain to be clarified (Gray and Smith, 2005).

4. Methods for identification and spatial analysis of hotspots

4.1. Approaches for hotspot identification

Identifying hotspots in soil is very challenging because: i) identification should focus on process intensities (and not on contents or concentrations), ii) the processes should be traced in undisturbed soil, without mixing of hotspots with bulk soil (Ruamps et al., 2011). It is very easy to postulate the existence of microenvironments with any required property but difficult to actually determine their existence and significance (Prosser, 1989). *This is especially challenging because nearly all soil analyses use mixed samples (Parkin, 1993) and are focused on determining contents (not intensities).* The first approaches to identify hotspots (Luster et al., 2009) involved i) light and electron microscopy, ii) microelectrodes or -sensors, iii) simple separation of soil adhered to roots (rhizosphere), iv) separation of the root zone with various gauzes and/or v) cutting of soil with increasing distance from the root surface (Helal and Sauerbeck, 1981; Kandeler et al., 2002). These approaches, however, are destructive, have many other limitations (Parkin, 1993) and are therefore not discussed here. The prerequisites for approaches to identify hotspots are: i) undisturbed soil should be analyzed, if possible by non-invasive approaches, ii) the analysis should be completed within a short time (much shorter than the duration of the hot moments), iii) the method should focus on process intensities (not solely on analyzing contents), iv) the spatial resolution of the method should be much smaller than hotspot size.

Only very few approaches fulfill these requirements (Table 4). The first trials to identify hotspots involved identifying microorganisms in thin sections (Jones, 1964) and autoradiography (Hendriks et al., 1981; Romheld, 1986). pH changes were visualized in gels (Hinsinger et al., 2009) or by installing pH and redox microelectrodes close to the roots (Flessa and Fischer, 1992). Autoradiography and its follow-up – imaging – enable localization of rhizodeposits (Rosling et al., 2004; Wichern et al., 2011; Rasmussen et al., 2013) and of nutrient uptake zones (Rubio et al., 2004). These localizations, however, do not necessary reflect microbial hotspots. Newly developed planar optodes enable the analysis of the 2D distribution of pH, O_2 and CO_2 partial pressures, temperature and ion concentrations in soil (Blossfeld, 2013; Rudolph et al., 2013). These parameters partly reflect microbial activity (CO_2/O_2 changes). Recently elaborated soil zymography identifies hotspots of activities of various enzymes: protease, amylase, acid and alkaline phosphatases, cellulase and chitinase (Spohn and Kuzyakov, 2013; Spohn et al., 2013). Microbial hotspots have been identified and their dependence on local environmental conditions better visualized (Rasa et al., 2012) by thin-section microscopy of fixed and polished soil samples stained with respective dyes (Nunan et al., 2001, 2002; Eickhorst and Tippkotter, 2008a).

The other group of very rapidly developing approaches is based on fluorescence in situ hybridization (FISH), which enables identifying not only microbial hotspots but also various microbial groups within the hotspots (Schmidt and Eickhorst, 2014). Combinations of FISH with catalyzed reporter deposition (CARD-FISH (Schmidt and Eickhorst, 2013), with MicroAutoRadiography (MAR-FISH) (Teira et al., 2004), with electron microscopy (Gold-FISH, (Schmidt et al., 2012), or nanoscale secondary-ion mass spectroscopy (Musat

Table 4
The most frequently used non-destructive approaches[a] to identify microbial hotspots in soil and the relevant parameters and processes.

Approaches[b]	Process/parameter	Conditions	Resolution	References
Autoradiography, Phosphor imaging	Rhizodeposition, nutrient uptake (P, K, Ca, …)	Lab, radioactive isotopes only	<100 μm	Pausch and Kuzyakov, 2011.
Microelectrodes	pH, Eh	Lab (field)	mm	Hinsinger et al., 2009.
Planar optodes	O_2, pH, CO_2, NH_4^+, PO_4^{3-}, Temperature, Eh	Lab	>100 μm	Blossfeld, 2013.
Zymography	Various enzymes	Lab (field)	< mm	Spohn et al., 2013.
Computer tomography[c]	Pore distribution and size	Lab		Peth et al., 2008; Schrader et al., 2007.
FISH, CARD-FISH, Gold-FISH	Various microbial groups	Lab	μm … mm	Eickhorst and Tippkotter, 2008b.
Polished soil samples	Bacterial groups	Lab (field)	mm	Eickhorst and Tippkotter, 2008a.
Thin sections microscopy	Bacterial groups, coupling with FISH, 16S-rRNA	Lab	μm	Eickhorst and Tippkotter, 2008a.
Biological thin sections	Bacterial cells	Lab	μm … cm	Nunan et al., 2001.

* Note that various methods allowing identification of individual microbial cells (not the colonies) are not mentioned here.
[a] The Table 4 gives short overview without details. The details can be found in respective reference papers.
[b] Only the approaches used for visualization of microbial colonies (compare Fig. 3) are mentioned here.
[c] These are the only 3D approaches (however, they were not used for identification of microbial hotspots).

et al., 2008) strongly improve the detection quality. They enable quantification and phylogenetic identification of microbial groups in 2D or even 3D hotspots, e.g. at root–soil interfaces.

X-ray computer tomography (CT) (Carminati et al., 2009; Tippkotter et al., 2009; Moradi et al., 2011) and neutron radiography (Carminati et al., 2007; Oswald et al., 2008; Zarebanadkouki et al., 2013) are the only approaches enabling identification of 3D structures. Their temporal dynamics help extend these approaches to 4D simulations (Carminati and Zarebanadkouki, 2013). Nonetheless, most applications of X-ray CT have focused on analyzing soil pore structure (Peth et al., 2008), water content and fluxes (Carminati et al., 2007), not on microbial hotspots.

Coupling the approaches is especially useful for understanding processes and their interactions in hotspots. This allows simultaneous spatial identification of 2 and more processes or parameters. Simultaneous identification of pH changes, O_2 and CO_2 partial pressures, and temperature by planar optodes (Borisov et al., 2011) is a promising approach to correlate processes in the rhizosphere (Blossfeld et al., 2011). Rhizodeposition hotspots (identified by ^{14}C imaging) were spatially correlated to acid phosphatase (analyzed by soil zymography), but showed very weak coincidence with hotspots of alkaline phosphatase (Spohn and Kuzyakov, 2013). We conclude that the development of methods for hotspot identification and analysis, as well as coupling the existing 2D (and 3D) approaches, are crucial for understanding microbial localizations and the effects of environmental factors.

4.2. Statistical approaches of hotspots analysis

Identifying 2D and 3D hotspot distribution in soil requires statistical analysis. The statistical approaches are necessary to clarify (Dechesne et al., 2003): i) hotspot size and form, ii) the distances/ranges between them and thus their contribution to total soil volume, iii) their distribution (random, clumped/aggregated, regular/uniform) to evaluate their facilitation and competition, iv) critical thresholds of process intensities sufficient to delimit hotspots and, especially important, v) their spatial correspondence to affecting factors: allocation and distribution of soil pores (Nunan et al., 2003), labile substrates, roots, particulate organic matter, organo–mineral associations, etc. This is necessary to identify the mechanisms and factors affecting hotspot origin, formation and functioning. Although the first discussions about the importance of statistical approaches for analyzing microbial hotspots were initiated more than 50 years ago (Parkin, 1993), this issue remains in the early stages of development. This is underlined by the fact that nearly all studies identifying microbial hotspots (references see above) merely visualized them but did not analyze them statistically.

A few attempts have been made to evaluate the distribution of microbial hotspots in soil. The classical geostatistics approaches showed the spatial autocorrelation of bacterial distribution in ranges of 1 mm and below, higher aggregation in topsoil, but no clear dependence on pore distribution (Nunan et al., 2003). Comparison of experimentally measured spatial distributions of bacterial microhabitats with six theoretical 3D distributions showed a higher microbial aggregation of pollutant degraders compared to NH_4^+ oxidizers (Dechesne et al., 2003).

In our opinion, other promising (but never used) approaches to analyze and to statistically evaluate the distribution of microbial hotspots are: spatial point pattern analysis, Log-Gaussian Cox processes, random probability maps, colocalization analysis, edge detection analysis, and mass fractal dimension analysis. These and similar spatial approaches permit upscaling and simulating hotspot distribution in soil with and without substrate addition (Kaiser et al., 2014; Raynaud and Nunan, 2014). They could also help model hotspot properties (Raynaud, 2010).

Table 5
Main microbial processes relevant in specific hotspots in soil[a].

Processes	Hotspots			
	Rhizosphere	Detritusphere	Biopores	Aggregate surface
Direct processes				
Decomposition	XX	XXX	X	X
Microbial activation	XXX	XXX	X	X
Microbial growth	XX	XXX	X	
Exoenzyme release	XX	XXX	XX	
Indirect processes				
Ammonification	XX	XXX	XXX	X
Nitrification	XX	XX	XXX	X
Denitrification	XXX		XXX	
N immobilization	XX	XXX	X	
CH_4 consumption	X	XXX	X	X
CH_4 production[b]	X	XX		
N_2O production[b]	X		XXX	X
N_2O consumption				
Redox changes	X		X	XXX
Fe oxidation/reduction	X		X	XXX
Priming effects	XXX	XXX	XX	?
Mineral weathering	XXX	XX	X	XX
$CaCO_3$ formation[c]	XXX		XXX	XX

[a] Here only the processes ongoing faster as in bulk soil are mentioned. The number of 'X' corresponds to the relative increase compared to bulk soil. The processes ongoing with rates similar as in bulk soil are not mentioned.

[b] These are the only processes ongoing slower in the 4 hotspot groups compared to the bulk soil. Hotspots of CH_4 and N_2O production are located within the aggregates, where the O_2 and other $\bar{e}$ acceptors are consumed by microbial activities. For details see other reviews (Parkin, 1987, 1993; Conrad, 1996; Groffman et al., 2009).

[c] This is an abiotic process of formation of $CaCO_3$ concretions related to water uptake by roots, or decrease of partial CO_2 pressure in large pores. It is ongoing only in the presence of Ca^{2+} in soil.

5. Ecological relevance

5.1. Main microbial processes in hotspots, process rates and priming effects

Much faster process rates in hotspots compared to bulk soil are especially pronounced for those processes directly or indirectly related to the input of labile C (Fig. 6). Directly affected are nearly all C transformations under oxidative conditions (hotspots are usually better aerated than bulk soil): decomposition and mineralization of plant litter, soil organic matter and rhizodeposits, microbial turnover and associated release of dissolved organics, CO_2, NH_4^+ and nutrients (Table 5). Indirectly affected are processes related to C turnover, such as microbial immobilization of N and other nutrients as well as the local consumption of O_2 and other electron acceptors (Table 5).

Various examples show that the process rates in hotspots are up to two orders of magnitude faster than in the bulk soil. The pH changes close to root tips may reach 2 units within a few mm (Marschner, 2011; Rudolph et al., 2013) or even within 0.2 mm around colonies of nitrifying bacteria (Strong et al., 1997). This corresponds to a 100-fold increase in H^+ concentration. The activity of H_2-oxidizing bacteria is about 10 times higher close legume nodules compared to bulk soil (Lafavre and Focht, 1983). The local concentration of organic acids in the rhizosphere is at least one order of magnitude higher than in root-free soil (Strobel, 2001; Christou et al., 2006). The acid phosphatase activity in the rhizosphere is about 5–10 times higher than in bulk soil (Spohn and Kuzyakov, 2013). Considering these much faster process rates in the hotspots, and that they occupy between 1 and 10% of the total area, we assess that *nearly all above-mentioned processes in soil are actually taking place in the hotspots* (inset in Fig. 1).

This calls for revising the rates of many processes in soil. The common opinion is that many processes, especially related to C turnover in soil, are very slow. This opinion originates 1) from the traditional sampling and analysis of mixed samples, where a very small hotspot volume is mixed with the remaining 95–99% volume of bulk soil (Parkin, 1993) and 2) from greenhouse gas emission studies in field or laboratory incubations, where the total fluxes are averaged for a soil surface or weight. Nonetheless, up to 100-times-higher process rates in hotspots clearly show that soils are very reactive systems. Especially C transformations can be boosted by removing the limitation by labile organics and by activating dormant microorganisms. Two groups of processes start at hot moments: i) production and release of exoenzymes that can decompose both the organics released by the input and the recalcitrant soil organic matter (SOM), and 2) microbial growth triggered by labile C requires other nutrients in stoichiometric ratios, leading to mining of these nutrients from SOM. Accordingly, both process groups accelerate SOM decomposition – leading to *priming effects*. The frequently measured accelerated SOM decomposition (priming) of 20–50% compared to that in bulk soil (Cheng et al., 2014) should therefore be related to hotspot volume (1–10%). Our conclusion is that the *real intensity of priming effects within hotspots is about 10–100 times higher than SOM decomposition in bulk soil.*

Some processes localized in small soil volumes and ongoing under O_2 limitation cannot be associated directly to one of the four hotspot groups mentioned above. Good examples of such processes are denitrification (Parkin, 1987, 1993; Grundmann et al., 2001; Groffman et al., 2009; Blagodatsky and Smith, 2012) or CH_4 production (Conrad, 1996). These processes occur in locations with low O_2 level (<10%) and high moisture, e.g. within aggregates, where intensive consumption of electron acceptors is not (or too slowly) replenished by O_2 diffusion (Focht, 1992; Grundmann et al., 2001; Blagodatsky and Smith, 2012). The four groups of hotspots under oxic conditions (Table 1, Fig. 2) are thus produced by fast inflow of labile C. In contrast, the hotspots under anoxic conditions and related denitrification and CH_4 production are triggered by slow diffusion of O_2 (Focht, 1992).

5.2. Pools and concentrations do not reflect the fluxes and processes

Microorganisms in soil hotspots take up the labile organics almost immediately (Fischer et al., 2010; Rousk and Jones, 2010) and consume them within a few hours (Jones et al., 2005). Such *quick uptake reflects the excessive pool principle* (Kuzyakov et al., 2009): the tiny fraction of microorganisms that is permanently active has excess uptake capacity (high V_{max}) for large amounts of labile C. This ability for fast uptake is especially pronounced at low substrate concentrations (low K_m = high substrate affinity). Therefore, the soluble C concentrations are usually very low and vary from several μg to maximally 100–200 μg C g^{-1} soil (Nguyen and Henry, 2002; Bastida et al., 2006; Waldrop et al., 2006). The high input of labile organics in the hotspots by roots or decomposed litter is compensated by very fast microbial uptake and decomposition. The high input of organics stimulates their faster utilization in the hotspots (Fig. 6). Thus, the *acceleration of fluxes (high input and output) is much higher than the increase of the stocks*. This complicates the analysis of hotspots because most analytical methods in soil science (and in the most other environmental sciences) focus on content and concentrations, not on turnover or fluxes.

6. Conclusions and outlook

This review analyzed the origin, properties and functions of microbial hotspots and hot moments in soil, aiming to underline the importance of spatial and temporal biological inhomogeneity of soils at the microscale. Soil physics has intensively investigated the spatial inhomogeneity of soils at nano- and micro- (but also at meso- and macro-) scales over at least the last 3-4 decades (Webster, 2000; Heuvelink and Webster, 2001). Although spatial microbial inhomogeneity in soil is tacitly accepted, only very few studies have focused on microbial hotspots and hot moments and on approaches allowing their experimental analysis, especially under field conditions. This discrepancy in the progress between soil physics and biology is because various soil physical parameters represent the rates of abiotic processes much better than they do microbial transformations. Thus, microbial biomass content in no way reflects microbial activity (Blagodatskaya and Kuzyakov, 2013). This calls for measuring microbial processes and C fluxes (which is much more difficult). Furthermore, the methods to separate, to sample, to analyze, and to statistically evaluate the spatial variability are much less developed in soil biology than in soil physics.

Most microbial hotspots are characterized by a high input of labile C and energy, temporarily (hot moments) removing the limitation common for bulk soil. The most important hotspots with primary input of C are the rhizosphere and detritusphere because labile C is released by living roots or decomposed litter. Most studies on hotspots have concentrated on the rhizosphere and detritusphere; few results are available on microbial activities and processes in other hotspot groups (biopores and drilosphere, aggregate surfaces, animal faeces and bodies).

Although hotspots occupy only a small portion of soil volume (usually between 1 and 5%, or even0.2% in subsoil), the process rates are up to two orders of magnitude faster than in bulk soil. Therefore, small spatial size is (over)compensated by (very) high process rates. Most processes measured in mixed soil samples are probably actually taking place in hotspots. This should be specified and quantified for the broad range of microbial processes in soil, as was done earlier for denitrification (Parkin, 1987).

It is necessary to develop approaches for visualizing, sampling and analyzing hotspots separately from the bulk soil in order to better understand soil processes. This is very challenging because any sampling leads to disturbance, potentially altering process intensities and even process directions compared to undisturbed conditions. Our research tools should correspond to the spatial distribution and temporal functioning of microorganisms – the main drivers of biogeochemical processes in soil. This is a prerequisite for understanding microbial mechanisms and for process-based modeling of biogeochemical cycles.

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