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Short communication

Community structure of prokaryotes and their functional potential in subsoils is more affected by spatial heterogeneity than by temporal variations

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ABSTRACT

Spatial and temporal dynamics of microbial community structure and function in subsoils have been rarely studied in the past. In this paper we present data on how bacterial communities as well as selected functional groups of microbes change in the rhizosphere, the drilosphere, and in bulk soil over time in topsoil as well as in subsoil. We show that the overall richness of bacteria and abundance of nitrifiers and denitrifiers decreases in bulk soil with soil depth. However, these effects were not or to a much lower degree observed in the rhizosphere and the drilosphere. Temporal fluctuations contributed by far less than spatial factors to the dynamics of bacterial communities and abundance of nitrifiers and denitrifiers in all compartments independent from the soil depth.

Structure and function of microbial communities in soils are highly dynamic over time and space (Fuka et al., 2009). This is indicated by the concept of "hotspots" and "hot moments" (McClain et al., 2003; Hagedorn and Bellamy, 2011). Therefore it is not surprising that much research has been done in the past in order to identify the pattern of microbial heterogeneity in soil and to identify abiotic and biotic drivers. The rhizosphere has been identified as a hotspot for microbial activity due to the secretion of root exudates (Marschner et al., 2001; Garbeva et al., 2008). The interface between plant litter and soil, called the detritusphere, can be considered as another focus point for microbes (Schulz et al., 2012) due to the presence of large amounts of nutrients directly after litterfall. Besides plants, soil animals also form hotspots for microbial activity in soil. For example several studies have indicated that the coating of earthworm channels, called the drilosphere, harbours a large number of microbes, which differ significantly in number and ecophysiology from those of the bulk soil (Dallinger and Horn, 2013). Besides the spatial pattern of heterogeneity, also the shifts of microbial communities over time have been of great interest. Next to the seasonal variations in temperature and moisture regime, the plant developmental stage as well as changes in the litter quality during the decomposition processes highly influence the microbial community structure and shifts in functionality (Molodovskaya et al., 2012; Lauber et al., 2013; Shade et al., 2013).

Despite the fact that subsoil systems have been identified as an important reservoir for nutrients in the last decade and thus will play a pronounced role in the future for sustainable plant production (Blume et al., 2002; Eilers et al., 2012; Fischer et al., 2013), the identification of hotspots and hot moments in subsoils has been so far mostly neglected. Especially in subsoil hotspots might be of a great importance as structural elements and nutritional pools for plant roots and microbes. However, in fact it is still unclear if the dynamics of microbes over time in deeper soil layers are comparable to those in topsoils or if the topsoil acts as a buffer and shifts over time are far less significant. Also, the role of plants and soil animals in the formation of hotspots in subsoils is still poorly understood.

Here we present data from a study where spatial and temporal heterogeneity patterns of soil microbes in top- and subsoils have been investigated in an agricultural field, which was cultivated with

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Table 1
Statistical evaluation of bacterial community structure and abundance of nitrifiers and denitrifiers by PerMANOVA. Significance code: $^{***}P \leq 0.001$, $^{**}P \leq 0.010$, $^{*}P \leq 0.050$. The plant development stage is indicated by week 14, 17, and 20, corresponding to early vegetative phase (BBCH 28-32), late vegetative phase (BBCH 34-38), and flowering (BBCH 55-65), respectively.

Factor	Data subset	16S rRNA gene diversity	Functional gene abundance g^{-1} dry matter
Compartment	Total	0.001***	0.001***
	Topsoil	0.001***	0.001***
	Subsoil	0.001***	0.001***
	Week 14	0.001***	0.001***
	Week 17	0.001***	0.001***
	Week 20	0.001***	0.001***
	C. intybus	0.001***	0.001***
	F. arundinacea	0.001***	0.001***
	M. sativa	0.001***	0.001***
Depth	Total	0.001***	0.001***
	Bulk soil	0.001***	0.001***
	Drilosphere	0.003**	0.001***
	Rhizosphere	0.023*	0.001***
	Week 14	0.001***	0.001***
	Week 17	0.001***	0.001***
	Week 20	0.001***	0.001***
	C. intybus	0.001***	0.001***
	F. arundinacea	0.001***	0.001***
	M. sativa	0.001***	0.001***
Vegetation state	Total	0.001***	0.001***
	Bulk soil	0.002**	0.001***
	Drilosphere	0.021*	0.001***
	Rhizosphere	0.039*	0.001***
	Topsoil	0.004**	0.001***
	Subsoil	0.008**	0.001***
	C. intybus	0.035*	0.001***
	F. arundinacea	0.013*	0.001***
	M. sativa	0.140	0.001***
	Bulk topsoil	0.001***	0.001***
	Bulk subsoil	0.001***	0.001***
	Drilosphere topsoil	0.069	0.001***
	Drilosphere subsoil	0.128	0.001***
	Rhizosphere topsoil	0.061	0.001***
	Rhizosphere subsoil	0.090	0.001***
Plant species	Total	0.001***	0.025*
	Bulk soil	0.104	0.301
	Drilosphere	0.012*	0.002**
	Rhizosphere	0.001***	0.357
	Topsoil	0.001***	0.043*
	Subsoil	0.001***	0.267
	Week 14	0.001***	0.086
	Week 17	0.001***	0.236
	Week 20	0.001***	0.286
	Bulk topsoil	0.001***	0.032*
	Bulk subsoil	0.414	0.252
	Drilosphere topsoil	0.006**	0.040*
	Drilosphere subsoil	0.065	0.001***
	Rhizosphere topsoil	0.001***	0.368
	Rhizosphere subsoil	0.001***	0.295
Compartment × depth	Total	0.001***	0.001***
Compartment × vegetation state	Total	0.001***	0.002**
Compartment × plant species	Total	0.001***	0.053
Depth × vegetation state	Total	0.081	0.005**
Depth × plant species	Total	0.004**	0.650
Vegetation state × plant species	Total	0.337	0.718

different crops with diverging root morphology. Besides the overall bacterial diversity, we measured copy numbers of selected functional genes (*nirS*, *nirK*, *nosZ* and *amoA*) per g dry soil, which were used as proxy for the abundance of nitrifiers and denitrifiers. Samples from three soil compartments were analysed (bulk soil, drilosphere, and rhizosphere). We hypothesized that in deeper soil layers differences in microbial community structure and function between hotspots like the drilosphere or rhizosphere and bulk soil become more pronounced than in the topsoil. Vice versa in topsoils temporal dynamics are higher than in subsoils due to the impact of abiotic factors like temperature and precipitation.

Soil samples were taken from a plot experiment which has been performed at campus Klein – Altendorf near Bonn, Germany, where *Festuca arundinacea* Schreb. with a rooting system characterized as a fibrous root system, *Cichorium intybus* L. and legume *Medicago sativa* L., both with a tap root system, were grown. In total 9 plots (each 10 × 6 m), located on the same field, were used in this study (3 plots per plant), which were randomly distributed according to a split-plot design and sampled separately in 2011. Per plot 5 subsamples (each 1 g) of bulk soil, drilosphere, and rhizosphere were taken from topsoil (10–30 cm) and subsoil (60–75 cm) and pooled, respectively. A sterilized spoon or tweezer was used to

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