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Soil bacterial communities and ecosystem functioning change more strongly with season than habitat in a restored floodplain

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ABSTRACT

Soil bacterial community structures and associated ecosystem functions are known to vary both in space and time but spatial and temporal patterns are rarely studied simultaneously. Dynamic floodplains offer an ideal setting to study these spatio-temporal patterns and to determine the relative importance of habitat diversity and seasons in shaping soil bacterial communities.

We studied the differences between habitats and seasonal patterns of soil bacterial communities (T-RFLPs) and soil environmental conditions (temperature, moisture and time elapsed since last inundation) and ecosystem functioning proxies (basal respiration, enzymatic activity, microbial C and N) over one year in seven habitats of a restored floodplain.

Soil bacterial community structures in the two habitats closest to the river were most divergent from the others. However, although bacterial community structures differed between habitats at all sampling times, their seasonal variability was substantially higher than the habitat differences. Most of the ecosystem functioning proxies were lowest in the most dynamic habitat (gravel bar). Furthermore, while both bacterial community structure and ecosystem functions varied in relation to environmental conditions, the two were not directly correlated, and the link between communities and functions was seasonally inconsistent. The ratio of seasonal vs. habitat variability of soil bacterial communities decreased from the most dynamic to the most stable (forest) habitat. Thus in dynamic ecosystems such as floodplains also external factors (flood disturbance, seasonally changing climatic conditions) might influence ecosystem functions and bacterial communities independently – possibly because of species functional redundancy – and are keys in maintaining floodplain taxonomical and functional diversity.

1. Introduction

Perturbation generates spatial and temporal variability in biotic communities and associated processes (Ward et al., 2002). Riparian floodplains, at the interface between the riverbed and the surrounding upland terrestrial ecosystems (Sedell et al., 1989), are among the most diverse environments at a global scale. Flood dynamics create an important spatial and temporal heterogeneity of habitats characterized by contrasted and changing physico-chemical conditions and biotic characteristics – and a gradient of perturbation from regularly flooded gravel bars to infrequently flooded riparian forests (Stanford and Ward, 1993; Tockner et al., 1997; Brunke et al., 2003). Riparian soils contain an unusually high diversity of microfauna and microflora, but this diversity is very heterogeneously distributed among the different functional processing zones (FPZ) of floodplains (Binkley et al., 1997). Functional processing zones are patches with distinct chemical and physical properties defined by specific hydromorphic influence that determine their ecological functions, such as microbial community composition, system metabolism, productivity, organic matter dynamics, and nutrient cycling (Thorp et al., 2006). Soils of floodplain thus offer an ideal setting to investigate

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the effects of spatio-temporal variation on soil bacterial communities and test whether these patterns are predictable based on abiotic characteristics and vegetation composition (i.e. revealing niche specialisation) or if they are instead random (i.e. in agreement with neutral theory; Langenheder and Szekely, 2011).

Soil bacterial communities vary over space, time and in response to environmental changes. Their spatial variation occurs at fine scale (Vos et al., 2013), in relation to soil micro-structure and organic matter distribution, and at broad geographical scale (Martiny et al., 2011). Soil and vegetation types are known to influence bacterial abundance and community composition across ecological gradients and succession (Pankhurst et al., 2001; Carney and Matson, 2006; Stromberger et al., 2007; Pietri and Brookers, 2009; Yu et al., 2012). Soil bacterial communities also vary temporally, over short (e.g. rain events) to longer (e.g. seasonal, ecosystem succession) time scales (Grundmann, 2004; Prosser, 2012) and also respond to perturbations (Allison and Martiny, 2008). Temporal dynamics are likely to dominate patterns of microbial diversity in ecosystems under recurrent perturbations, such as floods in riverine floodplains (Delong, 2010). However high habitat heterogeneity and contrasted microhabitats should also act as ecological controls on bacterial community structure (species sorting) and thus the relative importance of temporal and habitat differences should vary across gradients of perturbation (Lindström and Langenheder, 2012).

Here, we attempted to assess the relative importance of seasonal and habitat variability as drivers of soil bacterial community structures during on a one-year discontinuous monitoring of bacterial communities and selected indicators of ecosystem functions at morphologically distinct sampling sites in the riprarian zone of a river. The main factor separating them being distance from the riverbed and thus frequency and duration of flooding. Given the high habitat heterogeneity of floodplain ecosystems, we expected to find strong changes in bacterial communities among FPZs. Using terminal restriction fragment length polymorphism (T-RFLP) profiling, we analysed the habitat and seasonal variability of soil bacterial communities in relation to flood patterns, soil physico-chemical conditions and ecosystem functioning proxies such as respiration, enzymatic activity and microbial biomass in a lowland restored floodplain at Niederneunforn (river Thur) in Switzerland. These ecosystem functioning proxies can be linked to ecosystem services such as decomposition, nutrient cycling and carbon storage. Our study is part of an interdisciplinary project called RECORD (http://www.cces.ethz.ch/projects/nature/Record) (Linde et al., 2011; Pasquale et al., 2011; Samaritani et al., 2011; Schneider et al., 2011; Fournier et al., 2012; Shrestha et al., 2012). Along a transect in a restored floodplain several habitats corresponding to a succession gradient of plant colonisation were selected. We hypothesized (1) that bacterial community structures and ecosystem functioning proxies both would vary across habitats (from gravel bars to mature forests) and season. Given the very clear contrasts (e.g. in soil texture or vegetation structure) among the studied FPZs we hypothesized (2) that overall differences among FPZs would be greater than seasonal differences. However, given the clear gradient in inundation frequency and impact from the river to the floodplain forest, we also hypothesised (3) that the ratio of seasonal to habitat variability of soil bacterial communities would increase with the distance from the river.

2. Methods

2.1. Experimental design

River Thur covers a catchment area of 1700 km^2, from Mount Säntis, through the Swiss Plateau, and into the Rhine River. Lacking natural or artificial reservoirs, the river flow is subject to drastic and sudden changes in response to heavy rainfall events, especially in summer and autumn, and to snowmelt in spring. Long-term maximum, mean, and minimum flow rates are 1130, 50, and 2 $m^3\,s^{-1}$, respectively (1904–2005: http://www.hydrodaten.admin.ch/en/index.html). The mean annual precipitation at the study site is 908 mm and the average monthly temperature ranges from 0.9 °C in January to 19.0 °C in July (http://gate.meteoswiss.ch/idaweb). Glacio-fluvial sandy Gravels overlaying lacustrine clays dominate the Thur aquifer.

The river was first channelized in the 1890s to protect the river valley against floods. In the last 20 years, several river sections have been widened to allow the river to braid freely, in order to decrease the strength of the floods downstream and to increase the ecological value of the floodplain. The study site is located in the river corridor at Niederneunforn (Canton Thurgau, 8°77′12″ E; 47°59′10″ N), where a 2 km long section was widened from 50 to 110 m in 2002. The foreland in front of the levees was removed and the levees were lowered in some places to reconnect the old alluvial forest with the river during high floods. A strip of willow saplings was planted to reinforce the newly exposed banks.

Along the distance gradient from the riverbed, seven different habitats were identified based mainly on vegetation and topography and referred to as functional processing zones (FPZ)

Table 1
Physicochemical soil properties, hydrological and vegetation characteristics in the seven functional process zones of the study site in the Thur River floodplain, Switzerland. Soil properties are for the top 10 cm of soil.

Variable	Unit	Gravel	Grass	Willow bush	Mixed forest	Ash forest	Willow forest	Pasture
Flooding frequency	times $year^{-1}$	>10	>10	4–6	1–2	1–2	<1	<1
Flooding duration per event	days	>10	~10	~2	1	1	<1	<1
Gravimetric water content	%	21 ± 7	24 ± 8	26 ± 3	23 ± 4	29 ± 6	32 ± 4	21 ± 4
Texture (Sand/Silt/Clay)	%	81/14/5	66/26/8	44/44/12	38/47/15	33/50/17	25/58//18	65/27/8
pH (CaCl2)		7.6 ± 0.1	7.4 ± 0.1	7.5 ± 0.0	7.5 ± 0.1	7.5 ± 0.0	7.4 ± 0.0	7.5 ± 0.0
Organic C	g kg^{-1}	10.1 ± 3.7	16.3 ± 5.8	17.1 ± 3.2	21.4 ± 3.6	22.7 ± 2.1	24.8 ± 1.5	12.9 ± 2.9
Total N	g kg^{-1}	0.7 ± 0.2	1.0 ± 0.4	1.1 ± 0.3	1.6 ± 0.3	1.6 ± 0.2	1.8 ± 0.1	0.9 ± 0.2
Dominant vegetation		Various seasonal herbs, patchy	*Phalaris arundinacea*	*Salix viminalis*	*Acer pseudoplatanus* & *Fraxinus excelsior*	*Fraxinus excelsior*	*Salix alba*	Managed grassland dominated by *Trifolium* sp.
FPZ type		dynamic	dynamic	dynamic	stable	stable	stable	channelized
Distance from the river	m	3–6	5–15	10–25	50–70	70–80	70–80	40–50