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Microbial communities in floodplain ecosystems in relation to altered flow regimes and experimental flooding

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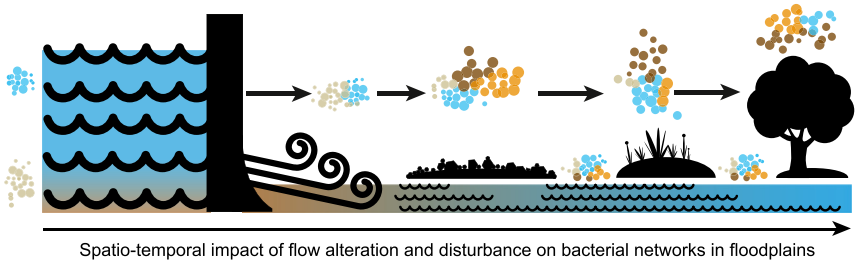
HIGHLIGHTS

- Floodplain habitat complexity caused high spatio-temporal microbial diversity.
- Experimental flood disturbance caused transient shifts in microbial communities.
- Seasonal and habitat effects overrode disturbance effects.
- More frequent flood disturbances might lead to an alternate microbial structure.

GRAPHICAL ABSTRACT



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ABSTRACT

River floodplains are spatially diverse ecosystems that respond quickly to flow variations and disturbance. However, it remains unclear how flow alteration and hydrological disturbance impacts the structure and biodiversity of complex microbial communities in these ecosystems. Here, we examined the spatial and seasonal dynamics of microbial communities in aquatic (benthic) and terrestrial habitats of three hydrologically contrasting (natural flow, residual flow, hydropeaking flow) floodplain systems. Microbial communities (alpha and beta diversity) differed more among floodplain habitats than between riverine floodplains. Microbial communities in all systems displayed congruent seasonal effects. In the residual and hydropeaking systems, an experimental flood was released from a reservoir to mimic a natural high flow event causing hydromorphological disturbance. The experimental flood caused a temporary shift in microbial communities by releasing microbes from the reservoir as well as redistributing communities among floodplain habitats. The flood-mediated shift in community structures had only a transient impact as pelagic bacteria did not persist within floodplain habitats over time after the flood. More frequent pulse disturbances might lead to an alternate structure of bacterial communities in floodplains over time.

1. Introduction

Microbes play a key role in the functional ecology of aquatic-terrestrial ecosystems, influencing biochemical and metabolic processes, and nutrient cycling such as decomposition and mineralization (Freimann et al., 2013; Hermans et al., 2020; Hotaling et al., 2017;

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Kaiser et al., 2016; Mayr et al., 2020). Microbial functioning in ecosystems is determined by community assembly in relation to the physico-chemical habitat template. Ecosystem landscapes comprise inter-connected habitats that allow bacterial dynamics to be placed in a metacommunity context. In this context, species sorting integrates source-sink dynamics (i.e., mass effects), patch dynamics and neutral processes in community assembly (Logares et al., 2013). In the context of floodplain habitats, mass effects occur continuously (as long as hydrologic connectivity persists) with a downstream directionality. Patch dynamics include the ability of species to disperse via the water column from an upstream to a downstream habitat. This requires species to become waterborn and to remain viable during transport. A successful coloniser then can outcompete a less competitive species present in a downstream habitat. The physico-chemical habitat template provides niches where species sorting can occur. Neutral processes, like speciation or demographic stochasticity, also influence community composition within a habitat. All these mechanisms interact with one another (Heino, 2013; Logue et al., 2011). How local bacterial communities respond to changes in these drivers at the regional scale likely depends on the relative strength of each process as well as intrinsic resistance and resilience properties. For instance, environmental change and mass effects can be seen as press disturbances to local bacterial communities, whereas seasonal shifts in the habitat template and periodic high flows can be considered pulse disturbances. How microbial communities respond and integrate across disturbances is still in debate (Febria et al., 2015; Shade et al., 2012; Zeglin, 2015).

Riverine floodplains are ideal model ecosystems to study microbial (meta) community dynamics in the context of ecosystem structure (habitat template), habitat linkages (ecohydraulics) and disturbance (hydrology). In their natural state, floodplains represent a complex, dynamic mosaic of contrasting aquatic-terrestrial habitats shaped by natural flow and sediment regimes that incorporate flow and flood pulses, ground/surface water exchange processes, and repeated erosion and deposition of sediments and organic matter (Amoros and Bornette, 2002; Doering et al., 2011; Poff, 1997; Stanford et al., 2005; Tockner et al., 2010; Wohl et al., 2015). Floodplain structural diversity along with a variable hydrologic and sediment regime links ecosystem function across habitats (respiration, organic matter and nutrient turnover). The coupling of aquatic-terrestrial habitats as well as ground-surface water exchange fosters and sustains an exceptionally high functional and biological diversity (Hauer et al., 2016; Tockner and Stanford, 2002; Ward et al., 1999) that is reduced with floodplain degradation and habitat alteration.

The increasing human demand for energy often results in dam construction that severely alters natural flow and sediment regimes in regulated rivers and subsequently degrades floodplain structure and function (Zarfl et al., 2015). As such, altered flow and sediment regimes downstream of reservoirs can directly impact floodplain habitats (Doering et al., 2012; Garofano-Gomez et al., 2013; Graf, 2006), reduce the abundance and distribution of species (Bunn and Arthington, 2002; Carlisle et al., 2011; Gabbud et al., 2019; Young et al., 2011) and limit functional processes (Aristi et al., 2014; Mbaka and Mwaniki, 2017; Sabater et al., 2018). Dams also act as physical barriers that restrict the exchange, dispersal and migration of material and organisms (Grill et al., 2019; Nilsson et al., 2005).

Over the last 20 years, mitigation policies have been implemented to restore the character of natural flow and sediment regimes in regulated rivers and floodplains. In particular, implementing high flows or managed floods (i.e., the controlled release of water from reservoirs to mimic the natural flow and sediment regime) is becoming a common management action to improve structural and functional conditions below dams (Gillespie et al., 2015; Konrad et al., 2011; Olden et al., 2014; Robinson et al., 2018; Yarnell et al., 2020). Although the response of regulated rivers to managed high flows and floods has been examined, most studies have focused on physical, biological and functional properties of higher organisms such as invertebrates and fish (Gillespie et al., 2015; Olden et al., 2014; Robinson et al., 2018). Further, most microbial assessments within river floodplains have focussed on either aquatic (Besemer et al., 2005; Freimann et al., 2013; Mayr et al., 2020; Nogaro et al., 2013) or terrestrial components of the floodplain (Argiroff et al., 2017; Samaritani et al., 2017; van Leeuwen et al., 2017). Only a few studies in stream networks demonstrated that the connectivity of microbial communities among terrestrial and aquatic ecosystems is of importance for overall microbial structural dynamics (Hassell et al., 2018; Hermans et al., 2020). To our knowledge, no integrative studies on aquatic and terrestrial microbial communities and their response to flow disturbance and mitigation measures in regulated floodplain rivers have been conducted to date.

The present study compared microbial communities in aquatic-terrestrial habitats of three hydrologically contrasting (natural flow, residual flow, hydropeaking flow) floodplain reaches over 1.5 years by community profiling using terminal-restriction fragment length polymorphism (T-RFLP). This was combined with examining the impact of a single experimental flood on microbial communities in different habitats of the residual and hydropeaking reach during the study period. The primary objective of the study was to compare the spatial and temporal variation of microbial communities among different floodplain habitats that included riparian forests, islands, open gravel bars, main channels and side channels (Table 1) in each reach. Due to the large variation in floodplain habitat characteristics, e.g., aquatic sediment vs. terrestrial soils and hydrological regimes, we predicted significant differences in microbial communities across space and time. The results were then used as baseline information for a second objective to assess the impact of the single experimental flood on microbial communities in the two hydropower (residual and hydropeaking) impacted floodplain reaches. We expected that flood disturbance would induce short-term changes in microbial communities in floodplain habitats in both reaches due to physical disturbance and sediment transport from the upstream reservoir and potentially influence community assembly in floodplain reaches and habitats over time. Specifically, we predicted more pronounced variation in the microbial community by flooding in the residual reach due to legacy effects of stable hydrological conditions compared to the hydropeaking reach with strong and frequent hydrological variations.

Table 1
Definitions of floodplain habitats examined in this study.

Habitat	Definition
Floodplain forest	Predominantly terrestrial habitat[a], characterized by developed soil and vegetation.
Island	Predominantly terrestrial[a] habitat with different vegetation stages. These habitats are surrounded by channel water or exposed gravel, and are characterized by sandy and pebble substrata and developed soil.
Open gravel bars	Predominantly terrestrial[a] area characterized by exposed gravel deposits.
Main channel	Lotic water body with upstream and downstream connections, characterized by coarse permeable gravel sediments.
Side channel	Lotic water body with at least upstream connection to the main channel, characterized by coarse permeable gravel sediments pebble or fine substrata.

[a] Terrestrial can become partly or completely aquatic habitat during hydrological variations and floods.

2. Material and methods

2.1. Study floodplains

The study floodplains are located on the Sarine and Sense rivers, two prealpine rivers in northern Switzerland (Fig. 1). The Sarine is 126-km long and drains a catchment of 1893 km^2. Mean elevation of study reaches was 575 m and annual precipitation 1075 mm. Upstream of Rossens dam (in operation since 1948), water is abstracted for hydropower production. Below the dam, an 13-km long floodplain reach experiences residual flow (2.5–3.5 m^3/s during the year). Downstream of this reach, water used for hydropower production (hydropower plant Hauterive) is released into the river again, resulting in a 8-km reach influenced by hydropeaking (daily flow increases up to 95 m^3/s). The Sense is about 35-km long and drains a catchment of 435 km^2. Mean elevation of the study reach was 810 m and annual precipitation 1345 mm. It is one of the most natural rivers in the region; it lacks large dams and has a natural flow and sediment regime (Hettrich et al., 2011). The geographical location, hydromorphological characteristics and flow regime of the three reaches - Sarine residual flow (SR), Sarine hydropeaking (SH) and Sense (SN) are shown in Figs. 1 and 2A–C. All three reaches comprise typical floodplain components, including floodplain forests, islands, open gravel bars, side channels, and a main channel (Table 1). Habitat components were categorized based on our previous studies (see Bodmer et al., 2016; Doering et al., 2011).

2.2. The experimental flood

An experimental flood was released from Rossens dam on 14–15 September 2016. Discharge at the dam was sequentially increased from 3.5 m^3/s (residual flow) to a maximum of 194.6 m^3/s. In total, 9.5 million m^3 of water was released over the course of 36 h leading to sediment transport and hydrological connection among floodplain habitats in SR and SH (Fig. 2D).

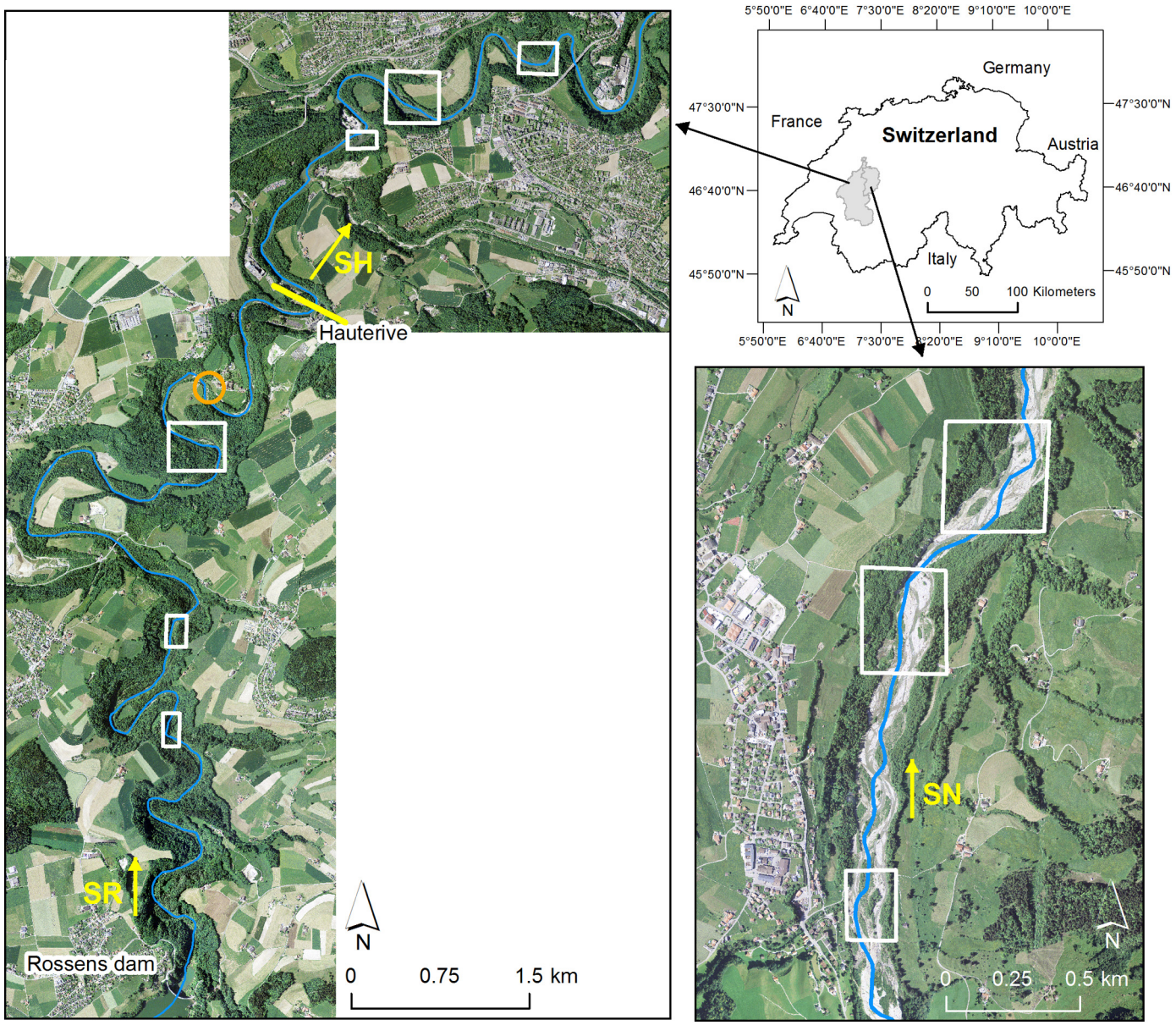


Fig. 1. Map of the study reaches and location of sampling sites. Left: Sarine residual flow (SR) including Rossens dam (water abstraction) and Sarine hydropeaking (SH) including hydropower plant Hauterive (water release). Orange circle marks the sampling site for sediment drift samples during the experimental flood. Right: Sense natural flow (SN). White rectangles indicate sampling sites ($n = 3$ per reach) including sampled habitats floodplain forests, islands, open gravel bars, main and site channels. Flow direction is from south to north. Orthophoto: Swissimage Geodata © Swisstopo.

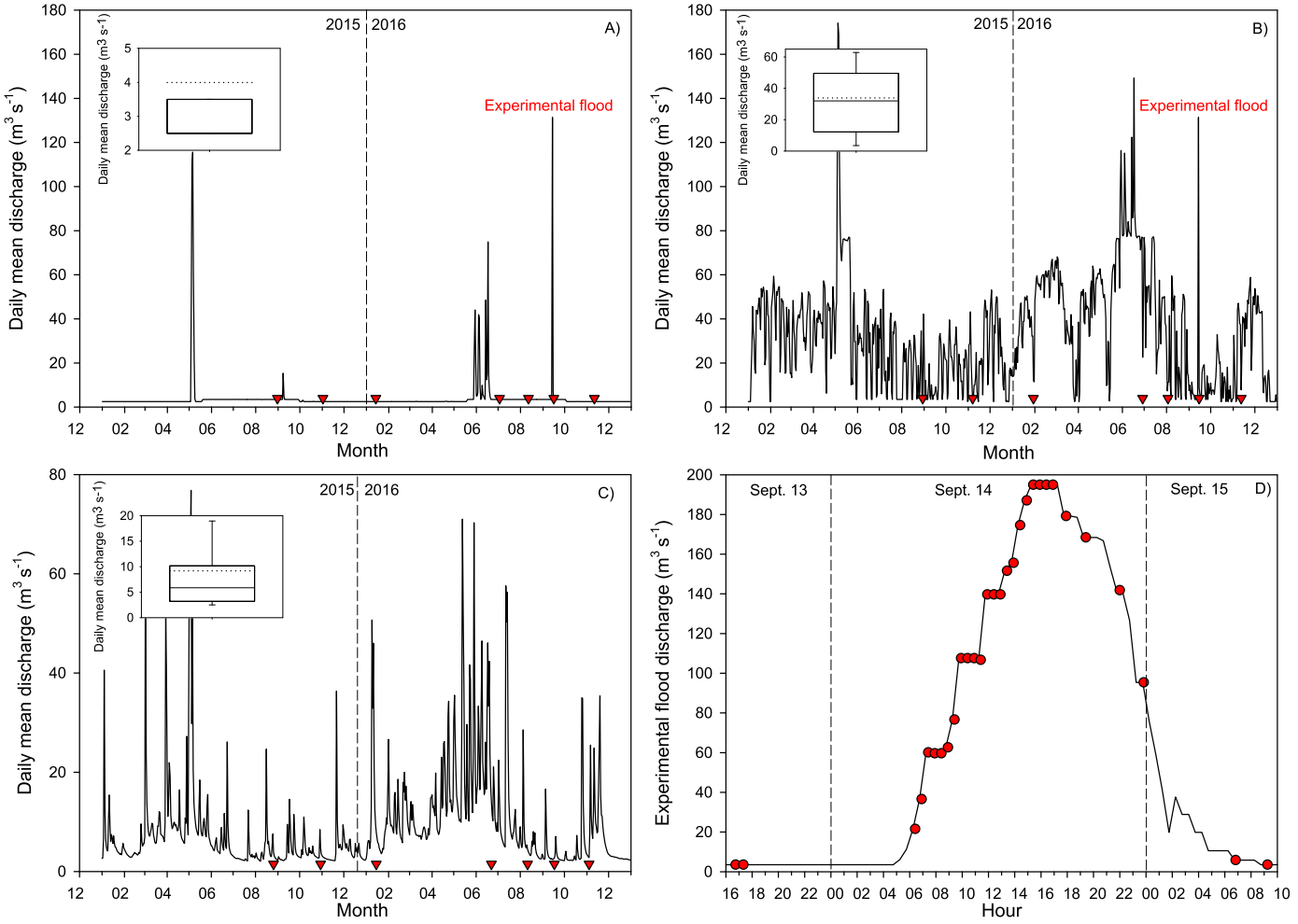


Fig. 2. Mean daily discharge (m^3/s) in the residual flow (A) and hydropeaking reach (B) of the Sarine floodplain and the natural flow reach (C) of the Sense floodplain for the years 2015 and 2016. Box plots show 25th and 75th percentile, median (straight line in the box), mean (dotted line), whiskers (90th and 10th percentiles). Red triangles lines show the sampling dates. D) Discharge (m^3/s) during the experimental flood event of September 2016 at the drift sampling site (Fig. 1). Red dots represent drift sample times. Discharge data for the Sarine were obtained from the hydropower company Groupe-e, for the Sense from the gauging station "Thörishaus – Sensematt" (ca. 20 km downstream of the Sense reach; Swiss Federal Office of the Environment).

2.3. Microbial sampling protocol

Sediment samples for analysis of microbes as well as abiotic sediment properties were collected as three composite samples each from floodplain forests, islands, open gravel bars, and side and main channel habitats at each sampling site ($n = 3$ per reach). Replicated samples ($n = 3$ per habitat type and sampling site) were collected seasonally from summer 2015 to autumn 2016 and two weeks after the experimental flood ($n = 7$) in all three floodplain reaches (SR, SH, SN) (see Fig. 1). For each sample, the upper ~10 cm of streambed sediments and soil was removed to avoid sampling microbial communities associated with bentic biofilm or plants. Sediment samples were mixed and sieved through an 8 mm and 2 mm sieve. Sediments <2 mm were separated for DNA extraction and for nutrient analysis using sterile 50 ml falcon tubes. Sediments <8 mm (~1000 g) were stored in plastic bags for analysis of total organic matter content, water content and grain size distribution. All samples were transported in a cooling box to the laboratory. Samples for DNA extraction and nutrient analysis were stored at −20 °C, and the other samples (<8 mm sediments) at 4 °C until processing. Sediment temperature at each sampling site was measured with a temperature needle probe (Multi-Thermometer DT-300, VOLTCRAFT, Switzerland) and averaged for each habitat.

Within 12 h from sampling, the water content (percentage water of sediment sample) was determined from sediments <8 mm by weighing, drying at 105 °C for 24 h and reweighing. To determine organic matter content, between 500 and 800 g of sediment was dried at 105 °C for 24 h, weighed, combusted at 500 °C for 3 h, and reweighed as ash free dry mass (AFDM) kg^{-1} dry weight. Combusted sediments were used to quantify grain size distribution of each sample using sieves (Retsch GmbH, Germany; mesh sizes 0.063, 2, 4, 8 mm). Total nitrogen and total carbon content of collected sediments (<2 mm) were measured and analysed by combustion using a Carbon-Hydrogen-Nitrogen-Analyzer (TrueSpec CHN Makro Analyser, Leco, USA).

Samples used to characterize the transport of microbes during the experimental flood were taken in the main channel of SR around 11 km downstream of Rossens dam. Sampling was carried out using a drift net (400 μm) just before the flood (BF; $n = 2$), during the ramping phase (DF1; $n = 14$), and during the peak (discharge above 140 m^3/s) and down-ramping phase (DF2; $n = 14$)(Fig. 2D). We pooled the peak and down-ramping phase samples in the statistical analysis as they showed little structural shift over time. Flow velocity (MiniAir2, Schiltkknecht AG, Switzerland) in front of the net and exposure time for each sample was measured to calculate the volume of water filtered during a sample.

2.3.1. Genetic analysis of microbes (T-RFLPs)

The microbial assemblage in each sample ($n = 316$, some habitats had less than 3 samples collected) was analysed using T-RFLP. Total genomic DNA of each sediment sample was extracted using a PowerLyzer

PowerSoil DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA) following the suppliers protocol. The partial 16S rRNA gene was amplified by PCR using the fluorescently labelled primers 8F_Red (5′-AGA GTT TGA TCC TGG CTC AG-3′) with fluorophore AT565 and 534R_Green (5′-ATT ACC GCG GCT GCT GGC-3′) with fluorophore AT532 (Microsynth AG, Balgach, CH) using standard conditions (Innis and Sninsky, 1990). PCR amplification was verified by gel electrophoresis. The PCR product was end-treated to correct for the effect of overhanging ends (Egert and Friedrich, 2005). PCR products were cleaned using a Millipore MultiScreen PCR μ96 filter plate (Merck KGaA, Darmstadt, Germany) and resuspended in 25 μl ddH_2O. Purified PCR amplicons were digested using the restriction enzyme *Alu*I (Promega, WI, USA) as prescribed by the manufacturer. From each digestion product, 1 μl was mixed with 18.65 μl formamide and 0.35 μl GS LIZ 600 Size Standard (Thermo Fisher Scientific™, MA, USA), denatured and analysed on an ABI 3500 capillary sequencer (Thermo Fisher Scientific).

2.4. Data analysis

T-RFLP profiles were analysed using GeneMapper® Software 5 (Applied Biosystems). Terminal restriction fragments (TRFs) between 40 and 500 bp were included in the analysis. Further data processing was carried out using the software T-REX (Culman et al., 2009). The software filters noise over true peaks (Abdo et al., 2006). Peak alignment was also performed in T-REX using the approach of the T-Align software program (Smith et al., 2005). Data analysis was conducted in R version 3.4.3 using the vegan, tsne and igraph packages, and Cytoscape version 3.6.1 (RCoreTeam, 2018; Shannon et al., 2003). Differences in alpha diversity between dates and floodplains were tested by non-parametric Kruskal-Wallis test followed by Dunn's test if models were significant (Hollander and Wolfe, 1973). Beta diversity within floodplains among seasons was assessed by multivariate homogeneity of groups' dispersion and differences tested as mentioned above (Anderson et al., 2006).

Strength and congruence in temporal assemblage shifts between the different floodplains were analysed by non-metric multidimensional scaling (NMDS). Absolute TRFLP frequencies were Hellinger transformed prior to analysis. Generalized additive models (GAMs) of log or logit (for percentage values) transformed environmental variables were fitted onto the NMDS to assess their potential influence on assemblage structure (Wood, 2003). Permutational multivariate analysis of variance (PERMANOVA) models were used to assess factors (i.e. floodplain, season, habitat) driving differences in community assembly within and between combinations of floodplains (Anderson and Walsh, 2013). Several models were built with significant terms being tested by Benjamini Hochberg *p*-value corrected pairwise PERMANOVAs. To support PERMANOVA outcomes, a factor fitting for floodplain, season and habitat was performed on the NMDS. Stochastic neighbor embedding (t-SNE) was used to visualize trajectories of bacterial communities from the flood (sites SR, SH) in relation to the reference floodplain (SN) (Maaten and Hinton, 2008). Perplexities were chosen according to pseudo-Bayesian Information Criterion (Cao and Wang, 2017).

Flood effects were examined further by constructing occurrence networks incorporating samples taken before, during and after the flood. The main goal was to see how OTUs (Operational Taxonomic Units) linkage to habitats (i.e., number of network edges) change due to the flooding. The presence and absence of edges during the time continuum gives us insight into mass effects and their long-term impact on bacterial communities. The networks were merged with co-occurrence networks based on Pearson correlations (non-sparse OTUs, Benjamini-Hochberg adjusted *p*-values <0.01 and 0.7 correlation cut-off). These networks depict OTUs that are found commonly together and therefore define core communities that were either found in the water column or the floodplain habitats. The definition of this core community is linked to the between habitat similarity (for land-born bacteria) and a permanently transported lotic community. Non-randomness of the Pearson networks were tested by comparing the networks to 10,000 random Erdös-Réyni networks with similar numbers of edges and nodes (Ju et al., 2014; Weiss et al., 2016) (Supplementary Table S1). Ultimately, the networks allowed us to quantify the impact of the flood on the spatio-temporal dynamics of bacterial communities induced by the experimental flood.

3. Results

3.1. Seasonal and spatial patterns in microbial communities

In the following section, we refer to the PERMANOVA models and their pair-wise PERMANOVA post-hoc tests presented in Supplementary Table S2.1. The conclusions drawn are the synthesis of the marked significant terms and term interactions and are also presented as take home messages in Supplementary Table S2.1. Models were built for single reaches and the combination among them. In general, seasonal effects influenced the community structure greater than habitat type among floodplain reaches, whereas habitat type influenced communities within each floodplain system (see r^2 and F-values, Supplementary Table S2.1). This finding was supported by the factor fittings on the NMDS as well (season: $r^2 = 0.34$, $p < 0.001$; habitat: $r^2 = 0.04$, $p < 0.01$; floodplain: $p > 0.05$, see Fig. 3 and Supplementary Table S2.2). Indeed, seasonal shifts in community assembly were roughly congruent among floodplain reaches with all seasons being distinct from one another within each floodplain (PERMANOVAs, $p < 0.05$, see Supplementary Table S2.1 for specific PERMANOVA model outcomes for specific reaches; Fig. 3A). Further, microbial communities mostly differed among floodplains within a particular season, except that SR and SH were similar in seasons S15, S16 (both summer) and W16 (winter), and SN was similar to SH and SR in seasons W16 and A16 (autumn) ($p < 0.05$, see specific PERMANOVA models in Supplementary Table S2.1).

Habitat types differed in assemblage composition depending on the floodplain, although differences were mostly evident between terrestrial and aquatic habitats in the different floodplains. For instance, side channel habitats differed from island and riparian forest habitats at SR, and island habitat differed from main channel and open gravel bar habitats at SH. Communities also differed between riparian forest habitat and main channel and open gravel bar habitats at SH. Lastly, island and riparian forest habitats differed from main channel, side channel and open gravel bar habitats at SN (PERMANOVA, $p < 0.05$). When the whole data set was taken into account, bacterial communities were similarly structured between island and riparian forest habitats as well as among main channel, side channel and open gravel bar habitats (PERMANOVA: $p < 0.01$). GAMs of grain size (0.063 mm) explained around 18%, temperature around 17% and of N around 14% of the assemblage variability (Fig. 3B; see Supplementary Table S3 for the analysis of the environmental variables).

Alpha diversity differed seasonally and with similar patterns among floodplain reaches over time (Fig. 4A). Seasons W16 and AF1 had the highest alpha diversity at all floodplains, whereas season A16 had the lowest alpha diversity (Kruskal-Wallis, $p < 0.001$, Supplementary Fig. S1C). In general, riparian forest and island habitats had higher alpha diversity than open gravel bar and side channel habitats among floodplains and seasons (Kruskal-Wallis, $p < 0.01$, Supplementary Fig. S1A). There was no consistent diversity pattern among habitats within a floodplain or season (see point distribution in Fig. 4A "Alpha Diversity"). Beta diversity showed similar seasonality among floodplains (Fig. 4B). Season AF1 (after flood) had the lowest beta diversity for all floodplains (Kruskal-Wallis, $p < 0.001$, Supplementary Fig. 1D). Beta diversity was lowest for island and riparian forest habitats relative to main channel, side channel and open gravel bar habitats among floodplains (Kruskal-Wallis, $p < 0.001$, Supplementary Fig. 1D).

3.2. Effects of the experimental flood

The experimental flood had a subtle impact on the regulated floodplains SR and SH (Fig. 5). Both floodplains had similar assemblage

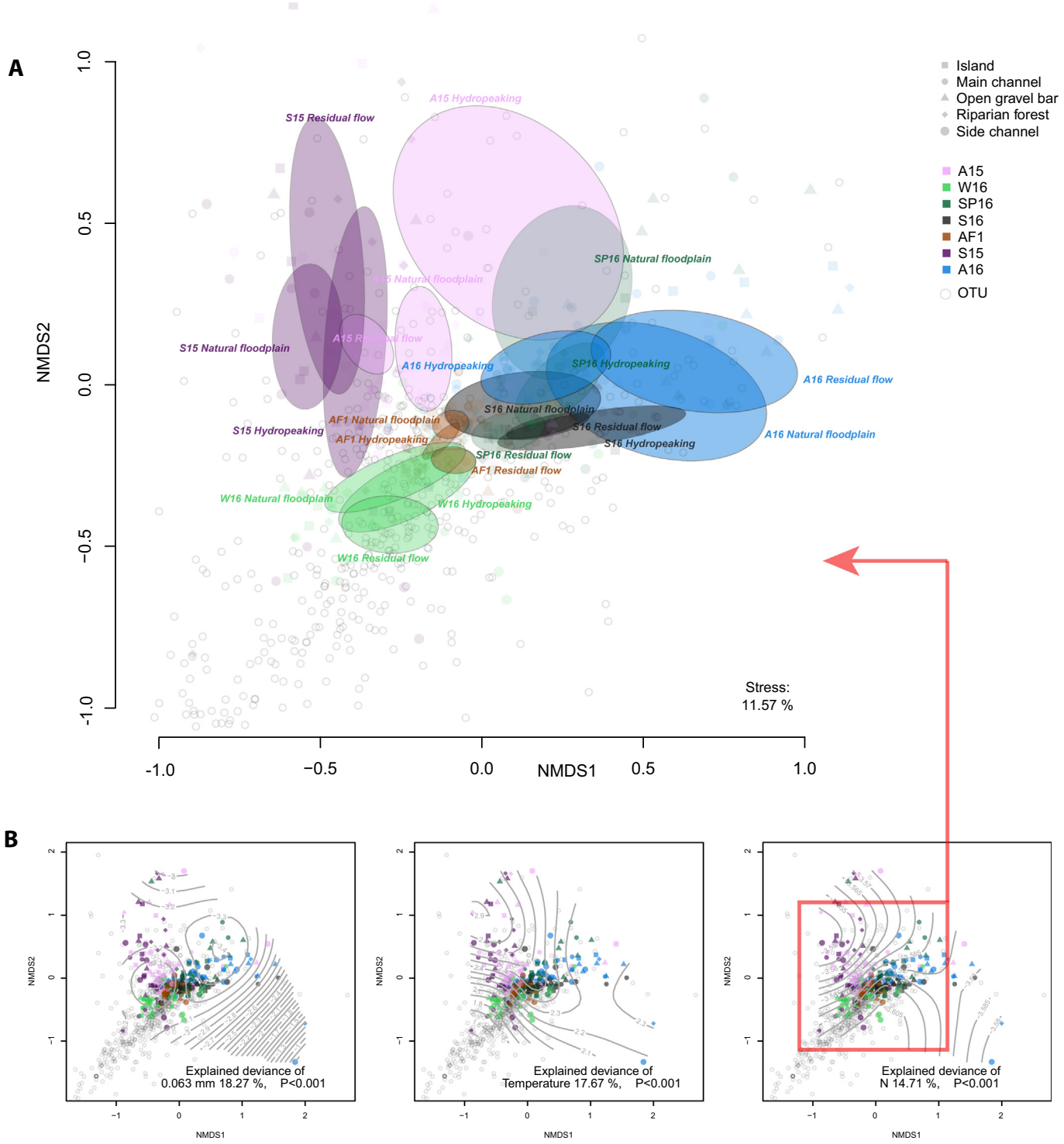


Fig. 3. Non-metric multidimensional scaling (NMDS) plot based on operational taxonomic units (OTUs) found within all regimes and seasons (SP = Spring, S = Summer, A = Autumn, W = Winter, AF = After flood). 90% confidence ellipses of the standard deviations of site scores of the regimes within the respective seasons are depicted. The site scores are shown in different symbols (i.e., habitats) and colors (i.e., seasons). OTUs species scores are depicted as light grey circles. The stress value for the NMDS is given (A). Generalized Additive Models (GAMs) of fitted environmental variables on the NMDS as depicted in panel A (B). Splines of the fitted variables are shown in grey. Explained deviance of the respective variables are given. Note that the NMDS in panel A has some site and species scores cut off (see red zoom box) in order to better visualize the dispersion ellipses.

structures before the flood (i.e., season S16) that were comparable to the reference floodplain SN. Microbial communities collected in transport showed a shift in structure before the flood (BF samples) from those during the ramping phase (DF1), likely due to microbial input from reservoir sediments being released during the flood. Microbial communities in transport then became more similar to those present in floodplain habitats during the peak and down-ramping phase of the flood (DF2) because of hydrologic connectivity (mixing) among floodplain habitats. Shortly after the flood (season AF1), SR and SH again had microbial communities that were similar to SN (Fig. 5A, B). In general, microbial communities following the flood were similar to those found among floodplain habitats for the respective season before the

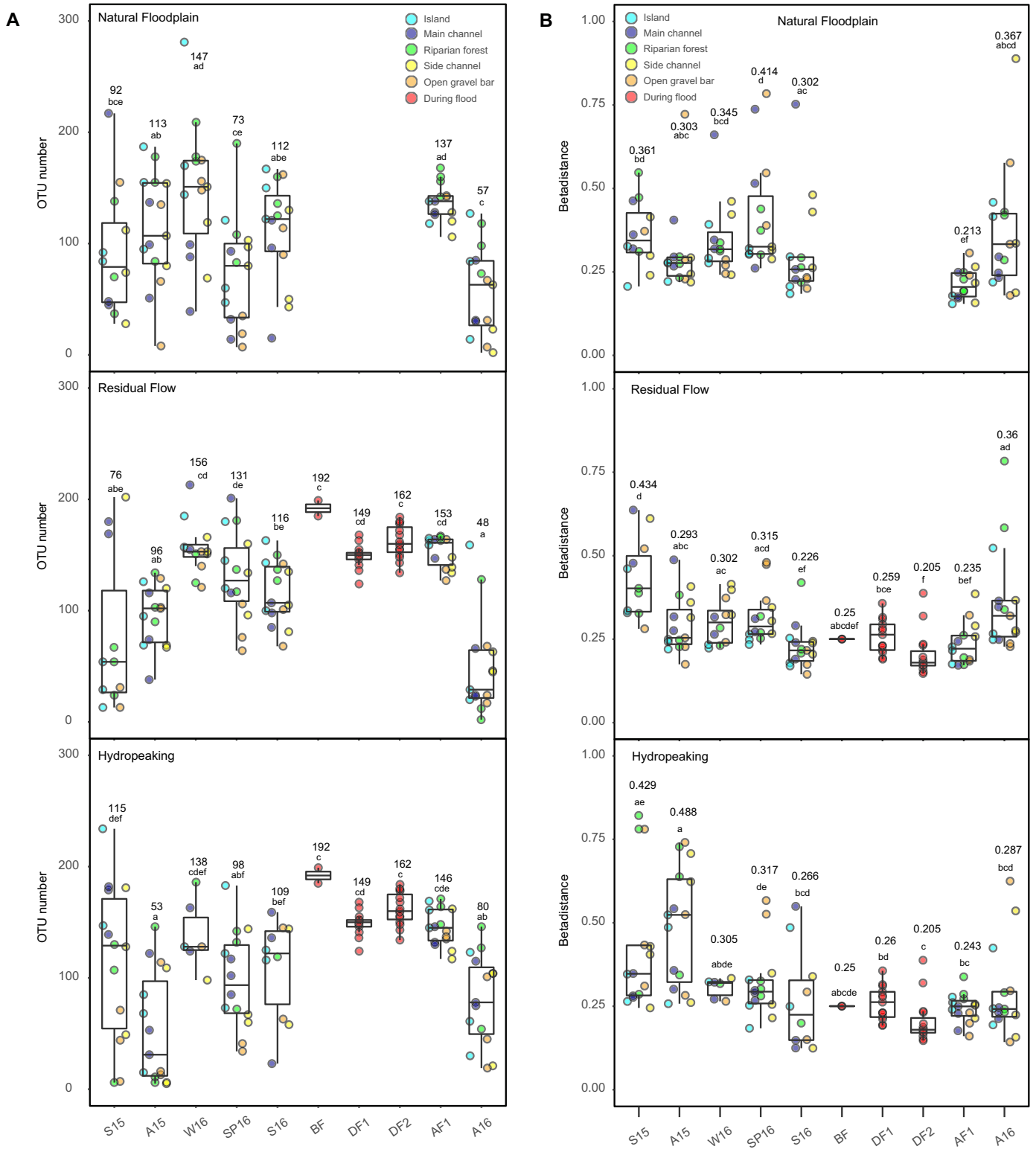
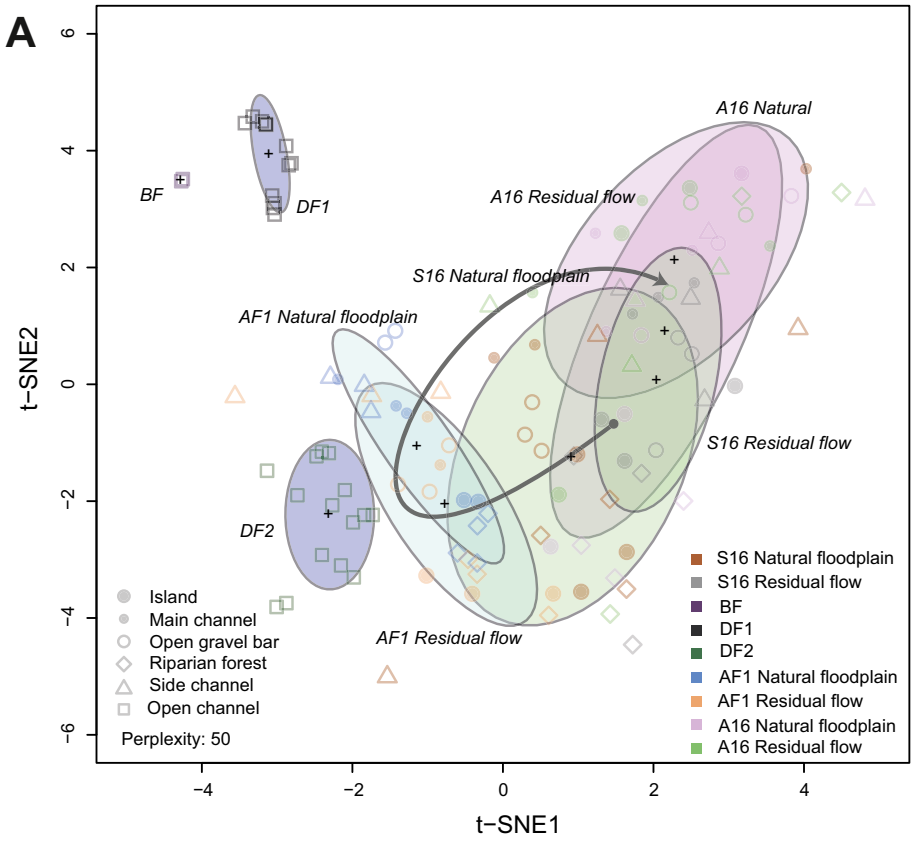


Fig. 4. Boxplot with jitter of bacterial alpha diversity (A) and of multivariate homogeneity of groups' dispersions (B) during different seasons (SP = Spring, S = Summer, A = Autumn, W = Winter, AF = After flood) and flood stages (BF = Before flood, DF = During flood) within the natural floodplain, residual flow and hydropeaking. Different habitats are depicted in specific colors. Whiskers indicate 1.5× interquartile range. Numbers indicate mean operational taxonomic unit (OTU) numbers or betadistances, respectively, whereas letters show group affiliation according to Dunn's-Test.

flood. Further, alpha diversity in SR and SH slightly increased after the flood as was observed in SN (Fig. 4A).

To further examine flood effects on microbial assemblage structure, we analysed the OTU presence/absence matrix in conjunction with co-occurrence patterns (Fig. 6, Supplementary Fig. S2, Supplementary Information - Cytoscape file). Different potential source/sink processes were found that influenced assemblage composition over time (Supplementary Table S4). Presented here are mean percentage values related to the total OTUs within floodplains SR and SH as both showed identical process patterns (see Supplementary Fig. S2). Here, OTUs were


A
A16 Natural
A16 Residual flow
S16 Natural floodplain
AF1 Natural floodplain
S16 Residual flow
BF
DF1
DF2
AF1 Residual flow
Island
Main channel
Open gravel bar
Riparian forest
Side channel
Open channel
Perplexity: 50
S16 Natural floodplain
S16 Residual flow
BF
DF1
DF2
AF1 Natural floodplain
AF1 Residual flow
A16 Natural floodplain
A16 Residual flow
t−SNE2
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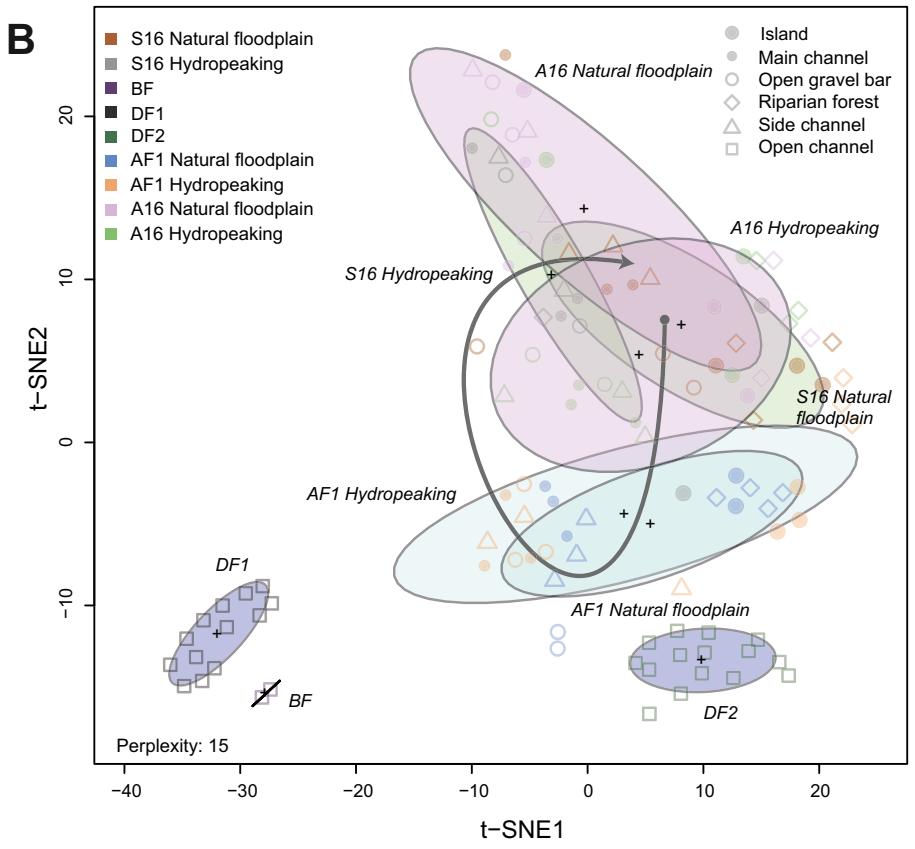
B
S16 Natural floodplain
S16 Hydropeaking
BF
DF1
DF2
AF1 Natural floodplain
AF1 Hydropeaking
A16 Natural floodplain
A16 Hydropeaking
Island
Main channel
Open gravel bar
Riparian forest
Side channel
Open channel
A16 Natural floodplain
A16 Hydropeaking
S16 Hydropeaking
S16 Natural floodplain
AF1 Hydropeaking
DF1
BF
AF1 Natural floodplain
DF2
Perplexity: 15
t−SNE2
t−SNE1

categorized as being aquatic or terrestrial. Some 10.8% of the OTUs were part of the Pearson correlation-based co-occurring "core" communities thought to originate from reservoir water washed into habitats and become partially established (i.e., larger number of edges connected to BF than to habitats in S16)(Supplementary Table S4). These core OTUs showed a high number of connections to habitats in season AF1, but decreasing connections in season A16. This result indicates a transient impact of reservoir water core OTUs on microbial communities in downstream habitats. Further, some OTUs were present only in transport (in BF but not in season S16, 8.8% of all OTUs), thus likely originating from reservoir water. These OTUs did not colonize any floodplain habitat following the flood (2.6% of all OTUs in SR and SH, respectively), and 4% of reservoir water OTUs were found in floodplain habitats in season AF1. However, some 2.2% of OTUs originating from reservoir water were able to persist in SR and SH (i.e., seasons AF1 and A16).

Some 10.5% of OTUs appeared to originate from reservoir sediments, as their signature was present in DF1 and DF2, but not in BF. Of these OTUs, 7.9% were transiently present and 1.6% persisted for a longer period, whereas only 1% were detected later in A16 but not directly AF. There were 8.7% aquatic and 10.9% reservoir sediment specific OTUs that were not detected in floodplain habitats at any date. Around 13.8% of the detected OTUs belonged to terrestrially derived microbes observed in seasons S16, AF1 and A16. Their signature was partially present in transport samples at BF and increased during DF1 and DF2, indicating washout from floodplain habitats during flooding (see Supplementary Table S4 and Cytoscape file). Another 18.2% of the OTUs were found in transport (present in BF), but 14% persisted until season A16 and 4.2% disappeared after season AF1. Further, 12.1% of the terrestrial OTUs were in transport during DF1 and DF2 with 9.7% of these found during seasons AF1 and A16, and 2.4% absent after season AF1. Lastly, 5.7% of detected OTUs were found during a specific season in some habitats and were not detected in transport before and during the flood. Only 0.8% of detected OTUs were in specific floodplain habitats before and after the flood without being found in transport.

4. Discussion

4.1. Variation in microbial communities across space and time

Flow and sediment regimes (timing, frequency, magnitude and duration) have been shown to impose strong ecosystem constraints on fish, invertebrates, microbes as well as ecosystem functions (Foulquier et al., 2013; Langhans et al., 2006; Poff et al., 1997; Rees et al., 2006; Robinson and Uehlinger, 2008). Mechanistically, these regimes introduce different hydrologic connectivity and disturbance patterns in fluvial landscapes. High flows, whether natural, experimental or generated by hydropeaking with repeated peaks and hydrologic connectivities between floodplain habitats, should cause convergence in microbial communities across habitats. For example, directed mass effects as well as frequent disturbance during high flows should lead to homogeneous microbial communities following an event as shown for macroinvertebrates (Chanut et al., 2019). Further, terrestrial inputs of organic matter constituents such as DOM into river channels is greatest during high hydrologic connectivity periods (Vazquez et al., 2011) and correlated with bacterial abundance (Caillon and Schelker, 2020). For macroinvertebrates, constant low flow conditions lead to a shift in habitat conditions and community composition (Bunn and Arthington, 2002). This result suggests that microbial communities may vary substantially among floodplain ecosystems in relation to local hydrology, specifically river floodplains experiencing residual flows, hydropeaking flows, natural flows and experimental flooding.

An important finding was that seasonal changes in microbial communities superceded any floodplain differences related to hydrology in all three floodplain reaches (Sarine residual flow-SR, Sarine hydropeaking-SH, Sense natural-SN). This seasonal shift in assemblage structure is likely linked to changes in key environmental drivers such as temperature, precipitation and nutrient levels (Garcia-Pichel et al., 2013; Nielsen et al., 2010; Staley et al., 2015). Indeed, assemblage variability was related to seasonal changes in temperature. Further, nitrogen concentration also influenced communities across seasons. The assemblage relations with environmental drivers across seasons correspond to other studies in streams (Hassell et al., 2018; Staley et al., 2015). Furthermore, aquatic-terrestrial floodplain studies examining ecosystem functions such as sediment respiration (Doering et al., 2011), bacterial abundances and enzyme activities (Bodmer et al., 2016), and electron transport system activities (ETSA) (Mori et al., 2017; Simcic et al., 2015), indicate the importance of season and habitat specific properties on floodplain dynamics. In contrast to the seasonal changes that are mirrored in temperature and N levels, there was a local and temporally stable component, i.e., grain size distribution, that we detected as a habitat specific community filter.

Community assembly was generally consistent among habitat types at the three study floodplain reaches. For instance, alpha diversity was highest in terrestrial floodplain habitats (riparian forest, islands), whereas beta diversity was lowest. A higher alpha diversity in terrestrial soils compared to aquatic sediments also has been shown for a New Zealand stream catchment (Hermans et al., 2020). The locally diverse (alpha diversity) but relatively homogeneous distribution (beta diversity) of microbial communities opposes the less diverse but more patchy distribution of communities in more aquatic floodplain habitats (gravel bars, main and side channels). Habitat conditions and potentially high functional redundancies of microbes likely influence assemblage similarity within and among terrestrial floodplain habitats (Allison and Martiny, 2008; Louca et al., 2018). Habitats with coarse sediments, e.g., gravel bars, are generally harsh for microbe development due to frequent physical disturbance from high flows but also because of high temperature variation. Here, increased carbon or nitrogen availability is most likely associated with vegetated areas and often are patchy in distribution. It has been shown that such habitats harbor more functionally specialized communities, thus variation in composition at a small scale can be expected (Freimann et al., 2013; Malard et al., 2002). Indeed, sediment properties of floodplain habitats differed among study floodplains, reflecting the differences in hydrology that ultimately influenced microbial communities in the different habitats within the different floodplains. Alternatively, the lack of a strong floodplain-specific assemblage structure might be coupled to biological buffering mechanisms. A previous study in an alpine floodplain found that only around 5% of assemblage composition was explained by hydrologic connectivity, whereas bacterial function measured in terms of enzymatic activities explained up to 40% (Freimann et al., 2015). The results suggest that local communities might display high functional redundancy. Thus, this redundancy causes them to be less influenced by hydrological differences among floodplains that reflects differences in solutes, organic matter concentrations, and dispersal dynamics.

4.2. Mass effects in community assembly in relation to experimental flooding

Mass effects in microbial communities have been shown important in coupled lake-stream systems (Adams et al., 2014) via inputs of terrestrial microbes into freshwaters (Hassell et al., 2018; Ruiz-Gonzalez et al., 2015). Headwaters of streams are considered reservoirs affecting

Fig. 5. t-Distributed stochastic neighbor embedding (t-SNE) plot of the bacterial community structure before, during and after the flood event (S = Summer, A = Autumn, BF = Before flood, DF = During flood, AF = After flood). Residual flow (A) and hydropeaking (B) are compared to the natural floodplain. Habitat types and specific seasons are depicted by different symbols and colors, respectively. The time trajectory of the communities is depicted as an arrow. Colored ellipses show the positioning of the seasonal clusters for a specific reach. T-SNE perplexity hyperparameters are given.

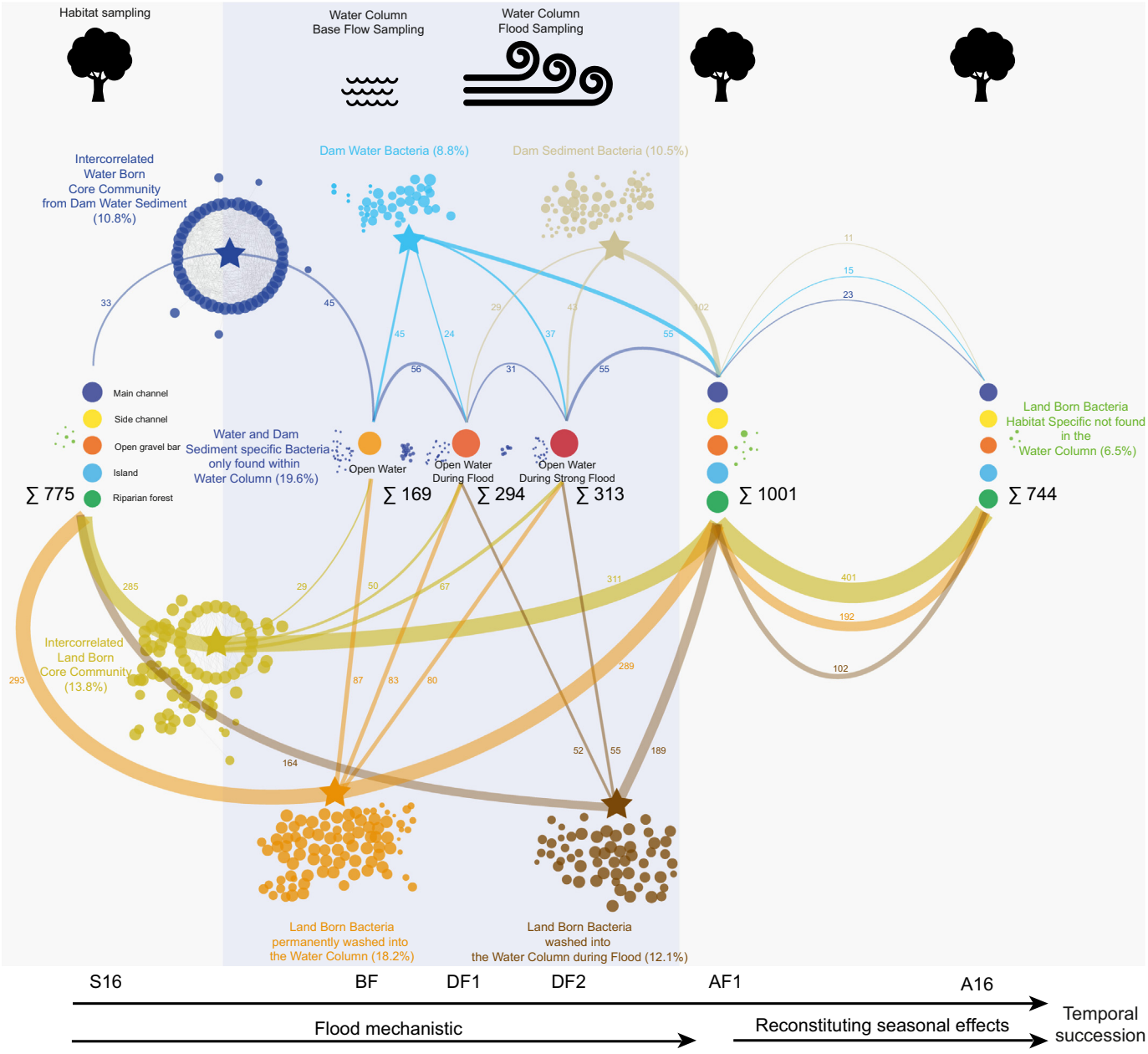

Fig. 6. Simplified temporal network of OTU appearance before, during and after the flood giving insight into flood related mechanistic and the overall impact of the flooding on forming bacterial communities. Habitat nodes before in summer (S16), two days after (AF1) and two month after the flood in autumn (A16) as well as open water column sample nodes before (BF) and during the flood (DF1 and DF2) are colored accordingly in the middle part of the network. Their temporal succession is indicated as an arrow at the bottom. Intercorrelated (i.e. Pearson correlation >0.7, $p < 0.01$) and non intercorrelated OTUs are depicted as grouped colored circles according to their origin and mechanistic appearance within the habitat or open water, respectively. The relative abundances of these mechanistic OTU clusters are given. Overall connectivity (edges) of the OTU clusters to the habitat groups or open water column are shown and sized to the number of edges. The sum of edges connecting OTUs with the habitat groups or water column is annotated. Sizes of the circles (nodes) correspond to their degree. The figure is based on the average values of the SH and SR networks found in Fig. S2 and Supplementary Table 4.

downstream microbial communities (Besemer et al., 2013). Longitudinal connectivity is a primary driver of microbial distribution and abundance in rivers and streams. Hydrologic transport directly affects microbial composition and frequent dispersal from source habitats into recipient habitats can influence local species pools (Hassell et al., 2018; Ruiz-Gonzalez et al., 2015). We found a core aquatic microbial assemblage that was present in both terrestrial and aquatic habitats at the residual and hydropeaking floodplains. This core assemblage likely originated upstream from the reservoir and influenced downstream habitats through a continuous mass effect. However, this core assemblage had little influence on local community assembly over the longer term, apparently being overridden (outcompeted) by internal habitat communities. This relation is supported by the low presence of this core community after the experimental flood, although a strong mass flux of the core assemblage into downstream habitats occurred. Adams et al. (2014) found that mass fluxes across habitats are important during significant hydrologic exchange, although species sorting predominately structured communities between exchange events. They also found that transplanted local communities were equal or less productive, depending on their origin. Nevertheless, up to 11% of the detected OTUs were in an interactive state between the water column and floodplain habitats in this study. Importantly, a microbial mass flux between floodplain habitats and river water was present in the residual-flow floodplain. This continuous microbial influx from upstream likely enhances the homogenization of communities among floodplain ecosystems.

There was a continuous input of a core terrestrial assemblage (14% of all detected OTUs) into the water column independent of the study floodplain. During the flood, there also was an increased signature of other habitat specific OTUs in the water column, indicating that aquatic and terrestrial habitats were hydrologically connected. Hydrological transport occurs in many organisms and was expected (Rohl et al., 2018). However, these microbes could not establish over the long term, likely due to habitat filtering mechanisms in the different habitats (Adams et al., 2014). Interactions among microbes also have been shown to constrain specific taxa (species sorting) in a similar way as habitat filtering (habitat template) (Hall et al., 2018). It was shown for macroinvertebrates that a single flood typically affects taxon richness immediately after a flood with quick recovery to pre-flood conditions after a few weeks (Robinson and Uehlinger, 2003; Robinson and Uehlinger, 2008). Although we found short-term effects of the flood on community assembly due to enhanced hydrologic connectivity, there was no clear long-term effect. The results suggest that seasonal and local habitat conditions override flood-induced mass effects among floodplain habitats. The proposed legacy effect of the different and contrasting hydrological variations in the different floodplain reaches was not found.

4.3. Ecological implications of altered hydrology and experimental floods

River impoundment has been shown to impact natural flow and sediment regimes, resulting in altered hydrologic connectivity and associated biotic and abiotic conditions in downstream waters. Contemporary water legislation is driving increasing interest among environmentalists and water resource managers regarding how these impacts can be mitigated in regulated rivers. The different hydrology among our study floodplains had little influence on local microbial communities. This finding suggests that the relatively large range of flow magnitudes and frequency types led to similar microbial communities across study floodplains.

The application of high flows or managed floods (i.e., the controlled release of water from reservoirs to mimic the natural flow and sediment regime) is becoming a common management action to improve environmental conditions below dams (Gillespie et al., 2015; Konrad et al., 2011; Olden et al., 2014; Robinson et al., 2018). Most of these studies assessed flood effects on fish and invertebrates, but no study examining microbial response has been conducted to date. Major flood events are severe pulse disturbances in rivers. How microbial communities respond to such disturbances is paramount in fluvial ecology as they are primary players in the functioning of ecosystems. Disturbance events such as floods can directly affect biotic communities or alter the environment, subsequently affecting biotic communities. Community stability is a consequence of resistance and resilience to disturbance along with time since disturbance (Shade et al., 2012). Further, ecosystem performance can be altered by disturbance induced biodiversity change (Naeem et al., 1994).

The degree of change in biotic communities, in general, following flood disturbance is inherently linked to microbial dynamics as well. This study provided information on microbial communities in river floodplain habitats under different hydrological regimes as well as local responses to an experimental flood. The results suggest that flood disturbance has a transient effect on microbial communities among floodplain habitats. The temporal input (mass effect) of microbes among floodplain habitats and potential changes in physicochemical habitat characteristics (i.e., organic matter inputs) was buffered so that the effected floodplains became similar to the natural floodplain. The results suggest that microbial communities show high redundancy among floodplains under different hydrologies and in response to high flow events, a finding in contrast to other biotic communities in regulated rivers.

We note that the herein used T-RFLP technique mainly mirrors the most abundant members of a microbial community. Therefore, this study provides a rather broad scale picture of the microbial dynamics. This implies that some less pronounced effects might have been overseen. Such small effects still can add up to importance on the ecosystem scale and should thus been incorporated in future studies. The use of next-generation sequencing of amplicons in combination with metagenomics can shed more light also on the functional part of this story. Overall, microbes serve as the processing and conversion base for most nutrients in ecosystems (Findlay, 2010; Madsen, 2011), thus it is imperative to understand microbial community assembly within fluvial landscapes under various environmental change scenarios. We conclude that additional research is needed to confirm and add generality to our research findings.

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CRediT authorship contribution statement

Michael Doering: Conceptualization, Methodology, Validation, Formal analysis, Writing – original draft, Funding acquisition. **Remo Freimann:** Methodology, Formal analysis, Software, Validation, Writing – original draft, Visualization. **Nadine Antenen:** Investigation. **Alexia Roschi:** Investigation. **Christopher T. Robinson:** Writing – review & editing. **Fabio Rezzonico:** Investigation, Resources. **Theo H.M. Smits:** Writing – review & editing. **Diego Tonolla:** Investigation, Visualization, Supervision, Project administration.

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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