Direct and indirect effects of flood regime on macroinvertebrate assemblages in a floodplain riverscape

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This document is the accepted manuscript version of the following article:

Chanut, P. C. M., Datry, T., Gabbud, C., & Robinson, C. T. (2019). Direct and indirect effects of flood regime on macroinvertebrate assemblages in a floodplain riverscape. *Ecohydrology*, 12(5), e2095 (16 pp.). <https://doi.org/10.1002/eco.2095>

Abstract: Floods are necessary for the functioning of floodplain ecosystems. Ultimately, flood effects on biota are spatially complex and unfold at various time scales. Yet, biodiversity conservation in regulated floodplains requires a sound quantification of the main pathways how floods affect riverine ecosystems. Here, we investigated the relative effects of flood frequency, magnitude and time elapsed since the last flood on macroinvertebrate communities of 24 parafluvial habitats in the Maggia river floodplain, Switzerland. Parafluvial habitats were sampled seasonally over one year and a combination of 2D hydrodynamic modelling and piecewise structural equation modelling was used to quantify the direct and indirect effects of local hydrological metrics on macroinvertebrate communities. We found that high flood frequency favoured rheophilic species (EPT taxa) over other groups (Coleoptera, Diptera) and prevented strong competitive interactions and competitive exclusion by maintaining low food resource levels. Importantly, we found that parafluvial habitats exhibited more lentic-like characteristics as time passed after a flood, which caused EPT taxa to be relatively more abundant and taxa richness higher immediately after flood disturbance. Lastly, overall taxa richness increased over time after a flood and even more so after larger floods. Our results suggest that variation in flood magnitude, frequency and return period maximizes beta diversity within floodplain riverscapes due to the independent and spatially-interactive responses of parafluvial habitats.

Keywords: floodplain, flood regime, stream invertebrates, ecological succession

Introduction

Alluvial floodplains are widely recognized as valuable features of our landscapes, for the goods and services they provide humans and for their intrinsic ecological value and high biodiversity (Tockner et al. 2010). Despite these values, human activities still threaten their integrity and ecological status globally by directly altering their morphological structure and natural flow regimes. For instance, 90% of floodplains are functionally extinct in Europe (Tockner and Stanford 2002). Preserving or restoring spatial heterogeneity in flow regimes (flooding) is a much-recommended measure in floodplain restoration (Paillex et al. 2009, 2013), yet restoring the natural flow regime in regulated rivers is rarely an option and instead compromises must be made between hydropower production, flood protection and ecological values.

Indeed, floodplains are pulsed ecosystems, where floods of different magnitude drive geomorphological, biogeochemical and ecological processes (Junk et al. 1989, Tockner et al. 1999, Stone et al. 2017). In particular, large floods (exceedance probability <5%) remodel the geomorphological structure of floodplains and maintain a high habitat diversity, including side arms, ponds, backwaters, gravel bars and vegetated islands (Arscott et al. 2002; Van der Nat et al. 2003), thus sustaining high biodiversity (Stanford et al. 2005, Datry et al. 2014).

In addition, low-to-medium magnitude floods exert a strong influence on primary production and biota within floodplains. During the flood, so called connection phase, organic matter and nutrients are exported to the floodplain, which triggers an increase in primary production when the flood recedes, so called disconnection phase (Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006). Lesser magnitude floods also affect biota directly through the mechanical removal/redistribution of individuals (Matthaei et al. 1997, Matthaei et al. 1999, Bond and Downes 2000) or increased ecological connectivity and dispersal during inundation (Paillex et al. 2007, Gallardo et al. 2008, Fernandes et al. 2014). They also can indirectly affect biota by changing local habitat conditions and primary production (Paillex et al. 2013, Fernandes 2014, Gallardo 2014). For instance, flooding scours bottom substrata and displaces individuals, thereby resetting communities to earlier successional stages (Amoros and Bornette 2002, Thomaz et al. 2007). Because parafluvial habitats have different thresholds and frequencies of inundation, the floodplain is often described as a mosaic of habitats at different successional stages (Bravard et al. 1986, Salo et al. 1986, Mouw et al. 2013, Whited et al. 2007).

Local physico-chemical conditions among parafluvial habitats largely result from the interaction between habitat positions within the geomorphological settings of the floodplain, which, e.g., determines water sources such as groundwater inputs (Malard et al. 2007, Capderrey et al. 2014). Local conditions also vary with the level of lateral connectivity to the main channel and vertical connectivity with alluvial aquifers, both of which can be pulsed or constant over time (Amoros and Bornette 2002, Brunke et al. 2003, Opperman et al. 2010, Capderrey et al. 2014). More specifically, physico-chemical attributes of parafluvial habitats are homogenized during phases of hydrological connection due to mixing and then diverge during disconnection phases, partly a result of differing water sources (groundwater, side-tributaries, etc.) and different properties in ecological succession (Thomaz et al. 2007). For example, typical habitat responses to decreases in hydrological connectivity include increases in electrical conductivity and ammonium concentration (Paillex et al. 2007, Paillex et al. 2009, Larned and Datry 2013), and decreases in dissolved oxygen (Gorski et al. 2013, Scott et al. 2011, Larned and Datry 2013).

Nutrient concentrations in parafluvial habitats also tend to increase with connectivity to the main channel and with groundwater seepage, but are also affected by water retention time as well as biological processes (Amoros and Bornette 2002, Brunke et al. 2003, Larned and Datry 2013). Lastly, water temperature is affected by connectivity gradients as well, where habitats with groundwater inputs typically have more constant temperatures through the year (Amoros and Bornette 2002, Larned and Datry 2013). These differences in local abiotic conditions driven by hydrological connectivity constrain biotic assemblages within parafluvial habitats of the floodplain (Brunke et al. 2003, Starr et al. 2014, Cadotte et al. 2017).

The coupling of environment-biota relationships is ubiquitous in fluvial systems, but parafluvial floodplain habitats are particular in that environmental conditions evolve over time during disconnection phases, effectively creating a time-varying environmental filter on biotic communities (Chang et al. 2016, Cadotte et al. 2017). For instance, macroinvertebrate assemblages are constrained by the dispersal mode of organisms in relation to the distance to potential sources of colonists following a flood and, mass effects excluded, by local conditions, resource availability and inter-patch hydrological connectivity (Amoros and Bornette 2002, (Tonkin et al. 2016). In the initial phase of colonisation, strong aerial dispersers can colonize habitat patches in priority, tracking favourable environmental conditions (Leibold et al. 2004, Cadotte 2007, Soininen 2014) as local habitat conditions diverge; i.e., the local environment dictates assemblage composition (Chang et al. 2016). As time passes after a flood, competitive interactions can gain importance as a structuring force of communities, see Figure 1 (Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2007).

Figure 1. Conceptual diagram outlining the effects of flood frequency and time since last flood on community assembly rules (full arrows), taxa richness and evenness (dashed arrow), primary productivity, abiotic conditions and community composition.

Species functional traits in relation to dispersal ability and niche breadth can be particularly useful in identifying the relative importance of specific processes such as environmental filtering in structuring communities (Thompson and Townsend 2006, Smith et al. 2015, Tonkin et al. 2016). Functional diversity, commonly defined as “the value and range of the functional traits of the organisms in a given ecosystem” (Diaz and Cabido 2001, Tilman 2001), has often been used by community ecologists to infer community assembly rules. This approach is based on the assumption that communities structured by the environment have low functional diversity because only adapted phenotypes (corresponding to specific ecological niches) are selected by the environmental filter (van der Valk et al. 1981, Keddy 1992, Diaz et al. 1999). In contrast, communities structured by strong interspecific competitive interactions have high functional diversity as a result of limiting similarity processes such as niche partitioning, whereby only species occupying non-overlapping ecological niches can co-occur (MacArthur and Levins 1967, Cornwell et al. 2009). In cases where strong competition leads to competitive exclusion, functional diversity also is low (Kraft et al. 2015, Cadotte et al. 2017, Passy et al. 2017). Although patterns of functional diversity must be interpreted with caution, they still provide robust evidence for different community assembly mechanisms when associated with sound understanding of the study system (Paillex et al. 2013, Li et al. 2015, Cadotte et al. 2017, Passy et al. 2017).

In this study, we aimed at quantifying the relative effects of long-term flood regime and recent flood history on macroinvertebrates inhabiting parafluvial habitats within a regulated floodplain riverscape. We sampled 24 parafluvial habitats seasonally for one year in a heterogeneous floodplain and developed a 2D hydrodynamic model of the floodplain to derive flooding frequencies and flood history. A piecewise structural equation modelling approach (SEM) was used to quantify the direct and indirect effects of flood regime through changes in local habitat and resource availability on the macroinvertebrate communities. We hypothesized that recent disturbance history (time elapsed since last flood) would be the main constraint of local habitat conditions and biota, with habitat characteristics (H_1) and communities (H_2) transitioning from lotic-like to lentic-like over time. Specifically, the time elapsed since last flood would affect the community composition directly by favouring strong dispersers early in assembly and indirectly through temporal changes in habitat conditions. Further, we anticipated that biofilm standing crops (food resource) would be lower in frequently flooded sites but increase over time after a flood (H_3), and that decreased biofilm standing crop would lead to increased competitive interactions and decreased community evenness (H_4).

Methods

Study site

The Maggia river is located in the south-eastern part of the Swiss Alps and flows southward into Lake Maggiore (Figure 2). It is one of the last remaining natural (non-urbanized) floodplains in Switzerland, and therefore has been declared a site of national importance (Kuhn

and Amiet 1988). Its catchment covers an area of 930 km² with elevations ranging from 200 to 3300 m a.s.l. Owing to the presence of two glaciers in the headwaters and snowfall precipitation in winter, the hydrological regime is classified as glacionival. Following the construction of a complex hydropower scheme in the headwaters in 1953, the flow regime of the river has been substantially modified (Pfamatter and Zanetta 2003, Molnar et al. 2008). The original high flows during snowmelt have been replaced by essentially constant flows (minimum flow requirements $\sim 1.5 \text{ m}^3/\text{s}$) with occasional flood peaks (Figure 3) with no correlation between magnitude and return period (Molnar et al. 2008, Perona et al. 2009). The alluvial floodplain used in this study is located in the middle of the valley; it is about 7-km long and nearly 2-km wide in some sections. Because of the fairly low storage of the hydropower scheme and high lateral hillslope runoff during major rain events, the larger flood peaks still occur (Figure 3) but the lesser magnitude floods do not (under $\sim 10 \text{ m}^3/\text{s}$).

Figure 2. Map of Switzerland showing the location of the Maggia River floodplain and the parafluvial habitats sampled.

Figure 3. Hydrograph of the Maggia River upstream of the modelling domain (gauging station Bignasco), from January 2010 to November 2016.

The combination of high flows and an abundance of bedload sediment (mean diameter of stones = 120 mm) maintains a diverse floodplain habitat. Within the floodplain, single-thread sections alternate with braided reaches where various types of parafluvial habitats occur: ponds, connected and disconnected side arms, and backwaters. For this study, we selected 24 permanently-wetted parafluvial habitats, specifically permanent ponds, disconnected side arms, and side arms connected at their downstream end with a shallow riffle.

Field sampling & laboratory analysis

Samples were collected once per season: in February 2016, in May 2016, August 2016 and October 2016. On each visit, a water sample (0.5 L) was collected from each habitat and stored on ice in the dark for chemical analysis in the laboratory. In the laboratory, water samples were analyzed for calcium (Ca, mg/L), nitrate (NO₃, mg/L), and pH using standard methods following Tockner et al. (1997). Spot measurements of dissolved oxygen (mg/L, Hach HQ40d connected to a LD10101 oxygen probe), water temperature (°C), and electrical conductivity (μS/cm, WTW meter, Germany) also were taken on each visit. At each sampling event, the order in which water samples and physico-chemical variables were measured was randomized among ponds to reduce bias of collection time. Additionally, a temperature sensor-logger (Thermocron, i-button) was deployed within each habitat for a period of 7 days following each visit that recorded water temperature hourly. The mean, standard deviation, range, minimum and maximum water temperatures were then calculated for each site and each season. Substrate size composition was measured using the zig-zag pebble count method where 50 cobbles were randomly selected along a reach and their b-axis measured (King et al. 1995). The structural diversity of the substratum within each habitat was calculated using the Shannon-Wiener index H (Cellot et al. 1994, Burnett et al. 1998, Brunke et al. 2003):

$$H = - \sum_{i=1}^S (p_i \ln (p_i))$$

With S being the number of Wentworth substrate size classes (Wentworth et al. 1922, Table S1 in supporting information) and p_i the proportion of the total sample belonging to the i th size class.

Surface biofilms (periphyton) were measured by randomly selecting 5 stones (cobble-size) within each habitat. The biofilm was removed from each stone by scrubbing with a wire brush into a plastic container with 100 mL of distilled water, and the scrubbed area measured (after Uehlinger 1991). The biofilm suspension was subsequently filtered through a glass fiber filter (0.45 μ m, Whatman GFF) and stored on ice in the dark. Chlorophyll-a extraction was conducted by incubating each half-filter in 6 mL 90% ethanol at 70°C for 10 minutes. Chlorophyll-a (μ g /L) was then determined using standard spectrophotometry (Hitachi 2000) following methods in Meyns et al. (1994). In parallel, the other half of each filter was dried at 60°C for 24h, weighed, then combusted at 450°C for 6h and reweighed for estimates of organic matter biomass as AFDM. Benthic macroinvertebrates were randomly collected ($n = 3$, at each site and date) using a Hess sampler (250 μ m mesh, 0.04 m² area) and preserved in 70% ethanol. In the laboratory, collected individuals were hand-picked, counted and identified to the lowest possible taxonomic level using Tachet et al. (2010). Of all taxa, 88% were identified to the family level, 6% to the class level and 6% to the order level.

Data analysis

Macroinvertebrate metrics - Macroinvertebrate taxa richness and community evenness were calculated for each site. To assess changes in community composition we also used the relative proportion (%) of the major groups: Coleoptera, Ephemeroptera, Plecoptera, Trichoptera, and Diptera. Functional diversity (FD) was calculated as the standardized effect size of Rao's quadratic entropy (SES-RaoQ), calculated as the standard deviation of the observed RaoQ from that of a null model. The null model was constructed by shuffling species abundances within each site and calculating RaoQ at each of 999 iterations. This type of null model approach, commonly used in functional diversity studies, has the advantage of removing the influence of differences in species richness on FD (Mason et al. 2013). For the analysis, we used all biological traits available in our database and used in previous studies on floodplain systems (e.g., Paillex et al. 2013, Van der Vorste et al. 2016), amounting to 41 categories distributed in 9 biological traits (Table S2, Supporting Information). Functional traits for all taxa were obtained from the Tachet database for each taxon (Tachet et al. 2010). To give the same weight to all traits in the diversity measure, affinity scores were standardized so that their sum for a given taxon would equal 1 (see Paillex et al. 2013).

Hydrodynamic model- We developed a 2D hydrodynamic model for the floodplain which enabled us to calculate two key hydrological metrics for each habitat: flood frequency over the two years preceding a sampling event and recent disturbance history represented by the number of days elapsed since the last flood. The model was constructed using Basement software (Faeh et al. 2010, developed at ETH Zurich: <http://www.basement.ethz.ch/>), which solves the depth-averaged shallow-water Saint-Venant equations to calculate water depth, current velocity and bottom shear stress for each element within the modelling domain. Because

of the spatial complexity of groundwater-surface water interactions in this alluvial floodplain that cannot be accurately simulated under the current state of system characterization, we only used the model to derive thresholds of discharge at which a given habitat becomes inundated with surface water as well as local bottom shear stress. Our modelling approach consisted of running steady-state simulations for the range of discharges corresponding to flood peaks that occurred between 13 March 2014 and the end of our study period on 28 October 2016. During this period, 45 identified flood events occurred (Table S3, Supporting Information), with a maximum discharge of 570 m³/s. For each discharge simulation, the model produced a simulated water depth for each cell of the modelling domain which was then overlapped with a map of our sampling sites to determine whether a particular habitat was flooded at a given discharge. We were then able to calculate a flood frequency for each habitat during the modelling period as well as the time elapsed since the last flood at each sampling campaign (February, May, August and October). We used the bottom shear stress values calculated by the model as a proxy for flood magnitude, as the effect of flooding on macroinvertebrates is dependent on bottom shear stress values (Borchardt 1993, Gibbins et al. 2007, Gibbins et al. 2009).

Floodplain bathymetry was obtained from a ground-proofed 6-cm resolution digital elevation model (DEM) derived from orthoimages captured from a drone flight on 10 February 2016. Because no major geomorphological changes occurred within the floodplain during the study period, we used the same DEM for all simulations for the four sampling events. The dimensions of the model mesh were chosen so as to minimize computation time and allow for an accurate representation of flow-paths within the floodplain (Table S4, Supporting Information). We used measurements of substrate size distributions in the following equation (1) (Meyer-Peter and Müller 1948) to estimate k_{str} , the initial Strickler coefficient for bottom friction:

$$k_{str} = \frac{21.1}{\sqrt[6]{D_{90}}}$$

Because of the uncertainty surrounding this coefficient, it was then incrementally adjusted as part of the model calibration procedure. The upstream boundary condition for the model was the discharge value being modelled and the downstream boundary was a discharge-stage relationship. For model calibration, we used discharge and stage data for the period 13 March 2014 – 28 October 2016 from an automated gauging station at the downstream end of the modelling domain. Given the flashy nature of floods in the Maggia (typical flood duration <1 day), no measurements of discharge-inundation relationships were made available, thus used a single gauge for calibration. The calibration to a single stream gauge was deemed robust, given the high vertical resolution of the bathymetry data and the fact that only one Strickler coefficient was used for the entire floodplain. The simulated stage-discharge relationship at the gauging station for each k_{str} value was compared with the measured one for the range of modelled floods and k_{str} was sequentially adjusted to minimize the root mean square error (RMSE). During the modelling period, 45 floods occurred, with a minimum discharge of 20.1 m³/s, a maximum of 570 m³/s, and average of 141.2 m³/s and standard deviation 164.8.

Habitat characterization- To summarize the physico-chemical attributes within each habitat, we performed a principal component analysis on selected physico-chemical variables after removing variables with Pearson's correlation greater than 0.7; variables included were nitrate concentration, electrical conductivity, dissolved oxygen (DO), mean water temperature (T) and standard deviation of water temperature.

Statistical analysis

We conducted a STATICO analysis to explore the relationship between macroinvertebrate community composition and environmental variables during the study period. STATICO is a three-way analysis coupling method designed to analyse the relationships between two series of tables: in our case a temporal series of environmental variables and one temporal series of species abundance data (Simier et al. 1999, Thioulouse et al. 2004, Thioulouse 2011, Slimani et al. 2017). Its usefulness in characterizing environment-biota relationships over time has been demonstrated in several studies (Carassou and Ponton 2007, Simier et al. 2006, Mendes et al. 2009).

We used piecewise structural equation modelling (SEM) to assess the direct and indirect effects of flood regime and history on macroinvertebrates. SEMs are adapted to model direct and indirect correlations in ecological systems while accounting for residual correlations between response variables (Bollen 1989, Grace et al. 2006). Piecewise SEMs differ from traditional SEMs in that instead of a variance-covariance matrix, they rely on local estimates to infer direct and indirect pathways (Grace et al. 2012, Pasanen-Mortensen et al. 2013). Because piecewise SEMs combine the information of multiple separate models into a causal framework, they allow for the use of random effects and release some of the assumptions made by traditional SEMs; they also accommodate smaller sample sizes. All pathways in the model were modelled using linear mixed effect models from the *lme* R package and combined into a structural model using the *PiecewiseSEM* R package (Lefcheck et al. 2016). Because of the repeated-measure structure of our dataset, we used site ID as a random effect in all models to account for unmeasured site-specific effects, and the season of each sampling event was included as fixed factor in each model to correct for seasonal effects. Following Grace et al. (2006, 2012), we

constructed an initial conceptual structural model based on literature and a priori knowledge on the functioning of alluvial floodplain systems (Figure 4).

Figure 4. Initial structural equation model corresponding to our a priori conceptual understanding of the system. Plain arrows represent positive correlations and dashed arrows represent negative correlations.

We then optimized this model using a stepwise backward selection procedure based on the AICc criterion for each separate GLMM (Pasanen-Mortensen et al. 2013, Theodorou et al. 2016). Based on the d-separation test implemented in the PiecewiseSEM package, we incrementally incorporated significant missing pathways that further improved the AICc of the overall model (Stenegren et al. 2017, Shipley et al. 2009, Shipley et al. 2013). The final model was the one with the lowest AIC and the most variables (Stenegren et al. 2017).

Model justification, with predicted responses

The original model was developed to be associated with our initial hypotheses with a summary of rationale or justification presented in Table 1. Specifically, to test H1 (see introduction) we included negative correlations between the habitat gradient (lotic to lentic) and both the time since last flood and the Y coordinate. To test H2, we initially assumed that the relative abundances of Coleoptera and Diptera would be positively correlated to the habitat

gradient and to the time since last flood, whereas the relative abundance of EPT taxa would be negatively correlated to these variables. To test H3, we initially included a negative correlation between biofilm biomass and flood frequency and a positive one between biofilm biomass and time since last flood. Finally, to test H4, we assumed that functional diversity and community evenness would be negatively correlated to biofilm biomass. We also tested whether taxa richness increased over time after flood, and whether it was higher in frequently flooded habitats because of higher structural diversity in the substrata. To that end we included a positive correlation between taxa richness and time since last flood, as well as a positive correlation path between flood frequency, sediment structural diversity and taxa richness.

Table 1. Justification and rationale for the initial structural equation mode

Justification	Response	Driver	Sign	References
Upwelling of groundwater in downstream reaches of the Maggia floodplain	Conductivity Nitrate	Y coordinate (increase downstream)	↗ ↗	Ruf et al. 2008, Larned and Datry 2013
Mixing of waters during flood, homogenization with main stem	DO Conductivity	Time since flood	↗ ↗	Paillex et al. 2009
Habitats become more isolated from surface and groundwater sources over time	Mean Temperature SD Temperature		↗ ↗	Rostan et al. 1987, Schwartz et al. 1996
All above relationships result in a general habitat gradient	Habitat gradient lotic to lentic	Time since last flood AND Y coordinate	↗	
Biofilm grows over time after being reset by the flood	Biofilm	Time since flood	↗	Biggs and Close 1989, Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006
The mechanical effect of floods tend to increase substrate heterogeneity	Substrate structural diversity	Flooding frequency	↗	Bornette and Amoros 1996
Direct removal of individuals, followed by recolonization	Taxa richness	Time since flood	↗	Matthaei et al. 1997, 1999
More ecological niches available with more diverse habitat structure		Structural diversity of habitat	↗	Brunke et al. 2003
Floods enable EPT taxa to readily disperse from the main stem where they abound. EPT are generally good aerial dispersers and therefore recolonize faster from adjacent patches after flood.	EPT relative abundance	Time since flood	↘	Alp et al. 2012 Brunke et al. 2003
EPT taxa are generally sensitive with a preference for lotic floodplain habitats		Flooding frequency	↗	
		Habitat lotic to lentic	↘	
Coleoptera and Diptera taxa are generally tolerant taxa with a preference for lentic floodplain habitats	Coleoptera and Diptera relative abundances	Time since flood Habitat lotic to lentic	↗ ↗	Brunke et al. 2003
Competitive interactions and therefore functional diversity should increase over time after flood	Functional Diversity	Time since flood	↗	Fairchild et al. 2000, Mouquet et al. 2003, Cadotte 2017 Townsend et al. 1997, Gallardo et al. 2009, Paillex et al. 2013
Functional diversity should be highest in rarely flooded habitats as a result of competitive interactions, short study duration is not expected to allow competitive exclusions		Flooding frequency	↘	
Low resource availability should favour interspecific competition and therefore lead to an increase in functional diversity.		Benthic primary productivity	↘	
The high interspecific competition at low resource availability should cause a decrease in community evenness as stronger competitors outgrow others.	Community Evenness	Benthic primary productivity	↗	Passy et al. 2017 Townsend et al. 1997, Gallardo et al. 2009, Paillex et al. 2013
Evenness should also be lowest in rarely flooded habitats as a result of competitive interactions		Flooding frequency	↗	
		Time since flood	↘	

Results

Hydrodynamic model

After calibration, the hydrodynamic model was able to accurately reproduce water depth at the gauging station (Figure S1, Supporting Information) for the range of modelled discharges with a $k_{str} = 26$. Equation (1) resulted in an initial value of 25 for k_{str} , this value was then changed by increments of 1 unit until a minimum RMSE was reached for all range of discharges. RMSE ranged from 0.14, 0.10, 0.07, 0.046, 0.047 for $k_{str} = 23, 24, 25, 26$ and 27, respectively. The k_{str} value of 26 gave the lowest RMSE among all tested values (0.046) and was therefore retained as the final friction parameter for the simulation of floodplain inundation. Discharge threshold values for habitat inundation ranged from 10 to 250 m^3/s (mean = 49 m^3/s , median = 35 m^3/s , standard deviation = 58 m^3/s). Flood frequency for the different parafluvial habitats ranged from 0.52 to 18.04 floods per year (Table S5, Supporting Information). Time elapsed since the last flood varied greatly among habitats at each date, owing to the wide range of inundation thresholds (Table S5, Supporting Information).

Habitat characteristics

The range of values in abiotic attributes indicated that the parafluvial habitats we selected in the floodplain were environmentally heterogeneous (Table S6, Supporting Information). PCA1 explained 48% of the total variation in physico-chemistry and therefore was used as indicator for “habitat” type in subsequent analyses (Figure 5).

Figure 5. Plot of the PCA performed on the variables: mean water temperature (Mean T, °C), standard deviation of water temperature (SD T, °C), dissolved oxygen (DO, mg/l), nitrate concentration (NO3.N, mg/l) and electrical conductivity (Condi. $\mu S/cm$).

PCA1 was primarily structured by the opposition between habitats with high DO and nitrate concentration on the positive side, and habitats with high and variable average water

temperatures as well as high electrical conductivity on the negative side (Table S7, Supporting Information).

Community composition

A total of 18 taxa were collected during the surveys, including species of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera, Heteroptera, Hydracharina, and Oligochaeta (Table S8, Supporting Information). Taxa richness changed little between seasons, it was lowest in February (10.9 taxa), then increased in May and August (11.1 and 11.5 taxa, respectively) and decreased in October (11.4 taxa). Macroinvertebrate density varied through time with 338 individuals/sample in February to 140 in May, 271 in August and 317 in October. Despite these temporal changes in abundances, there was little variation in community composition among seasons (Figure 6).

Figure 6. NMDS plot showing the composition of the macroinvertebrate communities at each sampling date; ellipses are 95% confidence intervals.

STATICO analysis showed that relationships between environmental variables and community composition were significant at all four dates (p values = 0.024, 0.006, 0.005 and 0.017 for February, May, August and October, respectively). The first axis accounted for 63.8% of the explained variance and the second axis for 21.1%. Axis-1 was primarily structured by the opposition between habitats with high DO and nitrate concentrations as well as coarse and diverse substrata on the one side and habitats with warm and variable water temperatures as well as high electrical conductivity on the other (Figure 7a).

Figure 7. Plots showing the results of STATICO analysis. (a) principal axes showing the contributions of environmental variables, and (b) principal axes showing the invertebrate community composition.

This result can be interpreted as a gradient from lentic-like habitats on the left side to lotic-like habitats on the other. Axis-2 was mainly constrained by periphyton biomass in the different habitats. Further, the analysis of species distributions revealed that Oligochaete, Corixidae, Ceratopogonidae, Hydracarina and Dytiscidae dominated communities at more lentic habitats (right hand side), whereas EPT taxa were more abundant at habitats with more lotic attributes (Figure 7b). The linkage between environmental variables and community composition was stronger in August and May and weaker in October and February (Figure S2, Supporting Information).

Piecewise SEM

The piecewise SEM after stepwise optimization was well supported by the data (Fishers'C = 104.54, $p = 0.175$, Figure 8). According to the final SEM model, both the distance downstream along the floodplain (estimate = -0.31, $p = 0.025$) and time elapsed since the last flood (estimate = -0.258, $p = 0.035$) negatively affected the habitat gradient (PCA1). This result means that habitats located further downstream or not recently flooded had lower DO and nitrate concentrations and higher electrical conductivity than other habitats. These habitats also had warmer and more variable water temperatures. Because the habitat gradient was correlated positively to taxa richness (estimate = 0.494, $p = 0.01$) and the proportion of EPT taxa (estimate = 0.265, $p = 0.033$), these habitat conditions mediated the negative effects of the longitudinal location of habitats and time since last flood on these two variables. In contrast to the model, periphyton biomass was not affected by time since last flood or flood magnitude, but was negatively related to flood frequency (estimate = -0.324, $p = 0.041$). Periphyton biomass was positively correlated to FD (estimate = 0.286, $p = 0.037$, Figure S3 Supporting Information), thus it mediated the negative effect of flood frequency on FD and the positive effect of flood frequency on community evenness through a negative correlation with this response variable (estimate = -0.386, $p = 0.011$).

Figure 8. Final structural equation model after optimization. Plain arrows represent positive correlations and dashed arrows represent negative correlations and annotations on arrows show the strength of the relationships. R^2 values correspond to marginal R squares. The thicknesses of the arrows are scaled to the strength of the correlations.

Lastly, the relative abundance of Coleoptera and Diptera were negatively correlated to flood frequency (estimate = -1.01 , $p = 0.0387$, estimate = -0.276 , $p = 0.04$, respectively). Flood frequency had a positive effect on substrate diversity (estimate = 0.419 , $p = 0.0003$), which was positively correlated to the relative abundance of EPT taxa (estimate = 0.78 , $p = 0.022$). Taxa richness was positively correlated to the interactive term between time since last flood and flood magnitude (estimate = 0.485 , $p = 0.02$, Figure S4, Supporting Information).

Discussion

In this study, we examined the relative effects of long-term flood frequency and time since the last flood on macroinvertebrate communities in 24 parafluvial habitats. We sampled habitats seasonally over one year and used a combination of 2D hydrodynamic modelling and piecewise SEM to quantify direct and indirect effects of local hydrological metrics on community composition, taxa evenness, taxa richness and functional diversity. Importantly, we found that high flood frequency favoured rheophilic species (EPT taxa) over more lentic groups (Coleoptera, Diptera) and limited strong competitive interactions and competitive exclusion to occur by maintaining low periphyton standing crops. Further, we found that habitat characteristics became more lentic-like as time passed after a flood. This relationship caused EPT taxa to be relatively more abundant and taxa richness higher immediately after flood

disturbance, although taxa richness increased over time after a flood and even more so after large floods.

Local conditions are affected by recent disturbance history and flood regime

The resulting hydrodynamic model accurately reproduced the stage-discharge relationship for the range of discharges considered. The single-value calibration of the bottom friction parameter was justified in this case, for only open gravel areas were flooded at the discharges considered and the spatial distribution of substrate size was relatively homogeneous. The wide range of modelled discharge thresholds for inundation of different parafluvial habitats reflected the geomorphological complexity of the floodplain. This heterogeneity also was apparent in the flood frequency values and time since last flood. The high average time since last flood in February reflected the glacial flow regime of the catchment; precipitation mainly falls as snow in the headwaters during winter, resulting in stable low flows. In contrast, the intermediate but variable values for time since last flood in May and August (median 24 and 63 days, respectively) together with high standard deviations (120 and 123, respectively) showed that medium-sized floods occurred during spring and summer, affecting some habitats but not others. Lastly, the low median time since last flood (5 days) in October showed that a large flood recently inundated most parafluvial habitats.

STATICO analysis revealed that the lotic to lentic habitat gradient had a strong effect on community composition, with more rheophilic EPT taxa predominantly occurring in the more lotic habitats. Temporal fluctuations in the strength of this environment-biota linkage (weaker linkage during winter and autumn compared to summer and spring) reflected the lower heterogeneity in habitat conditions in the floodplain in autumn and winter. Conversely, habitat conditions diverged more during spring and summer and the filtering effect on communities also was stronger. Results of this exploratory analysis confirmed that the environmental variables chosen to represent the effect of habitat type on communities in the subsequent SEM was adequate.

As expected, physico-chemical characteristics of floodplain habitats were strongly affected by their location along the longitudinal axis, with habitats further downstream (lower Y coordinate) exhibiting more “groundwater-dominated” waters with more stable and colder temperatures and high nutrient levels. Importantly, these differences in physico-chemical attributes were not solely explained by water origin, but also by the stage of succession a given habitat was at (Amoros and Bornette 2002, Thomaz et al. 2007). For instance, high DO levels are unlikely to be caused by groundwater inputs because the degradation of organic compounds in groundwater typically results in low DO levels. Instead, the negative relation of time since last flood on PCA axis-1 provided a parsimonious explanation to this pattern, confirming H₁. DO levels rose during floods with the influx of well-oxygenated river water, and remained high immediately after floods. As a habitat became disconnected from the main channel, biological processes consumed oxygen causing a decrease in DO levels over time. To summarize, a parafluvial habitat tends to be better oxygenated if recently flooded, and cooler and thermally more stable if receiving inputs of groundwater.

The decrease in substrate structural diversity with increasing flood frequency likely resulted from geomorphological differences among habitats, where least flooded habitats were

at a higher elevation compared to the river channel. Typically, these areas are zones of deposition and accumulation of smaller sized sediment during floods. This result was confirmed by the positive correlation between the Shannon index of structural diversity and median particle diameter ($r = 0.67$).

Counter to hypothesis H₄, periphyton biomass did not increase over time after a flood, but decreased with increasing flooding frequency. This direct effect suggests that periphyton levels remained low due to frequent flood disturbance (e.g., scouring). Another likely explanation is that high EPT abundance, especially mayflies, at regularly flooded habitats also kept biofilm standing crops to low levels by grazing. Grimm and Fischer (1986) hypothesized that periphyton growth rates are controlled by ambient nutrient concentrations and that maximum standing crops are primarily constrained by flood frequency (also see (Biggs and Close 1989, Robinson and Minshall 1986).

Community composition primarily responds to flood regime and local abiotic conditions

Hypothesis H₃ stated that community composition would change overtime after flood disturbance, partly reflecting the dispersal ability of taxa, was only partially supported by the data and the final model. No direct effect of time since last flood on community composition was observed, suggesting that local environmental filtering or biotic interactions played a larger role in structuring communities than the dispersal ability of taxa. However, the significant relationship between habitat characteristics and the relative abundance of EPT taxa suggests their high dispersal ability enabled them to track favourable environmental conditions (Tonkin et al. 2016), partially supporting H₃. Conversely, no relationship between habitat and the relative abundances of Coleoptera and Diptera suggests that the habitat gradient was too short to filter these species or that mass effects associated with very high dispersal rates overrode environmental constraints (Leibold et al. 2004, Holyoak et al. 2005). Independent of environmental constraints and recent disturbance history, the lower relative abundances of Coleoptera and Diptera at frequently flooded habitats indicated that these taxa were affected by flooding to a greater extent than EPT taxa. This difference could result from the high flood resistance of EPT taxa or their ability to recolonize rapidly from other source habitats (McMullen et al. 2012, Alp et al. 2012).

Taxa richness increases as time passes after a flood, and more so after major floods

We observed a linear increase in taxa richness over time after flooding (slope = 0.453), reflecting the temporal colonization of disturbed habitats by new species. The pattern of low richness post flood and recovery over time has been observed in many aquatic systems (Matthaei et al. 1997, Rader et al. 2007, Mundahl et al. 2011, Robinson 2012). The immediate decrease in taxa richness after a flood results from the physical removal of individuals, either by drifting or crushing, and the filtering of species according to their morphological or behavioural adaptation to flooding (Lytle and Poff 2004). Similarly, the positive interaction between flood magnitude and time since last flood on taxa richness showed that the increase in taxa richness after a flood is faster for larger floods than for smaller floods. Because it is independent of local environmental conditions, this general pattern can be attributed to the

direct physical effect of large floods on assemblages, where larger flood disturbances reset communities to earlier successional stages than smaller floods, resulting in a greater availability of ecological niches for colonization (Townsend et al. 1997, Robinson 2012). In contrast, direct recolonization from adjacent undisturbed substrate patches after small floods likely occurred before new species colonized from other habitats, resulting in similar taxa richness before and after small floods (Townsend et al. 1997, Francoeur et al. 1998, Matthaei et al. 1999, Robinson et al. 2003). Finally, high taxa richness at habitats with more optimal environmental conditions (positive PCA1) indicates that more taxa can live in these habitats in contrast to the other habitats containing more ‘tolerant’ species (Passy et al. 2017). This idea is supported by the low relative abundance of rheophilic EPT taxa at more lentic habitats (negative PCA1).

Resource availability mediates the effect of flood frequency on community assembly rules

The positive relationship between SES Rao’s Q and periphyton biomass suggested that limiting similarity processes associated with strong competitive interactions was a primary assembly rule at habitats with high resource availability, whereas environmental filtering by local abiotic conditions dominated habitats with low resource availability (further inferred by a negative functional diversity). This result was in accordance with hypothesis H₅. While this pattern may at first seem contrary to the expectation that competition would be stronger in habitats with low resources (Passy et al. 2017), these less productive habitats may instead exert a strong selective pressure on taxa through their mode of resource acquisition for instance (Bernard-Verdier et al. 2012).

The high community evenness in low resource habitats further suggested that no particular group of species was able to outcompete others. At high resource availability, low community evenness indicated that some taxa were able to outcompete others and dominate assemblages, as reflected in the higher functional diversity indicative of strong competitive interactions (Cotgreave and Harvey 1994, Hillebrand et al. 2007, Zhang et al. 2006, Gamfeldt et al. 2011, Larpkern et al. 2011). However, the lack of relationship between resource availability and the relative abundance of a particular taxon suggested that the identity of these dominant competitors differed between sites and thus largely constrained by stochastic processes (Tilman et al. 2004) or driven by site-specific external factors. It is likely that this study did not cover the full range of habitat conditions (higher resource availability) or time period (lower flood frequency) that favours interspecific competition because the outcome of such strong competition would likely be extirpation of poor competitors (Townsend et al. 1997), a reduction in functional diversity, and a potential increase in evenness (Paillex et al. 2013, Kraft et al. 2015, Cadotte et al. 2017).

Previous studies investigating functional diversity in floodplain macroinvertebrate communities found that FD peaked at intermediate levels of inundation frequency, being lower at low and high inundation frequencies (Gallardo et al. 2009, Paillex et al. 2013). These findings are in line with predictions of the intermediate disturbance hypothesis (e.g., Townsend et al. 1997) and dynamic equilibrium model (Huston 1979, 1994). Taken together, these concepts suggest that at high flood frequency and low resource availability, strong environmental filtering can occur, notably on species resistance to floods and respective dispersal capacities.

In contrast, strong competitive interactions and potentially competitive exclusion can develop in rarely flooded, highly productive habitats. Many studies have documented these colonization-competition trade-offs, where frequently disturbed habitats favour strong dispersers able to rapidly colonize recently disturbed patches and track favourable environmental conditions (Cadotte et al. 2007, Leibold et al. 2004, Soininen 2014, Tonkin et al. 2016), whereas strong competitors dominate community composition later in the assembly (Fairchild 2000, Mouquet et al. 2003, Cadotte et al. 2007).

In this study, the level of flood disturbance was negatively correlated to resource availability (periphyton biomass), which affected the relative importance of competition and environmental filtering. Our findings are in accordance with the predictions of Huston (1979 and 1994), Townsend et al. (1997) and Ward et al. (1999), in that low flood frequency at habitats with high resource availability did not limit the development of strong competitive interactions, whereas the combination of high flood-disturbance frequency and low resource availability acted as a strong environmental filter on assemblages. Overall, our findings showed that high flood frequency maintained low periphyton biomass levels and limited the development of strong competitive interactions (as shown by high positive FD) and competitive exclusion to occur (as shown by decreasing community evenness).

Implications for management: hydrological regime and floodplain biodiversity

Our findings, as discussed above, have direct implications for the management of river flow regimes and the conservation of biodiversity in alluvial floodplain systems. First, spatial heterogeneity in flood frequencies should be maintained to provide ecological niches among parafluvial habitats for both lotic and lentic species within floodplain riverscapes. In order to achieve this spatial heterogeneity in flood frequencies, habitats should differ in their connectivity (e.g., elevation differences) with the main channel and floods should differ in magnitude. This heterogeneity will sustain a spatial mosaic of habitat patches with differing resource availability. In more productive habitats, strong competitive interactions will emerge and strong competitors will tend to outcompete others, thus reducing local diversity but increasing beta diversity. Second, independent of long-term flood frequency, a high level of heterogeneity in flood return period should be maintained among parafluvial habitats. This heterogeneity would result in a mosaic of habitat successional stages, further enhancing macroinvertebrate beta diversity at the floodplain scale. Additionally, high heterogeneity in disturbance states among parafluvial habitats can act as ‘spatial’ insurance for ecosystem functioning and stability of floodplain riverscapes (Loreau et al. 2003). Finally, large floods also should be maintained, for they allow regeneration of ecological niches and colonization by novel taxa, thereby sustaining high taxa richness in floodplains.

Acknowledgments

This work was supported by a grant (407040_153942) from the Swiss National Science Foundation (SNSF) as part of the Energy Turnaround NRP70 program. Thibault Datry was supported by the AAP Risques entitled "META-RISC". We are especially grateful to Simone Blaser for her valuable help in the laboratory and with field work. We would also like to thank

Christa Jolidon, Jacques Chanut, Eduardo Martin and Hannele Penson for assistance during field campaigns.

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Supporting Information

Table S1. Wentworth substrate size classes

Size Code	Particle diameter range (mm)	Category
1	<0.062	silt/clay
2	0.062-0.125	very fine sand
3	0.125-0.25	fine sand
4	0.25-0.5	medium sand
5	0.5-1	coarse sand
6	1-2	coarse sand
7	2-4	fine gravel
8	4-5.7	medium gravel
9	5.7-8	medium gravel
10	8-11.3	coarse gravel
11	11.3-16	coarse gravel
12	16-22.6	small pebble
13	22.6-32	small pebble
14	32-45	large pebble
15	45-64	large pebble
16	64-90	small cobble
17	90-128	small cobble
18	128-180	large cobble
19	180-256	large cobble
20	256-362	boulder
21	362-512	boulder
22	512-1024	boulder
23	>1024	boulder
24	Bedrock	bedrock

Table S2. List of the 9 biological traits and the number of categories in each trait used to calculate the functional diversity of aquatic macroinvertebrates.

No.	Biological traits	Number of categories
1	Body size	5
2	Dispersal	4
3	Life duration	2
4	Reproduction	8
5	Locomotion	6
6	Aquatic stage	4
7	Feeding habits	6
8	Respiration technique	3
9	Voltinism	3

Table S3. Summary statistics of the 45 floods that occurred during the modelling period (March 2014 - November 2016).

	Discharge of Floods (m³/s)
Mean	141,2
Median	80.5
SD	164.8
Minimum	20.1
Maximum	570

Table S4. Characteristics of the model mesh.

	Mean area (m²)	Median area (m²)	Minimum area (m²)	Maximum area (m²)	SD area (m²)
Mesh elements	49.1	5.1	0.5	1949.9	96.9
Modelling domain	1,698,055	-	-	-	-

Table S5. Statistical summary of the modelled values for time since last flood and flooding frequency.

Time since last flood	Min	Max	Median	SD	Mean	CV (%)
February	131	463	131	86.6	187.9	46
May	24	553	24	120.2	63.8	188
August	53	653	63	123.9	85.2	145
October	5	715	5	147.8	54.6	271
Flood frequency (per year)	0.5	18.0	8.9	5.8	10.2	0.6

Table S6. Statistical distributions of the main environmental variables.

Variable	Mean	Median	SD	Min	Max
Conductivity ($\mu\text{S}/\text{cm}$)	72.8	73.1	14.9	36.1	101.0
pH	6.9	6.9	0.22	6.4	7.6
Nitrate (mg/l)	0.58	0.60	0.11	0.11	0.88
Dissolved Oxygen (mg/l)	9.1	9.1	1.5	4.5	11.8
Biofilm standing crop ($\mu\text{g}/\text{l}$)	7.7	6.6	4.4	0.9	22.3
Mean T ($^{\circ}\text{C}$)	10.8	10.2	3.9	2.2	19.2
SD T ($^{\circ}\text{C}$)	0.75	0.60	0.53	0	2.7
D ₅₀ (cm)	6.0	7.0	2.9	0.1	14.3
Substrate diversity	1.3	1.4	0.4	0	1.7

Table S7. Contributions of the selected environmental variables to PCA axes 1 and 2.

Variable	PCA-1	PCA-2
Conductivity	-0.416	-0.480
NO ₃ -N	0.565	0.259
Dissolved Oxygen	0.491	-0.453
Mean T	-0.418	0.581
SD T	-0.300	-0.397

Table S8. Summary of the occurrence and density of sampled taxa.

Taxa	SD density	Min density	Max density	Mean density	Mean occurrence
Oligochaeta	14.2	0	56.8	8.9	19.8
Hydracarina	7.0	0	27.3	6.2	21.0
Baetidae	38.1	0.25	178.0	14.9	20.8
Ephemerellidae	1.6	0	7.2	0.6	3.0
Heptageniidae	9.3	0	35.3	5.9	15.8
Leptophlebiidae	2.2	0	9.0	1.5	12.3
Plecoptera	17.5	1	69.8	18.5	23.3
Corixidae	97.0	0.25	458.0	46.8	20.3
Dytiscidae	3.9	0	16.3	2.6	12.3
Elmidae	2.9	0	13.5	1.2	8.5
Haliplidae	0.9	0	3.0	0.7	3.5
Hydroptilidae	40.9	0	169.0	23.2	19.0
Polycentropodidae	2.3	0	10.5	1.1	8.2
Ceratopogonidae	12.2	0	57.0	5.9	15.8
Chironomidae	165.0	7.5	708.0	133.0	23.3
Empididae	1.7	0	8.0	0.8	7.8
Limoniidae/Pediciidae	3.2	0	11.3	2.8	18.0
Tipulidae	7.3	0	32.8	5.5	15.5

Figure S1. Plot showing the modelled versus observed water depth at the gauging station for $k_{str} = 26$ and for a range of discharges.

Figure S2. Results of the STATICO analysis plotted separately for each sampling campaign. For clarity, species with projections values <0.05 on both axes of the factorial plan were not displayed.

Figure S3. Relationship between SES Rao's Q and biofilm standing crop (scaled values).

Figure S4. Plot showing the interactive effect of time since last flood and flood magnitude (modelled bottom shear stress, scaled values) on taxa richness.