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Long-term functional responses of macroinvertebrates to experimental floods and climate driven alterations in alpine streams

Master Thesis

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Abstract

Hydropower production is negatively affecting stream ecosystems in several Alpine catchments. Dams are among the greatest sources of hydropower-related environmental change in the area, altering the natural flow and sediment regime and releasing stable flows. Adaptive dam management aims at mitigating flow-related alterations, implementing ecologically sound water releases (environmental flows). In alpine rivers, seasonal spates play a fundamental role for stream and riparian ecosystems, sustaining important ecological processes. In regulated rivers, these seasonal high flows are lost after regulation but can be reintroduced by releasing experimental floods (i.e. controlled high-flows from dams). Alpine streams are also undergoing climate-driven environmental changes, which may alter water physico-chemical conditions by changing the contribution of different water sources (icemelt / snowmelt / groundwater), affecting also sediment dynamics and consequently habitat conditions for aquatic organisms. Understanding how climate change affects aquatic ecosystems is crucial to predicting future ecological responses. Further, knowledge on the response to flow restoration enables the development of environmental flow science based on empirical evidence. Here, using functional approaches, macroinvertebrate and environmental data collected during the monitoring of a 17-year experimental flood program on an alpine river, and of two unregulated reference streams with different glacial legacies, belonging to the same catchment (river Spöl) was analyzed. Fuzzy correspondence analysis, functional diversity indices and individual trait patterns were used to detect functional adaptions of the macroinvertebrate community to the experimental flood program, expecting a convergence towards reference streams. Furthermore, it was expected to find indications of climate-driven environmental alterations, and a consequent functional community shift mediated by different glacial signatures. The macroinvertebrate community in the flow-regulated river adapted to the new flow regime (experimental floods), showing multiple functional shifts following an increase in the frequency of traits linked to resistance/resilience. Although the macroinvertebrate community became more similar to the reference streams in terms of functional structure, functional indices and individual traits frequencies, the experimental flood program did not result in a complete ecological restoration. In the reference streams, gradual increases in water temperature and periphyton biomass (climate-driven) were observed. The functional response of macroinvertebrate communities differed between streams, highlighting the relevancy of glacial fingerprints in determining the magnitude and speed of such response. This study confirms the importance of long-term monitoring to evaluate the effects of climate change and flow restoration on stream ecosystems.

Content

1 Introduction

Alpine streams are extremely dynamic systems, often characterized by high discharge variability and large sediment load. Environmental conditions in these streams show strong seasonal fluctuations and, in general, ecosystems are subject to strong disturbance drivers. Periodic floods and sediment supply sustain geomorphological dynamics, and contribute to maintain spatio-temporal variability of habitat conditions (Lytle & Poff, 2004; Poff et al., 1997). Steep gradients and low water temperatures are typical in these systems and result in harsh environmental conditions. Instream physical habitats of alpine streams are normally characterized by high flow velocities, instable substrate and high discharge dynamics (Füreder, 1999; Sertić Perić et al., 2015). Flow regime and physico-chemical conditions in a stream strongly depend upon water source − icemelt (kryal), snowmelt (rhithral) and/or groundwater (krenal) − which vary depending on altitude, catchment size and glaciated surface (Brown et al., 2003; Füreder, 2007). Organisms living in such harsh environments have peculiar adaptations (life history, behavior) and follow and/or depend on the natural seasonal variability in flows. As an example, brown trout depend on floods to generate suitable spawning habitats (e.g. Füreder, 2007; Jacobsen & Dangles, 2012; Wharton, 2007) while macroinvertebrate assembly is determined i.a. by glacial flood intensity (Cauvy-Fraunié et al., 2014). This strong interplay between abiotic and biotic conditions is extremely sensitive to climate change. Warmer temperatures accelerate glacier snowmelt and alter rainfall/snowfall patterns, which in turn modify hydrological and environmental conditions in streams (e.g. Gobiet et al., 2014). Consequently, e.g. the window of opportunity for periphyton can change (Uehlinger et al., 2010) and the habitat range of macroinvertebrates can alter which in turn shift species abundance and richness (Brown et al., 2007; Giersch et al., 2017).

Hydropower electricity generation is an important economic pillar in montane areas, harvesting high-head waters potential. Hydropower networks are extremely developed in the Alps, where the hydropower potential has been almost fully expressed (Muhar et al., 2013; WWF EALP Freshwater, 2014). In recent years, the evidence of heavy impact on aquatic ecosystems is challenging the paradigm of hydropower as a completely sustainable energy source. In the Alps, water abstraction and water storage in reservoirs by the mean of dams is often used for hydropower production (Schmutz & Moog, 2018). These anthropogenic structures affect watercourses by producing lentic conditions upstream the dam (Kimmel & Groeger, 1984), leading to unnatural flow fluctuations (hydropeaking) further downstream as turbined water gets released (Greimel et al., 2018) and, between the water abstraction and release, leading to residual flow conditions. Residual flow reaches feature altered abiotic environmental conditions, as flow and sediment regime are disturbed, resulting i.a. in comparably low and stable discharge and in clogging of the substrate (Camenen, 2017; Carlisle et al., 2014; Dewson et al., 2007; Graf, 2006) which in turn can affect the assembly of aquatic organisms, such as macroinvertebrates (Bunn & Arthington, 2002; Robinson et al., 2018). Besides changes in habitat conditions, aquatic organisms in residual flow reaches experience direct impacts like the interruption of longitudinal migration and drift (Fette et al., 2007; Stanford et al., 1996).

In the last decade, the evidence of hydropower impacts led to the identification of mitigation measures and the development of environmental flows, for a sustainable and ecologically-sound management of hydropower facilities (Arthington et al., 2018; Poff et al., 2017). Environmental flows are intended to reproduce ecologically relevant natural flow patterns in residual flow reaches (so called functional flows, Yarnell et al., 2015). Floods and consequent disturbance are reintroduced via artificial high-flow releases (so called experimental floods; Gillespie et al., 2015, 2020; Konrad et al., 2011; Olden et al., 2014; Robinson et al., 2018). Experimental floods may partially restore habitat structure downstream a dam by flushing fine sediments and dense periphyton growth as well as reintroducing certain dynamic in the riverbed structure (Robinson et al., 2004; Mürle et al., 2003; Ortlepp & Mürle, 2003). As floods are seen as a main driver of community assembly and resilience (Death, 2010; Lytle & Poff, 2004; Resh et al., 1988), such experimental disturbance may further alter aquatic communities, e.g. by resetting flow-regulated macroinvertebrate compositions preferring stable conditions to more natural, resilient assemblages (Robinson & Uehlinger, 2008) or by favoring native fish species (Kiernan et al., 2012). Macroinvertebrate assemblies in flow-regulated reaches have shown to respond to experimental floods by adapting their taxonomical composition to the altered flow regime (Gillespie et al., 2020; Robinson et al., 2018). When assessing the ecosystem responses (e.g. macroinvertebrate community responses) to environmental flow programs, the importance of long-term studies and the use of adaptive management have been highlighted (Cross et al., 2011; Gillespie et al., 2015; Robinson, 2012; Robinson et al., 2018).

Trait-based approaches are being increasingly used as an alternative or a complementation to taxonomical analysis, assessing the effectiveness of flow restoration. Ecological/biological traits relate to functional aspects of aquatic ecosystems and have the potential to provide a mechanistic understanding of response patterns to natural and anthropogenic environmental changes (Arthington et al., 2010, 2018; Chen & Olden, 2018; Poff, 2018; Poff et al., 2017; Thompson et al., 2018; Van Looy et al., 2019; White et al., 2019). Traits are individual characteristics of a species that reflect functional adaptation to the environment (Menezes et al., 2010). One species e.g. could be able to disperse having an aerial adult stage (trait) and thus show increased resilience in fluctuating habitats (Townsend & Hildrew, 1994). Trait-based approaches have the potential to a) provide mechanistic understanding of the relationship between a species and its environment (Townsend & Hildrew, 1994; Verberk et al., 2013), b) allow comparisons across areas on different spatial scales because they do not rely on species identity (Dolédec & Statzner, 2010; Verberk et al., 2013; Webb et al., 2010), while being less sensitive to season and interannual fluctuations (Culp et al., 2011), and c) separate effects from different stressors (Lange et al., 2014). Trait-based approaches have numerous applications and can vary between single trait and trait-assemblage analyses (Chevenet et al., 1994). Multiple functional diversity indices can be calculated based on trait information, allowing e.g. the quantification of ecosystem stability (Goswami et al., 2017). Compared to taxonomic diversity indices, functional diversity indices may be more sensitive to identify disturbance effects (Liu et al., 2021) and underlie globally consistent shaping processes (Brown et al., 2018). Functional diversity indices and individual traits can provide information about the resistance and resilience of a macroinvertebrate community to environmental stress and allow to set goals to enhance ecological stability in the face of disturbance (e.g. Biggs et al., 2020; Van Looy et al., 2019). Individual functional responses of macroinvertebrates to both flow alteration (e.g. Wang et al., 2019) and climate change (e.g. Besacier Monbertrand et al., 2019; Khamis et al., 2014; Mbaka et al., 2015) in alpine catchments have been extensively studied, while community-level responses are still poorly assessed (Bruno et al., 2019). Mechanistic understanding of these relations is of paramount importance, as alpine streams often experience anthropogenic stress while being additionally exposed and sensitive to climate change related ongoing environmental alterations (e.g. Gobiet et al., 2014; Jacobsen et al., 2014; Milner et al., 2009, 2017). Furthermore, the long-term functional responses to experimental floods have not been addressed yet. A long-term perspective is crucial when studying the slow and fluctuating ecological responses to flow restoration as well as the ongoing directional climate-driven changes.

Here, a 22-years long-term macroinvertebrate dataset resulting from the monitoring of an experimental flood program in an alpine stream (Spöl) was analyzed using trait-based approaches. A focus was set on community's resistance and resilience patterns, which were related to the new restored flow regime. The long-term environmental and macroinvertebrate datasets of two free-flowing reference streams, Val da l'Aqua (Aqua) and Ova da Fuorn (Fuorn), were further analyzed, taking into account their differing glacial legacies (Sertić Perić et al., 2015). The aim is to gain insights on long-term functional responses of macroinvertebrate communities to a) flow restoration and b) climate-driven environmental change in alpine streams. Combining multivariate methods, functional diversity indices and single trait pattern analyses, it is hypothesized that:

- H1: Functional response of macroinvertebrate community to experimental floods (Spöl): Macroinvertebrate community on the river Spöl will show functional adaptations to the new flow regime (experimental flood program) and consequent environmental changes, reflecting observed structural community shifts. Specifically, it is expected that a) trait assemblage in the Spöl macroinvertebrate community will converge towards those of reference streams (Aqua and Fuorn). It is further expected that b) the frequency of traits conferring resistance/resilience to disturbance will increase in the Spöl community as a response to the experimental flood program (period 2000-2016). At the same time, it is expected c) that the discontinuation of the flood program (period 2016-2020) will result in a functional reversal to pre-flood conditions.

- H2: Functional responses of macroinvertebrate community to climate-driven environmental change (Aqua, Fuorn): With the use of long-term periphyton biomass and water temperature data, it is aimed to find evidence of climate-driven environmental change. Based on these results, it is expected a) to find clues of progressive functional shifts in the unregulated catchments of Aqua and Fuorn. It is further expected that b) glacial signature (i.e. the extent of glacial coverage in the catchment) will influence the intensity of these climate-driven functional shifts.

2 Methods

2.1 Study sites

The river Spöl (Figure 1) is a regulated river located in the central Alps, in eastern Switzerland, with a catchment of 286 km^2 (Scheurer & Molinari, 2003). The 5.7 km river reach interested by the experimental flood program is located downstream of the Livigno reservoir, at the Swiss-Italian border. This canyon-confined reach crosses the Swiss National Park before flowing into the Ova Spin reservoir. The sampling site is located in the Spöl Valley at Punt Periv, ~ 2.4 km downstream of the Punt da Gall dam. Mean residual flow from the dam is 0.55 m^3/s in winter and 2.5 m^3/s in summer, not taking into account the experimental floods (Robinson et al., 2018).

Two unregulated tributaries, Val da l’Aqua (Aqua; Figure 1) and Ova dal Fuorn (Fuorn; Figure 1) act as reference streams for the experimental flood program. Both study sites are located in the Swiss National Park. Their flow regime is typically alpine, with high flows in late spring/summer (snowmelt and glacial melt) and base flow in winter. Aqua drains a catchment of 4.3 km^2 containing a small rock glacier (0.2% of the catchment area; Robinson et al., 2004) and flows into the Spöl about 0.8 km downstream of the Spöl sampling site (Figure 1). An average discharge of 0.38 m^3/s (range 0.06–0.69 m^3/s; was measured between 1999 and 2000; Robinson et al., 2004). Fuorn drains a catchment of 57.6 m^2 of which 0.02% is covered by an ice field relic (Sertić Perić et al., 2015) and flows into the Spöl about 3.4 km downstream of the Spöl sampling site (Figure *1*). Mean annual discharge during the study was 1.05 m^3/s (range 0.2–7.3 m^3/s; Federal Office of the Environment; station Punt la Drossa). Riparian vegetation at all three study sites is dominated by larch and mugo pines (Sertić Perić et al., 2015) and stream substrate is characterized by alluvial cobbles and boulders; Robinson et al., 2004). Discharge data for Spöl and Fuorn used in the analysis originate from federal discharge stations located near the study sites (Spöl station: 46°37′42.454″N, 10°11′40.883″E, approx. 1.8 km upstream of the sampling site; Fuorn station: 46°39′18.619″N, 10°11′23.984″E, approx. 0.25 km downstream of sampling site). Due to the absence of a permanent gauging station, discharge was not regularly measured at Aqua.

2.2 Experimental flood program on the river Spöl

The Spöl catchment is part of the ramified EKW (Engadiner Kraftwerke) hydropower network. In the 70s, two pump-storage dams were built along its course (Punt da Gall and Ova Spin; Figure 1) to create storage reservoirs for hydropower electricity production (Scheurer & Molinari, 2003). After regulation, the constant residual flow from the Punt da Gall dam caused severe ecosystem alterations in the river Spöl. The lack of periodic disturbance promoted riverbed clogging by fine sediments and excess algal and moss growth, which determined dramatic habitat changes (Mürle et al., 2003; Uehlinger et al., 2003). The availability of trout spawning grounds declined, and *Gammarus fossarum* colonized and become dominant in the system (Ortlepp & Mürle, 2003). Macroinvertebrate assemblage changed, with species preferring stable conditions (including *Gammarus fossarum*) benefitting from residual flow conditions (Robinson et al., 2003). Further, reservoir deep-water releases changed water physico-chemical characteristics, resulting in lower water temperature and higher nutrient load (Scheurer & Molinari, 2003).

To mitigate these impacts, the Swiss National Park, EKW and the cantonal environmental agencies agreed on an experimental flood program starting in 2000. The aims were to a) enhance instream habitat conditions to improve substrate suitability for brown trout spawning, b) optimize the flood discharge necessary to maintain a near-natural ecological state and c) gain scientific knowledge regarding a long-term implementation of a regulated flow regime (Scheurer & Molinari, 2003). During the flood program, between 2000 and 2016, 32 experimental floods were released. These floods differed by timing and magnitude (Figure 2), depending on water availability and research objectives (Robinson et al., 2018). In March 2013, due to technical issues, water mixed with large amounts of fine sediments was released from Punt da Gall. It was estimated that this event killed ~64% of the trout population, and fine sediment deposition strongly reduced macroinvertebrates density (Robinson et al., 2018). The deposited sediments were successfully removed from the riverbed with a flushing flow in July 2013 (Task Force Spöl, 2015). In 2016, the experimental flood was suspended as a precautionary measure following a severe polychlorinated biphenyl (PCB) contamination, which were released during dam retrofitting (Swiss National Park, 2021).

Several studies analyzed the short- and long-term effects on the ecosystem in the Spöl and observed that experimental floods enhanced the ecological conditions of the river. The floods successfully reduced clogging, benthic organic material and periphyton biomass, and improved spawning conditions for brown trout (Mürle et al., 2003; Ortlepp & Mürle, 2003; Robinson et al., 2004, 2018; Robinson & Uehlinger, 2008). Macroinvertebrate densities and taxonomic richness decreased, resulting in community shifts. Originally highly abundant taxa (i.a. *Gammarus fossarum*) were reduced while more alpine-stream-associated taxa (mayflies and stoneflies) were favored (Robinson, 2012; Robinson et al., 2018).

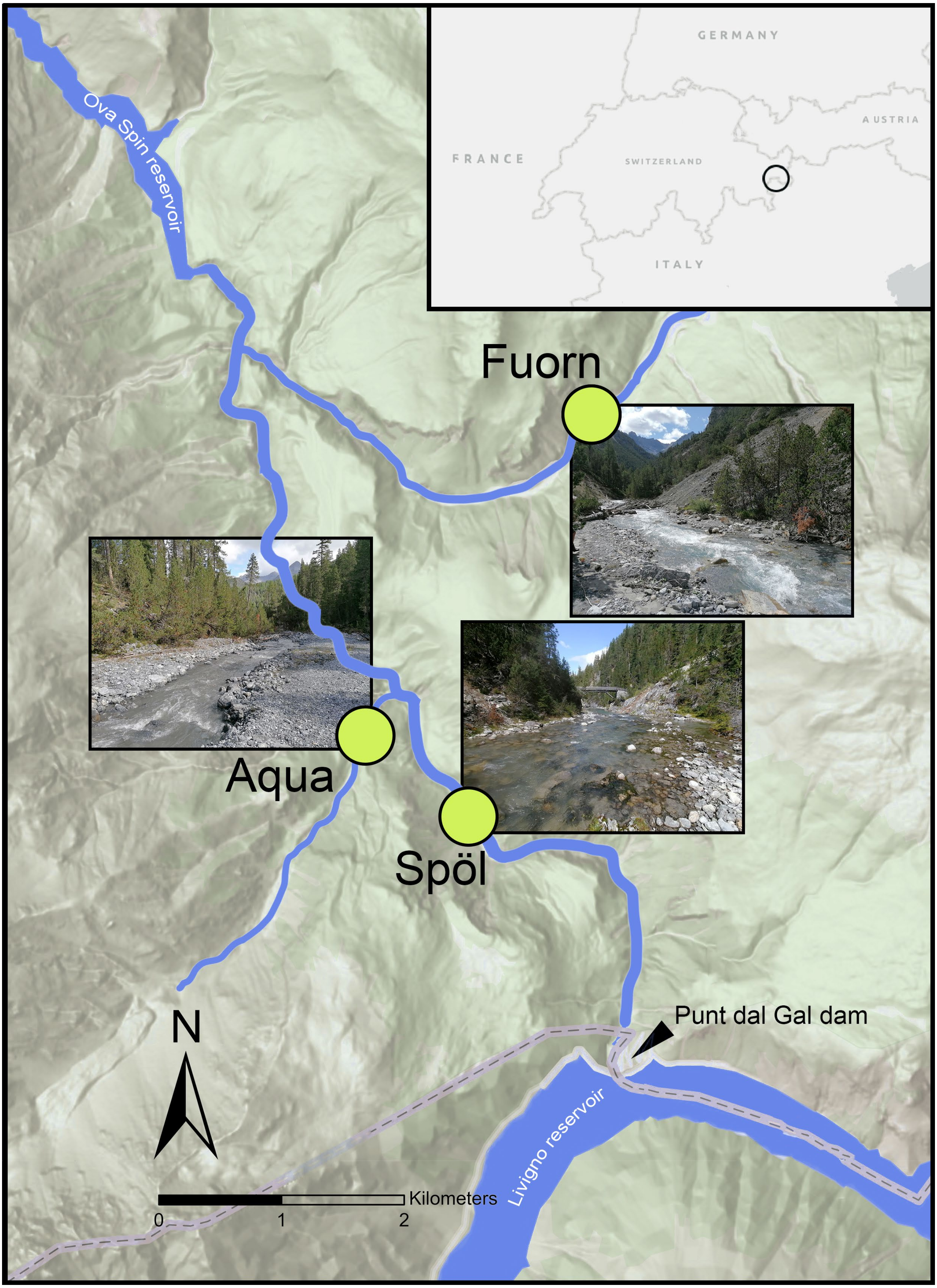
GERMANY
AUSTRIA
FRANCE
SWITZERLAND
ITALY
Ova Spin reservoir
Fuorn
Aqua
Spöl
Punt dal Gal dam
Livigno reservoir
N
Kilometers
0
1
2

Figure 1: Map showing the locations of the study sites (yellow circles) Spöl (46°38'13.777"N, 10°10'55.494"E; 1658 m a.s.l.), Aqua (46°38'26.447"N, 10°10'29.895"E; 1741 m a.s.l.) and Fuorn (46°39'24.270"N, 10°11'29.110"E; 1716 a.s.l.) together with pictures of the study sites (captured in August 2021). Black arrow indicates the location of the Punt dal Gal dam. Dashed line indicates the Swiss-Italian border. Data source: Swiss Federal Office of Topography & Esri.

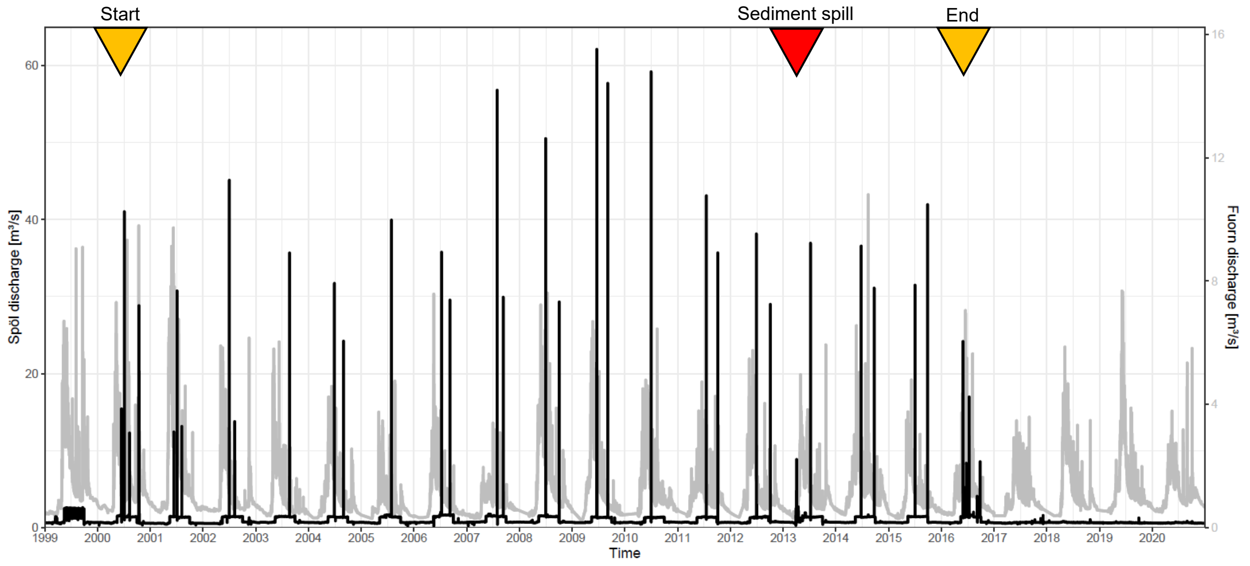

Figure 2: Hourly mean discharge during the study period at Spöl – Punt da Gall (left y-axis, black line) and Fuorn – Punt la Drossa (right y-axis, grey line). The experimental flood program started in June 2000 and ended with the last flood in May 2016. Orange triangles mark the start and the end of the flood program in the Spöl. Red triangle marks the time of the 2013 accidental sediment spill on the Spöl. Please note different scales on y-axes. Data source: Swiss Federal Office for the Environment FOEN.

2.3 Data collection and processing

Samples were collected for the long-term monitoring as described in Robinson et al. (2018). Benthic macroinvertebrates were collected from 1999 to 2020 on Spöl and Aqua, and from 2002 to 2020 on Fuorn, approximately every 5-6 weeks mainly from spring (April/May) to autumn (October/November). Winter months were not sampled due to difficult accessibility of streams (ice and snow on trails). At each sampling site and at each visit three macroinvertebrate samples were taken from riffle/run habitats using a Hess sampler (modified, 0.045 m^2, 250-µm mesh) and preserved with 70% ethanol until further processing. In the laboratory, macroinvertebrates were separated from organic and inorganic material and identified to the lowest practical taxonomic level (usually family or genus) using a stereo microscope (10x magnification). Similarly, periphyton was sampled at each sampling site and visit by randomly collecting five stones, which were stored at −20°C until further processing. In the laboratory, periphyton was scraped from the stones surface using a wire brush and water to rinse. A fraction of the resulting aqueous solution was filtered through glass-fiber filters (Whatman GF/F, precombusted) to retain the suspended periphyton. The filter was then dried (60°C) and burned (500°C at 4 h). Ash free dry mass (gAFDM) was calculated as the difference in weight before and after burning. Periphyton biomass (gAFDM/m^2) was estimated after Uehlinger (1991) by measuring stone's main axes (a-, b-axis) to estimate stone surface using the formula $a*b*\pi/4$. At each visit, conductivity and turbidity were measured, and a water grab (0.5 l) was collected for water chemistry analysis (data not used in this project). At each site water temperature (1 h intervals) was recorded using temperature loggers (VEMCO Minilog). Technical issues (e.g., dead batteries, logger launch failure) over the years resulted in some gaps in temperature time series (Figure 6).

2.4 Data analysis

2.4.1 Trait selection and allocation

A common distinction is made between biological traits (physiological and behavioural characteristics, e.g. body size, feeding preferences, dispersal strategies or life cycle duration) and ecological traits, reflecting habitat preferences such as water temperature or pH (Menezes et al., 2010; Tachet et al., 2010). Here, the functional community composition was characterized by selecting 11 biological traits (together containing 59 trait categories; Table 1): food preference, feeding habits, locomotion and substrate relation, respiration, body size, resistance forms, dispersal, types of aquatic stages, potential number of life cycles per year and life cycle duration. The response of these traits to environmental change has been analyzed before in the context of glacier-fed streams (Brown et al., 2018; Brown & Milner, 2012; Bruno et al., 2019; Cauvy-Fraunié et al., 2016) and/or climate change (e.g. Bonada et al., 2007). For later calculation of functional diversity indices, food preference, feeding habits, locomotion, body size and dispersal have been defined as effect traits, which can directly affect ecosystem properties and the provision of ecosystem services (Hevia et al., 2017). All trait information have been retrieved from the freshwaterecology.info database (Schmidt-Kloiber & Hering, 2015) and originate from Tachet et al. (2010). The Tachet trait information is available as fuzzy coded data which describes the affinity of a taxon to a given trait category (Chevenet et al., 1994). This approach allows the assignment of a taxon to more than one trait category using scores, from 0 (no affinity) to 3 or 5 (high affinity). The fuzzy codes for each trait category were further standardized per trait to account for the different fuzzy code scales. A trait database (traits x taxa; Q-table) was built for the occurring taxa in Spöl, Aqua and Fuorn (Appendix A). In most cases taxa were identified to the genus level, which has been identified as the ideal taxonomic resolution for trait studies (i.e. tradeoff between identification effort *vs* information detail; Statzner & Bêche, 2010). However, some years reported only family level identification. In these cases an aggregation of trait scores based on the species present in the catchment was applied, using a detailed species list available for the Spöl catchment (years 1997-2014; courtesy of Uta Mürle, Hydra AG). Family level should however still allow a realistic functional description of the macroinvertebrate community (Gayraud et al., 2003) and thus only have a minor impact on the accuracy of the results of this study. Hydracarina (0.05% of the total number of individuals) was excluded from the analysis due to a lack of trait information.

The three macroinvertebrate samples collected at each site/visit were pooled (mean), resulting in 161 samples for Spöl, 110 samples for Aqua and 90 samples for Fuorn. Following statistical analysis was performed using R version 4.1.1 (R Core Team, 2021). Log(x+1) transformation was applied to the abundance data (samples x taxa; L-table) to reduce the effect of highly abundant taxa (i.e. Chironomidae, Protonemura, Gammarus and Baetidae) with regard to further analysis steps (Májeková et al., 2016; Schmera et al., 2014). For the functional analysis of macroinvertebrates on a community level, community-weighted mean (CWM) trait values were calculated for each sample resp. community by combining the Q-table with the L-table as follows:

$$\sum_{i=1}^{n} p_i \, t_i$$

where n is the number of taxa in a community, p_i is the proportion of taxon abundance and t_i is the trait value of taxon (Garnier et al., 2004). CWM quantify the weight of each trait category in a community and sum up to 1 for each trait and were the basis for further analysis approaches apart from functional diversity indices. Spöl samples collected shortly (within 12 days) after an experimental flood were excluded from the analysis to reduce the impact of strong short-term flood effects on the long-term analysis.

2.4.2 Functional community composition and individual traits analysis

Fuzzy correspondence analysis (FCA) based on CWM was used to explore the functional structure of all macroinvertebrate samples at Spöl, Aqua and Fuorn. FCA is a multivariate approach that applies a correspondence analysis to fuzzy coded data, such as trait scores (Chevenet et al., 1994). FCA was generated using R package “ade4”

(Dray & Dufour, 2007). Pearson correlation with Bonferroni correction identified significant relationships between trait categories and the first two FCA-axes. Ellipses grouping the samples per study site (s.class function from the ade4 package) were plotted to show general differences between sites. Pairwise permutational analysis of variance (PERMANOVA) based on CWM was applied to test for general differences between sites (Anderson, 2001; Martinez Arbizu, 2020; McArdle & Anderson, 2001). PERMANOVA was accompanied by a permutational analysis of multivariate dispersion (PERMDISP) using Bray-Curtis distances between samples to test for homogeneity of multivariate dispersion (Anderson, 2006). Analysis of variance (ANOVA) was used to test for significance of PERMDISP. R packages “pairwiseAdonis” (Martinez Arbizu, 2020) was used for pairwise PERMANOVA and “vegan” (Oksanen et al., 2020) for PERMIDSP.

To visualize temporal shifts along the first two FCA-axes, eight separate temporal blocks have been defined according to shifts in taxonomic community composition at Spöl previously described by Robinson et al. (2012, 2018); 1999-2000, 2001-2002, 2003-2006, 2007-2010, 2011-2012, sediment spill (2013), 2014-2016 and post-flood (2017-2020). Ellipses grouping the Spöl samples according to these temporal blocks were further plotted in FCA ordination space. Individual trait categories that correlated significantly with at least one of the first two FCA-axes were used to investigate single trait patterns of response and differences between sites. Generalized additive model (GAM) smoothing splines were fitted to visualize these patterns at Spöl, while linear model (LM) smoothing splines were fitted for the reference sites, where linear relationships were assumed. Additionally, linear regression analysis was used for the reference sites to test for significant (Bonferroni corrected) increase or decrease over the study period. To account for autocorrelation, confidence intervals were expanded using heteroscedasticity and autocorrelation (HAC) robust standard errors (Zeileis, 2004).

2.4.3 Functional diversity

Five functional diversity indices were calculated to quantify community composition in functional space. Functional space can be defined as “a multidimensional space where the axes are functional traits along which species are placed according to their functional trait” (Mouillot et al., 2013). The indices calculated were: 1) Functional richness (FRic) which represents the volume within the functional space occupied by a community (Mason et al., 2005). 2) Functional dispersion (FDis) which is the mean distance of a community from the centroid of the functional space, affected by species richness (Laliberté & Legendre, 2010) and measures both functional richness and divergence (Mason et al., 2013). 3) Rao's quadratic entropy (RaoQ; Botta-Dukát, 2005; Rao, 1982) as a frequently used index for functional diversity of macroinvertebrates communities (Schmera et al., 2014). RaoQ measures both functional richness and dispersion (Mason et al., 2013). 4) Functional evenness (FEve) which describes the regularity of distribution of a community in functional space (Mason et al., 2005; Villéger et al., 2008). 5) Functional redundancy (FRed) which quantifies the extent to which taxa within a community share traits (Rosenfeld, 2002). Calculation of functional diversity indices followed the approach of Bruno et al. (2019) and consisted in a first step of building functional spaces using Gower dissimilarity matrices (Maire et al., 2015) adapted to fuzzy coded trait data (Pavoine et al., 2009). Functional diversity indices were calculated using the R packages "ade4" (Dray & Dufour, 2007) and "FD" (Laliberté & Legendre, 2010). Kruskal–Wallis test followed by a multiple comparison test and a Pairwise Wilcoxon Rank Sum Tests was used to test for general differences in functional diversity indices between the sites. Temporal patterns of the functional diversity indices over time were visualized fitting a GAM smoothing spline for Spöl, and a linear model for Aqua and Fuorn. For Aqua and Fuorn, a linear regression analysis was applied to test for significant (Bonferroni corrected) increase or decrease over the study period. To account for autocorrelation, confidence intervals were expanded using HAC robust standard errors (Zeileis, 2004).

2.4.4 Environmental data

Daily means of water temperature were calculated to detect potential long-term changes related to climate change. Linear regression analysis considering years without data gaps was applied to test for significant temperature increase at Spöl, Aqua and Fuorn. To account for autocorrelation, confidence intervals were expanded using HAC robust standard errors (Zeileis, 2004). The same approach was used to estimate changes in periphyton biomass for Aqua and Fuorn. For Spöl, temporal patterns of periphyton biomass were visualized using GAM smoothing splines. As for macroinvertebrates, periphyton samples collected within 12 days after a flood event were excluded from the analysis.

3 Results

3.1 Functional community composition and individual traits

On Spöl, the macroinvertebrate community composition over the entire study period was dominated (ca. 91% relative abundance) by six taxa: Chironomidae (31.9%), *Gammarus sp.* (23.9%), *Baetis spp*. (11.5%), *Protonemura spp.* (9.8%), *Leuctra spp.* (7.0%) and Simuliidae (6.7%). On Aqua (1999-2020), *Protonemura* was the most abundant taxon (37.8%) followed by Chironomidae (21.0%), Heptagenidae (12.4%), *Baetis spp.* (11.6%) and Limoniidae (7.2%). On Fuorn (2002-2020), most abundant taxa were Chironomidae (38.4%), *Protonemura spp.* (15.5%), *Baetis* spp. (11.8%), Heptagenidae (11.1%), *Leuctra spp.* (5.6%) and *Nemoura spp.* (5.4%).

FCA over the entire study period showed differences in functional structure between the macroinvertebrate communities of the three study sites, which mainly separate along the first FCA-axis (Figure 3). Pairwise PERMANOVA analysis based on CWM confirmed significant differences between the functional community composition of Spöl and Aqua ($R2 = 0.36$, $p < 0.01$), Spöl and Fuorn ($R2 = 0.17$, $p< 0.01$) and Aqua and Fuorn ($R2 = 0.07$, $p < 0.01$). PERMDISP analysis showed significant differences in multivariate dispersion between functional community composition of Spöl, Aqua and Fuorn ($p < 0.05$). Detailed results of pairwise PERMANOVA and PERMDISP are shown in Appendix B. Multiple trait categories correlated significantly with the first two axis of the FCA (Table 1). Ordination of FCA results with Spöl samples grouped in time blocks showed temporal shifts of Spöls functional community composition towards the reference sites, being most similar between 2007 to 2010 (Figure 4). Subsequently, a shift back towards pre-flood composition was observed between 2011 to 2013 before becoming again more similar to reference sites between 2014 to 2016. Post-flood (2017-2020) functional community composition at Spöl was similar to the on found in the first year of the flood program (2000-2004). Individual trait responses of Spöl, Aqua and Fuorn communities during the study period are shown in Appendix C. For Fuorn and Aqua, results from linear model fit to individual traits are shown in Appendix D.

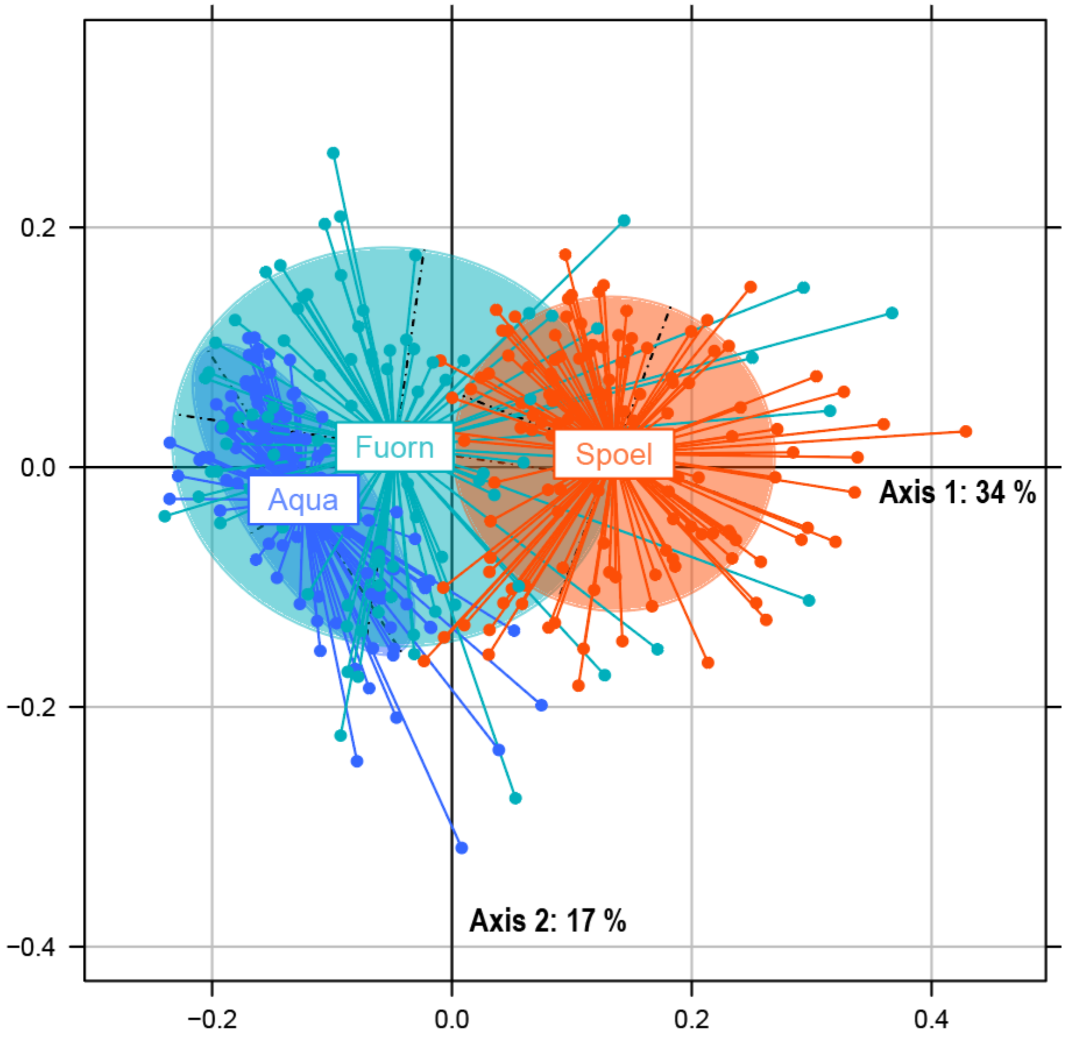

Figure 3: Ordination plot showing the results of FCA for macroinvertebrate community from Spöl, Aqua and Fuorn from 1999 to 2020. Each point represents a sampling visit (pooled sample). A) Distribution of samples along the first two FCA-axes. Explained variance of the first two axes is depicted. Ellipses separate samples between sites.

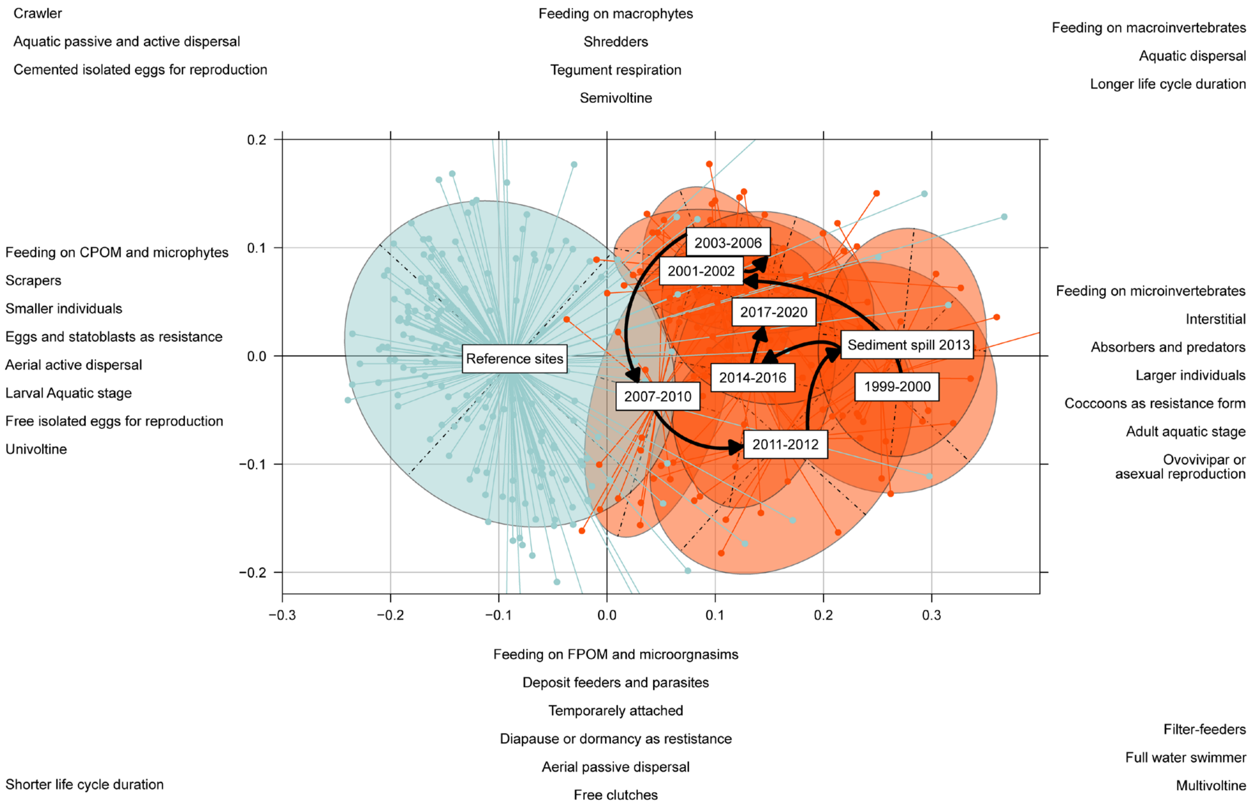

Figure 4: Ordination plot showing the results of FCA for the macroinvertebrate community from Spöl as well as Aqua and Fuorn (taken together as reference sites) from 1999 to 2020. Each point represents a sampling visit (pooled sample). Ellipses group the samples per temporal blocks for Spöl (orange), and reference sites (light blue). Black arrows indicate the temporal change in functional community composition along the first two FCA-axes. Trait categories correlating significantly ($R \geq 0.40$ and $p < 0.001$; Table 1) with one or both axes are listed along the FCA axes (explained variance axis 1 = 34%, axis 2 = 17%). Their position corresponds to the axis and the sign of the relationship (positive or negative). Trait categories located at the corner of the plot were significantly correlated to both axes (Table 1). Please note that single trait categories were aggregated in this figure to reduce complexity.

Table 1: Spearman correlation coefficients between traits and the first two axes of FCA for Spöl, Aqua and Fuorn. Bold coefficients correspond to strongly (R ≥ 0.40) and significantly (p < 0.001 after Bonferroni correction) correlated traits.

			R coefficient	
Traits	**Trait categories**	**Trait codes**	**Axis 1**	**Axis 2**
Food preference	Microorganisms	T1_1	-0.24	**-0.45**
	Detritus < 1mm	T1_2	-0.07	**-0.81**
	Dead plant ≥ 1mm	T1_3	**-0.55**	0.02
	Living microphytes	T1_4	**-0.77**	0.00
	Living macrophytes	T1_5	0.03	**0.60**
	Dead animal ≥ 1mm	T1_6	**0.47**	**0.40**
	Living microinvertebrates	T1_7	**0.86**	-0.10
	Living macroinvertebrates	T1_8	**0.56**	**0.45**
	Vertebrates	T1_9	0.02	0.23
Feeding habits	Absorber	T2_1	**0.47**	0.09
	Deposit feeder	T2_2	-0.06	**-0.41**
	Shredder	T2_3	-0.30	**0.41**
	Scraper	T2_4	**-0.46**	-0.15
	Filter-feeder	T2_5	**0.40**	**-0.67**
	Piercer	T2_6	0.02	0.23
	Predator	T2_7	**0.44**	0.32
	Parasite	T2_8	0.05	**-0.66**
Locomotion and substrate relation	Flier	T3_1	-0.09	0.03
	Full water swimmer	T3_3	**0.53**	**-0.41**
	Crawler	T3_4	**-0.65**	**0.52**
	Burrower	T3_5	-0.29	0.11
	Interstitial	T3_6	**0.83**	0.09
	Temporarily attached	T3_7	0.39	**-0.77**
	Permanently attached	T3_8	0.36	0.05
Respiration	Tegument	T4_1	-0.04	**0.40**
	Gill	T4_2	0.18	-0.27
	Plastron	T4_3	-0.09	0.03
	Spiracle	T4_4	-0.24	-0.31
Maximal potential size	≤ 0.25cm	T5_1	**0.47**	0.09
	> 0.25 - 0.5 cm	T5_2	0.24	**-0.72**
	> 0.5 - 1 cm	T5_3	**-0.73**	-0.11
	> 1 - 2 cm	T5_4	-0.29	**0.42**
	> 2 - 4 cm	T5_5	**0.82**	0.17
	> 4 - 8 cm	T5_6	0.11	-0.04
	> 8 cm	T5_7	**0.45**	0.14
Resistance forms	Eggs, statoblasts	T6_1	**-0.61**	0.12
	Cocoons	T6_2	**0.64**	0.28
	Diapause or dormancy	T6_4	-0.19	**-0.64**
	None	T6_5	0.14	0.04
Dispersal	Aquatic passive	T7_1	**0.60**	**0.41**
	Aquatic active	T7_2	**0.43**	**0.64**
	Aerial passive	T7_3	0.01	**-0.94**
	Aerial active	T7_4	**-0.81**	0.22
Aquatic stages	Egg	T8_1	**-0.63**	**0.64**

	Larva	T8_2	**-0.91**	-0.07
	Nymph	T8_3	0.34	**-0.78**
	Adult	T8_4	**0.93**	0.17
Potential number of cycles per year	< 1	T9_1	-0.25	**0.63**
	1	T9_2	**-0.82**	0.11
	> 1	T9_3	**0.82**	**-0.42**
Reproduction	Ovovivipar	T10_1	**0.84**	-0.18
	Free isolated eggs	T10_2	**-0.56**	-0.23
	Cemented isolated eggs	T10_3	**-0.67**	**0.50**
	Fixed clutches	T10_4	0.03	0.02
	Free clutches	T10_5	0.00	**-0.76**
	Terrestrial clutches	T10_7	0.39	-0.03
	Asexual	T10_8	**0.66**	0.23
Life cycle duration	≤ 1 year	T12_1	**-0.77**	**-0.50**
	> 1 year	T12_2	**0.77**	**0.50**

3.2 Functional diversity

Kruskal-Wallis test over the whole study period showed significant differences in functional indices FRic, FDis, RaoQ and FRed between Spöl and the reference sites, while no significant difference was found in FEve (Table 2 & Figure 5). FRic and RaoQ for Spöl were originally higher than at reference sites. The first ten years of the flood program resulted in a shift towards Aqua and Fuorn, meaning that the functional space occupied and the functional entropy at Spöl decreased. However, full overlap was never achieved and between 2011 - 2014, these indices increased, diverging from the reference sites. After flood discontinuation, RaoQ and FRic seem to be returning to pre-flood values. Similarly, FDis was overall higher for Spöl and showed similar patterns to FRic and RaoQ with a lower effect amplitude. The decrease in FDis corresponds to a reduction in deviation of community trait values from the center of functional space, resp. a functional homogenization. FEve did not show patterns related to the flow alteration at Spöl but followed a linear, stable trend and thus described a constant distribution of macroinvertebrate abundances and dissimilarities in functional space. Overall FEve at Spöl was similar to the reference reaches and showed no significant differences (Table 2 & Figure 5). Overall FRed for Spöl was lower than the reference sites and showed similar convergence pattern to FRic, FDis and RaoQ. The increase in FRed during the first decade of the experimental flood program indicated that more traits in the Spöl community were shared by the taxa.

No significant differences were found when comparing the functional diversity indices between Aqua and Fuorn (Table 2). Linear regression (Table 3) showed significant increases in FRed at Aqua and FRic at Fuorn during the study period as well as a decrease in RaoQ at Aqua.

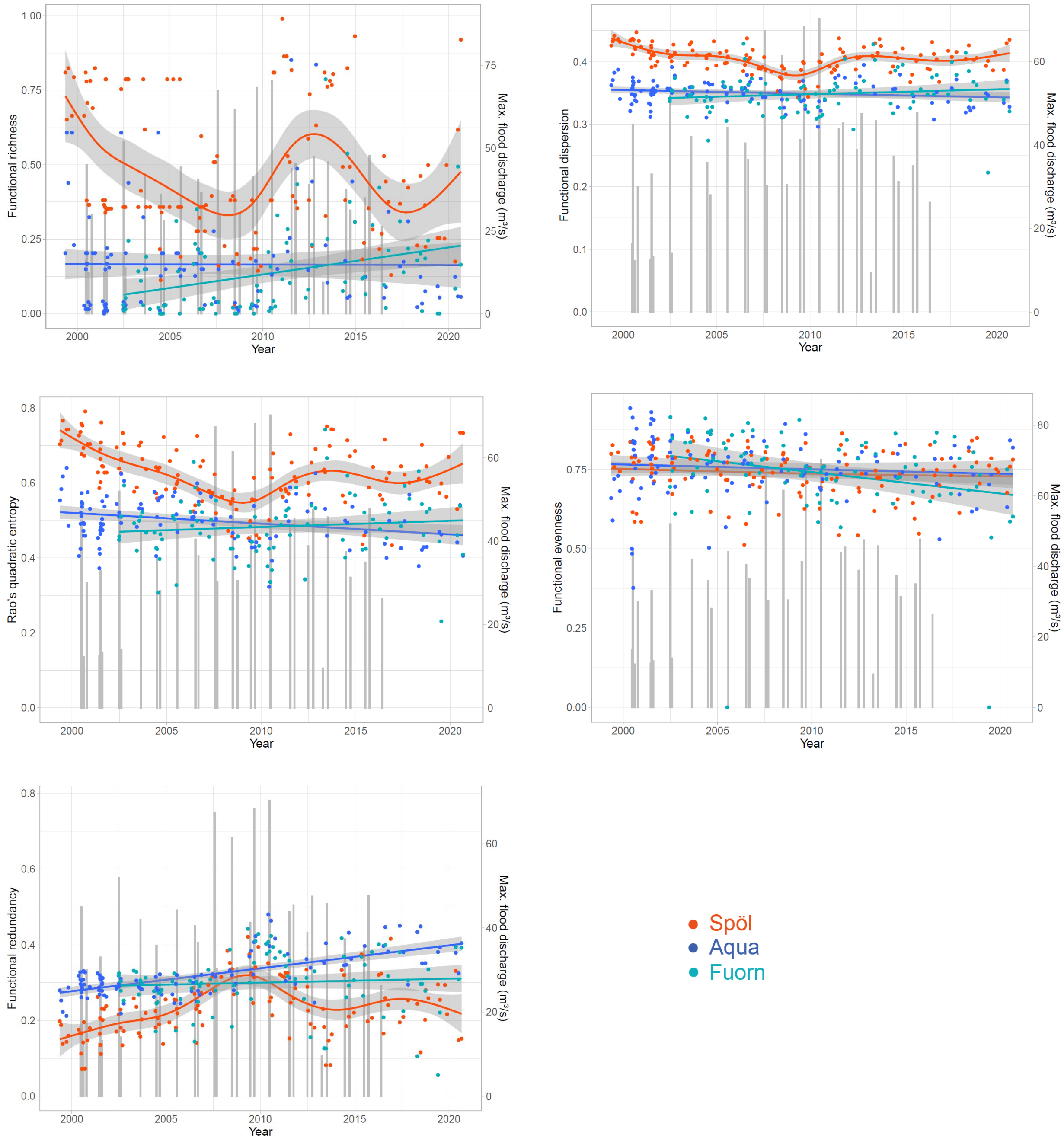

Figure 5: Functional diversity indices (left y-axis) calculated over the study period. Fitted GAM (Spöl) resp. LM (Aqua & Fuorn) splines are depicted together with 95% confidence bands (grey area). Maximum flood discharge of experimental floods (right y-axis) is shown as grey bars.

*Table 2: Results of Kruskal-Wallis, Kruskal-Wallis multiple comparison and Wilcoxon test comparing different functional diversity indices for Spöl, Aqua and Fuorn over the whole study period. Chi-square (χ^2) is given per comparison. Significant results are marked (***:p < 0.001).*

	Comparison	**χ2 RaoQ**	**χ2 FRic**	**χ2 FDis**	**χ2 FEve**	**χ2 FRed**
Kruskal-Wallis	Spöl – Aqua - Fuorn	149.87***	153.35***	194.62***	2.55	73.78***
Wilcoxon & multiple comparison	Spöl – Aqua	124.25***	125.35***	148.76***	19.19	99.61***
	Spöl – Fuorn	139.28***	141.17***	151.19***	13.16	80.39***
	Aqua - Fuorn	15.03	15.82	2.43	6.03	80.39

*Table 3: Results from linear regression model between the different FD indices and year for Aqua and Fuorn taking into account HAC robust standard errors. Adjusted R^2 and standard scores (z) are given. Significant results after Bonferroni correction are marked (***: p < 0.001, ** :p < 0.01).*

	Aqua		**Fuorn**	
FD index	**Adj. R2**	**z**	**Adj. R2**	**z**
RaoQ	0.08**	-2.62**	0.00	0.82
FRic	-0.01	-0.43	0.10**	3.23**
FDis	0.03	-1.61	0.01	0.88
FEve	0.00	-0.968	0.05	-1.94
FRed	0.45***	7.96***	-0.01	0.62

3.3 Water temperature and periphyton

Yearly mean water temperature during the study period was 5.3 ± 0.4°C (mean ± standard deviation (SD)) at Spöl, 2.8°C ± 0.2°C (mean ± SD) at Aqua and 4.8°C ± 0.3°C (mean ± SD) at Fuorn. Regression splines of annual water temperature data indicated an increase in mean water temperature at Spöl, Aqua and Fuorn from 1999 to 2020 (Figure 6). This trend was supported by the linear regression models with Spöl showing the strongest increase (beta coefficient (β) = 0.036; adj. $R^2 = 0.58$), followed by Fuorn ($\beta = 0.023$; adj. $R^2 = 0.35$) and Aqua ($\beta = 0.015$; adj. $R^2 = 0.12$). When using expanded standard errors, Spöl ($p < 0.001$) and Fuorn ($p < 0.001$) showed a significant increase in water temperature during the study period, but not Aqua ($p = 0.054$). Similarly, an increase in periphyton biomass during the study period occurred at both reference sites and was confirmed by the linear regression models with expanded standard errors (Figure 7). This increase was significant and similar for both Aqua ($\beta = 9.38 \cdot 10^{-9}$; adj. $R^2 = 0.12$; $p < 0.001$) and Fuorn ($\beta = 7.09 \cdot 10^{-9}$; adj. $R^2 = 0.08$; $p < 0.001$). GAM spline of Spöl periphyton biomass showed a strong decrease in the first ten years of the experimental flood program, (from 38.6 ± 23.9 gAFDM/m^2 in 1999 to 12.3 ± 8.4 gAFDM/m^2 in 2010). Confidence bands indicated greater fluctuations of periphyton biomass at Spöl compared to the reference sites (Figure 7).

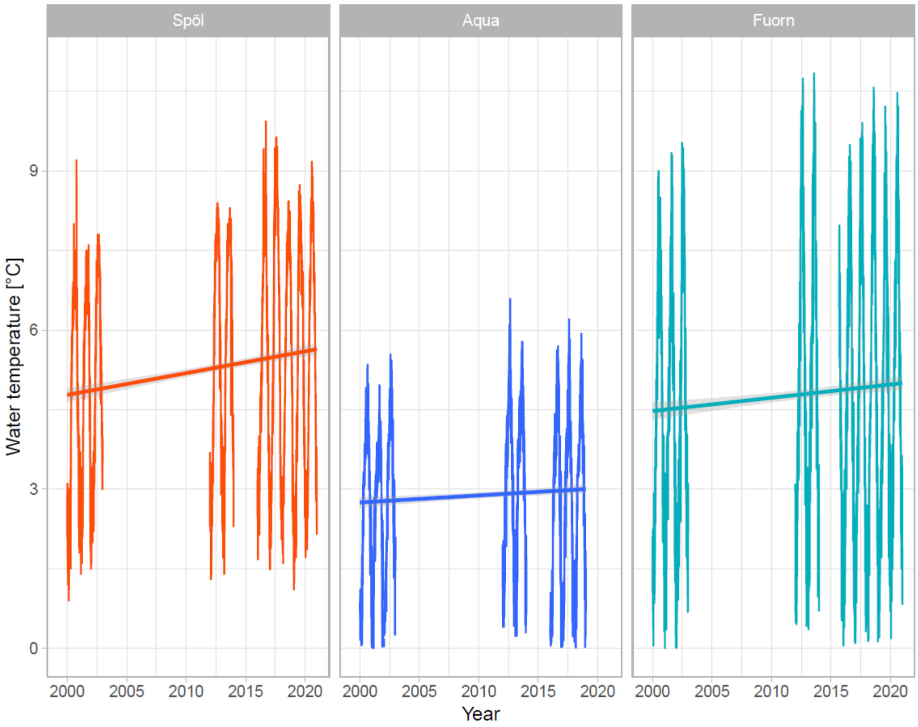

Figure 6. Daily mean water temperature (°C) measured at Spöl, Aqua and Fuorn. LM splines are depicted together with 95% confidence bands.

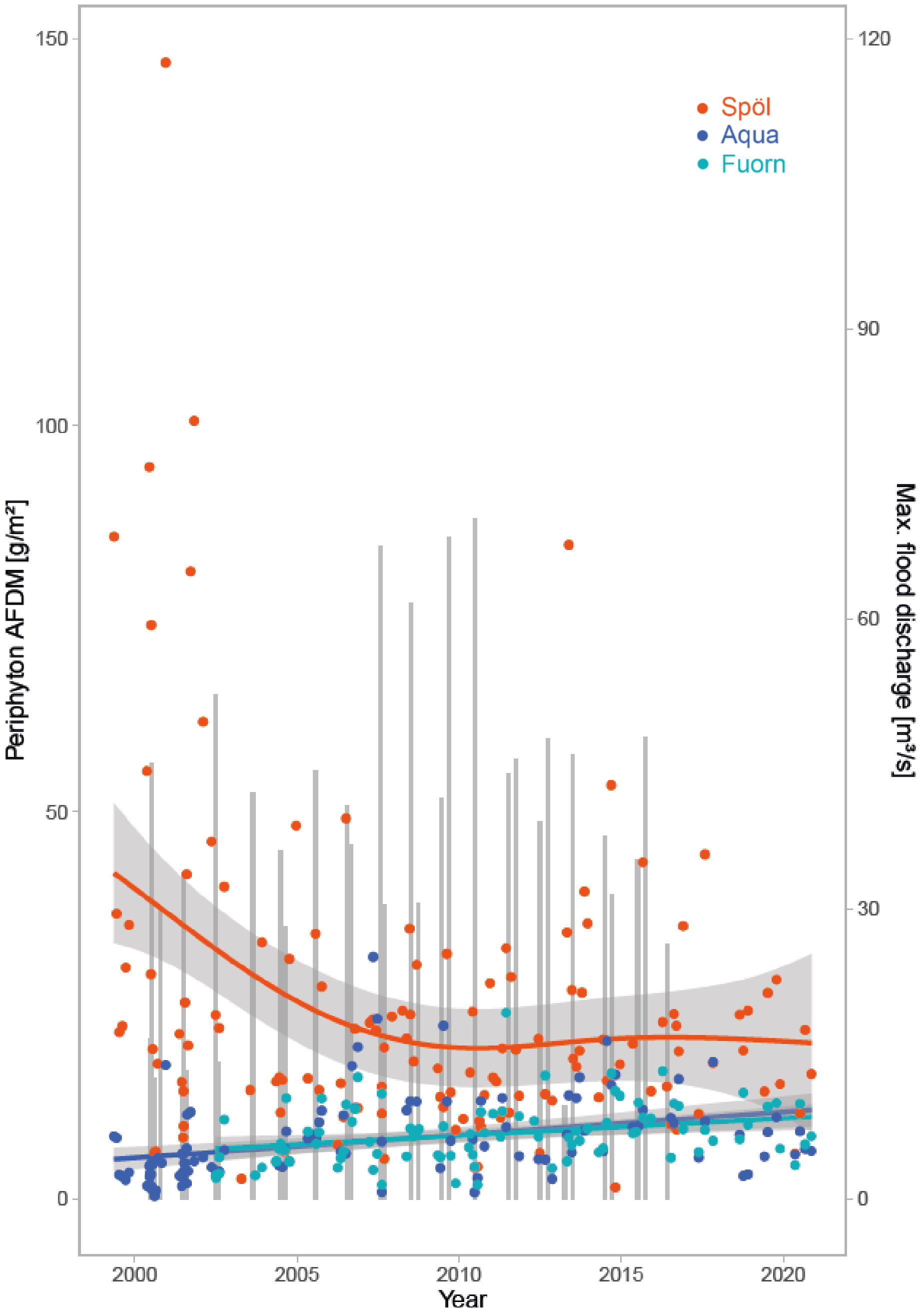

Figure 7: Periphyton biomass expressed as gAFDM (g/m^2) over the study period. Fitted GAM (Spöl) resp. LM (Aqua and Fuorn) splines are depicted together with 95% confidence bands.

4 Discussion

4.1 Long-term functional responses to experimental floods

4.1.1 Community responses

Flow regulation on the river Spöl resulted in a clear separation of its macroinvertebrate community compared to the unregulated streams, reflecting different functional adaptations to environmental conditions (stability *vs* disturbance). Separation in functional community composition as a response to flow regulation has been observed before in alpine catchments influenced by hydropower production (Bruno et al., 2019). Stable flow conditions as a consequence of damming come with a well-defined series of environmental changes, which clearly select for specific suits of traits. Functional strategies that rely on resistance/resilience, with the capacity of quick recovery after disturbance are not advantageous in residual flow environments. The expectation is that flow restoration would lead to a progressive functional shift towards communities characteristic of natural systems (Poff et al., 1997, 2017). The results of this study indicate that the experimental floods released over a 17-years period were successful in triggering functional community re-arrangement, but did not result in a complete ecological restoration. Experimental floods are point source of disturbance that generate both transient and more permanent changes in the river habitat template. On the Spöl, the functional goal (*sensu* Yarnell et al., 2015) of the flood program was to restore spawning habitat conditions for brown trout, and benthic invertebrates indirectly benefited from enhanced habitat conditions.

Temporal patterns (Figure 4) showed that functional community shifted between states over the years, but was close to reference conditions only between 2007 and 2010. A closer look at temporal dynamics reveals that shifts were unpredictable in direction and characterized by alternate community states (Robinson, 2012). It was observed that functional shifts were closely related to taxonomic shifts as observed in temporal structural studies (Robinson, 2012; Robinson et al., 2004, 2018; Robinson & Uehlinger, 2008). A strong functional shift took place in the early flood years (2001-2002), leading to a relatively stable community until 2006. The major shift in taxonomic macroinvertebrate assemblage in 2003 observed by Robinson et al. (2012, 2018) from an assemblage in transition to a stable assemblage was not reflected by a functional change. This indicates that shifting communities were somehow functionally redundant, suggesting that the structural change involved functionally equivalent taxa (Dolédec & Bonada, 2013; Rosenfeld, 2002). The following major shift was observed in 2007 (also observed in taxonomic composition) and resulted in a functional assemblage most similar to the reference conditions, which lasted until 2010. Robinson (2012) attributed these changes to colonization events by novel, more alpine-stream-associated taxa (e.g., *Nemoura* and other stoneflies). During the same period (2007-2010), also several functional diversity indices showed the closest resemblance to the reference sites (see Chapter 4.1.1.1). These were the years when the experimental floods were characterized by the greatest magnitude (i.e., every year one flood had peak discharge > 50 m^3/s, and the five highest peaks of the flood program were reached; Figure 2) suggesting that repeated high flood peaks may be an important driver of macroinvertebrate functional community assembly. Regarding hypothesis 1a, these assembly patterns as well as the development of functional diversity (see Chapter 4.1.1.1) suggest that the functional adaptions to the new flow regime took place over one decade of experimental floods. In the following years (2011-2012) Robinson et al. (2018) observed an ongoing increase in taxonomic richness that exceeded pre-flood values and presumed a further ecosystem state change initiated by the colonization of alpine-stream-associated taxa as a response to the new flow regime. Functional community composition changed as well, diverging from reference conditions towards functional assemblage typical of pre-flood years. While such patterns could reflect the intrinsic stochasticity of populations dynamics in natural systems (Rinaldo et al., 2020), the results if this study suggest that ecological restorations/environmental flows could result in unpredictable intermediate states, highlighting the importance of the long term perspective when evaluating ecological responses (Hsieh et al., 2022; Robinson et al., 2018).

The catastrophic sediment spill in 2013 caused another major shift resetting the functional community composition to pre-floods conditions. Sediment flushing events have been shown to be able to alter functional community composition of macroinvertebrates to an extent that prevent full functional recovery (Folegot et al., 2021). The mechanism driving these functional alterations caused by an increase in fine sediment may be also linked to burial of organic litter resp. the reduction of CPOM (Doretto et al., 2016; Wilkes et al., 2017) and thus temporally affect traits related to food preferences or feeding habits, such as shredders (Folegot et al., 2021; Wilkes et al., 2017). Similarly, a strong decrease in individuals feeding on CPOM following the sediment spill was found. The shift triggered by the sediment spill and the following quick recovery were also observed in taxonomic community assembly (Robinson et al., 2018). Fast recovery after such a major pulse disturbance suggests high resilience of the macroinvertebrate community likely gained through the experimental flood program. The observed increase in functional redundancy (FRed) supports these findings (see Chapter 4.1.1.1). The interruption of the flood program and the return to environmental conditions typical of stable flows resulted in another shift. However, functional transition is delayed, indicating a gradual process of adaptation to the new flow regime. Functional diversity indices confirm (see Chapter 4.1.1.1) that post-flood composition is in a transition phase, anticipating a complete return to the pre-flood state within a few years and thus supporting hypothesis 1c. While environmental filtering was presumably the main driver of functional community assembly on Spöl under experimental floods conditions, other regional and local assembly mechanism, e.g. dispersal or intraspecific competition, may gain importance under stable conditions (Brown & Milner, 2012; Crespo-Pérez et al., 2020; Sommer et al., 2014) together with climate-driven alterations (see Chapter 4.2).

4.1.1.1 Functional diversity

Functional indices confirmed the temporal shifts observed in functional community composition (Figure 4). FRic, FDis and RaoQ were significantly higher (Table 2; Figure 5) at Spöl compared to the reference reaches but responded to the experimental floods by decreasing during the first ten years. Similar to the patterns seen in functional community composition, these indices indicate a convergence to reference sites that peaked in the 2007-2010 period. Lower FRic, FDis and RaoQ are characteristic of free-flowing mountain streams, determined by harsh conditions as well as resource limitation (Ward, 1994; Zobrist, 2010) and low productivity (Petchey, 2003), i.e. lower periphyton biomass (Figure 7). Highly dynamic systems are characterized by strong environmental filtering, and functional diversity is typically lower if compared to stable systems (i.e. the Spöl without experimental floods; Crespo-Pérez et al., 2020). A decrease in FDis and RaoQ could further suggest reduced competition and/or the closing of niches (Milner et al., 2018; Statzner et al., 2004). While the other functional diversity indices responded to the flood disturbance, FEve was not affected suggesting that even though trait richness, dispersion and redundancy fluctuated during the study period, the occupation of the prevailing trait space by the community was constant (Mason et al., 2013). Scotti et al. (2020) measured similar FEve of macroinvertebrate communities in alpine streams of comparable altitude surrounded by coniferous forests. FRed was lower under flow-regulated conditions compared to the reference reaches and increased as a result of harsher environmental conditions (Bêche & Statzner, 2009). Higher FRed, a key component of resilience (Feit et al., 2019; Oliver et al., 2015), indicates that the Spöl macroinvertebrate community gained resistance and resilience (Biggs et al., 2020; Hooper et al., 2005; Naeem, 1998). This would confirm Robinson et al. (2018), who assumed an increase in ecosystem resilience to unpredictable perturbations as a positive effect of the flood program. In biological conservation, functional redundancy is considered an important indicator, as higher FRed holds the possibility of compensating losses in ecosystem functions resulting from a decrease in species richness (Schmera et al., 2017). It is further seen as the principal mechanism providing persistence against disturbances like floods (Angeler & Allen, 2016; Standish et al., 2014). Increase in FRed may also result from differences in taxonomic and functional shifts. While FRed started to increase after 2010, Robinson et al. (2018) showed that taxonomic richness already increased 4 years earlier, reaching pre-flood levels in 2007. Such decoupling of taxonomic and functional compositional changes indicates higher functional redundancy (Greenop et al., 2021; Jarzyna & Jetz, 2018). Increased ecosystem resilience may have allowed the macroinvertebrate community to recover after the sediment spill. The recovery patterns were found in FRic and, however less pronounced, in FDis, RaoQ and FRed (Figure 5). Increase in FDis following the sediment spill has been observed before as a response to a sediment flushing event in an alpine river (Folegot et al., 2021). FRic, FDis, RaoQ and FRed further suggest a shift back to flow-regulated ecosystem conditions after the discontinuation of the experimental flood program.

When comparing results of trait-based analyzing approaches based on a set of traits like the functional diversity indices (or FCA), it must however be noted that the selection and number of traits may influence the results (Zihao et al., 2021). E.g. FDis seems to be robust to such variation, while FRic and FEve showed to be more sensitive (Wilkes et al., 2020).

4.1.2 Individual trait patterns

Individual traits responded with variable patterns (Appendix C). Several traits showed convergence to the reference reaches peaking in the 2007-2010 period, by increasing or decreasing in frequency while other traits remained relatively stable or fluctuated during the study period. Most of the traits showing strong responses to experimental floods changed frequency towards pre-flood status after flood discontinuation, supporting hypothesis 1c. Comparison with reference conditions was sometimes made difficult by the existing temporal change occurring in Aqua and Fuorn (see Chapter 4.2). When analyzing multiple individual traits, it must be noted that alternative set of traits can confer resistance and/or resilience. A given species with small body size could e.g. gain resilience by having a short life cycle length while another species is large, highly mobile, and thus equally resilient. Therefore, no a priori predictions are possible on which or how many resilience traits should be present under flood disturbance (Townsend & Hildrew, 1994). This also applies to traits resisting other stressors, e.g. climate change (see Chapter 4.2). In general, when analyzing multiple traits, individual traits may not respond independently to environmental alteration. Phylogenetic constraints, statistical correlation or spatial effects (Menezes et al., 2010; Poff et al., 2006; Statzner & Bêche, 2010), especially at large scales (Wilkes et al., 2020) could result in traits correlation. Accordingly, the individual trait patterns observed may be a direct response to the experimental floods or else, be dependent from such traits, thus responding indirectly.

The response of multiple traits linked to resilience/resistance to the experimental flood program supported hypothesis 1b. The frequency (CWM) of individuals with a relatively small maximum body size increased at Spöl (Appendix C) while larger individuals decreased, both reaching reference sites frequencies ten years after start of the flood program. Smaller body size has been linked to an increased resilience in streams with hydraulic disturbance (Milner et al., 2018; Segura et al., 2013; Snook & Milner, 2002) whereas large-bodied individuals are expected in hydrologically more stable conditions (Kopp & Allen, 2021; Townsend & Hildrew, 1994). Resilience to extreme events, e.g. floods, can also be promoted by non-aquatic adult life stages (Poff, 2018). Accordingly, frequency of individuals with an aquatic adult life stage decreased in the Spöl. This trait response is likely linked to the decline in *Gammarus* density during the flood program (Robinson et al., 2018). Non-aquatic adult life stage implies active or passive aerial dispersal, of which former trait showed a response to the new flow regime at Spöl by increasing in frequency. Aerial dispersal promotes resilience to predictable disturbance (Townsend & Hildrew, 1994), allowing individuals to avoid flood disturbance by emerging before seasonal floods (Hershkovitz & Gasith, 2013; Lytle, 2002) and to recolonize afterwards (Gray, 1981). Aerial dispersal is an important response trait also to other anthropogenic impacts (e.g. agricultural land cover; Kopp & Allen 2021). Locomotion and substrate relation traits respond directly to physical habitat changes. The frequency of crawling individuals at Spöl increased and reached a peak ten year after start of the flood program suggesting augmented resilience (Ilg & Castella, 2006; Poff et al., 2006) while at the same time, full water swimmer showed lowest frequency, as it is supposed in streams with glacial signature, where attachment adaptions (e.g. claws) are more favorable to cope with high flow velocities (Crespo-Pérez et al., 2020; Cummins et al., 2008). Resistance to floods can be further gained by the type of reproduction strategy, e.g. by attaching eggs to a surface instead of laying them freely (Bêche & Resh, 2007). Correspondingly, the frequency of individuals with cemented isolated eggs increased in the Spöl to a level that could be found in Aqua. Also, the potential number and duration of life cycles are associated to resistance and/or resilience mechanism (e.g. Townsend & Hildrew, 1994). Hydrologically stable conditions before the flood program favored multivoltine taxa (Kopp & Allen, 2021), while flood disturbance promoted a decrease in frequency to a level found at Fuorn. However, differing responses of this trait to disturbance, resp. floods, have been observed. Bêche & Resh (2007) linked multivoltinism to enhanced resilience in Mediterranean-climate streams. As for the life cycle duration, frequent disturbance theoretically promotes short-lived individuals (Townsend & Hildrew, 1994), which is reflected in an increase of this trait frequency at Spöl following the floods. This could be due to higher chances of recolonization which are expected to be brought along with short life cycles (Van Looy et al., 2019). Considering the feeding habits, frequency of predators showed a strong adaption to the new flow regime by decreasing, suggesting that stable conditions may facilitate active hunting behavior of predators. Interestingly, this trait did not follow the shift around 2011 – 2013 but seemed to shift back to the pre-flood state after interruption of the flood program.

4.2 Long-term functional responses to climate-driven environmental change

Water temperature on Spöl and Fuorn showed a significantly increasing trend during the study period (Figure 6), most likely reflecting ongoing alterations of hydroecological conditions of alpine streams driven by climate change (Gobiet et al., 2014; Jacobsen et al., 2014; Milner et al., 2009, 2017). The difference in water temperature increase between reference sites (Fuorn: significant +0.51°C; Aqua: non-significant +0.33°C) points to differences in their glacial legacy (Sertić Perić et al., 2015). Rock glaciers are forms of permafrost and by thawing shape habitat conditions of streams (such as Aqua) by providing constant cold water. This higher kryal contribution at Aqua compared to Fuorn, where krenal/rithral water is likely to be a relatively more important driver of hydrochemistry, may act as a buffer for water temperature warming (Brighenti et al., 2019; Jones et al., 2019; Sertić Perić et al., 2015). Spöl showed the strongest increase in yearly mean water temperature (+0.79°C), which could relate to reservoir water warming (Zhao et al., 2021). The reservoir might also have acted as a buffer explaining the relatively lower water temperature amplitude observed at Spöl compared to Fuorn (Figure 6; Ward & Stanford, 1983). Periphyton biomass increased significantly at both reference sites (Figure 7) suggesting slightly increased primary production likely driven by increasing water temperature and nutrient availability (Boix Canadell et al., 2021; Sertić Perić et al., 2015; Uehlinger et al., 2010). The experimental floods on the Spöl reduced an initially very high periphyton biomass, however levels were always higher than reference (Figure 7). No long-term, climate-driven changes could be detected in the Spöl, as periphyton patterns were strongly influenced by the experimental floods.

4.2.1 Community responses and diversity patterns

Multivariate analysis of functional community (FCA) places Fuorn in an intermediate position between Aqua and Spöl. Functional diversity indices and individual trait patterns suggest that Fuorn appears to be undergoing a slow directed functional change towards Spöl. The individual stream sizes of the study reaches (Strahler stream order 5 at Spöl, 4 at Fuorn and 1 at Aqua) may have also contributed to overall functional differences (Vannote et al., 1980; Ward & Stanford, 1983). Functional diversity indices of Aqua and Fuorn (Figure 5; Table 3) remained mostly constant over the study period. Significant decrease was only found in RaoQ at Aqua and significant increase in FRed at Aqua and FRic at Fuorn, from which FRed underwent the strongest change. This in turn could indicate improved resistance and resilience (Biggs et al., 2020; Hooper et al., 2005; Naeem, 1998). FEve suggested a linear decrease at all three study sites, however not significantly, being most pronounced at Fuorn. Expected increase in importance of trait filtering and thus a clustering of co-occurring species' traits in trait space due to climate change may explain this development (Mason et al., 2013).

The distinct functional character found at reference sites represent their differing glacial influence and highlights the importance of rock glaciers (Aqua) in the context of climate change, as they can promote climatic resilience in alpine streams and maintain cold-water refugia (Brighenti et al., 2019; Harrington et al., 2017, 2018). Both reference study sites are on free-flowing postglacial tributaries lying at a comparable altitude, however they differ in glacial signatures and glacial body types. Aqua emerges from a small rock glacier, while Fuorns glacial cover consists of remnant ice fields (Sertić Perić et al., 2015). These differences were also reflected in functional community composition (FCA; Figure 3). Thus, regarding hypothesis 2b, Fuorn seems be to more prone to climate change driven alterations, showing changes in functional diversity. On the other hand, Aqua shows clear long-term changes in several individual traits but not in functional diversity suggesting the existence of buffer mechanisms that contrast this change. Such climate-sensitive traits may also be influenced by climate alteration in Spöl, however, a disentangling of stressors (flow alterations vs. climate change) was not possible, as functional response at Spöl was dominated by the experimental floods.

4.2.2 Individual trait patterns

Trait frequencies on Aqua and Fuorn were gradually changing or constant over time, and no abrupt changes, which could indicate a tipping point triggering a major functional shift (Scheffer et al., 2015), were detected. However, the time interval covered by this study is to the lower end when considering climate change as a driver of ecosystem alteration. For example, Bruno et al. (2019) could detect more pronounced climate-driven functional changes on macroinvertebrate communities over a 40-year period using similar functional analysis approaches.

Feeding preference traits appeared to be rather sensitive to climate-related environmental change in reference sites as multiple of these traits showed a significant change in frequency (Appendix C & D). As an example, the increase in frequency of microphytes (microalgae) feeding preference increased significantly at Aqua, a response that could be associated to the observed growth in periphyton biomass (Figure 7). Also other feeding traits changed in frequency, a fact that could indicate profound functional adjustments related to resource availability. The increase in frequency of traits such as interstitial space occupation and tegument respiration could be associated with physical habitat changes controlled by glacial signature (e.g. lower fine sediment load and deposition). However, Bruno et al. (2019) observed opposing patterns, suggesting that functional adaptation to changing environmental conditions is likely to be context dependent. The strong increase in frequency of semivoltine individuals at both sites, while univoltine at Fuorn and multivoltine individuals at Aqua decreased over the years can be associated to glacial retreat (Brown et al., 2018), indicating a progressive decline of glacial legacy followed by increasing habitat stability (Brown et al., 2015). Similarly, individuals with a long life cycle are slowly replacing short-lived ones, possibly suggesting an ongoing loss in resilience capacity (Townsend & Hildrew, 1994). Overall, the significant in- or decrease of multiple individual traits during the study period (together with implied changes in functional diversity, see Chapter 4.2.1) support hypothesis 2a.

4.3 Conclusions

This study confirms the importance of long-term monitoring to evaluate the effects of climate change and flow restoration on stream ecosystems. While functional macroinvertebrate community responses to climate change are frequently addressed in freshwater ecology, this likely is the first study examining macroinvertebrate traits in a context of long-term experimental floods. These floods modified the functional macroinvertebrate assembly towards a more natural composition, by promoting the occurrence of traits conferring resistance and/or resilience to flood disturbance, a common feature for organisms living in highly dynamic alpine streams. The observed patterns (shifts) were generally consistent with structural community responses on the Spöl (Robinson, 2012; Robinson et al., 2018). The findings of this study further corroborate the importance of periodic disturbance in regulated alpine streams to sustain the environmental dynamics leading to community reassembly, as it was observed that experimental floods discontinuation determined functional reversal towards pre-floods conditions. The progressive functional changes in unregulated alpine streams, associated to an increase in water temperature and periphyton biomass, indicate that macroinvertebrate communities are adapting to new climate-driven environmental conditions. Differences among sites were found and it is thus hypothesized that glacial fingerprint plays an important role in determining the magnitude and speed of such response. This highlights the need for further research to investigate mechanisms of response to multiple stressors (i.e. flow regulation and climate change combined; Bruno et al., 2019). In this study, the use of functional traits to analyze macroinvertebrate assembly patterns has proven to be an important complement to taxonomic approaches, i.a. by providing insights into the mechanism driving macroinvertebrate community responses regarding resistance and resilience and by allowing the comparision of observed trait patterns across ecoregions hosting a different taxonomic pool.

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II Appendix

Appendix A: Taxa x trait table

Appendix B: PERMANOVA & PERMDISP results

Appendix C: Individual trait frequencies (CWM)

Appendix D: Linear regression model results for Aqua and Fuorn

Appendix E: Plagiarism declaration

Appendix A

Table A1: Taxa x trait table showing taxonomic resolution and fuzzy coded trait values per trait code. Please note that trait categories T3_2, T4_5 and T6_3 are not shown, as no taxa showed affinity to these trait categories.

Taxon	T1_1	T1_2	T1_3	T1_4	T1_5	T1_6	T1_7	T1_8	T1_9	T2_1	T2_2	T2_3	T2_4	T2_5	T2_6	T2_7	T2_8
Allogamus	0	0	3	2	1	0	0	2	0	0	0	3	1	0	0	1	0
Baetis	0	2	2	5	1	1	0	0	0	0	1	0	3	0	0	0	0
Blephariceridae	0	0	0	5	0	0	0	0	0	0	0	0	3	0	0	0	0
Chironomidae	0.82	3.83	0.89	1.93	0.22	0.07	0.32	0.46	0	0	2.79	1.86	1.75	1.04	0	0.32	0.11
Coleoptera	0	1	0	3	0	0	0	0	0	0	0	1	3	0	0	0	0
Drusus	1	0	1	3	2	0	0	2	0	0	0	2	3	0	0	0	0
Empididae	0	0	0	0.5	0	0	0	5	0	0	0	0	0	0	0	3	0
Ephemeroptera	0.37	1.87	2.11	3.63	0.63	0.5	0	0	0	0	0.63	0.74	3	0	0	0	0
Gammaridae	0	1	5	2	1	2	2	1	0	0	0	3	1	0	0	0	0
Heptagenidae	0.74	1.74	2.22	2.26	0.26	0	0	0	0	0	0.26	1.48	3	0	0	0	0
Hirudinea	0	0	0	0	0	0.44	0.22	1.67	1.56	0	0	0	0	0	1.89	0.56	1
Leuctra	0	1	1	2	2	1	0	0	0	0	1	3	1	0	0	0	0
Limoniidae	0.04	0.04	0.38	0.12	0.08	0	0	0.35	0	0	0.22	0.22	0.17	0	0	0.39	0
Nemoura	0	1	2	1	0	0	0	0	0	0	0	3	0	0	0	0	0
Oligochaeta	0.96	2.89	0	1.19	0	0	0.12	0.08	0	0.89	2.92	0	0.19	0	0	0.12	0
Perloidea	0.11	0.22	0.11	1.78	0	0	1	4.22	0	0	0.11	3	0.89	0	0	1	0
Plecoptera	0.03	0.81	1.28	1.45	0.5	0.25	0.25	1.06	0	0	0.28	3	0.47	0	0	0.25	0
Protonemura	0	1	2	1	0	0	0	0	0	0	0	3	0	0	0	0	0
Rhyacophilidae	0	1	1	1	0	0	1	5	0	0	0	0	0	0	0	3	0
Simuliidae	0	0.63	0	0.25	0	0	0.15	0	0	0	0	0	0.25	0.75	0	0	0
Turbellaria	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0

Taxon	T3_1	T3_3	T3_4	T3_5	T3_6	T3_7	T3_8	T4_1	T4_2	T4_3	T4_4	T5_1	T5_2	T5_3	T5_4	T5_5	T5_6	T5_7
Allogamus	0	0	5	0	0	0	0	3	2	0	0	0	0	0	1	3	0	0
Baetis	0	3	4	0	1	0	0	1	2	0	0	0	0	3	1	0	0	0
Blephariceridae	0	0	2	0	0	2	1	1	3	0	0	0	0	3	0	0	0	0
Chironomidae	0	1.96	2.93	0.29	1	1.86	0	3	1	0	0	0	1.71	2.78	0.47	0.22	0	0
Coleoptera	1	0	4	0	1	0	0	1	3	3	0	0	3	0	0	0	0	0
Drusus	0	0	5	0	0	0	0	3	2	0	0	0	0	0	3	0	0	0
Empididae	0	0	2	1	1	0	0	1	0	0	1	0	0	3	0	0	0	0
Ephemeroptera	0	2	4.5	0	0.63	0	0	1	2.5	0	0	0	0	1.63	2	0	0	0
Gammaridae	0	2	3	0	1	0	0	0	3	0	0	0	0	0	2	2	0	0
Heptagenidae	0	1	5	0	0.26	0	0	1	3	0	0	0	0	0.26	3	0	0	0
Hirudinea	0	0.11	3.56	0.44	0	1.22	0	3	0	0	0	0	0	0.33	0.78	1.22	1	0.11
Leuctra	0	0	5	2	1	0	0	3	0	0	0	0	0	3	1	0	0	0
Limoniidae	0	0	0.3	0.7	0	0	0	0.08	0	0	0.92	0	0.05	0.42	0.26	0.16	0.11	0
Nemoura	0	0	5	0	0	0	0	3	0	0	0	0	1	3	0	0	0	0
Oligochaeta	0	0.31	0	0.72	0.98	0.04	0.04	3	0.17	0	0	0.19	0.23	0.23	0.36	0.1	2.66	0.17
Perloidea	0	0	4.11	0	1	0	0	3	0	0	0	0	0	1.11	2.45	0.33	0	0
Plecoptera	0	0	4.78	0.5	0.5	0	0	3	0.5	0	0	0	0.25	2.53	1.11	0.08	0	0
Protonemura	0	0	5	0	0	0	0	3	2	0	0	0	0	3	1	0	0	0
Rhyacophilidae	0	2	3	0	0	1	0	2	2	0	0	0	0	1	3	2	0	0
Simuliidae	0	0	0.29	0	0.15	0.57	0	0.55	0.18	0	0.27	0	0.33	0.67	0	0	0	0
Turbellaria	0	0	4	0	1	0	0	3	0	0	0	0	0	0	2	3	0	0

Taxon	T6_1	T6_2	T6_4	T6_5	T7_1	T7_2	T7_3	T7_4	T8_1	T8_2	T8_3	T8_4	T9_1	T9_2	T9_3	T10_1	T10_2	T10_3	T10_4	T10_5	T10_6	T10_7	T10_8	T12_1	T12_2
Allogamus	0	0	0	3	0	2	0	3	3	3	3	0	0	3	0	0	0	0	1	0	0	0	0	3	0
Baetis	2	0	0	2	3	2	1	3	3	3	0	0	0	2	3	0	0	1	3	0	0	0	0	3	0
Blephariceridae	1	0	2	0	2	1	0	1	2	3	2	0	0	3	2	0	0	0	3	0	0	0	0	3	0
Chironomidae	0	0	0.93	3	1.18	1	2.86	1	0	3	3	0	0	2.78	2.79	0.93	0	0	1	3	0	0	0	3	0
Coleoptera	0	0	0	3	2	1	0	2	3	3	0	2	0	3	0	0	0	0	3	0	0	0	0	1	3
Drusus	0	0	0	1	3	2	0	2	3	3	3	0	1	3	0	0	0	0	3	0	0	1	0	3	1
Empididae	0	0	0	3	1	1	0	2	0	2.5	3	0	0	3	1.5	0	0	0	0	0	0	2	0	3	0
Ephemeroptera	2	0	0.37	2	3	1.63	1	3	3	3	0	0	0.5	2.5	1.5	0	0.87	0.63	3	0	0	0	0	3	0.5
Gammaridae	0	0	0	3	3	2	0	0	3	3	0	3	0	0	3	3	0	0	0	0	0	0	0	1	3
Heptagenidae	2	0	0.74	2	3	1.26	1	3	3	3	0	0	1	3	0	0	1.74	0.26	3	0	0	0	0	3	1
Hirudinea	0	3	0	0	1.89	1.11	0.56	0	2.56	3	0	2.22	0.56	2.11	0.11	1.11	0	0.33	1.33	0.44	0	0.44	0	0.7	2.44
Leuctra	1	0	0	3	2	2	0	1	3	3	0	0	1	3	0	0	0	3	0	0	0	0	0	3	1
Limoniidae	0	0	0	1	0.23	0.31	0.15	0.31	0.53	0.47	0	0	0	0.75	0.25	0	0.75	0.25	0.53	0.47	0	0	0	1	0
Nemoura	0	0	1	3	2	2	0	2	3	3	0	0	2	2	0	0	0	3	1	0	0	0	0	2	2
Oligochaeta	0	1.35	0	2.48	1.38	0.15	0	0	2.74	2.74	0	2.74	0	0.78	2.22	0	0.23	0.12	2.66	0	0	0	0.46	0	1
Perloidea	1.78	0	0.78	1.44	2	2	0	1.78	3	3	0	0	2	2.78	0	0	0	1.33	1.78	0	0	0	0	0.11	3
Plecoptera	0.95	0	0.7	2.61	2	2	0	1.45	3	3	0	0	1.25	2.7	0	0	0	2.58	0.7	0	0	0	0	2.03	1.5
Protonemura	1	0	1	3	2	2	0	1	3	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0
Rhyacophilidae	1	0	2	3	3	2	1	2	3	3	3	0	1	2	1	0	0	3	0	1	0	0	0	3	2
Simuliidae	0.5	0	0.5	0	0.27	0.2	0.4	0.13	0.25	0.38	0.38	0	0	0.4	0.6	0	0.17	0	0.5	0	0	0.17	0	0.86	0.14
Turbellaria	0	3	0	0	1	2	0	0	3	3	0	3	0	3	0	0	0	0	3	0	0	0	1	0	3

Appendix B: PERMANOVA & PERMDISP results

Table B1: Results from pairwise PERMANOVA analysis. Tested pairs, sums of squares (SumsOfSqs), F-, R^2- and p-values are given. Significant results are marked (bold).

Pairs	SumsOfSqs	F	r^2	p
Spöl vs Aqua	**0.787**	**135.043**	**0.360**	**0.003**
Spöl vs Fuorn	**0.399**	**45.370**	**0.172**	**0.003**
Aqua vs Fuorn	**0.117**	**14.532**	**0.069**	**0.003**

Table B2: Results from PERMIDSP analysis. Sum of squares (SumsOfSqs), F-value, number of permutations and p-values are given. Significant results are marked (bold).

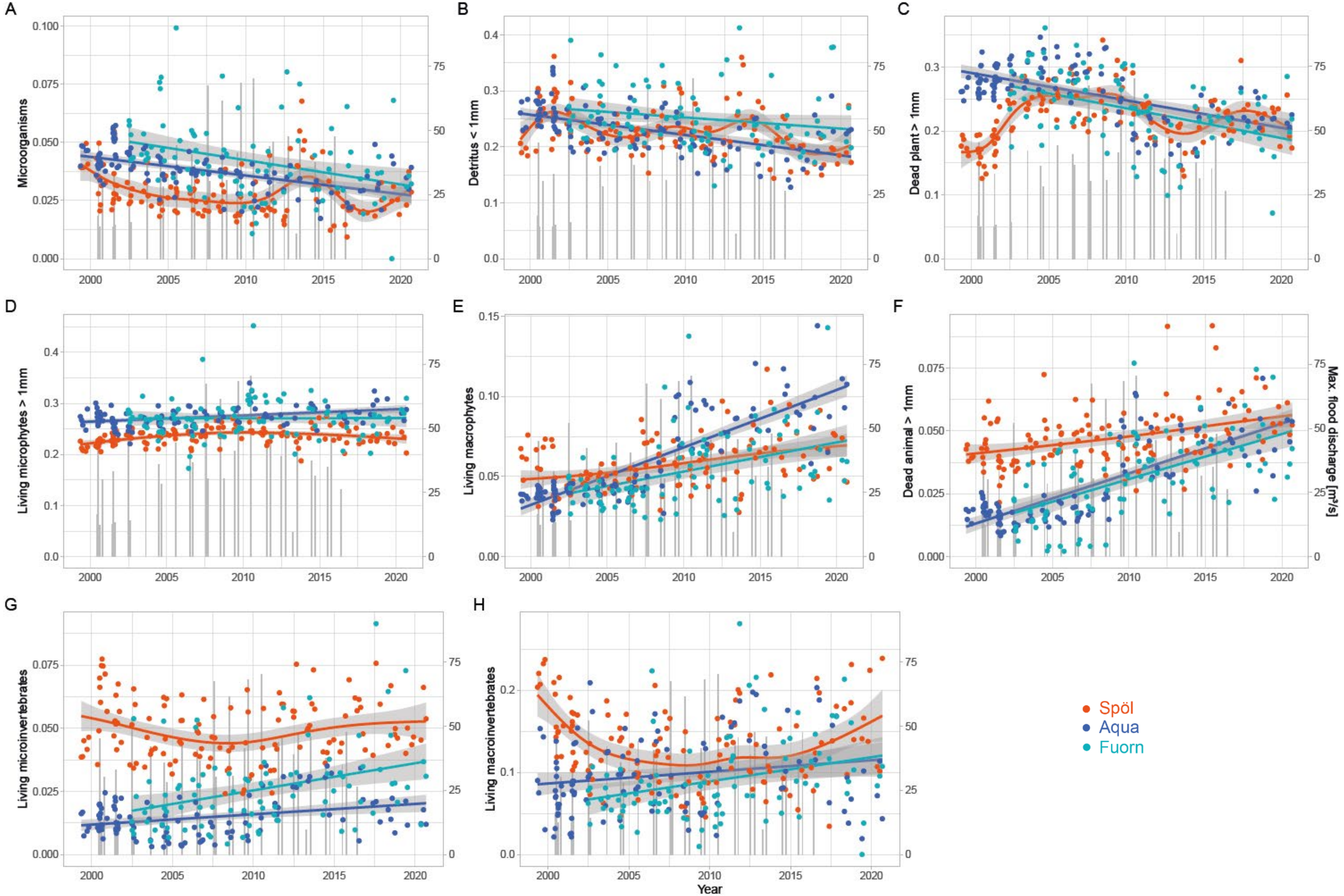
	SumsOfSqs	F	permutations	p
Groups	**0.067**	**39.681**	**99**	**0.01**

Appendix C

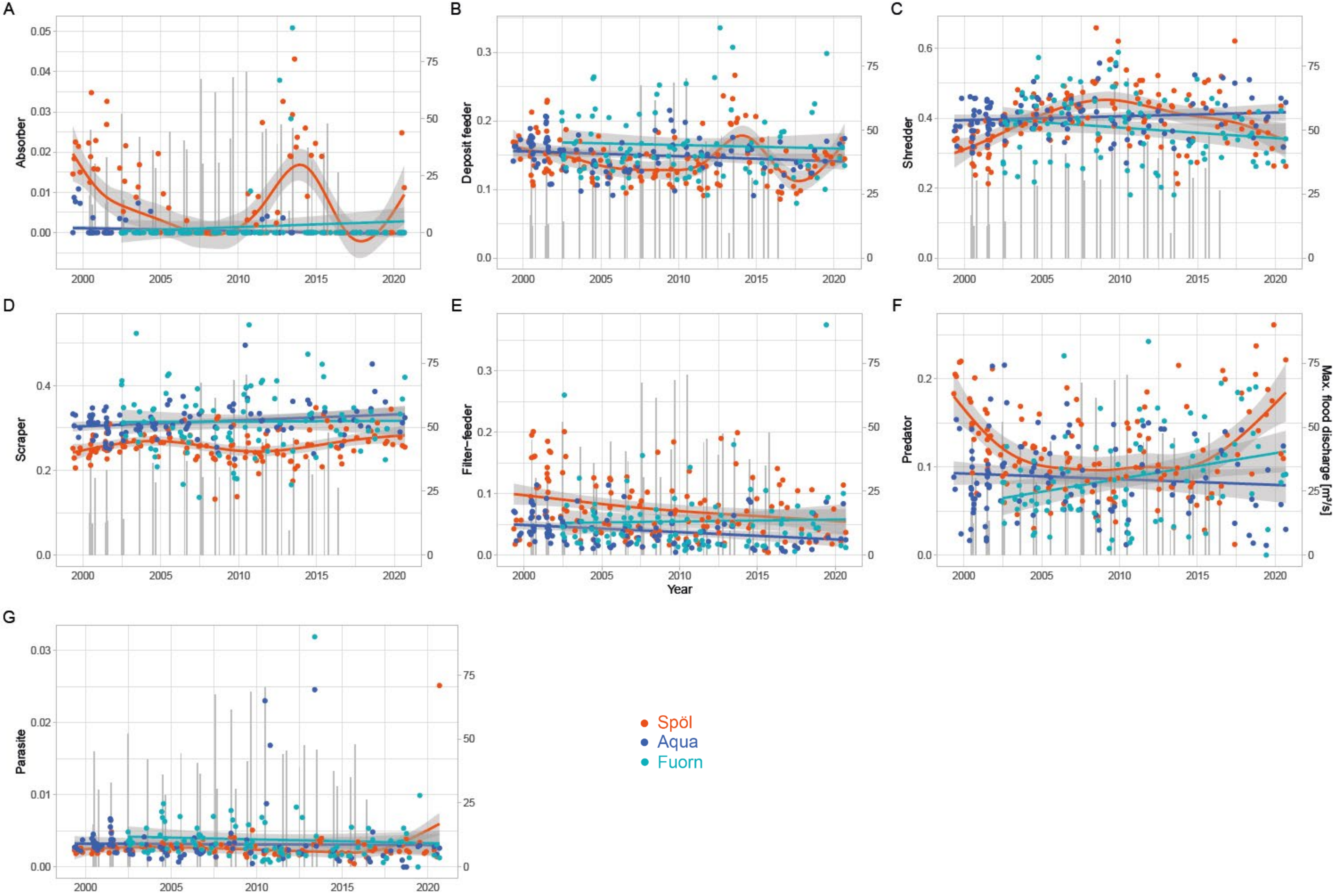
Individual trait frequencies

Development of individual traits CWM (left y-axis) over the whole study period. Fitted GAM (Spöl) resp. LM (Aqua & Fuorn) splines are depicted together with 95% confidence bands. Maximum flood discharge of experimental flood events (right y-axis) is shown as grey bars.

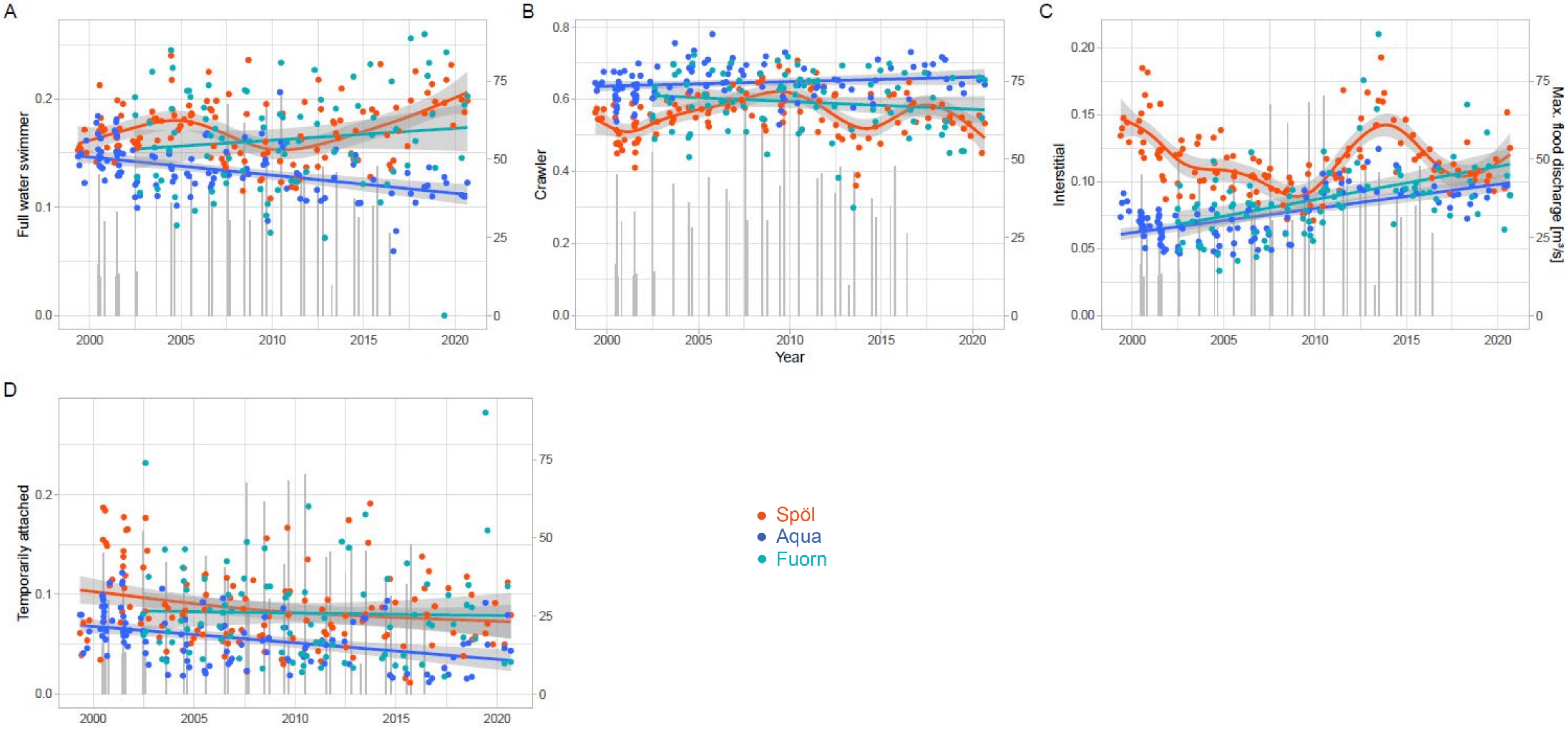
Food preference



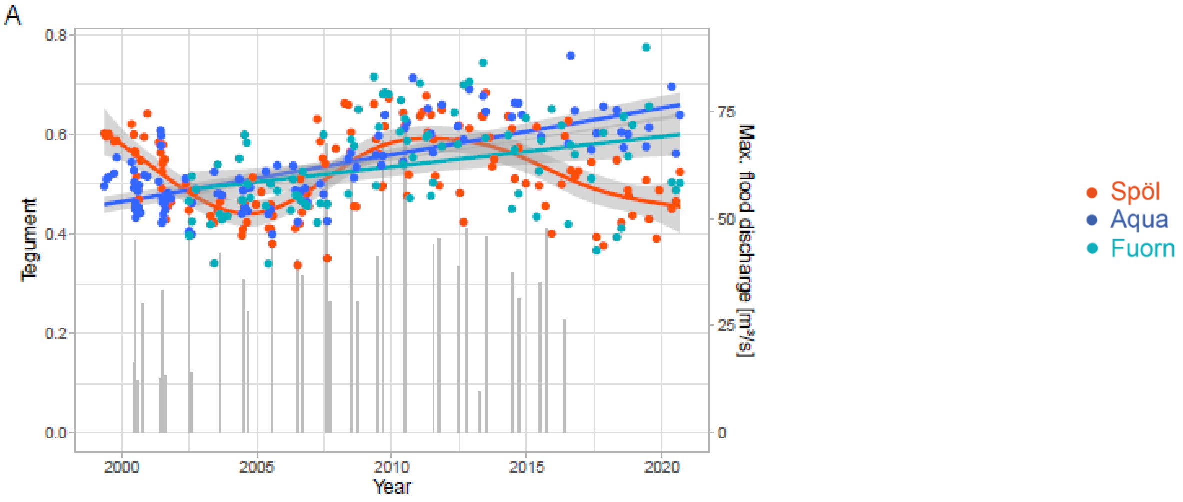
Feeding habits



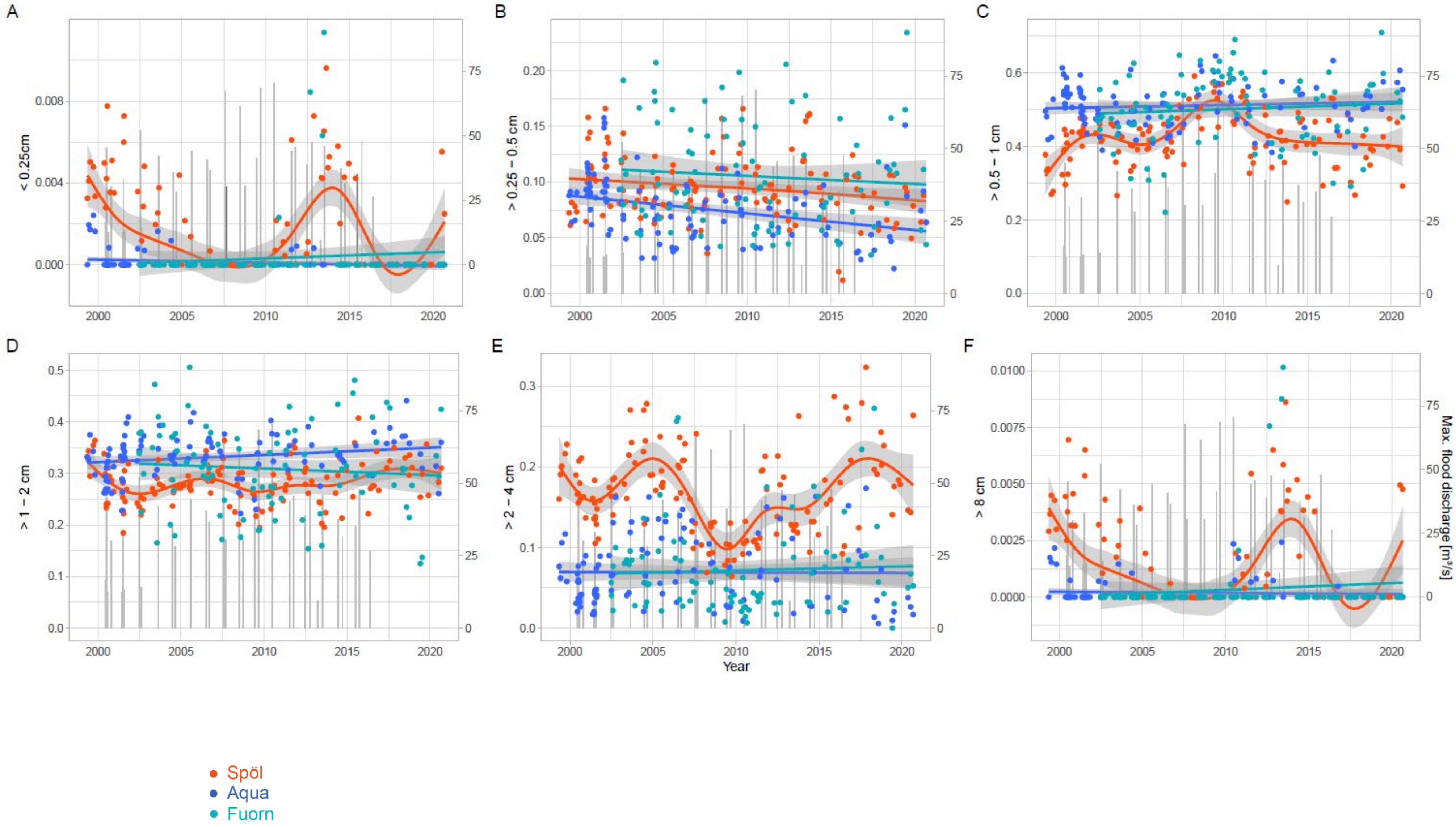
Locomotion and substrate relation



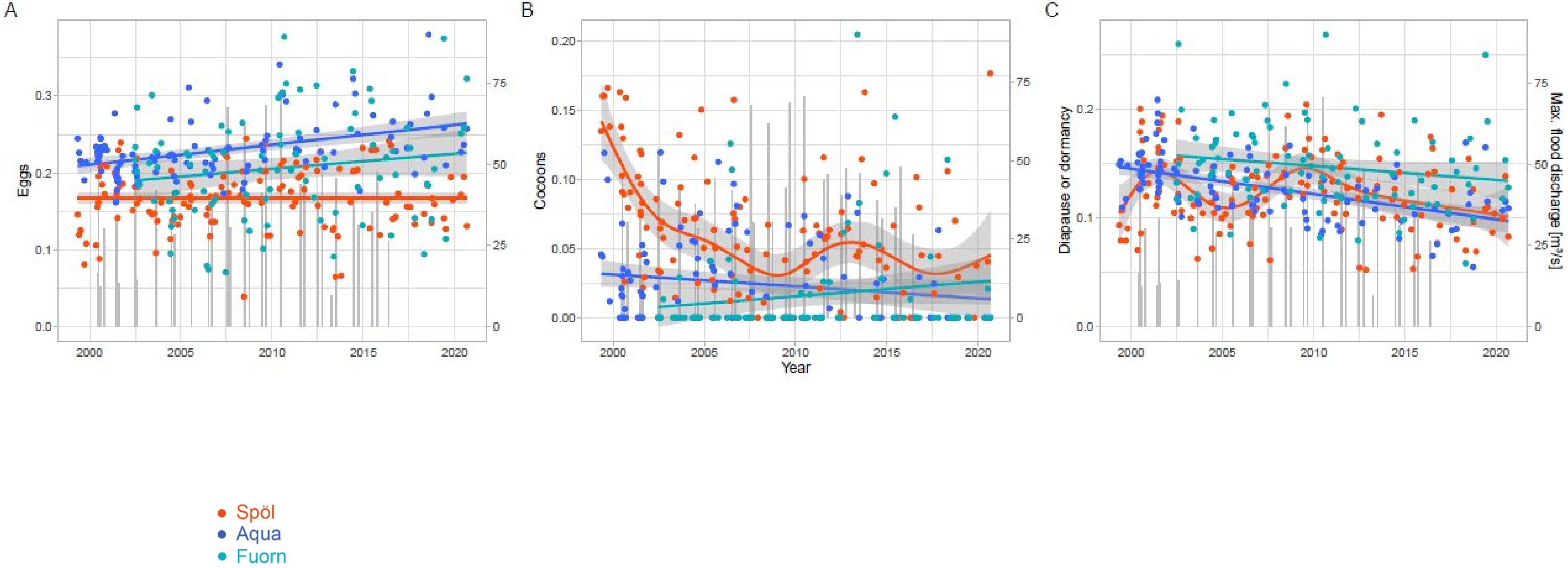
Respiration



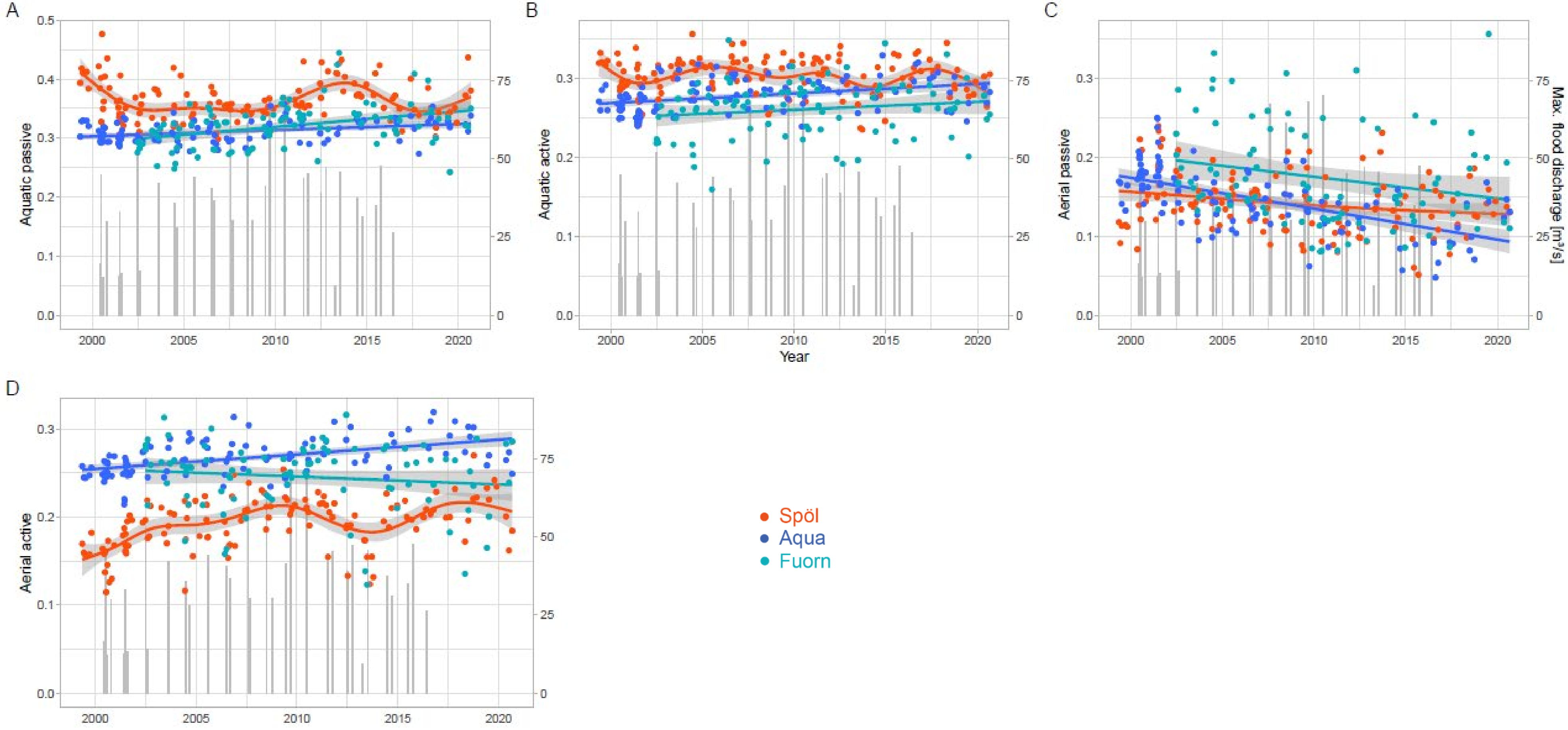
Maximal potential size



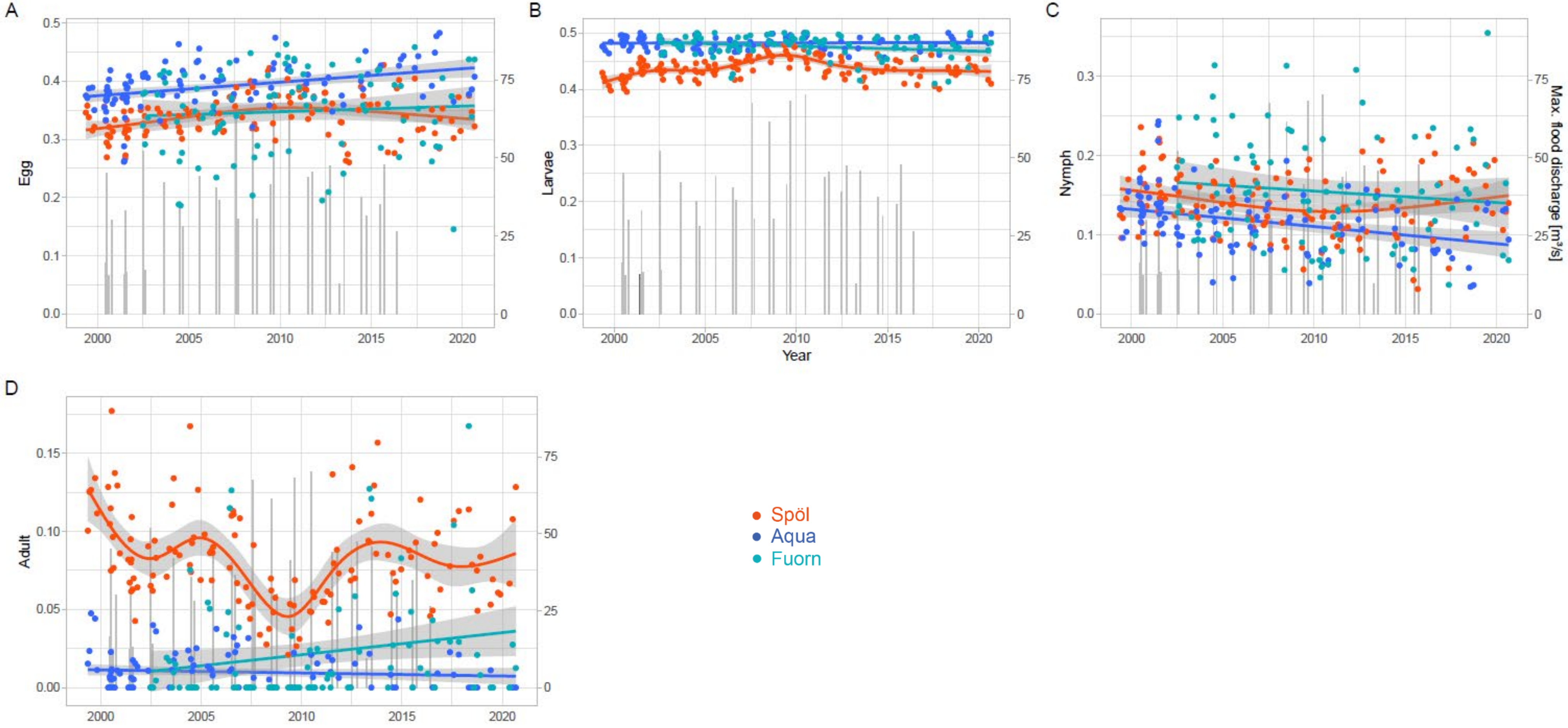
Resistance forms

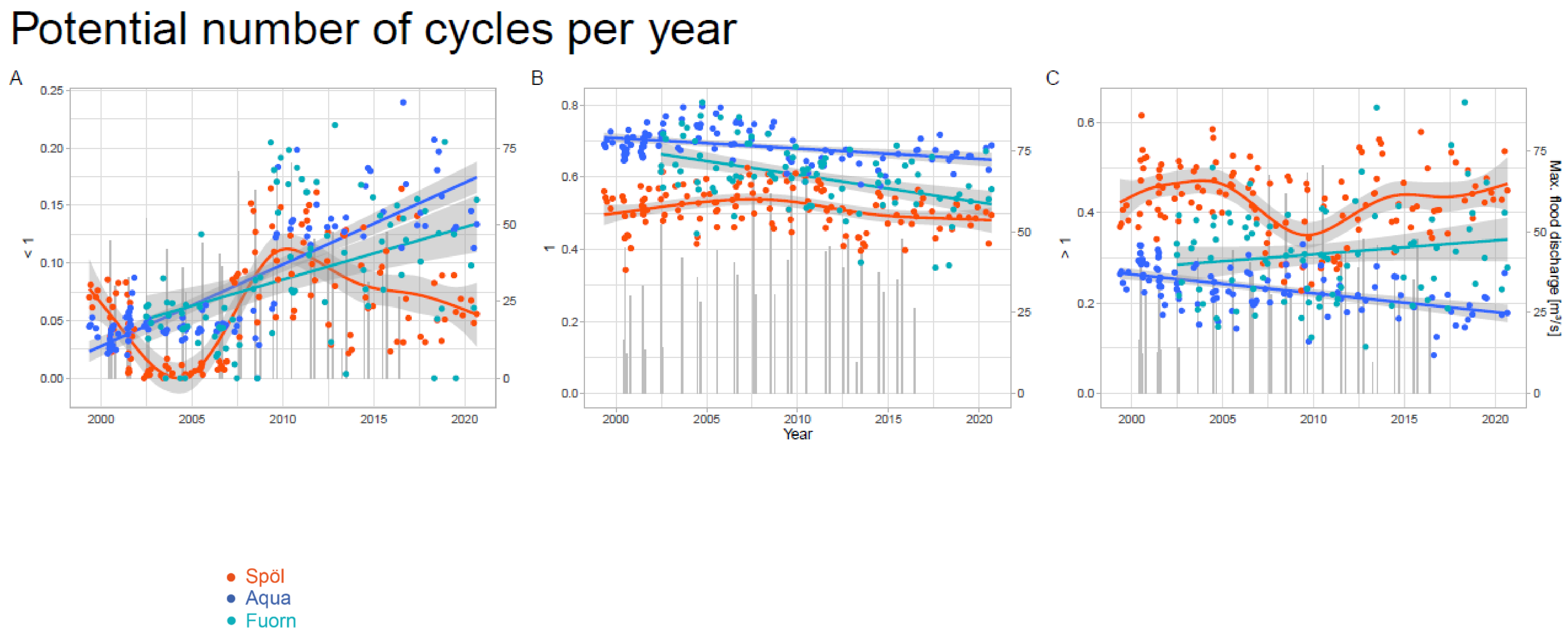


Dispersal

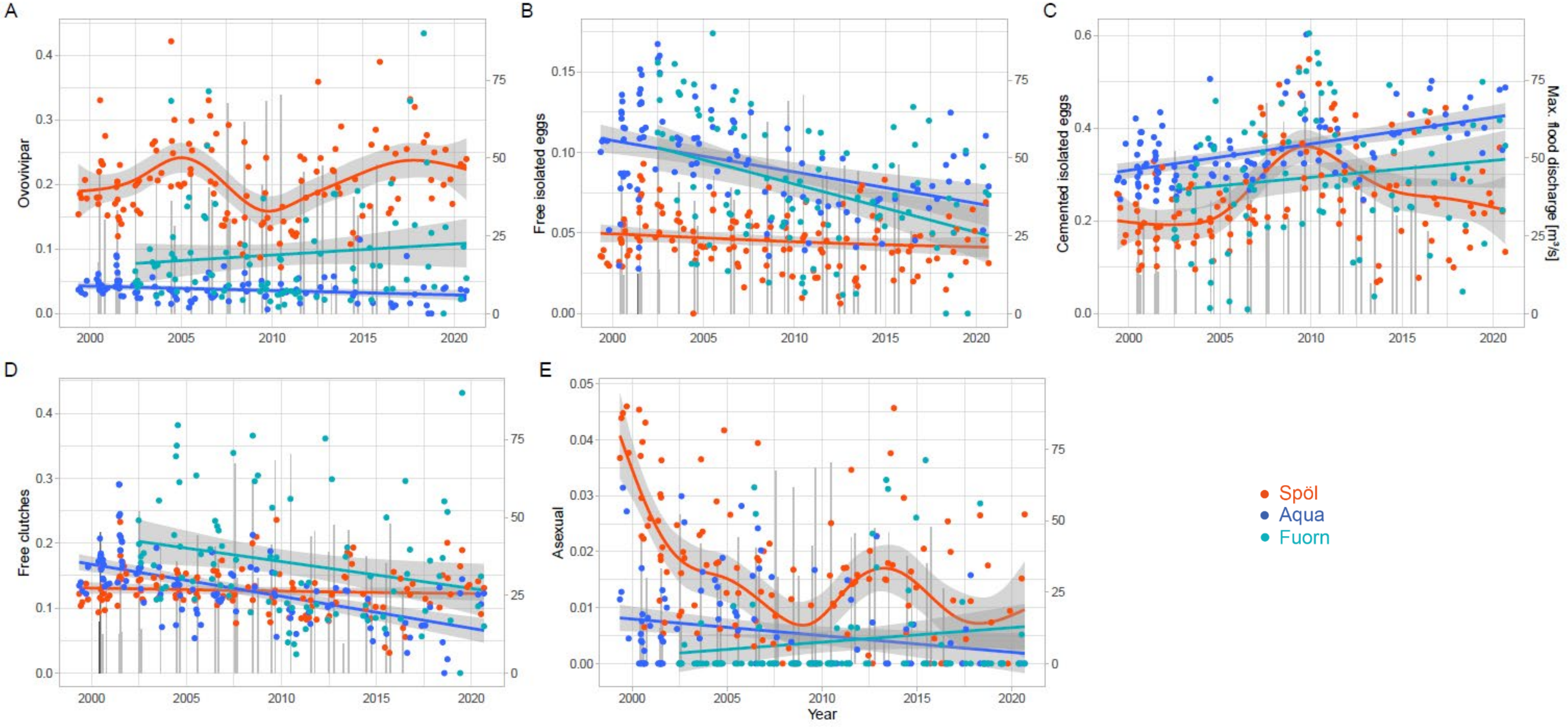

A
B
C
D
Aquatic passive
Aquatic active
Aerial passive
Aerial active
Year
Max. flood discharge [m³/s]
0.0
0.1
0.2
0.3
0.4
0.5
0
25
50
75
2000
2005
2010
2015
2020
Spöl
Aqua
Fuorn

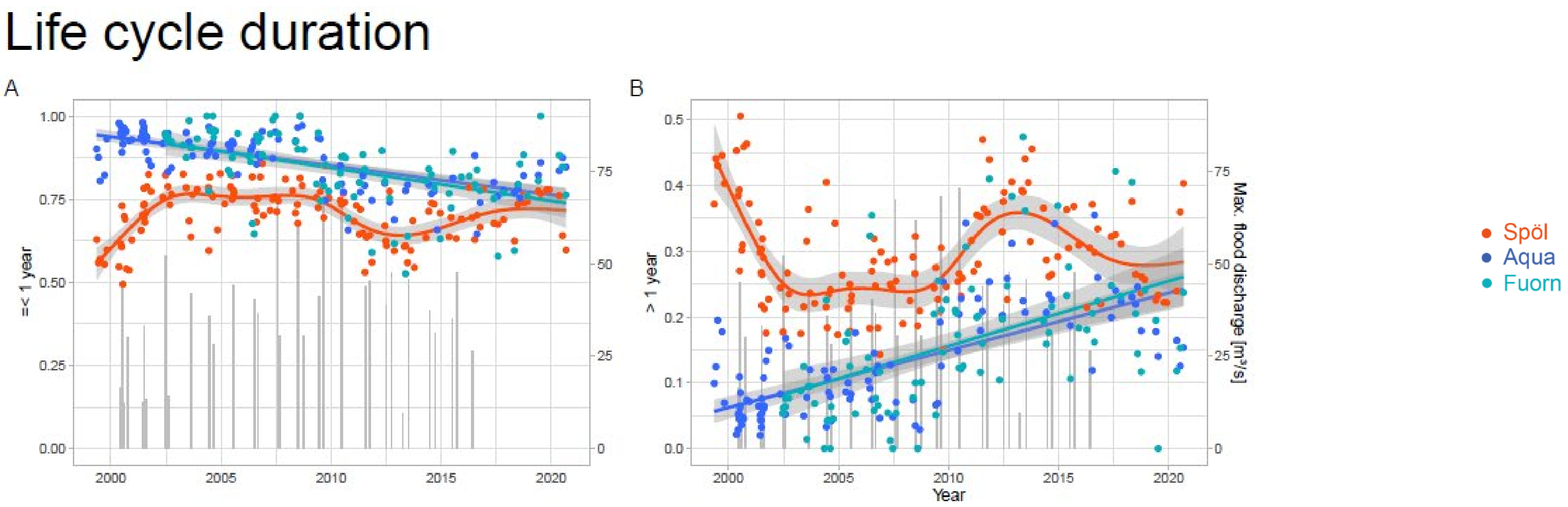
Aquatic stages




Potential number of cycles per year
A
< 1
0.25
0.20
0.15
0.10
0.05
0.00
75
50
25
0
2000
2005
2010
2015
2020
B
1
0.8
0.6
0.4
0.2
0.0
75
50
25
0
2000
2005
2010
2015
2020
Year
C
> 1
0.6
0.4
0.2
0.0
75
50
25
0
Max. flood discharge [m³/s]
2000
2005
2010
2015
2020
Spöl
Aqua
Fuorn

Reproduction




Life cycle duration
A
B
=< 1 year
> 1 year
Max. flood discharge [m³/s]
Year
1.00
0.75
0.50
0.25
0.00
0.5
0.4
0.3
0.2
0.1
0.0
75
50
25
0
2000
2005
2010
2015
2020
● Spöl
● Aqua
● Fuorn

Appendix D

Table D1: Results from linear regression model between individual traits (CWM) and year for Aqua and Fuorn taking into account HAC robust standard errors. Adjusted R2, coefficient estimates, standard scores (z) and p-values are given. Significant results are marked (bold). Bonferroni correction was taken into account (p<0.0011)

	Aqua			**Fuorn**		
Trait	**Adj. R2**	**z**	**p**	**Adj. R2**	**z**	**p**
T1_1	**0.33**	**-4.32**	**<0.001**	**0.10**	**-3.49**	**<0.001**
T1_2	**0.30**	**-3.64**	**<0.001**	0.03	-1.70	0.090
T1_3	**0.36**	**-4.56**	**<0.001**	**0.18**	**-4.53**	**<0.001**
T1_4	**0.15**	**3.29**	**<0.001**	-0.01	0.05	0.961
T1_5	**0.71**	**14.39**	**<0.001**	**0.17**	**4.43**	**<0.001**
T1_6	**0.63**	**8.80**	**<0.001**	**0.33**	**6.59**	**<0.001**
T1_7	0.10	2.36	0.018	**0.11**	**3.34**	**<0.001**
T1_8	0.03	1.21	0.226	0.08	2.76	0.006
T2_1	0.04	-1.38	0.168	-0.00	1.06	0.290
T2_2	0.02	-1.37	0.170	-0.01	-0.50	0.619
T2_3	0.01	1.15	0.250	0.02	-1.58	0.113
T2_4	0.04	1.86	0.063	-0.01	0.10	0.921
T2_5	0.07	-2.15	0.031	-0.01	0.29	0.835
T2_7	-0.00	-0.77	0.439	0.08	2.79	0.005
T3_3	**0.20**	**-4.36**	**<0.001**	0.00	0.99	0.320
T3_4	0.02	1.09	0.274	0.01	-1.34	0.182
T3_6	**0.38**	**4.30**	**<0.001**	**0.19**	**4.85**	**<0.001**
T3_7	0.15	-2.91	0.004	-0.01	-0.22	0.829
T4_1	**0.53**	**6.72**	**<0.001**	0.01	2.48	0.013
T5_1	0.04	-1.38	0.168	-0.00	1.06	0.289
T5_2	0.11	-2.46	0.014	-0.01	-0.71	0.475
T5_3	-.0.00	0.66	0.509	-0.00	0.63	0.528
T5_4	0.04	1.51	0.130	-0.01	-0.62	0.536
T5_5	-0.01	-0.06	0.950	-0.01	0.32	0.750
T5_7	-0.01	0.46	0.646	-0.00	0.99	0.323
T6_1	**0.18**	**4.15**	**<0.001**	0.01	1.38	0.166
T6_2	0.02	-1.63	0.103	0.01	1.33	0.182

T6_4	**0.28**	**-5.46**	**<0.001**	0.02	-1.54	0.123
T7_1	**0.12**	**3.51**	**<0.001**	**0.13**	**2.92**	**<0.001**
T7_2	0.12	2.81	0.005	0.01	1.50	0.134
T7_3	**0.37**	**-4.42**	**<0.001**	0.04	-2.04	0.041
T7_4	**0.24**	**3.95**	**<0.001**	0.00	-1.10	0.271
T8_1	0.14	3.06	0.002	-0.01	0.63	0.527
T8_2	-0.01	0.21	0.836	0.04	-2.04	0.042
T8_3	0.12	-2.89	0.004	0.00	-0.99	0.321
T8_4	0.01	-0.89	0.372	0.34	1.50	0.135
T9_1	**0.69**	**9.24**	**<0.001**	**0.16**	**4.17**	**<0.001**
T9_2	0.15	-3.19	0.001	**0.20**	**-4.21**	**<0.001**
T9_3	**0.27**	**-5.11**	**<0.001**	0.01	1.42	0.154
T10_1	0.04	-2.18	0.029	0.00	0.75	0.453
T10_2	0.15	-2.54	0.011	**0.14**	**-3.72**	**<0.001**
T10_3	**0.26**	**5.74**	**<0.001**	0.01	1.35	0.178
T10_5	**0.36**	**-4.82**	**<0.001**	0.05	-2.23	0.026
T10_8	0.05	-2.39	0.017	0.01	1.35	0.176
T12_1	**0.46**	**-4.96**	**<0.001**	**0.23**	**-3.44**	**<0.001**
T12_2	**0.46**	**-4.96**	**<0.001**	**0.23**	**-3.44**	**<0.001**

Appendix E

PLAGIARISM DECLARATION

Master’s thesis for the School of Life Sciences und Facility Management

The student declares that all sources in the text (including Internet pages) and appendices have been correctly disclosed. This means that there has been no plagiarism, i.e. no sections have been partially or wholly taken from other texts and represented as the student’s own work or included without being correctly referenced. Any misconduct will be dealt with according to paragraphs 39 and 40 of the General Academic Regulations for Bachelor’s and Master’s Degree Courses at the Zurich University of Applied Sciences (dated 29 January 2008) and subject to the provisions for disciplin ary action stipulated in the University regulations (Rahmenprüfungsordnung ZHAW (RPO)).

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Wädenswil, 11.01.2022
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Signature:

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