

## RESEARCH ARTICLE

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# Patchiness in flow refugia use by macroinvertebrates following an artificial flood pulse

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## Abstract

Flow refugia, locations that maintain substrate stability and low hydraulic stress during periods of high flow, can ensure riverine resilience in the face of increasing hydrological unpredictability. Despite their known importance, they have been overlooked in recent years with work on drought refugia currently seeing greater attention. Moreover, research on the role of flow refugia during artificial flood pulses in regulated rivers, where flood disturbances are no longer part of the hydrograph, is essentially absent. Here, we compared flow refugia for benthic macroinvertebrates among six habitats (main channel, side channel, riffle, margin, lentic including a floodplain pond, and inundated floodplain) within four different sites in response to an artificial flood pulse. We found that the grain-size distribution and macroinvertebrate community composition changed at each site following the flood. Macroinvertebrate assemblages became longitudinally homogeneous, but within-site beta diversity and taxa richness remained temporally stable following the flood pulse, suggesting the presence of flow refugia. In this respect, margin, inundated floodplain and lentic (a floodplain pond) habitats provided important flow refugia locations, particularly for the mobile mayfly *Rhithrogena* sp. In contrast, low substrate stability in riffle and side channels resulted in limited refugia potential for most taxa. Refuge use was however patchy with high levels of intra-habitat variability being evident for *Rhithrogena* sp. and the amphipod *Gammarus fossarum* in margin and side channel habitats. Further work is required to advance our knowledge of flow refugia in rivers with differing flow regimes to enable their integration into management and restoration schemes.

## KEYWORDS

benthic macroinvertebrates, experimental flood, habitat diversity, patchiness, stability

## 1 | INTRODUCTION

Hydrological variability is widely acknowledged to play a pivotal role in the structuring of aquatic ecosystems, including the presence of natural flood pulses (Karaouzas, Theodoropoulos, Vourka, Gritalis, &

Skoulikidis, 2019; Palmer & Ruhi, 2019). Increased shear stress, substrate instability and scouring are some of the primary processes associated with floods that can lead to negative implications for benthic organisms (Cobb, Galloway, & Flannagan, 1992; Nakayama & Asami, 2020; Resh et al., 1988). Despite these sporadic and often

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intense disturbances, macroinvertebrate communities are highly resistant, often returning to pre-flood densities in a few weeks or months (Angradi, 1997; Matthaei, Uehlinger, & Frutiger, 1997; Robinson, Uehlinger, & Monaghan, 2003). An important factor that can mitigate the impact of flood disturbance on benthic assemblages is the use of refugia which enables recovery times to be shorter than the generation times of most invertebrate species (Sedell, Reeves, Hauer, Stanford, & Hawkins, 1990; Van Looy et al., 2019).

Despite the relative importance of refugia in maintaining ecosystem resilience (Sedell et al., 1990; Van Looy et al., 2019), research specifically examining the role of refugia is heavily skewed towards drying events or drought (e.g., Dodemaide, Matthews, Iervasi, & Lester, 2018; Doretto et al., 2018; Hill & Milner, 2018; Sarremejane et al., 2021; Vander Vorste, Obedzinski, Nossaman Pierce, Carlson, & Grantham, 2020). Many of the characteristics that define refugia functioning for differing disturbances show some degree of overlap such as the use of resistance strategies by the organisms (Gjerløv, Hildrew, & Jones, 2003; Lancaster & Belyea, 1997; Townsend, Doledec, & Scarsbrook, 1997) and the spatio-temporal availability of refugia, including connectivity to residential habitats (Sarremejane et al., 2021; Sedell et al., 1990). Importantly however, the physical characteristics of the disturbance (Effenberger, Sailer, Townsend, & Matthaei, 2006; Townsend, Scarsbrook, & Dolédec, 1997) dictates that the role of refugia will differ significantly among disturbance type and as such the role and the functioning of refugia should be examined specifically to each disturbance type.

Flow refugia are locations that maintain substrate stability and low hydraulic stress during periods of high flow, thereby allowing taxa to resist the disturbance (Fuller, Griego, Muehlbauer, Dennison, & Doyle, 2010; Lancaster & Hildrew, 1993a). Refugia can be present at various spatial scales, ranging from individual particles (Biggs, Duncan, Francoeur, & Meyer, 1997; Matthaei, Arbuckle, & Townsend, 2000; Townsend, Scarsbrook, et al., 1997) to woody debris and marginal vegetation (Borchardt, 1993; Palmer, Arensburger, Martin, & Denman, 1996; Thompson et al., 2018). At the larger scale, inundated riparian areas, backwaters and the hyporheic zone can act as important refugia for a variety of organisms (Dole-Olivier, Marmonier, & Befly, 1997; Matthaei & Townsend, 2000; Sueyoshi, Nakano, & Nakamura, 2014). Of the limited work conducted on the importance of flow refugia, a large majority of these studies have focussed on natural flood pulses in relatively natural floodplains (Matthaei & Townsend, 2000; Sueyoshi et al., 2014) as well as channelised river reaches (Negishi, Inoue, & Nunokawa, 2002). However, flow regulation remains a significant ongoing threat to freshwater diversity (Belletti et al., 2020; Reid et al., 2019) and globally artificial floods are being used to restore flood pulses in flow-regulated rivers (Konrad et al., 2011; Olden et al., 2014). Although the positive implications of artificial flood programmes have been documented for ecosystem health (Melis, Korman, & Kennedy, 2012; Ortlepp & Mürle, 2003; Robinson, Siebers, & Ortlepp, 2018; Robinson & Uehlinger, 2008), little is known about the role of flow refugia in maintaining ecological persistence during these artificial flow pulses (but see Robinson, Aebischer, & Uehlinger, 2004).

Anthropogenic activities continue to modify riverine ecosystems globally, diminishing habitat diversity and the potential availability and quality of refugia habitats (McCluney et al., 2014; Wohl, 2019). It is therefore urgent that the role of refugia is better quantified for different river types that cover a range of flow regimes, especially as high flows are being increasingly implemented in river restoration schemes. Further, this urgency is particularly relevant given that climatic change is leading to more unpredictable hydrological conditions with both flood and drought events predicted to increase in frequency and intensity (Asadieh & Krakauer, 2017; Yuan, Jiao, Yang, & Lei, 2018). Identifying habitats which could act as flow refugia during flood disturbances is therefore vital to ensure the persistence of freshwater biodiversity globally. This knowledge would enable freshwater refugia habitats to be conserved and incorporated in management and restoration strategies, something that is currently absent (Hermoso, Ward, & Kennard, 2013; Keppel et al., 2015; Selwood & Zimmer, 2020). As working on the implications of flood events is inhibited by the relative unpredictability of flood events and the logistics of working during high flows (Death, 2008), artificial flow pulses can also provide valuable scientific opportunities for testing ecological theories (Konrad et al., 2011; Olden et al., 2014).

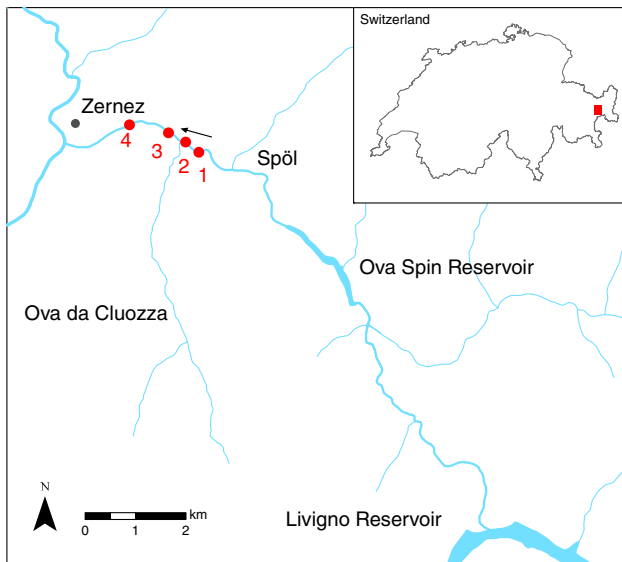
In this study, we therefore sought to assess how substrate stability affected the provision of instream habitats that provide flow refugia from an artificial flood pulse in the regulated river Spöl, Switzerland. The objectives were to: (a) assess the role of flow refugia in maintaining the core taxa present in the Spöl despite potential reductions in abundances following the artificial flood; (b) assess the implications of the artificial flood pulse on substrate stability and the provision of in channel refugia habitats; and (c) assess the effectiveness of different habitats to act as flow refugia during an artificial flood pulse.

## 2 | METHODS

### 2.1 | Study location

The river Spöl is located in the central Alps, flowing into Switzerland from Italy in the lower Engadine (Figure 1). The river is regulated by two hydroelectric dams before entering the Inn River at Zernez, Switzerland. Flow regulation in the form of residual flow (a minimum discharge that is set) commences downstream of Livigno reservoir (Punt dal Gall dam) where the Spöl flows ~5.7 km through a canyon-confined valley in the Swiss National Park and into the lower Ova Spin reservoir. From this reservoir, the Spöl flows a further 5.5 km to its confluence with the Inn. For more details regarding the hydropower setup on the river Spöl please see Scheurer and Molinari (2003).

Prior to regulation in 1970, the river Spöl exhibited a natural snowmelt / glacial meltwater flow regime, with high flows in summer and low flows in winter. Periodic floods from heavy rainfall occurred during summer / early autumn with peak discharges between 20 and 60 m<sup>3</sup>/s (Robinson et al., 2018). The average annual flow of the Spöl at the Punt dal Gall fluctuated between 12.5 and 6.6 m<sup>3</sup>/s, but post-



**FIGURE 1** Map of the study sites on the river Spöl in the Swiss National Park. The artificial flood was released from the Ova Spin Reservoir in September 2018 [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/rm.3941)]

completion of the dam the residual flow was set to an average flow of  $1 \text{ m}^3/\text{s}$ . In the lower flow regulated section from Ova Spin to Zernez, the flow is even lower, being permanently set to  $1 \text{ m}^3/\text{s}$  in summer and  $0.3 \text{ m}^3/\text{s}$  in winter (Scheurer & Molinari, 2003).

Land use within the  $295 \text{ km}^2$  catchment (Bundesamt für Umwelt, 2020) is predominately coniferous forest (*Picea excelsa* and *Pinus mugo*) with some grassland and sedges present in the lower floodplain. Climate in the region is continental with high seasonal variations in temperature, but low precipitation (Barry, 1992). River sediments originate primarily from dolomitic and calcareous scree from rocky, high gradient valley slopes and locally from remnant glacial moraines (Trachsel, 2001; Trümpy, Schmid, Conti, & Froitzheim, 1997). Bedrock is present in many areas of the riverbed. In many places, forest vegetation has colonised gravel bars, and roots of woody vegetation have stabilised banks decreasing riparian dynamics often present in natural free-flowing rivers (Mürle, Ortlepp, & Zahner, 2003).

## 2.2 | Artificial flood, study sites and habitats

The most notable feature of the flow regime of the regulated Spöl was the absence of peak flow events. As a result, the Engadine power company, Swiss National Park and state authorities began to implement artificial floods, predominately in the upper regulated part of the Spöl in 2000. Thirteen artificial floods have also been undertaken in the lower flow regulated section (2000–2017; Kevic, Ortlepp, Mürle, & Robinson, 2018). In September 2018 (the focus of this study), a controlled artificial flood was released in the lower flow regulated section, from the outlet of the Ova Spin reservoir over an 8-hr period. A peak discharge of  $25 \text{ m}^3/\text{s}$  was achieved during the

flood that lasted around 2 hrs, with rising and falling limbs being incremental. Although the event was shorter than natural flood events, previous artificial floods of similar discharge have been shown to be sufficient enough to mobilise bed sediments and reduce algal levels without causing high fish mortality (Mürle et al., 2003; Ortlepp & Mürle, 2003; Uehlinger, Kawecka, & Robinson, 2003). It should be noted that there were no implications for water temperature during the studied flood as the dam is a hypolimnetic release reservoir, and thus the thermal regime remains relatively constant (Jakob, Robinson, & Uehlinger, 2003).

The effects of the 2018 artificial flood were monitored at four locations over a 1.5 km section of the lower river Spöl downstream of the Ova Spin reservoir with the first site (site 1) located ca. 2.7 km downstream of the Ova Spin outlet (Figure 1). Two sites (sites 1 and 2) were located upstream of the unregulated Ova da Cluozza tributary, and two sites (sites 3 and 4) were located downstream of the confluence. The upstream sites (sites 1 and 2) are located in a canyon-confined channel, whereas the lower two sites (sites 3 and 4) are in a more open floodplain valley where the channel takes on a braided form (Figure 1). The four sites represented a gradient of sediment conditions with heterogeneous substrates present at sites 1 and 2 and a more homogenous riverbed at sites 3 and 4 (see Figure S1 for site photographs). Sampling was conducted before and after the artificial flood with pre-flood sampling taking place the week prior to the flood. Substrate samples were conducted immediately following the artificial flood and again 10-months later to assess the temporal longevity of flood effects. Macroinvertebrate sampling was conducted 1 and 7 days after the artificial flood to assess the utilisation of potential refugial habitats. Sampling methodology details can be found below.

At each site, sampling was conducted at the habitat level. A total of six potential refugial habitats were visually identified as occurring at one or more sites. These comprised of three in-channel gravel-bed habitats: (a) the main channel (subjected to high velocities at all sites, average  $0.99 \text{ m/s}$  pre-flood, and periodic floods at sites 3 and 4 from the Ova da Cluozza tributary); (b) side channels (reduced velocities at average  $0.41 \text{ m/s}$  pre-flood) with the majority maintaining connectivity with the main channel under residual flow conditions and; (c) riffle at site 1 only (average velocities pre-flood of  $0.70 \text{ m/s}$ ). Three habitats lacking gravel substrate being comprised of sand / silt or terrestrial vegetation were also identified: (d) lentic (comprising an unconnected floodplain pond under residual flow conditions and 1–2 samples in a pool per time period at site 2); (e) river margins (taken at the river shoreline and which encompassed terrestrial vegetation at site 3 during flooding) and; (f) inundated floodplain (encompassing a channel that formed on the grassy floodplain following the flood and was connected at either end to the main channel at site 4). See Table S1 for a summary of all flow velocities for site-specific habitats before and after the flood and Table S2 for a breakdown of the sampled habitats on each occasion. As refugial habitats were sampled when present, some habitats were sampled only at one site (e.g., floodplain and riffle) and some were sampled on one or two occasions for some sites.

## 2.3 | Sampling methods

### 2.3.1 | Grain-size distributions

To assess the grain-size distribution (GSD) of surface substrates, 100 to 200-count Wolman samples (dependent on habitat area) were conducted at each in-channel gravel-bed habitat ( $n = 3$ ) where present at each site. Grains were selected by conducting longitudinal transects within each habitat, blindly selecting a grain at each step and measuring the b-axis via a gravelometer (Wolman, 1954). Wolman counts were conducted before (hereafter termed pre-flood) and after the artificial flood (hereafter post-flood) to determine how bed conditions changed due to the flood. In addition, habitats were surveyed in June 2019, approximately 10 months post-flood (hereafter 10 months post-flood).

### 2.3.2 | Benthic macroinvertebrates

Benthic macroinvertebrates were sampled at each study site via 30 s kick samples ( $n = 3$ –5 per habitat dependent on habitat area) using a standard pond net (1 mm mesh size) and preserved in the field in 70% ethanol. Habitats at each study site were sampled on three occasions; before the artificial flood, 1 day after the flood and ~7 days after the flood ( $n = 155$  samples; 47 at Site 1, 45 at Site 2, 39 at Site 3 and 24 at Site 4). All benthic invertebrates were identified to the lowest taxonomic level possible in the laboratory (most to species or genus with the exception of some Diptera families (Ceratopogonidae, Blephariceridae, Chironomidae, Simuliidae, Empididae, Stratiomyidae and some Limoniidae), Oligochaeta, Zonitidae, and Hemiptera (family).

## 2.4 | Statistical analyses

### 2.4.1 | Grain-size distributions

Grain size percentiles of D16, D50, D84 and statistical parameters of mean, sorting, skewness and kurtosis (Bunte & Abt, 2001) were derived from pooled site data to characterise benthic substrate composition over time. Sorting coefficients were calculated based on Folk and Wards (1957) sorting classification. Cumulative GSD curves were constructed for Wolman counts based on pooled habitat data.

### 2.4.2 | Benthic macroinvertebrates

Differences in community composition between pre-flood, 1 day post-flood and 7 days post-flood were examined via Principal Coordinates Analysis (PCoA) centroid plots. Two centroid matrices were derived from Bray–Curtis similarity coefficients by calculating the averages of all samples per time period; one by site and one by each habitat (regardless of site). Statistical differences in community composition associated with the additive explanatory factors of site, time,

habitat, and the interaction of habitat  $\times$  time and site  $\times$  time were assessed via PERMANOVA using the 'adonis' function in the vegan package using all samples (Oksanen et al., 2019). Where significant differences occurred by time, pairwise comparisons of differences were performed using the 'pairwise.adonis' function (Arbizu, 2019). To assess if beta diversity of SpöL assemblages varied over time (i.e., all sites combined) and over time by site, homogeneity of multivariate dispersions among assemblages were examined using the 'betadisper' function and tested for statistical differences via Tukey post hoc tests.

Taxa driving differences in community composition associated with the artificial flood were examined via the Similarity Percentage (SIMPER) using the 'simper' function. Subsequently, the abundance of the top four taxa identified through SIMPER in addition to total abundance and taxa richness were statistically tested via linear mixed-effects models (LMMs) using the 'lmer' function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). All metrics were  $\log(x + 1)$  transformed. Here, taxa richness was assessed as proxy for refugia provision following Van Looy et al. (2019). Should refugia be present, taxa richness should demonstrate a non-significant effect associated with time. All models were fitted with the fixed effects of time (pre-flood, 1 day post-flood and 7 days post-flood), habitat and their interaction. Site was fitted as a random effect to account for potential spatial and temporal autocorrelation. Post-hoc pairwise comparisons of groups were performed where a significant effect of time was returned using estimated marginal means within the 'emmeans' package (Lenth et al., 2020). All analyses were conducted in the R environment (R v3.6.0; R Development Core Team, 2019).

## 2.5 | Results

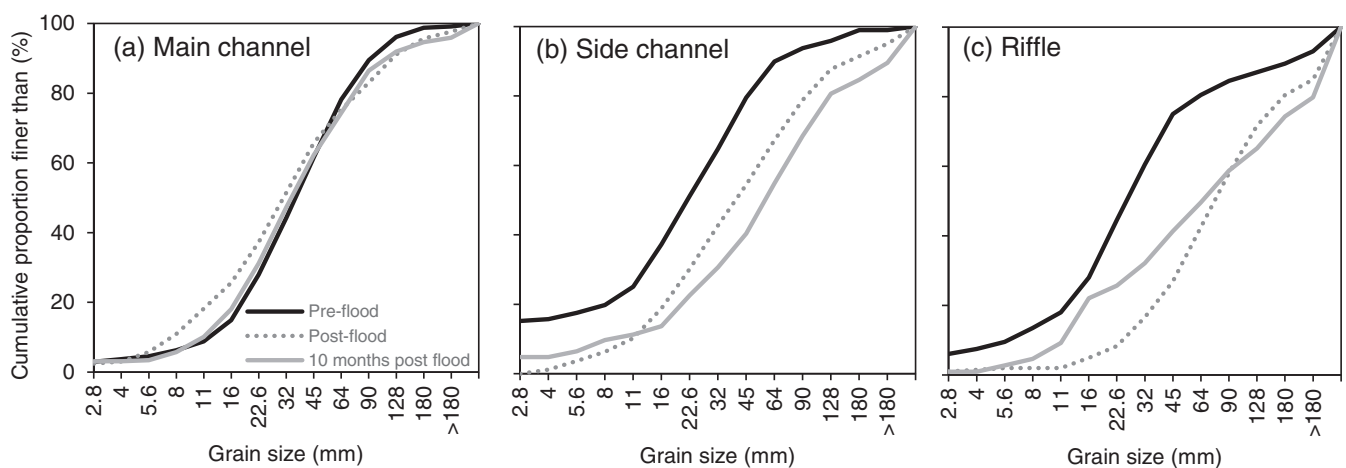
### 2.5.1 | Grain-size distributions

The GSD of benthic substrates changed following the flood pulse, being habitat and site dependent. At the site level, changes in the GSD were most evident at sites 1 and 2, with gravels becoming coarser immediately following the artificial flood, indicating the loss of fine sediment surficial deposits (Table 1). At sites 3 and 4, changes in GSD were not as substantial but still present, with some increases in the fine – medium pebble fractions (4–16 mm) at both sites, resulting in a finer distribution (Table 1). Ten months post-flood, sites 1 and 2 displayed little change in post-flood GSD conditions. In contrast, GSD at sites 3 and 4 demonstrated a considerable shift to coarser substrate conditions 10 months post-flood (Table 1). Sorting coefficients were generally similar across time, with grains being classified as moderately well sorted (Folk and Ward coefficients of 0.5–1.0). However, at site 2 in both post-flood periods and at site 1 10 months later, fractions were classified as being well sorted (coefficients in the range 0.35–0.50). Kurtosis values did not vary over time (Table 1).

At the habitat level, there were no differences in GSD profiles over time at the main channel habitats (Figure 2a). In contrast, considerable changes in the GSD were evident at side channel and riffle habitats with coarsening evident following the flood (Figure 2b,c). Riffle

**TABLE 1** Summary of grain size metrics for the study period based on Wolman pebble count. Post-flood is immediately after the artificial flood

Metric	Site 1			Site 2			Site 3			Site 4		
	Pre-flood	Post-flood	10 months post-flood	Pre-flood	Post-flood	10 months post-flood	Pre-flood	Post-flood	10 months post-flood	Pre-flood	Post-flood	10 months post-flood
D16 (mm)	7.8	11.1	8.9	10.1	9.2	9.5	9.9	6.5	10.9	9.6	6.9	16.2
D50 (mm)	21.2	30.5	24.0	26.9	43.8	36.0	21.0	18.5	25.2	23.7	18.5	33.2
D84 (mm)	50.9	81.3	121.9	65.0	144.3	111.0	39.0	47.0	67.0	43.7	39.0	58.0
Mean (mm)	23.9	38.3	38.7	30.8	57.5	44.8	22.2	21.8	31.8	25.0	20.5	35.0
Sorting	0.55	0.53	0.40	0.54	0.37	0.45	0.65	0.52	0.54	0.58	0.57	0.62
Skewness	0.91	1.08	1.24	0.91	0.72	0.88	0.93	0.93	1.11	0.83	0.90	0.89
Kurtosis	0.18	0.20	0.16	0.22	0.25	0.17	0.24	0.22	0.21	0.27	0.26	0.31

**FIGURE 2** Grain-size distribution (GSD) profiles of benthic substrates as determined by Wolman counts at the three in-channel habitats (a) main channel, (b) side channel and (c) riffle. Post-flood is immediately after the artificial flood

habitats displayed fining 10 months later with an increase in the fraction <30 mm, whilst no further change was present in the side channel habitats.

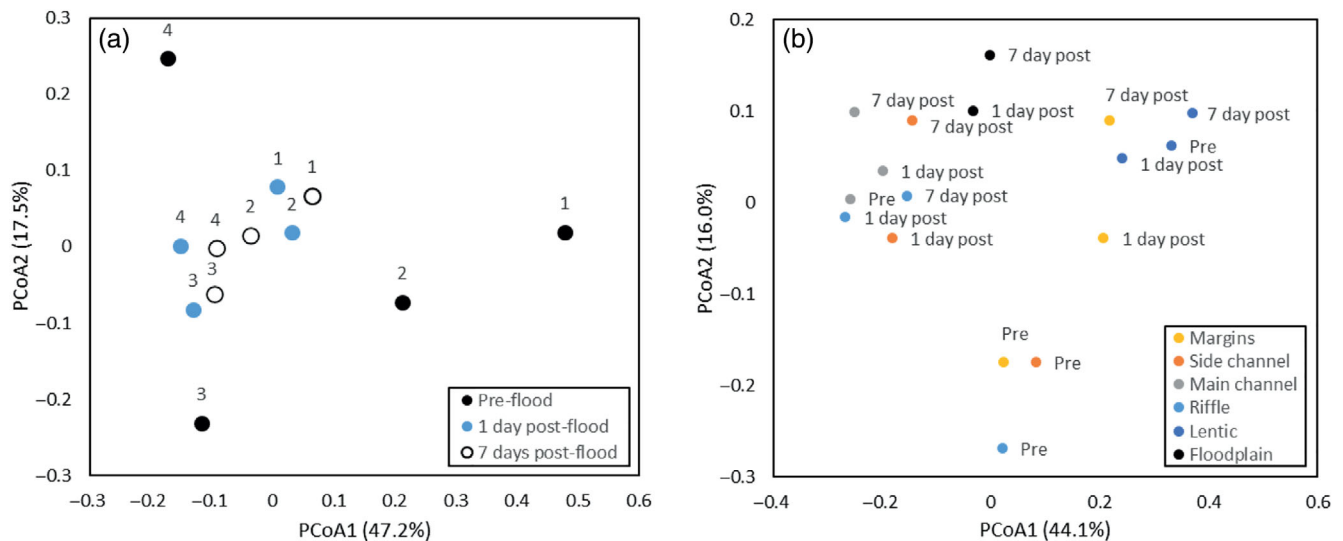
## 2.5.2 | Benthic macroinvertebrates

A total of 18,672 individuals comprising 38 taxa (and 3 semi-aquatic taxa) were recorded in the 155 benthic samples. The most abundant taxa overall were *Gammarus fossarum* (47.8% of total benthic abundance) followed by *Baetis* sp. (21.7%), Chironomidae (12.0%) and *Rhithrogena* sp. (5.4%). Three predominately lentic taxa, most likely originating from the reservoir, were found only post-flood (Ptychoptera, Stratiomyidae, Ceratopogonidae, totalling 9 individuals).

PCoA centroid site plots indicated a shift in community composition following the artificial flood at all sites (Figure 3a). Pre-flood community composition between sites was heterogeneous with sites plotting discretely in ordination space. In contrast, post-flood communities from all sites clustered towards the centre of the ordination

space with the composition of each site converging indicating a more homogenous assemblage across all sites. Beta diversity of SpöL assemblages reflected this with a significant reduction in community heterogeneity following the artificial flood in both 1 day and 7 day post-flood assemblages relative to pre-flood assemblages ( $p = .04$  and  $p = .05$ , respectively).

PERMANOVA indicated that community composition differed as a function of sample time, site and habitat in addition to the interaction of site  $\times$  time and habitat  $\times$  time (all factors  $p < .002$ ), with habitat accounting for the greatest amount of variation ( $R^2$  of 17%). Pairwise PERMANOVA indicated that community composition of pre-flood communities differed relative to 1 and 7 day post-flood communities ( $F = 4.01$ ,  $R^2 = 0.04$ ,  $p = .014$  and  $F = 9.34$ ,  $R^2 = 0.09$ ,  $p = .001$ , respectively), but there were no differences between 1 day and 7 day post-flood communities ( $p > .05$ ). SIMPER indicated that reductions in *G. fossarum*, *Baetis* sp., Chironomidae, *Rhithrogena* sp. and *Protonemura* sp. were the primary driver of differences between pre- and post-flood assemblages (Table S3). Despite alterations to SpöL assemblages following the flood, beta diversity



**FIGURE 3** Principal Coordinates Analysis (PCoA) centroid (a) site, and (b) habitat plots using Bray–Curtis similarity coefficients of benthic communities from the river Spöil associated with an artificial flood in September 2018. In plot labels for a = sites (1–4) and for b = time period (Pre = pre-flood, 1 day post = 1 day post-flood and, 7 days post = 7 days post-flood). Note inundated floodplains were only sampled after the flood [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/rm.3941)]

**TABLE 2** Summary of LMMs testing the influence of sample time (pre-flood, 1 day post-flood and 7 days post-flood), habitat and their interaction on total abundance, taxa richness and abundance of individual taxa

Factor	Time		Habitat		Time × habitat	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Total abundance	9.71	<b>.008</b>	33.72	<b>&lt;.001</b>	5.78	.762
Taxa richness	0.01	.996	14.16	<b>.015</b>	12.20	.202
<i>Gammarus fossarum</i>	2.96	.228	45.74	<b>&lt;.001</b>	8.22	.512
<i>Baetis</i> sp.	33.84	<b>&lt;.001</b>	70.36	<b>&lt;.001</b>	14.88	.094
Chironomidae	28.55	<b>&lt;.001</b>	210.54	<b>&lt;.001</b>	31.19	<b>&lt;.001</b>
<i>Rhithrogena</i> sp.	5.32	.069	38.24	<b>&lt;.001</b>	15.03	.090

Note: Significant terms are emboldened.

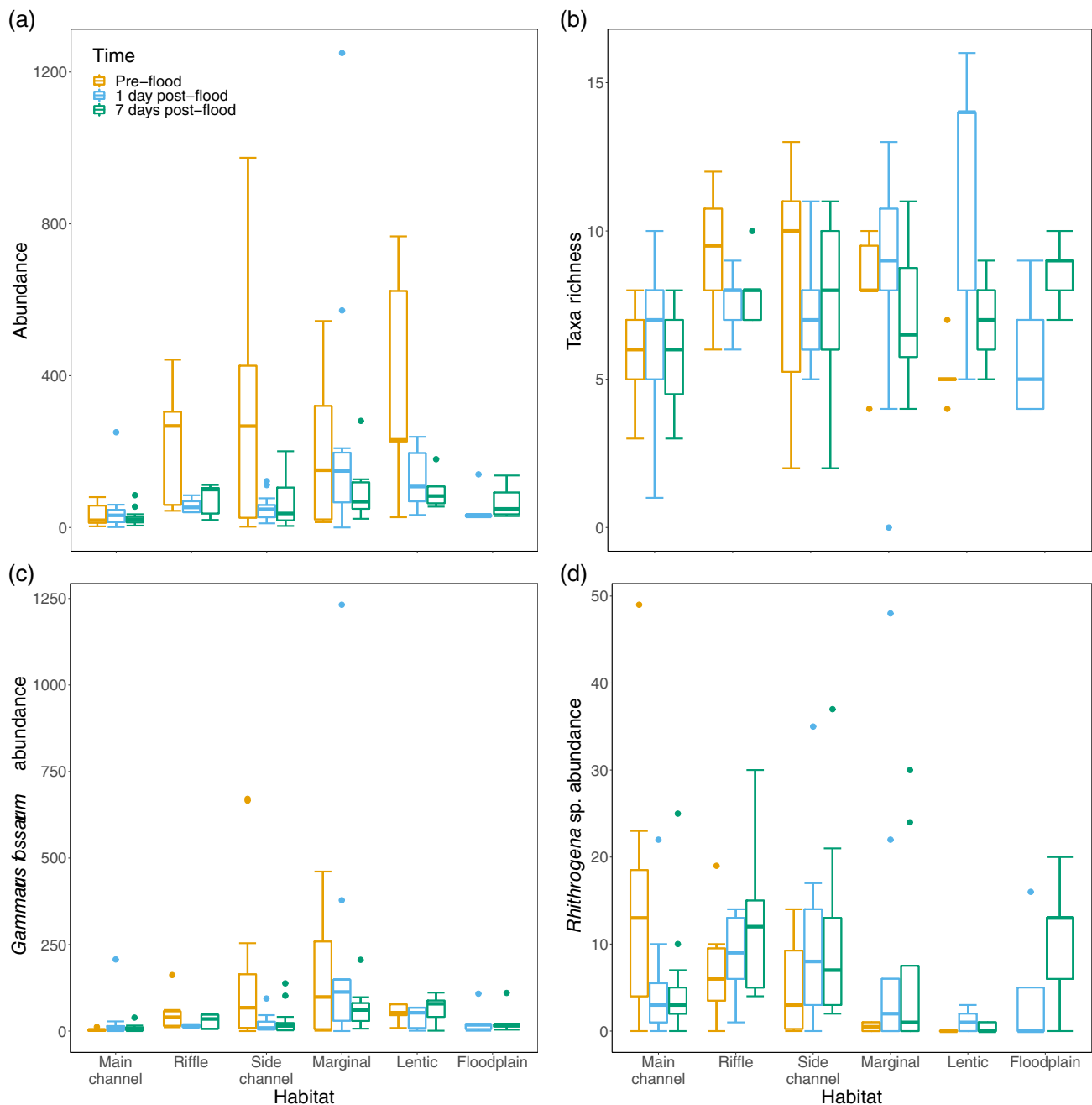
remained stable at the individual sites over time ( $p > .05$ ), with the exception of site 1 which saw a significant increase in heterogeneity following the artificial flood ( $p = .026$ ).

PCoA habitat centroid plots indicated a shift in community composition associated with habitat type. Pre-flood margin and side channel communities were most similar, with riffle communities also occupying a similar ordination space. In contrast, main channel and lentic habitats supported discrete communities (Figure 3b). Following the flood, riffle and side channel communities became more comparable to main channel communities, whilst margin communities demonstrated a shift in composition similar to lentic assemblages and still supported discrete communities post-flood (Figure 3b). Floodplain communities represented a ‘bridge’ between the two clusters of instream and margin / lentic habitats (Figure 3b).

Benthic total abundance, and the abundance of *Baetis* sp. and Chironomidae demonstrated a statistically significant negative effect of sample time (Table 2). Taxa richness and abundances of *G. fossarum* and *Rhithrogena* sp. did not differ by time (Table 2). Total abundance reduced immediately following the flood in all habitats with the

exception of main channel communities that remained stable 1 day after the flood (Figure 4a; Table S4). Taxa richness demonstrated highly patchy and variable responses to the artificial flood (see Figure 4b), although only the lentic habitat exhibited a significant increase 1-day after the flood. Taxa richness in some habitats did not change following the flood (e.g., main channel), displayed a reduction for some habitats (e.g., riffle and side channel), or increased immediately post-flood then displayed reductions 7 days post-flood (e.g., lentic, margin; Figure 4b).

*G. fossarum* were highly abundant (>100 individuals per 30 s sample) at marginal and side channel habitats pre-flood, but were markedly reduced in side channels immediately following the flood (Figure 4c). Use of habitats by *G. fossarum* 1-day following the flood was highly variable with marginal habitats supporting abundances of ~1,250 individuals (per 30 s kick) in one instance. *Rhithrogena* sp. abundances in margin and side channel habitats showed significant increases 1 day post-flood with the floodplain also supporting comparable numbers (Figure 4d; Table S4). Post-flood abundances remained stable in side and margin habitats but



**FIGURE 4** Boxplot of (a) total abundance; (b) taxa richness; (c) *Gammarus fossarum* abundance, and (d) *Rhithrogena* sp. abundance of benthic macroinvertebrate communities as a function of habitat and sample time (pre-flood, 1 day post-flood and 7 days post-flood). Note inundated floodplains were only sampled after the flood [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

continued to expand in floodplain habitats 7 days post-flood. The main channel displayed a marginally insignificant reduction in *Rhithrogena* sp. following the flood (Figure 4d). As with *G. fossarum*, highly variable habitat use following the flood was evident for *Rhithrogena* sp. with considerable positive outliers evident in side channel and margin habitats both 1 and 7 days following the flood pulse (Figure 4d). *Baetis* sp. abundances were significantly reduced in riffle, side channel and margin habitats and Chironomidae abundances in lentic and riffle habitats following the flood (Figure S2a, b; Table S4).

### 3 | DISCUSSION

We examined how benthic macroinvertebrates responded to an artificial flood associated with the provision of differential habitats acting as flow refugia. Prior to the artificial flood pulse, benthic macroinvertebrate communities at each site represented discrete communities, most likely reflecting the habitat heterogeneity present at the different sites. However, following the flood pulse, communities became more homogenous with little variation between sites being present both 1 and 7 days post-flood. Despite the

homogenisation of Spöl assemblages associated with the flood, within-site beta diversity remained temporally stable in all but one instance. The stable temporal beta diversity at the site level suggests that refugia provision was present in the Spöl with taxa being able to persist through the flood, but that the more tolerant generalists dominated. The exception to this was at site 1 that supported the highest taxa richness pre-flood, and which comprised a core set of taxa but also some rarer species. It is likely that the flood eradicated some of these rarer taxa with some remaining in a few samples, thereby causing the observed increase in community heterogeneity post-flood. The provision of refugia also can be assumed through the lack of significant differences in overall Spöl taxa richness pre- and post-flood. Taxa richness can provide a good proxy to assess the presence of refugia during periods of disturbance (following Sueyoshi et al., 2014; Van Looy et al., 2019). Given the stability in this metric, we can assume that refugia were present in the Spöl and therefore that refugia provision was essential in enabling the resistance of benthic taxa to the artificial flood (also see Robinson, Aebischer, et al., 2004).

Following the flood, lateral margin areas and the inundated floodplain displayed increased abundances and the lentic habitat (comprising a previously disconnected floodplain pond) displayed increased taxa richness, suggesting either active flow refuge seeking behaviour to avoid unfavourable conditions in the river channel, or passive draft/transport during the flood followed by persistence in the refugial habitats. Robinson, Aebischer et al. (2004) and Matthaei and Townsend (2000) also recorded high invertebrate drift within inundated riparian areas following floods and shoreline / marginal areas have been similarly cited as refugial areas (Rempel, Richardson, & Healey, 1999). Margin habitats exhibited a shift in composition to one similar to lentic habitats in our study, reflecting the refugial role both these habitats played for taxa preferring slow-flowing waters. Sueyoshi et al. (2014) similarly found that habitats with slow-flowing water acted as refugia during a snowmelt flood. In contrast, the instream habitats of riffle, side and main channel habitats became more homogenous in their community composition post-flood. Reductions in abundance and taxa richness were also evident in the riffle and side channel habitats, most likely reflecting a considerable loss of taxa. Inundated floodplain communities represented a 'bridge' between the two clusters of instream (riffle, side and main) and margin / lentic habitats, suggesting some degree of intermediate habitat conditions. The active use of riparian and floodplain habitats as refugia highlights the importance of river systems being able to maintain lateral connectivity during hydrological flood disturbances (Chanut, Datry, Gabbud, & Robinson, 2019; Matthaei & Townsend, 2000; Ward, 1989). Globally, many river channels are increasingly being channelised, resulting in flood peaks being funnelled within the channel with little connection with lateral riparian / floodplain areas that naturally would occur. This lack of lateral connectivity in highly modified river channels limits habitat provision and in turn the likelihood of taxa finding suitable refugia (Negishi et al., 2002; Sueyoshi et al., 2014; Williams et al., 2020). Our results provide further evidence that lateral connectivity is essential to maintain biodiversity following hydrological disturbances.

Flow refugia use was particularly evident for the mayfly *Rhithrogena* sp. with occupation in the floodplain habitat, and increased abundances in margin and side channel habitats following the flood. This result was mirrored by a reduction in abundances in their dominant habitat of the main channel prior to the flood. Refugia use has been found to be highly species dependent (Lancaster & Hildrew, 1993b; Sueyoshi et al., 2014), however Rempel et al. (1999) also cited *Rhithrogena* sp. as showing active refugia behaviour following a large flood. This taxon is highly mobile, being observed as early recolonists following instream disturbances (Matthaei, Uehlinger, Meyer, & Frutiger, 1996) and therefore can seek refugia when hydraulic stress increases during flood events.

Mobility in accessing refugia is also crucial to ensure that taxa are not stranded in temporary habitats formed during a flood, such as inundated floodplains or marginal areas (Matthaei & Townsend, 2000). In the case of the studied flood pulse, morphological change in the channel form dictated that marginal and inundated floodplain habitats were still present 7 days after the flood. Therefore, it can be expected that taxa would have been able to make it back to their residential habitats with low risk of stranding following the flood. In contrast to *Rhithrogena* sp., the mayfly *Baetis* sp. and the dipteran Chironomidae displayed significant reductions in abundance following the flood. Bruno, Cashman, Maiolini, Biffi, and Zolezzi (2016) found that these two taxa were particularly sensitive to dislodgement from high flows, demonstrating the highest drift rates during hydropeaking flood pulses. Although both taxa are particularly affected during artificial flood pulses, they have been recorded to exhibit rapid recovery to pre-disturbance abundances (Robinson et al., 2003; Robinson, Uehlinger, & Monaghan, 2004).

Use of refugia is often highly patchy in space, reflecting the microdistribution of hydraulic stress and substrate stability amongst other factors (Dole-Olivier et al., 1997; Lancaster & Belyea, 1997; Palmer et al., 1996). This patchiness was evident in the Spöl with *G. fossarum* and *Rhithrogena* sp. demonstrating considerable abundances in individual samples that were an order of magnitude greater than in other samples. For example, abundances of 1,232 individuals were recorded in one 1-day post-flood margin sample for *G. fossarum* (maximum pre-flood abundance of 666 in side channel habitat), whilst a large number of outliers were evident in both 1 and 7 day post-flood samples within the margin and side channel habitats for *Rhithrogena* sp. This patchiness highlights the need for high habitat diversity under baseflow conditions, which in turn dictates a high likelihood of habitat diversity under hydrological stress, with a small proportion of these habitat patches representing suitable refugia for different taxa. The patchy nature of refugia use also highlights the difficulties in assessing refugia potential, particularly associated with the unpredictable nature of floods (Death, 2008). Artificial floods in this sense represent a unique scientific opportunity to further our knowledge base of flow refugia (Konrad et al., 2011; Olden et al., 2014).

The importance of refugia habitats in the Spöl can be placed in the context of changing sedimentological conditions. High hydraulic stress during flood events can lead to significant displacement of benthic macroinvertebrates, whilst stable riverbed patches can act as flow



refugia (Effenberger et al., 2006; Lancaster & Hildrew, 1993a). We observed that all sites underwent changes in their GSD, which may partially explain the altered composition of macroinvertebrate communities following the flood. In particular, riffle and side channel habitats underwent considerable coarsening with the artificial flood mobilising fine sediments. Other studies examining the role of artificial floods in the river Spöl under earlier flood settings also observed a coarsening of riverbed sediments, with active transport of bed material and the deposition of loose gravel (Mürle et al., 2003). We observed similar in this study. The high degree of sediment transport most likely explains why these habitats displayed the greatest changes in macroinvertebrate communities following the flood in terms of composition, abundance and richness, with large-scale drift often being initiated via dislodgement due to saltating grains or enhanced shear stresses (Gibbins, Batalla, & Vericat, 2010; Gibbins, Vericat, & Batalla, 2007). In marked contrast to the side and riffle habitats, the main channel, although also being subjected to the highest hydraulic pressures of the flood pulse, displayed no changes in the GSD. This habitat was subjected to high energy velocities prior to the flood pulse and it can be expected that the artificial flood would not change the structure of the riverbed. Here, taxa richness and abundances were low prior to the flood but remained temporally stable as did community composition to some degree. Understanding substrate stability is therefore vital to be able to assess the relative importance of refugia for maintaining resilience.

Our knowledge of flow refugia remains severely limited compared to that of drought / low flow refugia. Our results provide additional knowledge to this neglected resilience concept in the context of an artificial flood pulse. We found that although macroinvertebrate assemblages became homogenised longitudinally at the four river locations monitored, the diversity of invertebrate communities at the site scale remained similar to pre-flood levels and taxa richness remained stable over time. Overall, these results indicated that although generalist taxa dominated the community following the flood, sufficient refugia must have been present to enable the persistence of more flow-sensitive taxa that contribute to diversity. Riparian margin areas, inundated floodplains and lentic habitats (a floodplain pond) acted as important refugia areas. Low substrate stability in riffle and side channels resulted in limited refugia potential. However, our results also highlight that refugia use is patchy in space, with significant intra-habitat variability being evident. We believe this study and the recognition of refugia as a means of river resilience by Van Looy et al. (2019) should stimulate further research on flow refugia functioning, which although prominent in the late 1990's has since been essentially neglected. Ensuring refugia functioning under increasingly unpredictable hydrological extremes by incorporation into restoration and management schemes is vital to ensure the persistence of freshwater biodiversity and management (Selwood & Zimmer, 2020).

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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