PRIMARY RESEARCH PAPER

Long-lasting effects of experimental flow intermittency on alpine stream macroinvertebrates (Val Roseg, Switzerland)

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Abstract Changing weather patterns and receding glaciers are predicted to increase flow intermittency in alpine streams. If aquatic macroinvertebrate communities largely comprise taxa adapted to perennial flows, an increase in flow intermittency substantially reduces biodiversity and affects functional processes. We conducted a before-after-control-impact field experiment to examine how macroinvertebrate communities in an alpine headwater stream responded to and recovered from a repeated experimental increase in flow intermittency. Flow in one channel was manipulated to simulate increased summer intermittency (June–September) over two consecutive years, whilst an adjacent channel served as a control. We monitored the density of benthic macroinvertebrates, periphyton and organic matter at approximately monthly intervals over three years during the snow-free period. Before manipulation, both channels had similar ecological properties. The flow manipulation reduced the overall macroinvertebrate density, and especially the proportional rheophile density, across both years. Recovery of the macroinvertebrate community following experimental flow intermittency took more than a year, and longer than our study period. This could be due to long aquatic life stages, dispersal limitation and biotic interactions. We conclude that climate-induced changes in alpine stream flow regimes can lead to a fundamental shift in macroinvertebrate assemblages through local extinctions, mostly of rheophilic species.

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Introduction

Alpine streams harbour a high level of biodiversity and play an important role in biogeochemical cycling in fluvial networks (Hotaling et al., 2017; Milner et al., 2017; von Schiller et al., 2017). Aquatic macroinvertebrate communities in glacier-fed alpine waters are shaped by a distinct flow regime (continuous high flow in summer and low flows in winter) and low temperatures (Milner et al., 2017). However, changing weather patterns and disappearing glaciers can lead to an increase in flow intermittency, especially in summer (Piano et al., 2019; Muelchi et al., 2021). This is expected to have substantial long-term effects on aquatic macroinvertebrate communities in alpine streams (Cauvy-Fraufrom & Dangles, 2019; Piano et al., 2019; Paillex et al., 2020).

Flow intermittency is a strong driver of benthic macroinvertebrate abundances and composition (Stubbington et al., 2017). In alpine streams, community density and diversity may decrease with increasing frequency and duration of intermittency if most macroinvertebrates are adapted to perennial flows (Ward, 1994; Menezes et al., 2010; Windsor et al., 2017; Paillex et al., 2020). During short dry periods (i.e., a few days or weeks), some taxa in intermittent streams can persist in a desiccation-resistant stage or using refuges, like the hyporheic zone (Stubbington, 2012; Stubbington & Datry, 2013; Vander Vorste et al., 2016b). Where resistance traits are common, recovery to the original community might thus take place within a few weeks following flow resumption (Fowler, 2004; Vander Vorste et al., 2016b; Van Looy et al., 2019).

Impacts on stream biota typically increase with the duration of the dry period: relative desiccation-resistance and local refuges become insufficient mechanisms for population persistence (Fowler, 2004; Van Looy et al., 2019). Macroinvertebrates then recolonise the rewetted streambed from nearby perennial waters; e.g., via drift and aerial dispersal (Doretto et al., 2018, 2020; Alther et al., 2019; Siebers et al., 2020). As summer drying of streams often coincides with aquatic life stages of insects in alpine streams (Ward, 1994; Robinson et al., 2010), it can shift assemblage composition to include more multivoltine, generalist taxa and fewer rheophilic, univoltine, drying-sensitive and specialized taxa (Doretto et al., 2018; Piano et al., 2019; Siebers et al., 2020). Several experimental studies that increased intermittency for relatively long time periods (i.e., several months up to a year) showed relatively slow recovery after normal flow resumption; macroinvertebrate assemblages remained impacted 6 to 16 months after rewetting (Cauvy-Fraufrom et al., 2016; Piano et al., 2019; Siebers et al., 2020).

The persistence of populations and assemblages at a landscape scale are, therefore, most likely to be affected by drying events over multi-year timescales. Most experimental and field studies only characterise intermittency effects over short time periods; i.e., from single measurements up to a year, or from single channels and uniform experimental setups (Doretto et al., 2018; Siebers et al., 2020; Gruppuso et al., 2021). Yet, the multi-year effects of the expected increase in summer flow intermittency in alpine streams remain unknown.

Here, we conducted a three-year before-after-control-impact (BACI) field experiment in an alpine headwater stream to gain insight into the response and recovery of macroinvertebrate communities to an increase in summer flow intermittency. We manipulated flow in a channel to simulate the expected climate change-induced increase in summer intermittency (June–September) over two consecutive years. An adjacent channel was used as a reference/control. Recovery was monitored between flow manipulation periods and then for a year after normal flow resumption. Siebers et al. (2020) describe the immediate responses to the first flow manipulation. In the current study, our objectives were to (1) assess the multi-year effects of an experimental increase in summer intermittency on the macroinvertebrate community in an alpine channel, (2) compare changes in macroinvertebrate communities between the two summer flow manipulations to establish if repeated summer intermittency had cumulative effects, and (3) characterise recovery of the manipulated channel in comparison to the control stream. We predicted that (1) the increase in summer intermittency would cause the macroinvertebrate community in the manipulated channel (i.e., the manipulated community) to have fewer taxa, fewer rheophilic taxa in particular, and lower densities; (2) the manipulated community would show

cumulative repeated effects over the two summers with increased flow intermittency; and (3) the manipulated community would not return to an ecological state similar to the control channel within a year.

Methods

Description of catchment and experimental site

Val Roseg is a glaciated catchment of the Inn River located in the Bernina massif (Fig. 1) in the eastern Swiss Alps (46°25′39″ N 9°51′31″ E). The valley has two retreating glaciers, Roseg and Tschierva, and a glacial lake that feed the braided channel system (*Ova da Roseg*) in the upper catchment. Here, headwater streams are fed by variable contributions of glacial meltwater, groundwater, snowmelt, and rainwater. Discharge in the *Ova da Roseg* has a strong annual pattern of low winter discharge due to glacial freezing, and a higher discharge during spring and summer as snowmelt and glacial meltwater increase (Ward et al., 1999; Uehlinger et al., 2003; Fischer et al., 2014).

Headwater streams in the Roseg catchment can be highly intermittent, with an estimated 80–90% of the network drying at least once a year (Siebers et al., 2020). Winter freezing of surface water is most common, but short periods (a few days) of periodic summer drying are also widespread (Malard et al., 2006; Robinson et al., 2016; Siebers et al., 2020). A more detailed catchment description can be found in Siebers et al. (2020) and Ward and Uehlinger (2003). We conducted our experiment in a reach in which the study stream splits into two channels for around 350 m. The adjacent study channels (each 100 m) are 10–15 m apart, and similar in altitude (2041 m asl), slope (1.2°) and riparian vegetation. During winter, the study channels can dry (or freeze), or groundwater inputs can maintain baseflow (Robinson et al., 2016; Paillex et al., 2020; Siebers et al., 2020).

Experimental design and data loggers

The experiment used a before-after-control-impact (BACI) design. A temporary barrier that prevented water from entering one channel (MC: manipulated channel) was installed during the summer of 2018 (5 June to 20 September) and 2019 (4 June to
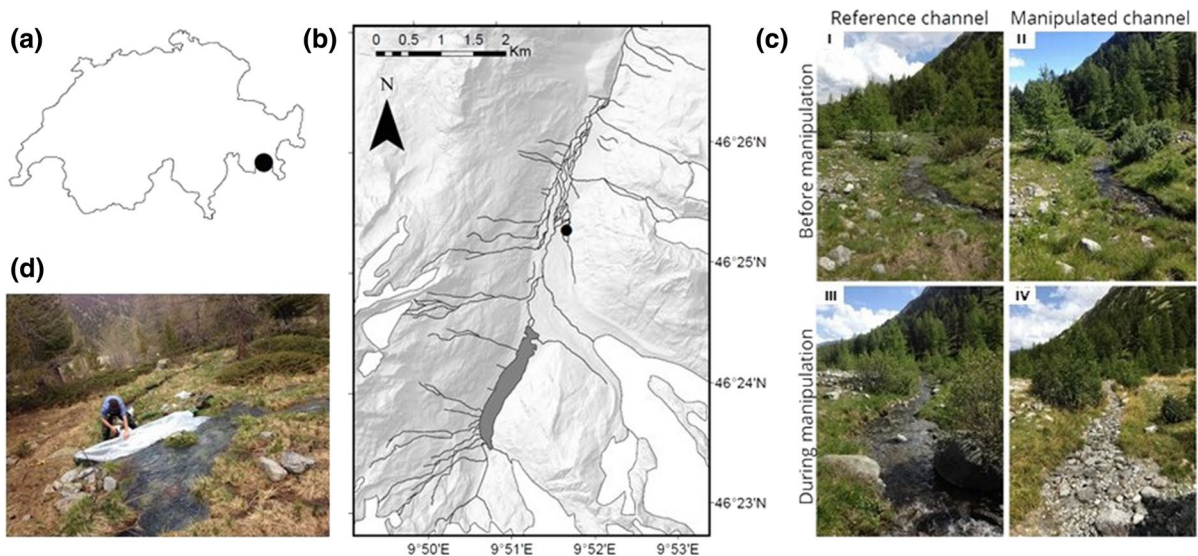
Fig. 1 a Location of the catchment in Switzerland; and **b** location of reference and manipulated channel within the stream network. Glaciers are coloured white, and the glacial lake is coloured in grey. Hill shade is derived from altitude data from the 25 m digital elevation model of Switzerland (swisstopo 2018, swissTLM3D & swissALTI3D, Bundesamt für Landestopographie (Art.30 Geo IV): 5704 000); **c** the reference channel (I, III) and manipulated channel (II, IV) before the flow manipulation in June 2018 (I, II) and during the flow manipulation in August 2018 (III, IV), adapted from Siebers et al. (2020); and **d** installation of the flow manipulation barrier

19 September) to induce surface drying (Figs. 2, 3). No flow manipulation took place in 2020. This flow manipulation period was chosen to coincide with the regular timing of summer drying in intermittent streams in the Roseg catchment; streams usually dry from late June onwards and their surface flow resumes in late September due to a general increase in precipitation (Paillex et al., 2020).

To measure flow intermittency, we used HOBO Pendant Temperature/Light 64 K data loggers (Onset Computer Corporation, Bourne, MA, USA) modified to measure electrical resistance, which registered presence/absence of liquid water (as relative conductivity) and temperature (Paillex et al., 2020). The loggers were placed on the streambed, in the thalweg of each stream, and protected by PVC pipes with open ends aligned with the streamflow. Standing water is uncommon in Val Roseg, so the presence of water largely correlates with surface flow (Paillex et al., 2020; Siebers et al., 2020). The logging period was approximately 2 years; loggers were installed on 1 December 2017, removed once (13–22 October 2018) for maintenance, and the data were downloaded on 12 December 2019. The loggers were inspected every 3 months and fine sediments removed to maintain logger function.

Both channels dried in winter 2017/2018 and started to flow again in early April 2018 (Fig. 2). The reference channel (RC) flowed for the remainder of the study period. During the first 25 days of the first flow manipulation, The MC dried during the daytime (likely due to evapotranspiration (Mutzner et al., 2015)) and flowed during the night and early morning (due to local bank storage and hyporheic upwelling; pers. obs., authors). Longer drying events (> 1 day) occurred between the end of June and September. Major rainfall events occasionally resulted in flow in the MC for several hours (Siebers et al., 2020). In total, the MC was dry for at least one hour on 82 of 107 manipulated days. Flow in the MC resumed immediately after removal of the barrier (20 September 2018). In between the first and second flow manipulation, the MC dried during the winter months, whereas the RC continued to flow. During the second flow manipulation period, longer drying events (> 1 day) again occurred between the end of June and September. The MC was dry for at least one hour on 67 of 107 manipulated days during the

second period, and flow resumed immediately after removal of the barrier (Fig. 2).

Temperature in the RC followed characteristic seasonal patterns around a low, stable mean (mean ± SD: 3.0 ± 2.1 °C, Fig. 2a). The temperature in the MC followed a similar pattern outside of the manipulation periods (1.7 ± 2.1 °C, Fig. 2b) and was substantially higher and more variable during both manipulation periods (11.1 ± 6.6 °C and 11.5 ± 6.7 °C in 2018 and 2019, respectively).

Sample collection and analysis

Sample collection and analyses followed Siebers et al. (2020). In brief, each channel was sampled 17 times: before manipulation ($N = 3$, in September 2017 and May & June 2018), during the first manipulation ($N = 5$, once in July, and twice in August & September 2018), in between the manipulation periods ($N = 4$, October & November 2018 and May & June 2019), during the second manipulation period ($N = 3$, July, August & September 2019), and after the second flow manipulation ended ($N = 2$, October 2019 and September 2020). The streams were sampled twice (instead of once) in June and July of 2018. Snow cover prevented sampling between December and March during the whole study period.

We collected benthic macroinvertebrate samples, a water sample, and periphyton samples on each sampling occasion in each channel. A benthic macroinvertebrate sample was taken at three representative locations (five locations in June and July 2018 to obtain higher definition for the samples just before and after the first dam installation) along both study reaches (100 m) with a Hess sampler (mesh size = 250 μm, area: 0.0425 m²) for 30 s, and stored in ethanol. This relatively short sampling time is suitable for this type of very 'clean' stream, as it still yielded a great quantity of individuals (e.g., ca. 10,000 ind/m² in the reference stream during summer). When the streambed was dry, macroinvertebrates were sampled by excavating the same depth and area as a Hess sampler (see Siebers et al. 2020). In the laboratory, macroinvertebrates were identified to the lowest common, practical taxonomic level (family for most insects, order for Plecoptera and Coleoptera, and other taxa grouping for non-insects) after Tachet et al. (2010), with additional references for Plecoptera (Lubini et al., 2012), Trichoptera (Waringer & Graf, 2011), Ephemeroptera
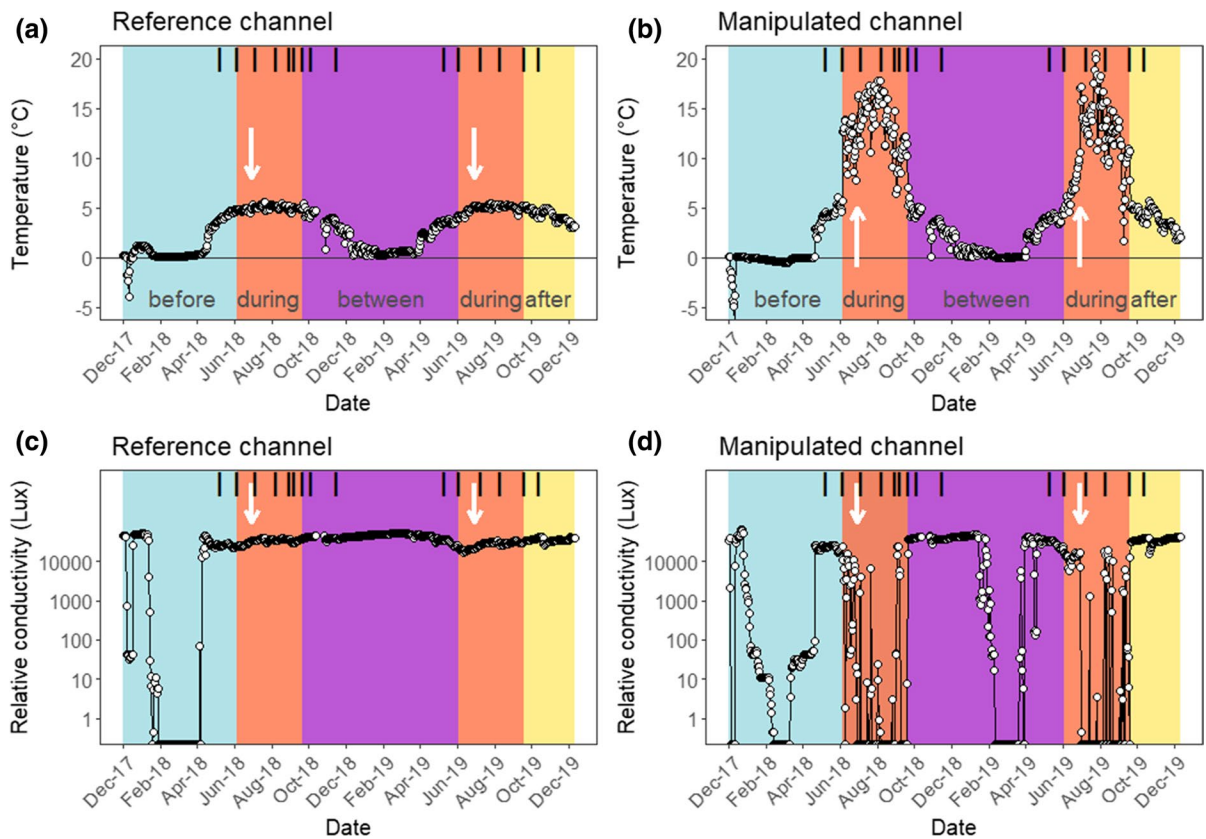
Fig. 2 Temperature (**a**, **b**) and relative conductivity (**c**, **d**) in the reference channel (RC) and manipulated channel (MC), respectively. During dry periods in MC, the logger registered air temperature. Relative conductivity values of zero indicate an absence of liquid surface water (due to freezing or drying). Colours indicate experimental periods (blue: before, red: during, pink: between, yellow: after). The white arrows indicate the onset of regular summer drying periods (end of June) in intermittently flowing streams in the catchment. The break in logging data (October 2018) is due to maintenance. The black vertical lines indicate sampling dates during the logging period. Two sampling dates fell outside the logging period (11 September 2017, 22 September 2020)

(Bauernfeind & Humpesch, 2001), Coleoptera (Lucht et al., 1998) and Diptera (Eiseler, 2010). The coarse resolution restricts our ability to compare life history traits amongst taxonomic groups, although most families were represented by ≤ 3 functionally similar genera (e.g., *Baetis* spp. for Baetidae) and many taxonomic groups at our identification level have broadly similar ecological traits (e.g., most Alpine Plecoptera are rheophilous). Only one sample per channel was processed from October 2019 due to spoiling of the other samples.

Water samples were taken in triple-rinsed 0.5 L polypropylene bottles without headspace and stored at 4 °C until analysis the following day. Samples were analysed for alkalinity, pH, dissolved organic carbon (DOC), total nitrogen (TN), nitrate (NO_3–N), total phosphorus (TP), soluble reactive phosphate (SRP; PO_4-P), and silicate (H_4SiO_4), following methods in Tockner et al., (1997). The water chemistry was similar in the MC and the RC throughout the experiment (see Online Resource 1).

Periphyton samples were taken as biomass scrubbed from a measured area of five randomly selected cobbles on all dates except September 2017. Benthic organic matter (ash-free dry mass, AFDM) was taken from the remainder of each macroinvertebrate sample after initial analysis (see Siebers et al. (2020) for details on periphyton and benthic organic matter). The standing stocks of periphyton and benthic organic matter remained comparable throughout the experiment (see Online Resource 3).

Data analysis

The BACI design was used to test if flow intermittency affected macroinvertebrate assemblages, with the RC as a control. The comparisons for all analyses were based on 10 groups: the two channels during the five experimental periods (Fig. 2): before ($N=3$), during1 ($N=5$), between ($N=4$), during2 ($N=3$), and after ($N=2$). All analyses were performed in R 4.0.2 using RStudio (RStudio Team, 2020; R Core Team, 2021).

To visualise variability of macroinvertebrate assemblages in space and over time, we generated non-metric multidimensional scaling (nMDS) ordinations using Bray–Curtis similarity matrices calculated from Wisconsin standardised, square-root transformed mean densities per sample date via the function "metaMDS" with R package *vegan* (Oksanen et al., 2020). We also used *vegan* to assess if assemblages differed between channels and amongst the experimental periods with a permutational multivariate analyses of variance (PERMANOVA, via the function "adonis2"). We analysed the multivariate homogeneity of groups dispersions [PERMDISP2, variance analysis with *vegan* (Anderson et al., 2006; Oksanen et al., 2020)] to compare beta diversity of the two channels via the function "betadisper" with Tukey multiple comparisons to check for significance. To identify which taxa contributed the most to the overall Bray–Curtis similarity, we performed an indicator species analysis (ISA), also known as IndVal, with the package *indicspecies,* via the function "indicators" (Dufrêne & Legendre, 1997; Cáceres & Legendre, 2009).

We calculated four biological metrics to assess biodiversity differences between the two channels over time: macroinvertebrate density (individuals per square meter), proportional rheophile density (percentage of total individuals identified as rheophilic), number of taxa, and proportional rheophile taxa (percentage of total taxa identified as rheophilic). We chose proportional abundances over raw numbers for rheophilic individuals and taxa to facilitate comparisons between the channels across experimental periods with contrasting densities and number of taxa. The rheophilic preference of taxa (see Online Resource 2, Table S2) was classified based on Schmedtje & Colling (1996), Banning (1990), and Tachet et al. (2010) via *freshwaterecology.info* (Schmidt-Kloiber & Hering, 2015).

Differences in (a) macroinvertebrate density (individuals per square meter), (b) proportional rheophile density (percentage of total individuals identified as rheophilic), (c) number of taxa, and (d) % rheophile taxa (percentage of total taxa identified as rheophilic) were tested. To test whether these four biological metrics differed between the two channels across five experimental periods, we used a generalised linear model (GLM) for pairwise comparisons between the two channels in the same period (families: negative binomial distribution for density, Poisson for proportion of rheophilic density and taxa; Conway-Maxwell Poisson distribution for number of taxa). We use estimated marginal means (also known as least-squares means) for these comparisons, which are the predicted mean values extracted from the GLMs (Lenth, 2020), as sample sizes between groups being compared were not always equal. We used the R package *AER* to check overdispersion, and *emmeans*, *MASS*, and *glmmTMB* for the GLMs (Venables & Ripley, 2002; Kleiber & Zeileis, 2008; Brooks et al., 2017; Lenth, 2020). For visualisations, we used plyr, devtools, ggpubr, ggplot2, viridis, hrbrthemes, reshape2, ggrepel (Wickham, 2007, 2011, 2016; Garnier, 2018; Kassambara, 2020; Rudis, 2020; Slowikowski, 2020; Wickham et al., 2020).

Results

Before the flow manipulations, the reference channel (RC) and manipulated channel (MC) had similar macroinvertebrate assemblages dominated by Chironomidae, Simuliidae and Plecoptera (Figs. 3, 4; Table 2: ISA $P > 0.05$, Table S3 in Online Resource 2). All four biological metrics were also similar in the RC and the MC (Fig. 5, Table 1).

During the first manipulation period, the MC had significantly lower macroinvertebrate densities and a lower proportional density of rheophilic individuals (% rheophile density) than the RC (Fig. 5a, b; Table 1). The proportion of rheophilic taxa (% rheophile taxa) remained similar, and the number of taxa was not significantly lower (Fig. 5c, d; Table 1). Chironomidae dominated both RC and MC assemblages (RC=53%, MC=65%). Compared to the RC, the MC had fewer Baetidae (RC=10%, MC=3%) and Plecoptera (RC=23%, MC=13%; Table S4 in Online
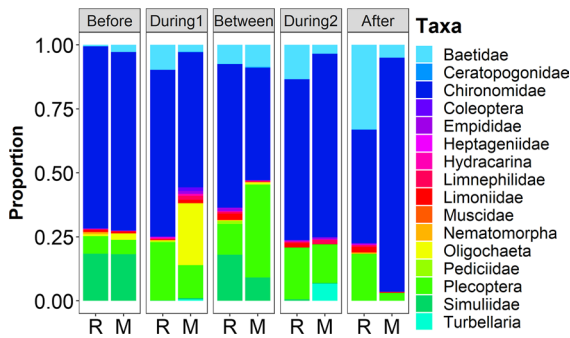
Fig. 3 The proportional abundance of each taxon (or proportional taxa abundance) in each experimental period (before, during first, between, during second, and after manipulation) in the reference (R) and manipulated (M) channel. See Table S4 for precise percentages
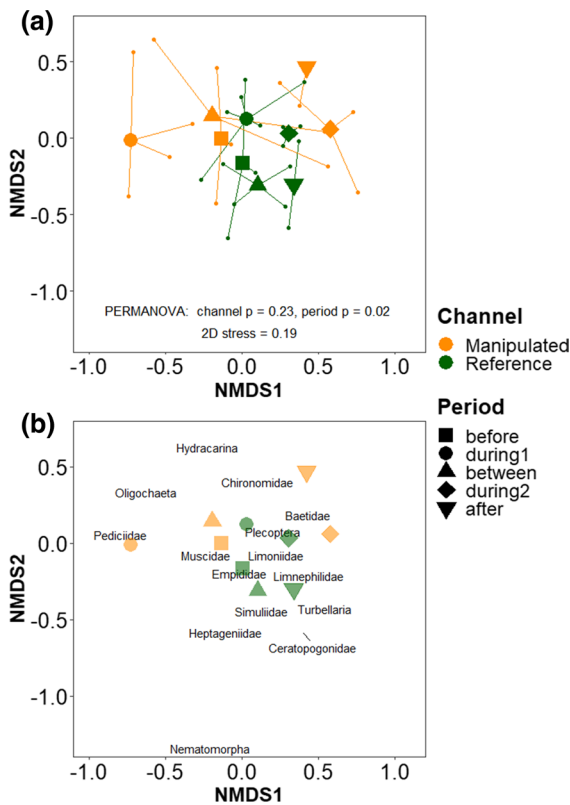

Fig. 4 Non-metric multidimensional scaling (nMDS) plots of **a** the macroinvertebrate assemblages in the reference (green) and manipulated channel (orange) based on densities on each sampling date. Lines link the assemblages on individual dates (small circles) to the experimental period centroid; and **b** the positioning of taxa in the ordination, taxa names are slightly separated to avoid overlap. The true position of "Ceratopogonidae" is indicated with a line, as the text has been moved to reduce overlap

Resource 2). The RC had several significant indicators with moderately high indicator values in this period: Baetidae, Chironomidae, Hydracarina, Muscidae, and Plecoptera (see Table 2). The MC had two significant indicators with low indicator values: Oligochaeta and Coleoptera (see Table 2).

During the autumn and spring between the manipulation periods, the RC had a relatively stable assemblage composition (Fig. 4a). In contrast, the MC assemblages were highly variable during this period; the individual sampled assemblages plotted further away from the centroid (Fig. 4a). Macroinvertebrate density partly recovered between the flow manipulation periods but remained considerably lower in the MC than the RC (Fig. 5a; Table 1). The MC also had a significantly lower % rheophile density, and a significantly lower number of taxa (Fig. 5b, c; Table 1). The proportion of thiophilic taxa was not significantly different between the channels (Fig. 5d; Table 1). The RC was characterised by dipterans (Limoniidae, Empididae, Simuliidae, Pediciidae) and trichopterans (Limnephilidae) (see Table 2: ISA $P < 0.05$ for all). In contrast, the MC harboured only a few dipterans and no significant indicators. In autumn, MC communities were dominated by low-density chironomid populations, which expanded and were joined by Plecoptera, Baetidae and Simuliidae by early spring (see Table S3 and S4 in Online Resource 2).

During the second flow manipulation, MC macroinvertebrate densities were highly variable, with a significantly lower % rheophile density than the RC (Fig. 5; Table 1). The MC also had fewer taxa than the RC, although this was marginally non-significant. No taxa were indicative of either channel (Table 2). Again, Chironomidae dominated both assemblages (RC = 62%, MC = 70%; Table S4 in Online Resource 2), and the MC had fewer Baetidae (RC = 13%, MC = 3%) and Plecoptera (RC = 20%, MC = 15%) than the RC.

After the flow manipulations, assemblages in the MC remained substantially different from RC. The MC macroinvertebrate densities increased and were statistically comparable to those in the RC (Fig. 5; Table 1). However, the % rheophile density and the number of taxa remained significantly lower compared to the RC. The RC assemblage had no significant indicators and mainly consisted of Chironomidae (45%), Baetidae (33%), and Plecoptera (18%). The assemblage of the MC was strongly dominated
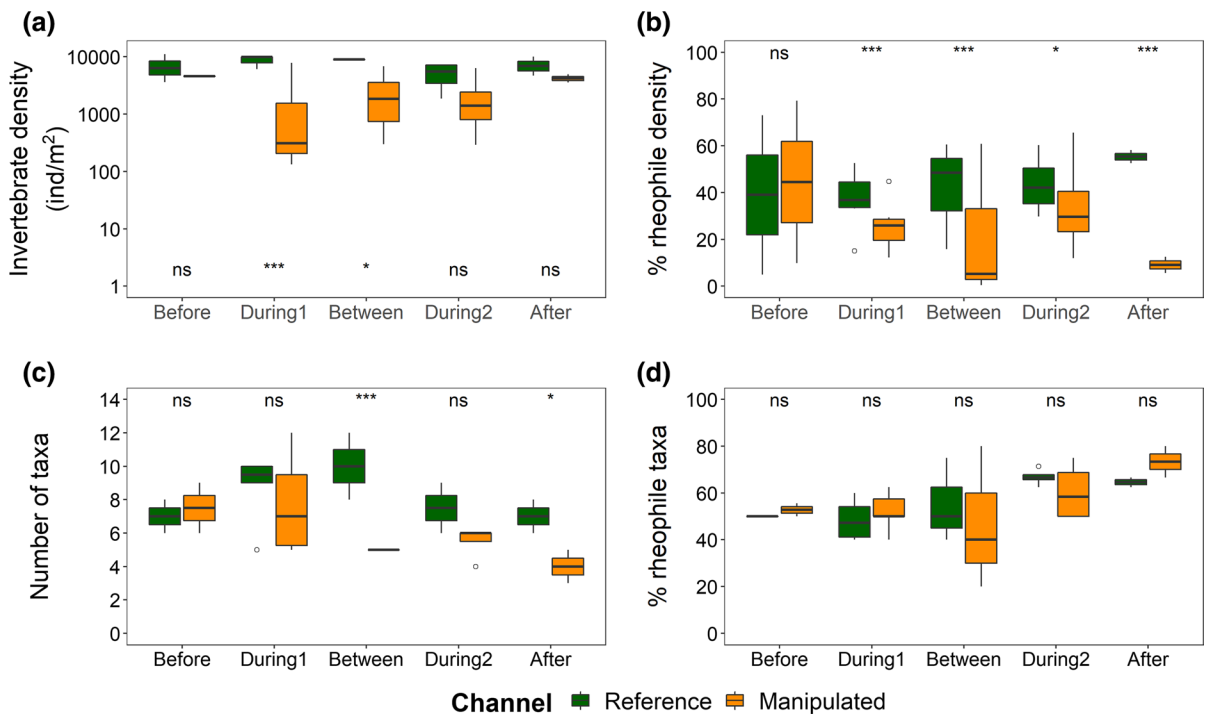
Fig. 5 Differences in **a** macroinvertebrate density (individuals per square meter), **b** proportional rheophile density (percentage of total individuals identified as rheophilic), **c** number of taxa, and **d** % rheophile taxa (percentage of total taxa identified as rheophilic) between the reference and manipulated channels during the five experimental periods (before, during1, between, during2, after). Open circles indicate outliers. Significance of the pairwise comparisons (generalised linear model) of means are indicated with ns ($P > 0.05$), *$P \leq 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$

by Chironomidae (92%) on both post-manipulation sampling dates (Fig. 4b), with a much lower proportion of Baetidae (5%) and Plecoptera (3%) and no significant indicators either (Table 2, Table S3 in Online Resource 2). The MC also had much fewer Limoniidae than the RC (RC = 2.2%, MC = 0.4%). Interestingly, the differences in macroinvertebrate assemblages are present in both sampling dates after the flow manipulations (September 2019 and 2020), so the channels remain different even one year after normal flow has resumed (see Table S3).

Overall, the macroinvertebrate assemblages significantly differed between manipulation periods (PERMANOVA: $R^2 = 0.231$, $P = 0.022$), but not between the two channels ($R^2 = 0.036$, $P = 0.256$). The MC assemblages varied more over time than the RC assemblages (PERMDISP, MC = 0.34, RC = 0.50, $P < 0.001$), as evidenced by the wider distribution of both the MC centroids and their associated assemblages (Fig. 4a).

Discussion

We found that a multi-year increase in summer drying strongly affected macroinvertebrate assemblages of an alpine stream. In particular, the macroinvertebrate densities and proportion of rheophilic macroinvertebrate densities (% rheophile density) decreased in the flow-manipulated channel (MC) compared to the reference channel (RC). The number of taxa first seemed relatively unaffected, but it also decreased significantly over the study period. Macroinvertebrate density recovered relatively quickly, but recovery of % rheophile density and number of taxa in the MC was incomplete when the study ended after more than one year of normal flow resumption.

Changes in macroinvertebrate assemblages

As per our first prediction, an increase in summer drying decreased macroinvertebrates densities and number of taxa in the MC compared with the RC. In

addition, variability in macroinvertebrate assemblage composition and density were higher in the MC than the RC. Lower macroinvertebrates densities and number of taxa (especially of rheophilic taxa) commonly occur in intermittent streams across climatic zones when compared to similar perennial stretches, especially in streams experiencing recent shifts to intermittent flow (Datry et al., 2014; Soria et al., 2017; Piano et al., 2019; Crabot et al., 2021b). Low flows and drying events in summer restrict the macroinvertebrate taxa which can sustain viable populations (Vander Vorste et al., 2016a; Crabot et al., 2021b). Alpine rheophilic taxa (e.g., many Plecoptera, Baetidae, and Limoniidae) are particularly sensitive to flow intermittency, as they require flowing water with high oxygen levels or they often have longer (1 + year) life cycles (Tachet et al., 2010; Birrell et al., 2020). These alpine taxa are often well-adapted to winter drying (as their life cycles include winter resting stages), but they are not well-adapted to summer drying (Hynes, 1976; Irons et al., 2011; Robson et al., 2011; Tolonen et al., 2019). The reductions in density and number of taxa caused by our experiment were thus likely driven by declines in rheophilic macroinvertebrates that may

be resistant to winter freezing, but not to summer drying periods.

We found a reduction in the density of rheophilic taxa in the MC, with a reduction in or absence of Ephemeroptera (Baetidae, Heptageniidae) and Plecoptera, as well as some dipterans (Empididae, Limoniidae). The MC had a higher abundance of Chironomidae and Oligochaeta than RC. These differences in macroinvertebrate assemblages could be explained by taxa-specific life histories. Other flow experiments that experimentally induced summer drying have also found that taxa with long-lived larval/juvenile stages (e.g., Plecoptera and certain Ephemeroptera) are less resistant to increased summer intermittency than multivoltine taxa with short life cycles (e.g., Chironomidae) (Doretto et al., 2018; Piano et al., 2019; Crabot et al., 2020). Additionally, a high proportion of Chironomidae in benthic communities is characteristic of intermittent alpine streams, likely because they have high tolerance to environmental harshness (e.g., low temperatures and substrate instability) and a high recolonisation ability due to multivoltine development and aerial dispersal (Klein & Tockner, 2000; Rüegg & Robinson, 2004). Our results suggest that

Table 1 Pairwise comparisons (generalised linear models) of the metrics calculated to compare macroinvertebrate assemblages in the reference channel (RC) and manipulated channel (MC) during the five experimental periods (before, during1, between, during2, after): macroinvertebrate density, proportional rheophile density (%), number of taxa, and proportion of rheophilic taxa

	Before		During1		Between		During2		After	
	RC	MC	RC	MC	RC	MC	RC	MC	RC	MC
Macroinvertebrate density										
P value	0.849		<0.0001		0.052		0.189		0.503	
Estimated marginal means	7380	8639	14,626	1898	11,095	2986	5132	2378	7388	4243
Standard error	4320	5057	4943	642	5303	1427	2124	985	4325	2484
Proportional rheophile density (%)										
P value	0.400		<0.0001		<0.0001		0.034		<0.0001	
Estimated marginal means	39.0	44.5	36.8	26.0	41.7	22.2	43.6	34.2	55.4	9.1
Standard error	4.4	4.7	2.5	2.1	3.7	2.1	3.3	2.9	5.3	2.1
Number of taxa										
P value	0.751		0.235		0.001		0.070		0.042	
Estimated marginal means	7.0	7.5	8.8	7.7	10.0	5.0	7.5	5.5	7.0	4.0
Standard error	1.0	1.1	0.7	0.7	1.0	0.8	0.8	0.7	1.1	0.8
Proportion of rheophilic taxa										
P value	0.969		0.927		0.886		0.910		0.916	
Estimated marginal means	0.50	0.53	0.48	0.51	0.55	0.47	0.67	0.60	0.65	0.73
Standard error	0.5	0.5	0.3	0.3	0.4	0.4	0.4	0.4	0.6	0.6

Table 2 Indicator species analysis (ISA) results (*P* value and indicator value) for the reference channel (RC) and manipulated channel (MC) during the five experimental periods (before, during1, between, during2, after) for each macroinvertebrate taxon

	Before		During1		Between		During2		After	
	RC	MC	RC	MC	RC	MC	RC	MC	RC	MC
Baetidae										
P value	0.920	0.745	0.030	1.000	0.290	0.665	0.255	0.960	0.055	0.690
Indicator value	0.005	0.034	0.373	0.001	0.138	0.032	0.109	0.001	0.242	0.021
Ceratopogonidae										
P value	1.000	1.000	1.000	0.660	0.160	0.130	1.000	1.000	0.375	1.000
Indicator value	0.000	0.000	0.000	0.000	0.273	0.127	0.000	0.016	0.036	0.000
Chironomidae										
P value	0.250	0.260	0.005	0.995	0.360	0.905	0.575	0.970	0.535	0.440
Indicator value	0.124	0.123	0.356	0.015	0.148	0.047	0.072	0.002	0.046	0.055
Coleoptera										
P value	1.000	1.000	1.000	0.005	1.000	0.360	1.000	1.000	1.000	1.000
Indicator value	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.001	0.000	0.000
Empididae										
P value	0.460	0.815	0.185	0.850	0.010	1.000	0.425	0.765	0.220	1.000
Indicator value	0.033	0.011	0.243	0.000	0.375	0.000	0.045	0.000	0.034	0.000
Heptageniidae										
P value	1.000	1.000	0.175	1.000	0.075	1.000	0.440	1.000	0.315	1.000
Indicator value	0.000	0.000	0.145	0.000	0.182	0.000	0.030	0.000	0.091	0.000
Hydracarina										
P value	0.535	0.140	0.050	0.640	0.600	0.670	0.335	0.720	1.000	1.000
Indicator value	0.012	0.062	0.263	0.004	0.012	0.008	0.042	0.000	0.000	0.000
Limnephilidae										
P value	0.465	0.870	0.175	0.880	0.025	0.580	0.440	0.670	0.210	0.910
Indicator value	0.078	0.015	0.131	0.000	0.292	0.045	0.081	0.002	0.105	0.004
Limoniidae										
P value	0.385	0.415	0.740	0.940	0.005	1.000	0.185	0.955	0.125	0.710
Indicator value	0.062	0.089	0.062	0.008	0.422	0.000	0.129	0.000	0.150	0.007
Muscidae										
P value	1.000	1.000	0.025	1.000	0.170	1.000	1.000	1.000	1.000	1.000
Indicator value	0.000	0.000	0.400	0.000	0.167	0.000	0.000	0.000	0.000	0.000
Nematomorpha										
P value	0.105	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.145	1.000
Indicator value	0.228	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.158	0.000
Oligochaeta										
P value	0.340	0.060	0.430	0.045	0.650	0.710	1.000	1.000	1.000	1.000
Indicator value	0.083	0.280	0.117	0.078	0.025	0.028	0.000	0.001	0.000	0.000
Pediciidae										
P value	1.000	1.000	0.150	0.785	0.020	0.480	1.000	1.000	1.000	1.000
Indicator value	0.000	0.000	0.225	0.000	0.279	0.029	0.000	0.001	0.000	0.000
Plecoptera										
P value	0.715	0.775	0.005	1.000	0.500	0.315	0.415	0.955	0.310	0.900
Indicator value	0.045	0.037	0.464	0.001	0.119	0.146	0.087	0.021	0.071	0.007
Simuliidae										
P value	0.080	0.070	0.865	0.905	0.010	0.505	0.660	0.850	1.000	1.000
Indicator value	0.174	0.174	0.001	0.030	0.289	0.040	0.004	0.002	0.000	0.000

Table 2 (continued)

	Before		During1		Between		During2		After	
	RC	MC	RC	MC	RC	MC	RC	MC	RC	MC
Turbellaria										
P value	0.130	1.000	0.570	0.195	1.000	1.000	1.000	0.105	1.000	1.000
Indicator value	0.033	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000

rheophilic taxa can depend on flowing water during summer development periods, and summer drying thus constitutes a major disturbance (Brittain, 1990; Erba et al., 2003). Other taxa that either hatch from eggs or develop during spring may be more drying-tolerant, as their least drying-resistant stages (i.e., early instars) may occur during stable flows derived from spring snowmelt.

Functional feeding traits could explain some of the shifts we observed in macroinvertebrate assemblages: shredder (Limnephilidae) and scraper (Heptageniidae) densities were lower and generalist collector gatherer (Chironomidae) densities were higher in the RC compared to the MC. Studies from other flow experiments in alpine intermittent streams found similar results (Piano et al., 2019, 2020; Siebers et al., 2020). The change in feeding mode could be mediated by a shift in basal resource quality in stream food webs; e.g., reduced microbial conditioning of terrestrial organic matter in drying alpine streams could lead to lowered lability for stream macroinvertebrates, or drying could reduce the productivity of algae in biofilms (Niedrist & Füreder, 2017; Siebers et al., 2019). However, we did not identify any differences in benthic organic matter or periphyton densities between the two channels, and Siebers et al. (2020) found no change in food quality measured as organic matter C:N ratios in the first half year of flow manipulation and recovery. Changes in resource availability or quality are also likely to represent less of a disturbance than the drying events themselves, particularly for rheophilic taxa (e.g., Heptageniidae), and may thus amplify rather than drive declines in macroinvertebrate abundances. More experimental work is needed to clarify the mechanisms causing the changes in assemblage structure resulting from increases in flow intermittency over longer timescales.

Effects of sequential flow manipulation years

In contrast to our second prediction, we did not find a strong cumulative effect of the two consecutive manipulations. In fact, the effects on macroinvertebrate density were stronger during the first than the second flow manipulation, and assemblage composition was more dissimilar between RC and MC during the first than second manipulation. An incomplete recovery after the first flow manipulation may have 'primed' the experimental channel with an assemblage that included fewer drying-sensitive taxa before the onset of the second flow manipulation, a legacy effect (e.g., Cauvy-Fraunié et al., 2016).

From the first manipulation onwards, the MC was dominated by largely multivoltine taxa such as Chironomidae. The two summer drying events would have affected different cohorts of these taxa that were unaffected during egg-laying or early development in spring (see above), and would thus represent independent rather than consecutive disturbance events in the context of this life history. Seasonality in development may also have sheltered some taxa from the effects of drying altogether. For example, Simuliidae were present in the spring before the first and second manipulation, but not following the second year of drying. Whilst this primarily spring-associated taxon can shorten its development periods in intermittent streams (Rüegg & Robinson, 2004), it was also largely only present in samples here from May and June: it is thus difficult to assess whether this taxon might have been affected by recurrent years of flow intermittency. Whether consecutive years of drying affects macroinvertebrates interactively or independently is thus likely tied to taxon-specific seasonality in life history.

Slow, partial recovery following increased summer drying

In line with our third prediction, the MC showed only a partial return to similarity to the RC after normal flow resumed following the second flow manipulation. The number of taxa and proportional rheophilic density were still substantially lower in the MC than the RC a year after normal flow resumption. In contrast, the proportion of rheophilic taxa was never significantly lower in the MC and the overall density in the MC returned to levels statistically comparable to the RC after normal flow resumption. Similarly, previous field studies have found that a temporary increase in intermittency can have long-term effects (6–16 months after normal flow resumption) on community composition and density (Cauvy-Fraunié et al., 2016; Piano et al., 2019; Gauthier et al., 2020; Siebers et al., 2020).

A return to a pre-disturbance assemblage depends on the resilience and resistance of its taxa (Bogan et al., 2017). Taxa might display resilience by recolonizing after a disturbance via aquatic or aerial dispersal, or tolerate desiccation by surviving as drying-resistant life forms or in refuges like pools or the hyporheic zone (Bogan et al., 2017; Hotaling et al., 2017; Van Looy et al., 2019). A potential resistance mechanism could be the presence of drying-resistant life forms by some taxa. The higher densities of Plecoptera between flow manipulations occurred in spring, which may reflect development of dormant, desiccation-resistant eggs or juveniles when favourable conditions returned. For example, several Plecoptera families (e.g., Capniidae and Nemouridae) that occur in Val Roseg are known for these strategies (Poff et al., 2006; Tachet et al., 2010). Larvae and nymphs might also tolerate drying using in situ refuges. However, pools are an unlikely refuge in our study area: pool formation is uncommon in Val Roseg's high gradient streams, especially in streams near the side-slopes like our study stream (Malard et al., 2000; Robinson & Matthaei, 2007). Recovery from the hyporheic zone also likely played a minor role, as recolonisation by individuals in the hyporheic zone should have been more rapid (several days or weeks) than we observed in the MC (Datry, 2012; Vander Vorste et al., 2016b)—possibly because of water table depletion during the long dry periods. Hyporheic

sampling would be required to determine its potential contribution to assemblage recovery.

Aquatic or aerial dispersal from adjacent waters with surface flow are also likely recovery processes that contributed to resilience of the macroinvertebrate community in the MC. For example, Limnephilidae are common in the hyporheos of Val Roseg (Malard et al., 2003), yet individuals in intermittent streams likely originate almost entirely from perennial stream source populations (Shama et al., 2011). In particular, Siebers et al. (2020) observed a pulse of drifting macroinvertebrates immediately following rewetting in the MC, yet some of the families represented (Perlodidae, Baetidae) were not found in subsequent samples from the MC. Their results suggest that macroinvertebrates, either from the hyporheos or from inflowing drift, may selectively drift away from previously dry reaches upon flow resumption rather than contributing to local assemblage recovery. Studies by Leys et al. (2017) and Shama et al. (2011) revealed that local dispersal dynamics are important in maintaining populations of some taxa in intermittent streams of Val Roseg (also see Brown et al. (2003) and Finn et al. (2010)). Local populations might be dispersal-limited due to habitat fragmentation and the flight abilities of aerial dispersers (Hynes, 1976; Crabot et al., 2020; Gauthier et al., 2020). However, the short distances between the MC and nearby flowing waters (including the RC, only 10–15 m away) make it unlikely that dispersal limitation plays a major role.

The timing of drying in summer coincided with key life cycle events for some rheophilic taxa, which might explain the ongoing effects observed one year after flow resumed. Rheophilic taxa were most abundant during the summers in the RC, but their densities were much lower in the MC. The absence of fast-flowing water likely hampered summer oviposition in the MC for many aquatic macroinvertebrates with aerial adult stages (Hynes, 1976; Brittain & Sartori, 2009; Bogan & Boersma, 2012), and thus reduced recruitment of new cohorts via oviposition. Our results suggest that one year of normal flow was insufficient to alleviate the combined effect of desiccation and reduced oviposition on rheophilic taxa during the two drier summers.

This slow, partial recovery of the original community could also reflect a shift in biotic interactions, such as predator–prey interactions or competitive

exclusion (Holomuzki et al., 2010; Walters, 2011; Cauvy-Fraunié et al., 2015; Hotaling et al., 2017), which altered assemblage composition long after normal flow had resumed. For example, Chironomidae are often described as facultative predators or cannibals (Zah et al., 2001; Niedrist & Füreder, 2017), and may have shifted diets to include some of the prey previously consumed by larger predators (e.g., Plecoptera, Empididae) that were excluded by drying events. This dietary plasticity may have provided Chironomidae with a competitive advantage over specialist grazers (e.g., Baetidae) in the months following flow resumption. Further determination of the food web in alpine intermittent streams to a fine taxonomic resolution is necessary to determine the contributions of these processes.

Conclusions

We observed relatively long-lasting (> 1 year), but no interactive effects, of increased summer flow intermittency on the macroinvertebrate community in an alpine channel, especially on densities of rheophilic taxa. We also saw a gradual reduction in number of taxa. We observed a partial recovery of the manipulated community in our study period. Our study only included a single manipulated channel and identified taxa to a relatively coarse level, which limits the generality of our findings to how flow intermittency might affect entire alpine fluvial networks. Despite this, our results align with the wider consensus that rheophilic taxa in alpine areas will be hit hardest by climate change (Hock et al., 2019). The predicted increase in summer flow intermittency (Tramblay et al., 2021) could have dramatic consequences on some aquatic insects in alpine landscapes. Alpine streams assemblages could thus shift to a new composition that is adapted to the summer drying disturbance regime, which could rapidly reduce genetic diversity, homogenize community composition and cause local species extinction (Cauvy-Fraunié et al., 2015; Hotaling et al., 2017; Birrell et al., 2020; Crabot et al., 2021a).

Declarations

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