Flow intermittency affects structural and functional properties of macroinvertebrate communities in alpine streams

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Abstract
1. Flow regime is a major determinant of the structure and functioning of aquatic ecosystems. Under climate change, flow intermittency is becoming more prevalent in glaciated alpine catchments, but the effects of increasing dryness on aquatic biodiversity remain largely unknown.

2. We characterised flow intermittency patterns in 30 streams of a glaciated alpine catchment over 15 months and separated these streams into four intermittency categories: perennial streams, winter-drying streams, moderately intermittent streams with occasional drying in summer, and periodically intermittent streams with extensive dry periods throughout the year. We then examined how these drying patterns affected structural and functional properties of benthic macroinvertebrate communities, and whether these changes were primarily deterministic or stochastic.

3. At the taxonomic level, we observed a response at the highest intermittency levels, with $\alpha$ diversity lower and $\beta$ diversity higher in periodically intermittent streams than in other stream types. This result suggested that local biota were well adapted to intermediate intermittency levels (mostly during winter) but not to high intermittency during summer. In contrast, functional diversity indices at the $\alpha$ and $\beta$ levels (based on trait abundances) did not differ across intermittency categories. Considering the moderate level of functional redundancy, we interpreted this as an indication that changes in taxonomic diversity may have resulted primarily from stochastic processes.

4. Analysis of community and trait composition indicated that deterministic selection may indeed have occurred with increased intermittency, but this process was likely to be minor in comparison to stochastic extinctions. Notably, community evenness was highest in periodically intermittent streams and lowest in perennial streams, suggesting that frequent drying prevented competitive exclusion.

5. Our results suggested that most macroinvertebrate populations are resilient to intermediate intermittency levels but are filtered at high intermittency, irrespective of their resilience capacities. However, more research is needed to clarify the specific roles of different facets of flow regimes, specifically frequency,
1 | INTRODUCTION

Hydrological extremes such as flooding and drying are major structural forces in aquatic ecosystems (Lake, 2003; Poff et al., 1997). With climate change, these disturbances are becoming more frequent and severe in many parts of the world, with far-reaching consequences on the biodiversity and functioning of aquatic ecosystems (Cisneros et al., 2014; Seneviratne et al., 2012; Woodward et al., 2016). Mountainous regions are particularly sensitive to climate change with a warming rate more than twice as high as the global average, and presently are experiencing substantial temporal shifts in precipitation patterns (Hock et al., 2019; Horton et al., 2006; Pepin et al., 2015; Zemp et al., 2006). These changes, together with the recession of glaciers, are causing a drastic alteration of hydrological regimes in alpine catchments, including an increasing prevalence of flow intermittency (Beniston, 2012; Milner et al., 2009).

Glaciated alpine catchments encompass a diversity of water sources and hydrological processes, sustaining a mosaic of flow intermittency regimes within stream networks (Brown et al., 2003; Ward, 1994). For instance, kryal streams (glacier-fed) are subject to drying during winter when glacial melt is minimal, whereas rhithral streams (fed by precipitation and/or snow melt) may dry at the end of the snow-melt season in early summer. Finally, krenal streams (groundwater-fed) typically flow all year round (Brown et al., 2003; Paillex et al., 2020; Rüegg & Robinson, 2004). Since the 1960s, various studies have examined the environment and biota of alpine streams, but with an overwhelming emphasis on kryal streams and the importance of a glacial influence (Alther et al., 2019; Hieber et al., 2005; Lods-Crozet et al., 2001; Ward & Palmer, 1994). Comparatively, little attention has been given to the effects of flow intermittency in alpine catchments (but see Donath and Robinson, 2001; Rüegg and Robinson, 2004; Robinson, Tonolla, et al., 2016; Siebers et al., 2019, 2020).

The effects of flow intermittency on aquatic macroinvertebrate communities are strongly dependent on the resistance and resilience of the taxa present (Lake, 2000). Species may possess traits that enable them to survive drying events in situ (resistance); for instance, the ability to produce dormant life stages to undergo aestivation, or smaller body sizes allowing them to find refuge in the hyporheic zone when water levels recede (Bonada, Dolédec & Statzner, 2007; Strachan et al., 2015). Another set of traits, such as short generation times and strong dispersal abilities, may allow species to recover faster between dry spells and thus be more resilient (Chester & Robson, 2011; Van Looy et al., 2019). Some feeding strategies can also provide an advantage, depending on the type of resources available after rewetting (Aspin et al., 2019; Sarremejane et al., 2020). For example, flow cessation may negatively affect taxa with specialised feeding strategies such as those feeding exclusively on biofilms or leaf litter, while favouring generalists such as omnivores in general (Piano et al., 2019; Sarremejane et al., 2020). Finally, the presence of in-stream refuges such as permanent pools, organic debris, and hyporheos can play a major role in increasing the resilience of communities (Chester & Robson, 2011; Stubbington, 2012).

Benthic macroinvertebrate communities tend to be more resilient than resistant to drying (Datry et al., 2014) and to physical disturbances in general (Death, 2010). However, the relative importance of resistance and resilience strategies for community recovery is largely dependent on the biogeographic setting of streams. For instance, in drier Mediterranean regions, where desiccation episodes are recurrent and a central aspect of the hydrological regime, many taxa are adapted to either resist or avoid drying events (Bonada, Dolédec, et al., 2007; Hershkovitz & Gasith, 2013; Robson et al., 2013). Similarly, in lowland gravel-bed rivers, many invertebrate taxa have the ability to migrate to the hyporheos during drying events, and communities may therefore be resilient to drying (Del Rosario & Resh, 2000; Stubbington, 2012; Vander Vorste et al., 2016). In contrast, intermittent headwater streams are often steep and bedrock-dominated, resulting in shallow or absent hyporheos, and macroinvertebrate communities tend to show more reliance than resistance for survival (Chester & Robson, 2011).

Flow cessation can thus cause major reductions in macroinvertebrate abundances and species richness as well as substantial changes in community composition (Piano et al., 2019; Rüegg & Robinson, 2004; Siebers et al., 2020). A commonly reported pattern of changing community composition with increasing intermittency is a reduction in rheophilic taxa such as many EPT species (Ephemeroptera, Plecoptera, Trichoptera) in most systems (Boulton, 2003; Datry et al., 2014; Stubbington et al., 2009), and in alpine streams in particular (Siebers et al., 2020). Alpine macroinvertebrate communities may take several months to recover from drying events (Drost et al., 2022; Siebers et al., 2020), probably because alpine macroinvertebrates have low resistance to drying.

The main processes by which flow intermittency and disturbance in general affect communities may be deterministic,
stochastic, or a combination of the two (Chase, 2007; Thompson et al., 2020; Vellend, 2010). Stochastic processes may dominate through random extinctions and random changes in community structure where species differ little in their resistance and resilient traits at the landscape scale (Chase, 2007). In this case, the least abundant taxa are more likely to become extinct first, and changes at the taxonomic level (in species richness and community composition) generally do not correlate with changes at the functional level (functional richness [FRic] and functional community composition). In contrast, deterministic niche selection may occur where species differ widely in their resistance and resilience capacities (Keddy, 1992; Siefert et al., 2013). As the least resistant and resilient taxa are filtered out, community changes will occur at both taxonomic and functional levels. Similarly, drying may reduce taxonomic and functional variability among communities (β diversity) when homogeneous deterministic selection dominates. In contrast, where stochastic processes dominate, drying can increase taxonomic β diversity (Sarreemejane et al., 2018) while leaving functional β diversity unchanged (Mouchet et al., 2010; Sokol et al., 2011; Stegen & Hurlbert, 2011). Beta diversity can be further partitioned to assess whether it is primarily made of assemblages of different taxa (turnover) or nested subsets of similar taxa (nestedness; Baselga, 2010). High turnover generally reflects the selection of different species by different environmental conditions or disturbance levels, or stochastic processes such as ecological drift or dispersal limitation (Randall Hughes et al., 2007; Vellend, 2016). High nestedness can arise if high disturbance levels or harsh environmental conditions extirpate the most sensitive species (Ballinger et al., 2007; Daniel et al., 2019; Pandit et al., 2009).

As flow intermittency in alpine streams increases, a better understanding of the ecological linkages between intermittency regimes and aquatic biota is essential. Indeed, the characterisation of macroinvertebrates for different intermittency regimes in alpine streams remains largely incomplete, thus limiting this understanding (Hotaling et al., 2017). Here, we characterised intermittency regimes and macroinvertebrate communities in 30 streams of a glaciated alpine catchment. We separated streams into four intermittency categories (ICs) and examined whether differences in diversity resulted from deterministic selection or stochastic processes. We hypothesised that species would mostly differ in resilience traits, and thus taxonomic and functional a diversity would be lower in the most intermittent streams because of deterministic selection, and highest in perennial streams (H₁). Further, we expected that highly intermittent streams would have lower abundances of the least resilient taxa and low-resilience traits (H₂). Finally, we expected that β diversity among ICs would primarily result of high nestedness, and that structural and functional β diversity would be lower in highly intermittent streams because of strong homogeneous deterministic selection (H₃).

2 | METHODS

2.1 | Study catchment and characterising intermittency

This study was conducted in Val Roseg, a glaciated alpine valley in the Swiss Alps with a catchment covering an area of 66.5 km² and elevations ranging from 1,760 to 4,049 m above sea level (asl). The elevation of sampling sites in this study ranged between 2,002 m and 2,181 m asl (average 2084 m asl). Two major glaciers cover the upper parts of the valley to the south, and an extensive floodplain occurs in the mid-section where the main stem regularly expands. Headwater streams included in this study were tributaries to the main stem and were sampled just upstream of the point where streams entered the floodplain (see Paillex et al., 2020). The study streams were selected for approximately consistent width (c. 1-3 m wide) and lengths to control for variation across sites (Paillex et al., 2020). Our study streams comprised three types of water origin and associated intermittency regimes described in Paillex et al. (2020): perennial krenal streams, kryal streams that dry seasonally between autumn and spring, and rhithral streams where drying occurs both in winter and summer on a periodic basis. We used the same streams as Paillex et al. (2020), but here 15 months of data on flow intermittency were available (compared to 11 months for their study), which enabled a more refined classification of intermittency regimes. HOBO Temperature/Light 64K sensors modified to measure electrical resistance (Chapin et al., 2014) were used to record water presence/absence and water temperature hourly between July 2017 and October 2018 (Paillex et al., 2020).

2.2 | Field sampling

The 30 streams were sampled three times: September 2017 (Alpine autumn), June 2018 (spring), and August 2018 (summer). On each occasion, a 500-ml water sample was collected and stored on ice in the dark. The water samples were later analysed for pH, concentrations of silicate (mg H₂SiO₄⁻ L⁻¹), nitrate (µg N L⁻¹), total phosphorus (µg/L), total organic carbon (TOC; mg/L) and dissolved organic carbon (DOC; mg/L) as in Tockner et al. (1997). Biofilm was sampled by randomly selecting five stones (cobble-size) within each habitat. The biofilm was removed from each stone by scrubbing with a wire brush into a plastic container with 100 ml of distilled water, and the scrubbed area measured (after Uehlinger, 1991). The biofilm suspension was subsequently filtered through a glass fibre filter (0.45μm, Whatman GFF) and stored on ice in the dark. Each filter was dried at 60°C for 24 hr, weighed, combusted at 450°C for 6 hr, and then reweighed for estimates of organic matter biomass as ash-free dry mass. Benthic macroinvertebrates were randomly sampled (n = 3, at each site and date) using a Hess sampler (250μm mesh, 0.04m² area) and preserved in 70% ethanol. Streams were not sampled
for macroinvertebrates when surface water was absent ($n = 3$ in autumn, $n = 6$ in summer). In the laboratory, collected individuals were hand-picked, counted, and identified to the family level using Tachet et al. (2010). Depending on the context, higher taxa (family or genus) may or may not be suitable to elucidate patterns of diversity and community composition (Beketov et al., 2009; Heino & Soininen, 2007; Rossier, 2017). However, higher taxa performed well for studying community composition at small spatial scales in systems with low faunal diversity and low species to higher taxa ratio (<2–3; Carneiro et al., 2010; Heino, 2011; Heino & Soininen, 2007; Timms et al., 2013). Here, the spatial scale of our study was small (headwaters of a single alpine catchment) and it is well established that such alpine streams typically exhibit low faunal diversity because of the harsh environmental conditions (Ward, 1994). In addition, Alther et al. (2019) found that the diversity of genera and species within macroinvertebrate families in non-glacial streams of the Val Roseg were relatively low, except for Chironomidae. Further, Siebers et al. (2020) showed that macroinvertebrate families responded strongly to increased intermittency in a stream of the Val Roseg. We therefore considered that family-level identification was adequate to address the questions of our study, given the low diversity and probably low species to higher taxa ratio. In addition, Datry et al. (2014) showed that responses of macroinvertebrate assemblages to flow intermittency were congruent for different levels of taxonomic resolution at a global scale. This, together with further evidence that linkages between environment and community composition in stream macroinvertebrates are usually well preserved across species, genera and families (Arscott et al., 2006; Beketov et al., 2009; Datry et al., 2014; Furse et al., 1984), suggested that family-level identification was suitable for our study.

Benthic organic matter (BOM) was collected at the same time as macroinvertebrates with a Hess sampler ($n = 3$ at each site and date) and its biomass was quantified as ash-free dry mass.

2.3 Taxonomic and functional community metrics

For each site at each sampling date, we calculated total invertebrate abundance (total count within the three replicate samples), taxa richness and community evenness. We also calculated dissimilarity matrices based on log-transformed taxa abundances (Bray–Curtis index) and occurrences (Soerensen index). We then performed principal coordinate analyses (PCoAs) on these matrices and used the first two PCoA axes to describe variation in community composition among streams.

To describe functional attributes of the communities, we extracted 54 functional traits divided into 10 categories. We only selected traits that may affect resistance or resilience to drying (after Crabot et al., 2020; Datry et al., 2014; see selected traits in Table S1.2). Functional traits for all taxa were obtained from the Tachet database (Tachet et al., 2010) and trait values were averaged within families. This database provides an affinity of a given taxa for a particular trait class using a fuzzy coding approach ranging from 0 for low affinity to 3 for high affinity. Importantly, averaging trait values to the family level implies that all patterns at the functional level need to be interpreted with care, especially for the families encompassing a high diversity of trait modalities. For instance, the family Chironomidae encompasses many species that differ largely in feeding mode (Robinson, Thompson, et al., 2016). Considering the very high relative abundance of Chironomidae in our samples, averaging all trait scores within that family could potentially affect all trait analyses and especially those based on trait abundance matrices, because of the very high abundance of average trait values overshadowing patterns associated with other taxa. We therefore also completed the functional analysis with Chironomidae excluded, and showed that our findings remained unchanged (Supporting Information S2).

We calculated functional dispersion (FDis) as a measure of functional diversity (Laiberté & Legendre, 2010) and FRic based on log-transformed taxa abundances to describe functional attributes of communities (Brown et al., 2018; Laiberté & Legendre, 2010). Prior to using trait information, trait affinity scores were standardised so that their sum for a given family would equal 1 (Pailex et al., 2013). We calculated matrices of trait abundances and occurrences by multiplying the taxa by traits matrix with the taxa abundances and occurrences matrices, respectively. We then calculated pairwise Gower dissimilarity matrices on the trait abundance and trait occurrence matrices for each date, performed PCoAs, and used the first two axes to describe changes in community composition and structure at the functional level. Finally, we calculated functional redundancy using the SYNCSA package (Debastiani & Pillar, 2012) as the difference between taxonomic diversity and Rao’s quadratic entropy based on taxa functional similarity, divided by taxonomic diversity (Crabot et al., 2020; de Bello et al., 2007).

2.4 Data analysis

For each stream, we used the readings of the electrical resistance loggers to calculate the percentage of dry observations (equivalent to percentage of time dry during the study) and the number of drying events (where one drying event is a consecutive suite of dry observations separated by wet periods). We calculated the Euclidean distance between sites based on the standardised values of these two metrics and conducted a cluster analysis with a Ward agglomeration method to separate streams into different ICs. We also conducted a PERMDISP analysis on this distance matrix to test whether the variability in drying attributes within each IC differed. We used the hourly temperature readings to calculate the mean temperature for each stream as well as the coefficient of variation (CV) to describe thermal variability. Because the most intermittent streams dry in the summer months when water temperature is the highest, we used a linear model to test whether mean water temperature varied with the percentage of dry events.

We tested whether the different ICs were associated with differences in mean water temperature and its CV, BOM biomass,
periphyton biomass, electrical conductivity, as well as concentrations of dissolved and total organic carbon (DOC and TOC, respectively), total phosphorus, and silica. We also tested whether community metrics at the structural (taxa richness, evenness, total abundance, and PCoA axes on Bray–Curtis and Soerensen dissimilarity matrices) and functional levels (Fdis, Fric, functional redundancy, and PCoA axes on Gower dissimilarity matrices) differed among ICs and sampling dates. To do so, we used linear mixed models with each environmental parameter or community metric as a response variable and the different ICs as well as the sampling date as fixed effects. We added site ID as a random effect to account for the repeated measures design. To assess whether ICs differed in environmental conditions, we used a likelihood ratio test to compare three model structures: one including only the date as fixed effect, one including both date and ICs as fixed effects, and, finally, one including an interaction term between date and IC (Siebers et al., 2019). If the likelihood ratio test indicated differences across all ICs, we assessed post hoc contrasts among ICs by calculating estimated marginal means (EMMs) and comparing them among ICs using the Emmeans R package (Searle et al., 1980). In addition, we used likelihood ratio tests to assess whether adding an environmental variable as a fixed effect improved the model fit. We then compared pairwise contrasts using EMMs. Differences among dates were only reported when the best performing model in the likelihood ratio test included the interaction term between date and IC.

For each date separately, we used pairwise Bray–Curtis and Soerensen dissimilarity indices to describe taxonomic β diversity and pairwise Gower dissimilarity indices (based on abundances and occurrences) to describe functional β diversity. We then used a permutational analysis of multivariate dispersions based on 999 permutations (PERMDISP) to assess whether taxonomic and functional β diversities differed among ICs. PERMDISP tests whether the average distances from sites to group centroids differ among the different groups. When PERMDISP indicated that the distances between groups differed, we performed a Tukey’s HSD test to examine pairwise contrasts and obtain adjusted p values for multiple testing.

In addition, we calculated average pairwise Soerensen (occurrences) dissimilarities for each IC and date separately, and partitioned them in turnover and nestedness components (Baselga, 2010).

When PERMDISP indicated variations in β diversity among ICs, we used β deviations to test whether these differences might be due to deterministic selection processes or to stochastic and random processes. Specifically, we used the swsh_both.c and the quasiswap algorithms within the oecosimu function to simulate 999 random communities based on abundance and occurrence, respectively, separately for each date. We then computed the appropriate pairwise dissimilarity matrices on each of these communities (Bray–Curtis and Soerensen for taxa abundances and occurrences, and Gower for trait abundances and occurrences). Finally, we calculated the β deviations as the difference between observed pairwise dissimilarities and their mean expected dissimilarities (across the 999 simulations), divided by the standard deviation of the expected dissimilarities (Kraft et al., 2011). We then performed a PERMDISP on these β deviations (Sarremejane et al., 2020). PERMDISP tests that indicated differences in both β diversity and β-deviations among ICs would indicate that these differences primarily result from deterministic selection processes, whereas a PERMDISP result that indicated no difference between β-deviations would suggest that differences in β diversity result from random processes. We visualised taxonomic and functional communities by plotting the first two PCoA axes.

Finally, we used multivariate generalised linear models (MGLMs) separately on taxa abundances and trait abundances, to assess differences in taxonomic and functional community composition among ICs. We used the negative binomial distribution and checked its adequacy by plotting the residuals of the model. We ran separate models for each date because MGLM does not support random effects. We assessed the contribution of individual taxa or traits to these differences with the univariate procedure included in the ManyGLM function of the mvabund package, and assessed pairwise differences among ICs using post hoc GLMs and the EMMs comparison procedure. In the results section, we only present taxa for which post hoc EMMs indicated a difference between ICs. For traits,
TABLE 1 Results of the linear mixed models testing the effect of the different intermittency categories as well as the interaction with sampling date on species richness, total density, species evenness, functional diversity (SES-FDis), functional richness (FRic) and functional redundancy

<table>
<thead>
<tr>
<th>Type</th>
<th>Richness L ratio</th>
<th>p value</th>
<th>Density L ratio</th>
<th>p value</th>
<th>Evenness L ratio</th>
<th>p value</th>
<th>FDis L ratio</th>
<th>p value</th>
<th>FRic L ratio</th>
<th>p value</th>
<th>Functional redundancy L ratio</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type:Date</td>
<td>10.12</td>
<td>0.119</td>
<td>6.13</td>
<td>0.408</td>
<td>5.46</td>
<td>0.487</td>
<td>3.96</td>
<td>0.68</td>
<td>7.52</td>
<td>0.275</td>
<td>10.02</td>
<td>0.123</td>
</tr>
</tbody>
</table>

we show a subset of trait responses, because trait values are highly correlated.

All analyses were conducted in R 4.0.5 (R Core Team, 2021). We used the nlme (Pinheiro et al., 2021) and mvabund (Wang et al., 2012) packages for the linear mixed models and MGLMs, respectively. The vegan package (Oksanen et al., 2020) was used to calculate taxa richness, dissimilarity matrices, generate null models and perform PERMDISP. We used the function dbFD from the FD package (Laliberté et al., 2014; Laliberté & Legendre, 2010) to calculate FDis and FRic.

3 | RESULTS

3.1 | Flow intermittency and stream classification

Twenty-four of the 30 streams (80%) dried at least once during the 15 months of study. The cluster analysis separated sites into four categories (Figure 1). The first category represented perennial streams, except for one stream where one single short drying event occurred (Table S1.1). The second category (winter-drying—WD) described streams with intermediate total drought duration (26.8% dry observations on average) but low number of drying events (5.7 on average). These streams predominantly dried seasonally, between late October and March (Figure S1.1). Streams in the third category (moderately intermittent—MI) also had intermediate total drying durations (17.0% dry observations) but higher number of drying events (33.6 on average). These streams also dried during the colder months but some short drying events could also occur during late spring and summer. Finally, streams in the fourth category (periodically intermittent—PI) dried more often (40.1 drying events on average) and had the most dry observations (51.7% of dry observations on average). These streams experienced extensive dry periods throughout the whole year.

3.2 | Flow intermittency and local environment

Average water temperature was higher in WD and PI streams compared to MI and perennial streams, and the CV in water temperature was higher in MI streams compared to PI streams (Tables S1.3 and S1.4). Average water temperature was positively related to the percent dry events (F = 28.24, R² = 0.49, p < 0.001; Figure S1.2). Dissolved silica concentration was on average higher in perennial streams than in WD streams. Electrical conductivity was higher in perennial streams than in PI and WD streams. The biomass of BOM differed among ICs overall, but not across any specific pairwise comparisons, suggesting only a weak effect of ICs on BOM. Biofilm biomass and concentrations of DOC, TOC, and total phosphorus did not differ among stream types (Table S1.3 and S1.4). Spearman correlations between environmental variables are described in Table S1.5.

3.3 | Flow intermittency and α-level metrics

Taxa richness was lower in PI streams than in all other stream types, with an average of 4.9, 8.1, 7.4, and 7 for PI, MI, WD, and perennial streams, respectively. Total abundance was lower in PI streams than in perennial streams (82.8 and 1,422.2 individuals on average, respectively), but did not differ among other stream types. Community evenness was lower in perennial streams than in PI streams (0.13 and 0.29, respectively) but was not different among other stream types (Table 1; Figure 2a–c). Neither FRic, FDis, nor functional redundancy differed among ICs (Table 1; Figure 3a–c).

The analysis of PcoA scores indicated interactions between sampling date and ICs. For taxa abundances, PcoA1 scores were lower in PI streams compared to other ICs, except for WD streams in June. PcoA2 scores did not differ among ICs. For taxa occurrences, PcoA1 scores did not differ among ICs. PcoA2 scores were higher in PI streams than all other ICs, but only in August (Table S1.6; Figures S1.3 a, b; S1.4). PcoA1 scores also decreased with elevation for taxa abundances, while PcoA2 scores increased with elevation.

At the functional level, PcoA1 scores based on trait abundances were higher in PI streams than all other ICs, whereas PcoA2 scores were lower in PI than WD streams (Table S1.6; Figures S1.3 c, d; S1.4). PcoA1 scores based on trait occurrences were higher in PI streams than all other ICs but only in August. PcoA2 scores based on trait occurrences were lower in PI streams than all other ICs but only in August.

3.4 | Effects of intermittency regime on communities

Difference across ICs in taxa abundance were indicated by the MGLMs in September (dev. = 114.1; p = 0.049) and June (dev. = 102.2; p = 0.018), but univariate tests did not indicate differences for all taxa (Table S1.7). In contrast, for August, three taxa...
(Baetidae, Chironomidae, and Nemouridae) showed different abundances between ICs in the MGLM, but post hoc tests yielded differences only for Chironomidae (Table S1.8). MGLMs conducted on trait abundances also showed overall effects in June and September, but univariate tests did not (Table S1.9). In August, univoltine and multivoltine taxa were more abundant in perennial streams than in PI streams (Table 2; Figure 4). A similar pattern was observed for the scraper, shredder, and filter-feeder feeding groups. Finally, taxa belonging to size classes 0.25–0.5, 0.5–1, 1–2 and 2–4 cm were also all more abundant in perennial than PI streams (Table 2; Figure 4).

3.5 Flow intermittency and β diversity

Bray-Curtis β diversity (abundances) did not differ among ICs in June and September, but was higher in PI streams than in other
stream types in August (Table 3; Figure 5). Soerensen $\beta$ diversity (occurrences) differed among ICs but tests of pairwise comparisons did not indicate any difference, suggesting that the overall differences were minor. Bray–Curtis (abundances) $\beta$-deviations did not differ among ICs at any date ($F = 0.92, p = 0.476$). Functional $\beta$ diversity based on trait abundances did not differ among ICs at any date (Table 3; Figure 6). In August, functional $\beta$ diversity based on trait occurrences was higher in PI streams than all other stream types and functional $\beta$ deviations (occurrences) were higher in PI streams than in WD streams ($F = 6.03, p = 0.02$). On average across dates,
turnover accounted for a larger fraction of β diversity between ICs than nestedness (61% and 39%, respectively; Table S1.10).

4 | DISCUSSION

With this research, we examined the effects of flow intermittency on benthic macroinvertebrate diversity at the structural and functional levels in alpine streams. We characterised flow intermittency patterns over 15 months in 30 streams of a glaciated alpine catchment. We then examined the linkages between these drying patterns and different diversity metrics as well as taxa and trait abundance patterns. We found that streams could be divided in four categories based on their intermittency regimes: perennial streams; streams with one long drying event during autumn and winter (WD); streams with drying events predominantly during autumn and winter but occasionally during summer (MI); and streams with long and frequent drying events in autumn and winter as well as during summer months (PI). At the taxonomic level, PI streams had

<table>
<thead>
<tr>
<th>Taxon or trait</th>
<th>Deviance</th>
<th>p</th>
<th>Effect (from post hoc test)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chironomidae</td>
<td>24.42</td>
<td>0.001</td>
<td>Perennial &lt; PI, MI</td>
</tr>
<tr>
<td>Baetidae</td>
<td>18.43</td>
<td>0.008</td>
<td>Non-significant</td>
</tr>
<tr>
<td>Nemouridae</td>
<td>22.8</td>
<td>0.003</td>
<td>Non-significant</td>
</tr>
<tr>
<td>1 life cycle/year</td>
<td>23.62</td>
<td>0.008</td>
<td>Perennial &gt; MI, PI</td>
</tr>
<tr>
<td>&gt;1 life cycle/year</td>
<td>22.97</td>
<td>0.009</td>
<td>Perennial &gt; MI, PI</td>
</tr>
<tr>
<td>Scraper</td>
<td>23.60</td>
<td>0.008</td>
<td>Perennial &gt; PI</td>
</tr>
<tr>
<td>Filter feeder</td>
<td>24.575</td>
<td>0.006</td>
<td>Perennial &gt; PI</td>
</tr>
<tr>
<td>Shredder</td>
<td>26.78</td>
<td>0.004</td>
<td>Perennial &gt; PI</td>
</tr>
<tr>
<td>Size: 0.25–0.5 cm</td>
<td>22.659</td>
<td>0.009</td>
<td>Perennial &gt; PI</td>
</tr>
<tr>
<td>Size: 0.5–1 cm</td>
<td>23.76</td>
<td>0.007</td>
<td>Perennial &gt; MI, PI</td>
</tr>
<tr>
<td>Size: 1–2 cm</td>
<td>25.221</td>
<td>0.005</td>
<td>Perennial &gt; PI</td>
</tr>
<tr>
<td>Size: 2–4 cm</td>
<td>21.864</td>
<td>0.010</td>
<td>Perennial &gt; MI, PI</td>
</tr>
</tbody>
</table>

Abbreviations: MI, moderately intermittent; PI, periodically intermittent; WD, winter drying.
lower $\alpha$ diversity (taxa richness) but higher $\beta$ diversity (Bray–Curtis) than the other stream types. At the functional level, we showed that FRic, functional diversity, and functional $\beta$ diversity based on trait abundances remained unchanged among stream types. These patterns suggest that most taxa were negatively affected at high intermittency levels (PI streams), irrespective of their high resilience capacities. Therefore, changes in taxonomic $\alpha$ and $\beta$ diversity at high intermittency probably resulted primarily from stochastic processes, as opposed to deterministic filtering of species based on their resistance/resilience capacities.

4.1 | Flow intermittency and environmental conditions

In a previous study of flow intermittency patterns and hydrology of Val Roseg, Paillex et al. (2020) defined three classes of intermittency linked to differences in stream water origin. Here, with additional data on presence/absence of water, we were able to further refine their initial classification of streams according to intermittency regimes. Specifically, we separated the seasonally drying streams into WD and MI streams. There

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**FIGURE 5** Ordination plots showing communities (dots) plotted on the two first principal coordinate analysis (PCoA) axes calculated on Bray–Curtis dissimilarities (taxa abundances). Ellipses represent 95% standard error areas. MI, moderately intermittent; PI, periodically intermittent; WD, winter drying.
were no strong relationships between IC and local environmental conditions except for the high electrical conductivity and dissolved silica concentration in perennial streams, reflecting their groundwater origin (Paillex et al., 2020). The higher percentage of dry observations was strongly linked to higher average water temperatures probably because the additional drying duration predominantly occurs during colder months (Figure S1.1). This result suggests that differences in water temperature among ICs were due to different wetted periods rather than differences in water origin. There thus appear to be no differences in water origin between seasonally drying streams that might have affected the composition of macroinvertebrate assemblages, particularly in the prevalence of glacial melt (Brown et al., 2003).

### 4.2 The effects of intermittency on \( \alpha \)-level metrics

The lower macroinvertebrate abundance in PI streams compared to perennial streams was in accordance with the general expectation...
that flow intermittency acts as a strong disturbance to benthic macroinvertebrates (Arscott et al., 2010; Datry, 2012; Fenoglio et al., 2007; Sarremejane et al., 2020). In addition, and in partial accordance with H1, we found that taxa richness did not differ between ICs, except in PI streams where it was lower. This suggested that several taxa were adapted to intermediate levels of intermittency, especially during winter, but were unable to establish viable populations at the highest intermittency levels. Importantly, the changes in taxa richness were not reflected in FRic or functional diversity, although the level of functional redundancy was moderate (comparable to other studies in intermittent streams, see Crabot et al., 2020), suggesting that taxa became extinct irrespective of their resistance or resilience capacities. Additionally, the comparable level of functional redundancy among stream types showed that no similar trait profiles were selected in any given IC (which would show as high functional redundancy in a particular IC). Finally, differences in community composition among ICs (shown with the PCoA scores and the MGLM results) were minor, with reduced abundances of Chironomidae in PI streams, suggesting that deterministic selection was minimal. This was in stark contrast with other studies that reported much stronger selection effects of drying on macroinvertebrate communities, including substantial reductions in abundances of rheophilic taxa such as some EPT (Datry et al., 2014; Doretto et al., 2020; Piano et al., 2019; Siebers et al., 2020).

Overall, the lack of correlation between taxonomic and functional diversity metrics, together with the lack of evidence for deterministic selection of taxa could indicate that the reduced taxa richness in PI streams was primarily the result of stochastic processes (Boersma et al., 2014; Crabot et al., 2020; Sarremejane et al., 2020; Vellend, 2010). Here, we argue that the discrepancy between our findings and that of other studies from lower elevation systems might be due to biogeographical differences and specifically the high environmental harshness in alpine catchments. Macroinvertebrate assemblages in high-altitude streams are probably already filtered for their high resilience, by harsh environmental conditions including low temperatures, substrate instability, and ubiquitous drying during winter (Brown et al., 2003; Paillex et al., 2020) and drying events may therefore act on an already depauperate functional pool at the landscape level, resulting in smaller effects than increased drying in lower-altitude streams (Tolonen et al., 2019).

The fact that the taxa pool was potentially highly resilient to moderate intermittency might also explain why, in contradiction to H2, there was no evidence of trait filtering or differences in taxonomic diversity at intermediate levels of intermittency (between perennial and WD streams for instance). At high intermittency levels, however, it seems that a threshold was exceeded above which most populations could not be maintained, irrespective of their resilience capacities, and this resulted in the abrupt decrease in total abundances, taxa richness, and abundances of most trait categories.

Overall, this suggests that resistance and resilience traits may not be useful to predict the response of community composition to drying in these harsh alpine environments, because resistance and resilience capacities may be homogeneously high within the taxa pool (i.e., low contrast in these trait values among taxa), compared to lower elevation systems (Bonada, Rieradevall & Prat, 2007; Crabot et al., 2021; Fenoglio et al., 2007). Alternatively, it is possible that some mechanisms were poorly captured by the set of traits we used and that a more refined characterisation of traits related to resilience in these alpine systems could yield a better understanding of the mechanisms underpinning community response to drying. Specifically, accounting for finer differences in life history and phenology (such as the timing and duration of different life stages) could help explaining some of the community responses to the different duration, frequency, and timing of drying in PI streams. For instance, strong filtering is expected if the duration of vulnerable life stages of a particular taxon exceeds the return period of drying events (Jacquet et al., 2020; Wallace, 1990). Similarly, it seems taxa were mostly adapted to winter drying but could not cope with additional summer drying. Precise information on the timing of life cycle of different taxa in this alpine environment could potentially help explain some of these effects. It is also worth noting that colonisation in these systems is largely reliant on aerial dispersal, dispersal limitation may thus be an important factor at specific times, depending on the timing of drying with respect to the timing of aerial stages (Wallace, 1990).

The interpretation of assembly processes from functional patterns should be considered carefully here because the averaging of trait values within families could also partially explain the lack of functional responses. However, here, three main points provided some confidence in these analyses. First, Alther et al. (2019) found that the diversity of genera and species within families were relatively low in the Val Roseg, except for Chironomidae. Second, we could show that our results remained largely unchanged when we removed Chironomidae from the analyses, the most functionally diverse family. Third, Siebers et al. (2020) found that an experimental increase in intermittency caused strong responses in the abundances of different macroinvertebrate families in a stream of the Val Roseg.

Finally, we found that community composition changed along a gradient of elevation (the elevation of our sampling sites was highly correlated with latitude, equivalent to longitudinal location along the main stem), independently of other environmental variables. Considering the narrow range of elevations between our sites, it is unlikely that such differences in elevation had a direct filtering effect on populations. Interestingly, Burgherr and Ward (2001) found that macroinvertebrate diversity and abundances of most taxa decreased with elevation in the upper reaches of the main stem in Val Roseg because the glacial influence increased upstream. In our tributary streams, glacial influence was unrelated to elevation (Paillex et al., 2020); it is therefore possible that the differences we observed with elevation resulted from different colonisation patterns from the main channel, especially for potentially poorer dispersers such as Oligochaeta and Chironomidae. Alternatively, it is also possible that some important environmental variables were left unmeasured (substrate quality for instance).
Lastly, in contrast to our expectations, community evenness was highest in PI streams and lowest in perennial streams, suggesting that, despite the higher taxa richness, certain taxa (Chironomidae in particular) dominated assemblages in the absence of drying events. This pattern of higher evenness (or diversity) in highly disturbed environments can be common, however, and probably results from the fact that regular disturbance prevents competitive exclusion (Harvey et al., 2018; Valladares et al., 2015; Violle et al., 2010). In summary, high intermittency caused lower taxa richness, probably through stochastic processes, but also prevented certain taxa from dominating assemblages, potentially by limiting competitive exclusion.

4.3 The effects of intermittency on \( \beta \)-level metrics

In contrast to our expectation that increased intermittency would decrease \( \beta \) diversity through homogeneous selection (H3), Bray–Curtis (abundance) \( \beta \) diversity was higher in PI streams compared to all other stream types. This pattern could result from several mechanisms, including deterministic heterogeneous selection (if variability in abiotic conditions was higher among PI streams), stochastic processes linked to high mortality across the species pool, or dispersal limitation. Here, it is unlikely that dispersal limitation caused the differences in \( \beta \) diversity among ICs. This is because the streams within each ICs were well distributed spatially with respect to each other and to the main stem, which may to some extent act as a source of colonists (Paillex et al., 2020). In this context, high connectivity between sites may also have ameliorated the effect of drying events in WD or MI streams (e.g., Rosset et al., 2017).

The variability in drying attributes (percent dry and drying duration) was higher among PI streams than among perennial and WD streams. While this pointed towards heterogeneous deterministic selection as the cause of differences in \( \beta \) diversity, several patterns suggested that this was not the case. First, there were no differences in taxonomic \( \beta \) deviations among ICs, a strong indication that stochastic processes may have dominated as a structuring process (Sarremjeane et al., 2020). Second, contrary to our expectation (that patterns of functional and taxonomic \( \beta \) diversity would be broadly similar), we found that functional \( \beta \) diversity based on trait abundances did not differ among ICs. This, together with the fact that functional redundancy was rather low in this system in general, could suggest that periodical drying in summer increased taxonomic \( \beta \) diversity via stochastic processes. Similarly, Stubbington et al. (2019) found that increasing drying duration led to higher \( \beta \) diversity through heterogeneous selection in moderately intermittent streams (0%-25% drying duration), whereas stochastic extinctions caused an increased \( \beta \) diversity in the highly intermittent Albarine River (drying duration 0%-60%). Interestingly, in our study the differences in \( \beta \) diversity were only present immediately after the summer drying season, either in August (Bray–Curtis) or in August and September (Soerensen). The effects of summer drying may therefore have been rather short lived and communities could converge during autumn and winter.

Contrary to our expectations, we did not find that nestedness was higher than turnover among ICs. Instead, the turnover component was generally slightly more important than the nestedness component. While the balance of these two components does not allow for a clear identification of assembly mechanisms, this was further indication that increased intermittency in this system did not act as a strong deterministic filter of taxa based on their resistance and/or resilience capacities (Ballinger et al., 2007; Daniel et al., 2019; Pandit et al., 2009). Here, the alpine environment may already act as a strong pre-filter on community composition before drying occurs (Hieber et al., 2005). For example, Leigh and Datry (2017) found that \( \beta \) diversity peaked at intermediate levels of intermittency across both Australian and European streams, probably because environmental heterogeneity also peaked at intermediate intermittency and caused strong heterogeneous selection. We found that both \( \beta \) diversity and \( \beta \) deviations were higher in PI streams, suggesting that heterogeneous selection occurred at that level. However, despite our confidence in the reliability of functional analysis (see Section 2), trait averaging within families could also partially explain the lack of functional diversity patterns, and these results should be considered with caution.

4.4 Perspectives and implications

At both \( \alpha \) and \( \beta \) levels, we observed that differences in diversity or community structure predominantly occurred between the most extreme ICs (perennial and PI), and these probably resulted primarily from stochastic processes. We interpreted this as an indication that most taxa could not survive past a threshold of drying duration and/or frequency in PI streams. There would be great value for future research in investigating these thresholds in macroinvertebrate community composition responses along gradients of drying frequency and duration.

While the differences in macroinvertebrate communities we observed between ICs were probably due to harsher conditions associated with shorter hydroperiod (through increased drying frequency or duration), two other factors may also have played a role: differences in timing and predictability of drying. For instance, not only did PI streams dry for longer and more frequently than other stream types, but they also tended to dry more during summer months and in a less predictable manner (as opposed to WD streams for instance). It is well known that both timing and the degree of predictability of disturbance events can strongly determine their effects on biota (Lytle, 2001; Wallace, 1990), as species in regularly disturbed environments may develop adaptations to avoid or survive predictable disturbance such as that caused by drying (Lytle & Poff, 2004). It is known that flow intermittency will become more prevalent in alpine catchments, and especially in summer as the reduction in snow and ice covers will result in less meltwater being released into kryal and rhithral streams (Beniston, 2012; Milner et al., 2009). We
Therefore argue that future work should focus on disentangling the relative importance of the increased duration and frequency of drying events, and the changes to their timing and predictability. We showed that community changes at the functional level were limited, but we argue that future research should focus on examining the changes in functional capacities (for instance the capacities of ecosystems to process organic matter, uptake nutrients, or maintain energy flow through food webs) along intermittency gradients in alpine streams. The open questions in that area can include: does the higher community evenness in PI streams compensate for the lower tax richness in terms of functional capacities; and how do changes in community structure with drying affect functional rates (e.g., OM decomposition) in alpine stream networks?

Finally, our findings suggest that the recovery of communities after summer drying was relatively rapid because communities were similar in September and June. This implies that recolonization rates were high in this catchment, probably as a result of high ecological connectivity (Leys et al., 2016; Siebers et al., 2019). However, previous studies have also shown that when summer drying events occur in alpine streams that used to flow throughout the season, macroinvertebrate densities and richness are greatly reduced and assemblages are slow to recover (Drost et al., 2022; Plano et al., 2019; Siebers et al., 2020). Assemblages in Val Roseg may therefore be adapted to the current prevalence of flow intermittency at a network scale given that flow intermittency has been widespread across the valley for—at the very least—over a decade (Robinson, Thompson, et al., 2016). As the distribution of intermittency regimes within the landscape is shifting under climate change and glacial retreat, it is urgent to characterise the resilience of communities at the scale of entire stream networks by specifically including seasonal changes in ecological connectivity, with respect to the dispersal capacities of different species.

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**CONFLICT OF INTEREST**
The authors declare no conflict of interest for this study.

**DATA AVAILABILITY STATEMENT**
Data are available from the authors upon reasonable request.

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