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Abstract

Alpine streams face rapid hydrological changes due to the effects of global warming, glacier melting, and increased water uses such as hydropower production. Defining environmental flows (e-flow) is crucial to mitigate the ecological impacts of flow alterations. Among e-flow assessment methods, hydraulic habitat models predict changes in habitat suitability for aquatic species under different flow scenarios. They couple hydraulic models of stream reaches with biological models relating the abundance of taxa to microhabitat hydraulics. However, there is currently no suitable biological models for alpine, often fishless streams. In this study, we develop biological models for dominant macroinvertebrate taxa in alpine streams and compare their responses to hydraulics with those published in lowland streams. Using data collected in 150 microhabitats along a gradient of shear stress within five alpine streams, we performed generalized linear mixed models relating macroinvertebrate abundance to microhabitat hydraulics (shear stress, flow velocity, Froude number and water depth). We developed biological models for 41 taxa, and observed significant microhabitat selection for shear stress (18 taxa), velocity (20), Froude number (21), and depth (11). Most of them presented consistent responses across studied alpine streams, with shear stress and velocity as the main drivers. For common taxa, shapes of macroinvertebrate responses to hydraulics were comparable with those observed in lowland streams. Nevertheless, taxa preferred slightly lower shear stress in alpine streams compared to lowland streams, probably due to high-fine sediment and oxygen concentrations, especially for taxa feeding on autochthonous organic matter. Many (23%) abundant taxa are rheophilic in alpine streams, thereby threatened by flow reduction, including the glacial stream specialists Diamesinae and *Rhithrogena delphinensis*, which will be also affected by glacier retreat. Combined with hydraulic models, our biological models will facilitate more robust e-flow assessments, thereby reducing the impacts of flow alterations on alpine aquatic ecosystems.

KEYWORDS

benthic macroinvertebrates, glacial rivers, hydraulic preference models, hydraulic variables, mixed-effect models

1 | INTRODUCTION

Flow alteration has been identified as a major pressure on river eco-systems with many direct and indirect effects (Allan et al., 2021). In particular, alpine environments face rapid hydrological changes due to the combined effects of global warming and increased water abstractions linked to growing water demand. Increased air temperature and associated snow cover reduction affect both the quantity and the timing of snow meltwater flow, occurring earlier in spring (Confortola et al., 2013; Matiu et al., 2021). After a first increase in glacial meltwater, glacier shrinkage will lead to significant glacier runoff reduction, especially in summer, until complete ice disappearance (Huss et al., 2008). In addition, there are more and more water intakes for irrigation, drinking water, artificial snow production in touristic areas (Calianno et al., 2018; Vanham et al., 2009), and a growing number of small hydropower plants in mountainous regions in the current political context of greenhouse gas reduction (Lange et al., 2018; Zarfl et al., 2015). All these changes modify the hydrological regime of alpine streams (Barnett et al., 2005; Viviroli et al., 2011), and consequently their hydraulic conditions (Cauvy-Fraunié et al., 2014; Consoli et al., 2021), sediment regimes, morphologies (Baker et al., 2011; Bunn & Arthington, 2002), and physico-chemical conditions (Meier et al., 2003).

In turn, modifications in local habitat conditions induce changes in aquatic biodiversity. For example, Jesús et al. (2004) observed reduced macroinvertebrate richness downstream a small hydropower plant due to hydrological regime alteration. Quadroni et al. (2016) highlighted an alteration of benthic communities after sediment flushing from a small alpine reservoir, probably linked to rapid turbidity increase and channel instability (Gabbud et al., 2019). Hydropeaking also lead to macroinvertebrate drift, with sometimes pronounced effects in pools compared to riffles (Aksamit et al., 2021). In addition, Cauvy-Fraunié et al. (2016) observed that a 30% reduction in flow in a glacial stream had significant impact on the community composition, with positive effects on generalist herbivores but negative effects on filter feeders (Cauvy-Fraunié et al., 2014). Similarly, Rosero-López et al. (2022) highlighted a significant increase in benthic cyanobacteria with a 60% reduction in flow in the Andes. In this context, tools are needed for predicting biological responses to habitat modifications and mitigating ecological impacts.

Impacts of flow alteration can be mitigated by implementing environmental flows (e-flow), defined as the quantity, timing and quality of water flows required to sustain river ecosystems while satisfying societal needs (Arthington et al., 2018). A large number of e-flow assessment methodologies are available worldwide, which can be classified into hydrological, hydraulic rating, hydraulic habitat models and holistic approaches (Tharme, 2003). Hydraulic habitat models couple hydraulic models of stream reaches with biological models. Coupling both components allows predicting change in habitat suitability for aquatic taxa under different flow scenarios. Firstly, the hydraulic component predicts the frequency distributions of microhabitat hydraulic conditions at various discharge rates. Microhabitat refers here to a spatial scale small enough for reflecting the current hydraulic

environment of aquatic organisms. The hydraulic component can be a hydrodynamic numerical model that provides spatially-explicit description of within-reach hydraulic variability (Sinha et al., 1998). Hydrodynamic models are costly but particularly useful to study the spatial behaviour of individuals, or the effects of morphological restoration or hydropeaking on river habitats (Lamouroux et al., 2017). Statistical habitat models have also been proposed as alternative to numerical ones (Lamouroux & Capra, 2002; Wilding et al., 2014). These simplified models estimate the statistical distributions of hydraulic habitats within reaches, but do not provide spatially-explicit results. They are particularly useful in complex stream morphologies where numerical hydraulic approaches are challenging (Girard et al., 2014). Secondly, the biological component (hereafter called hydraulic preference models) describes the variation of taxon abundance with microhabitat hydraulic conditions (e.g., water depth, flow velocity, near-bed shear stress; Forcellini et al., 2022), based on repeated field observations at the microhabitat scale (Jowett, 2003; Shearer et al., 2015). Hydraulic preferences can vary according to the life stage (Capra et al., 2017; Dolédec et al., 2007; Statzner, 1993) and the environmental context (e.g., sedimentary conditions, dissolved oxygen; Leftwich et al., 1997; Rempel et al., 2000). Nevertheless, hydraulic preference models of many aquatic taxa exhibit a high degree of transferability across streams and dates and are thereby particularly suited for e-flow assessment (Forcellini et al., 2022; Lamouroux et al., 2013; Plichard et al., 2020).

Transferable hydraulic preference models have been developed for plants (Biggs, 1996), dozens of fish (Dunbar et al., 2012; Plichard et al., 2020) and macroinvertebrate taxa in European lowland streams and rivers (Dolédec et al., 2007; Forcellini et al., 2022; Mérigoux et al., 2009). However, despite the numerous ecological studies on alpine streams, few examined the relationship between the hydraulic conditions and macroinvertebrates at the microhabitat scale. While Snook and Milner (2002) highlighted that macroinvertebrates presenting traits associated to low turbulence occurred exclusively at low flow velocities and macroinvertebrates with traits offering resistance and/or resilience to turbulence were ubiquitous in a Pyrenean glacier-fed catchment, Cauvy-Fraunié et al. (2014) showed that certain taxa occurred exclusively in turbulent habitats in an Andean glacier-fed catchment. Thus, our knowledge is still incomplete, and hydraulic preference models still lack in the specific context of alpine environments. The complex morphologies of alpine streams, due to steep slope and heterogeneous substratum, generate particular hydraulic habitats (e.g., torrential flow with high relative roughness; Rickenmann & Recking, 2011). Vertical velocity profiles can differ from conventional ones in alpine streams, suggesting that bed shear stress could be more relevant than water column velocity for describing the microhabitat selection of benthic macroinvertebrates (Statzner & Müller, 1989). In addition, compared to lowland streams, alpine streams are generally colder, with less organic matter, higher concentrations of dissolved oxygen due to turbulent flows, and higher turbidity when glacier-fed (Füreder et al., 2001). Finally, alpine streams are often fishless and exhibit specific macroinvertebrate communities (Becquet et al., 2022; Brown et al., 2009). Therefore, it is

urgent to develop new biological models for alpine organisms to assess the impact of flow alteration on alpine aquatic communities.

In this study, we used benthic macroinvertebrates, particularly suited to assess the impacts of flow alterations in alpine stream biodiversity, as they dominate the macrofauna of alpine streams and display a wide range of habitat requirements and biological traits (Wallace & Webster, 1996). We aimed to (1) develop hydraulic preference models for dominant macroinvertebrate taxa in alpine streams, (2) test whether responses to hydraulics varied among alpine streams, particularly between streams with or without glacial influence, (3) identify the hydraulic variables that best explain microhabitat selection by alpine taxa, (4) compare hydraulic responses with those obtained in lowland streams and (5) assess which taxa are the most sensitive to hydrological alterations. For this purpose, we collected 150 macroinvertebrate samples (30 microhabitats × five alpine stream reaches) and characterized microhabitats with four hydraulic variables: bed shear stress, water column velocity, water depth, and Froude number following the approach of Forcellini et al. (2022). We first expected (hypothesis H1) consistent responses to hydraulics across sites within the same stream type but different responses between glacier-fed and no glacier-fed streams for certain taxa, due to the particular environmental conditions characterizing glacier-fed streams (Milner & Petts, 1994). We also expected (H2) stronger macroinvertebrate responses to benthic shear stress than average water column velocity

(Statzner & Müller, 1989), and a lower explanatory power of water depth than other variables as benthic macroinvertebrates make little use of the entire water column (Walton, 1980). Finally, we hypothesized (H3) that responses to hydraulics might vary between alpine streams and lowland streams for at least certain taxa due to the environmental specificities of alpine streams (e.g., higher concentrations of dissolved oxygen associated with turbulent flows).

2 | MATERIALS AND METHODS

2.1 | Study sites and their environmental characteristics

Our study was conducted in five stream sites with contrasted glacial influence and located between 1193 and 1732 m a.s.l. in two catchments in the French Alps (Table 1). As these sites were also studied in Becquet et al. (2022), where detailed maps are available, we used the same acronyms here. Sites Z9, Z10 and Z11 were located in the Arvan catchment in the Grandes Rousses massif and sites X15 and X29 in the Arve catchment in the Mont-Blanc massif. Their general environmental characteristics (Table 1) were derived from Becquet et al. (2022) as well as additional point physico-chemical measurements made during repeated field surveys for this study or others (Table 1).

TABLE 1 Environmental characteristics of the study sites. Physico-chemical variables were measured on several occasions since 2018 ($n = 13$ for Z10 and Z11, $n = 5$ for Z9, X15 and X29; see Becquet et al. (2022) for methods and instruments used). Hydraulic variables at the microhabitat scale were measured while sampling macroinvertebrates. For physico-chemical (temporal repetitions) and hydraulic microhabitat variables (spatial repetitions), the first line corresponds to the average and standard deviation of point values and the second line corresponds to the minimum and maximum values

Site codes	Z9	Z10	Z11	X15	X29
General characteristics (Becquet et al., 2022)					
Catchment	Arvan	Arvan	Arvan	Arve	Arve
GCC (%)	0.0	4.4	4.2	27.6	1.3
Altitude (m a.s.l.)	1732	1467	1430	1193	1203
Slope (°)	12	5	6	1	14
Physico-chemical characteristics					
Temperature (°C)	7.0 ± 2.3 (4.3–10.0)	7.9 ± 3.5 (1.2–12.4)	8.1 ± 4.0 (0.8–13.4)	8.1 ± 1.5 (6.2–10.1)	6.7 ± 1.1 (5.5–8.1)
Turbidity (NTU)	7.3 ± 5.0 (2.0–15.5)	177 ± 255 (5.0–795)	353 ± 794 (5.8–2842)	21.8 ± 14.2 (10.0–45.0)	2.4 ± 2.0 (1.0–5.9)
Oxygen (mg L^{-1})	9.5 ± 0.5 (8.6–10.0)	9.7 ± 0.8 (8.5–11.3)	9.7 ± 1.0 (8.6–11.5)	10.1 ± 0.6 (9.3–10.6)	10.4 ± 0.5 (9.8–11.1)
Hydraulic microhabitat variables					
Shear stress (HFST)	7.3 ± 3.7 (0–13)	10.6 ± 5.5 (0–20)	8.8 ± 5.4 (0–19)	9.9 ± 5.6 (1–20)	10.7 ± 4.8 (2–20)
Flow velocity (m s^{-1})	0.29 ± 0.23 (−0.04–0.71)	0.57 ± 0.52 (−0.05–1.77)	0.46 ± 0.37 (−0.02–1.29)	0.52 ± 0.48 (−0.07–1.48)	0.50 ± 0.42 (0.00–1.80)
Froude number (−)	0.29 ± 0.21 (0.00–0.71)	0.44 ± 0.42 (0.00–1.46)	0.39 ± 0.33 (0.01–1.27)	0.38 ± 0.33 (0.01–1.13)	0.44 ± 0.36 (0.00–1.28)
Water depth (m)	0.11 ± 0.03 (0.07–0.24)	0.21 ± 0.10 (0.09–0.42)	0.17 ± 0.10 (0.08–0.47)	0.22 ± 0.07 (0.11–0.37)	0.15 ± 0.06 (0.06–0.28)

Sites Z10, Z11 and X15 were glacier-influenced, with respectively 4.4%, 4.2% and 27.6% of glacier cover in the catchment (GCC, calculated by dividing the glacier area in 2015; estimated from satellite, Paul et al., 2020). These glacier-influenced sites were characterized by low slopes (between 1 and 6°) and high mean turbidity (e.g., 353 NTU for Z11, measured with a digital sensor, Table 1). They also exhibited high temporal variability in both turbidity (e.g., SD = 794 NTU for Z11) and temperature (e.g., SD = 4.0°C for Z11). The two remaining sites, Z9 and X29, were not glacier-influenced, had steeper slope (12° and 14° respectively) and lower mean turbidity (≤7.3 NTU). They exhibited lower temporal variability in both turbidity (e.g., SD = 2.0 NTU for X29) and temperature (e.g., SD = 1.1°C for X29). Dissolved oxygen concentrations of the five sites were always higher than 8.5 mg L^{-1}, with a maximum value of 11.5 mg L^{-1} (Z11, 03/03/2020). Note that X29 was not considered as a glacier-influenced stream due to a very small glacier area (0.04 km^2 in 2015; Paul et al., 2020), a low GCC (1.3%), and the presence of a lake below the glacier buffering the environmental conditions associated with glacial influence (Hieber et al., 2002).

2.2 | Biological data

Biological and hydraulic data collection was performed in late August and early September 2019. At each site, we sampled 30 microhabitats with a Surber net (0.05 m^2, mesh size 250 μm). Microhabitats were selected regularly along a gradient of shear stress. Samples were preserved in the field in 96% ethanol. In the laboratory, samples were rinsed through 250 μm, 500 μm and 2 mm sieves and sorted thoroughly by hand in a standardized manner, under a binocular magnifier (Leica MZ 125). Macroinvertebrates were identified under a binocular microscope (Leica M 205C, magnification 160X). Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera orders were identified to genus or species when possible, while the majority of Diptera were identified to family or subfamily. We identified 10%, 33% and 48% of sampled individuals to species, genus, and family, respectively, the others belonging to higher taxonomic ranks. The list of references used for identification is available in Supporting Information (Appendix S1). To run models on a consistent dataset, we removed taxa determined at the order or higher taxonomic level (12 taxa removed, e.g., Cyclopoida, Nematoda and Oligochaeta).

Within a family, individuals identified at the genus or species level were retained, but for individuals identified at the family level (e.g., first instars or damaged individuals), two options were considered. (1) When the individuals identified at the family level represented less than 50% of the total abundance of this family, they were removed from the dataset (eight taxa removed). (2) When the individuals identified at the family level represented more than 50% of the total abundance of this family, an additional family-level taxon was created, grouping all individuals belonging to the family (two families concerned). For these, the suffix 'tot' was added to family name (Chloroperlidae tot and Limnephilidae tot). Similarly, within a genus,

individuals identified at the species level were retained, while for individuals identified at the genus level only, we created an additional genus-level taxon grouping all individuals belonging to the genus (12 genus concerned) if the individuals identified at the genus level represented more than 50% of the total abundance of this genus. For these, the suffix "tot" was added to genus name (e.g., Nemoura spp. tot). For example, for the genus Nemoura, Nemoura mortoni (Ris, 1902) included all individuals identified at this species level, Nemoura spp. included all individuals identified only until the genus level, and Nemoura spp. tot included all individuals identified at both species and genus levels (i.e., Nemoura spp. plus Nemoura mortoni). Taxa Capniidae/Leuctridae, Brachyptera/Rhabdiopteryx and Baetis alpinus/melanonyx included individuals of the two mentioned families, genus, and species, respectively, when individuals were too small to identify them more precisely. As all individuals of the taxon Baetis spp. were early instars (<500 μm) that could not be reliably identified beyond genus level, we renamed this taxon as Baetis spp. juv.

After these groupings, for the numerical convergence of models, we considered only taxa with a total abundance higher than 30 individuals in the data set. Similarly, we considered only taxon × site combinations with at least five individuals of the taxon in each site, and at least two sites where this condition was respected. With these filtering, a total of 41 taxa were considered for the analyses.

2.3 | Hydraulic variables

At each microhabitat (n = 150), we measured water depth (D, m) and flow velocity at 40% of the water depth above the bed (V40, m s^{-1}), with a flow meter (Marsh McBirney Flo-Mate 2000, HACH, Loveland, CO, United States). This velocity V40 theoretically corresponds to the average water column velocity when the velocity profile is logarithmic. Similarly to many previous studies (Consoli et al., 2021; Dolédec et al., 2007; Lorenz & Wolter, 2019; Mérigoux et al., 2009), we measured near-bed shear stress (HFST, dimensionless) using 'Fliesswasserstammtisch-hemispheres' (HFST hemispheres), developed by Statzner and Müller (1989). These numbered hemispheres (HFST = 0 to 24) of similar shape but different densities are sequentially put on a plate on the riverbed, and the heaviest hemisphere moved by the flow is used to estimate shear stress (from 0.77 to 712 N m^{-2}). Finally, we calculated the Froude number (Fr, dimensionless) as:

$$Fr = \frac{V40}{\sqrt{gD}},$$

with g is the acceleration of gravity (9.81 m s^{-2}). This variable discriminates tranquil vs. torrential flows and habitats such as pools, runs and riffles. To describe the hydraulic patterns in our alpine study streams, we examined the correlation among each hydraulic variable with Ranged Major Axis (RMA, Model II) linear regressions (Legendre & Legendre, 1998) using random permutations (N = 999, significance threshold p = 0.05), adapted to our data where estimates of variables have comparable variance of errors compared to their means.

2.4 | Microhabitat selection models

2.4.1 | Model description

Following the approach of Plichard et al. (2020) for fish and Forcellini et al. (2022) for macroinvertebrates, we used generalized linear mixed models (GLMM) to model macroinvertebrate abundance responses to microhabitat hydraulics, involving B-spline transformations of the hydraulic variable (enabling non-linear responses) and assuming a negative binomial distribution of macroinvertebrate counts (accounting for abundance overdispersion). As variations in average abundance among sites can be due to many factors other than hydraulics (e.g., biogeography, temperature, water quality; Hart & Finelli, 1999), all our GLMM considered the site as a random factor and were used to assess the effects of hydraulics on abundance within sites (Dolédec et al., 2007).

We performed four nested models with increasing complexity (M1, M2, M2g and M3) on the 41 selected taxa. The basic M1 model assumed that abundance does not depend on hydraulics. The 'average' model M2 considered that abundance depends on hydraulics (transformed using a spline function), with a similar non-linear influence on abundance among all sites. The 'by-stream type' model M2g was similar to M2 but the influence of hydraulics could differ between the two groups of sites with or without glacial influence (considered here as a binary presence/absence factor). Note that M2g has only been performed on taxa occurring in the two stream types ($n = 23$). Finally, the 'by-site' model M3 considered that abundance depends on hydraulics and that the influence of hydraulics can vary at each site. In detail, models assumed:

$$y_{ij} \sim NB(\mu_{ij}, \theta),$$

where y_{ij} is the abundance of a given taxon in microhabitat i of site j, μ_{ij} its expected mean value, NB is the negative binomial probability density function, and θ its taxon-specific dispersion parameter. Relations between the expected abundance μ_{ij} and hydraulic variables varied across models as:

$$\text{M1 (no microhabitat selection)} : \log(\mu_{ij}) = \beta_0 + u_{0j},$$

$$\text{M2 ('average' microhabitat selection)} : \log(\mu_{ij}) = \beta_0 + u_{0j} + f(x_{ij}),$$

$$\begin{aligned}\text{M2g ('by} - \text{stream type' microhabitat selection)} : \log(\mu_{ij}) \\ = \beta_0 + u_{0j} + u_{1g} x_{ig} + f(x_{ij}),\end{aligned}$$

$$\text{M3 ('by} - \text{site' microhabitat selection)} : \log(\mu_{ij}) = \beta_0 + u_{0j} + u_{1j} x_{ij} + f(x_{ij}),$$

where β_0 is the fixed component of the intercept, u_{0j} is a site-level random intercept, u_{1g} is a stream-type-level random slope, and u_{1j} is a site-level random slope. In M1, M2 and M2g, u_{0j} follows a normal distribution. In M3, (u_{0j}, u_{1j}) follows a bivariate normal distribution among sites. Finally, $f(x)$ is a spline transformation of the hydraulic

variable x. In practise, we fitted M2, M2g, and M3 using the glmer.nb function of the lme4 package (Bates et al., 2015) combined with spline functions (R Development Core Team 2018). To avoid overparametrisation, and because more flexible site-specific models were not very convincing in previous studies on fish (Plichard et al., 2020), we used splines with two degrees of freedom only (with a single knot positioned at the median x value). M1 was fitted using the glmadmb function (Fournier et al., 2012), due to numerical difficulties with the function glmer.nb when estimating site-level random effects with low standard deviations.

2.4.2 | Model evaluation metrics

The mixed-effects modelling approach enabled us to compare models without microhabitat selection (M1), models with a similar microhabitat selection among sites (M2), models with variable selection between stream-types (M2g) and models with variable selection between sites (M3). We used likelihood ratio tests (LRT, comparing M2, M2g, and M3 with M1) to assess if taxa abundance response to microhabitat hydraulics was statistically significant. Then, following Plichard et al. (2020), we used the non-parametric Spearman Rho rank correlation (Spearman, 1904) for describing fits. This statistical parameter indicates how hydraulic preference models explained the ranks of observed abundance, which is an intuitive statistic for strongly overdispersed data with very high abundance values in a few samples. We noted Rho_{M1}, Rho_{M2}, Rho_{M2g} and Rho_{M3} the rank correlations between fitted and observed abundance values (for the corresponding model), and defined five summary statistics to describe the explanatory power ('gain') of the models:

$$\text{M2}_{\text{Gain}} = (\text{Rho}_{M2} - \text{Rho}_{M1})/(1 - \text{Rho}_{M1}),$$

$$\text{M2g}_{\text{Gain}} = (\text{Rho}_{M2g} - \text{Rho}_{M1})/(1 - \text{Rho}_{M1}),$$

$$\text{M3}_{\text{Gain}} = (\text{Rho}_{M3} - \text{Rho}_{M1})/(1 - \text{Rho}_{M1}),$$

$$\text{M2}_{\text{Proportion}} = \text{M2}_{\text{Gain}}/\text{M3}_{\text{Gain}},$$

$$\text{M2g}_{\text{Proportion}} = \text{M2g}_{\text{Gain}}/\text{M3}_{\text{Gain}},$$

where M2_{Gain}, M2g_{Gain} and M3_{Gain} respectively reflected how the 'average,' 'by-stream type' and 'by-site' models explained observed abundance variations within sites (additional gain relative to M1). $\text{M2}_{\text{Proportion}}$ and $\text{M2g}_{\text{Proportion}}$ are bounded between 0 and 1 and indicate the gain of M2 and M2g relative to M3. We considered that taxa had significant microhabitat selection when M3 significantly improved M1 ($p < 0.05$ according to LRT) and explained a minimum of abundance variability ($\text{M3}_{\text{Gain}} \geq 0.05$, following Forcellini et al. (2022)). Among taxa with significant microhabitat selection, we considered that taxa presented relevant 'average' and 'by-stream type' models when M2 and M2g were significantly better than M1 ($p < 0.05$

according to LRT) and explained most of the observed abundance ranks ($M2_{Proportion}$ ≥0.5, and $M2g_{Proportion}$ ≥0.5). We considered that M2g provided a better prediction of macroinvertebrate abundances than M2 when M2g was relevant and the gain of M2g compared to M3 was greater than M2 ($M2g_{Proportion}$ > $M2_{Proportion}$).

2.4.3 | Model outputs

For taxa with relevant 'average' microhabitat selection among sites (relevant M2: significant LRT for M2 and $M2_{Proportion}$ ≥0.5), we developed an operational preference model. Due to the log-link in M2 formulation, abundance was modelled as proportional to $\exp[f(x)]$, with thereby $\exp[f(x)]$ equivalent to a habitat suitability index or preference curve (Nestler et al., 2019). As previous studies on microhabitat modelling (e.g., Consoli et al., 2021; Dolédec et al., 2007), we rescaled this index between 0 and 1, by dividing it by its maximum value over a fixed range of the hydraulic variable x (e.g., [0–20] for HFST; Appendix S2). For some taxa (6/17 relevant M2 for HFST, 5/19 for V40, 4/20 for Fr, and 2/6 for D), M2 fits had undesirable edge effects, corresponding to unsatisfactory spline extrapolations for extreme hydraulic values. In such cases, we proposed expert modifications of the numerical results and reported these changes in Appendix S2. As a typical example, the U-shape fit obtained for the genus *Dicranota* spp. is due to a few points with HFST >12 (see points in Appendix S3), whereas the average response of the taxa is a decreasing abundance with HFST. In this case, we held the preference index for HFST >12 constant and equal to the preference index observed for HFST = 12 (Appendix S2).

To obtain an average hydraulic preference of taxa with similar microhabitat selection among sites (relevant M2) and facilitate comparisons with other studies, we defined AVG_HFST as the average of HFST values weighted by their habitat suitability index. Thus, AVG_HFST summarized the hydraulic preference of the taxa and corresponded to the average HFST that would be used if all HFST values were equally available in a site. Similarly, we calculated AVG_V40, AVG_Fr and AVG_D.

2.4.4 | Comparisons of responses to hydraulics

To identify which hydraulic variables best explained microhabitat selection by alpine taxa, we compared the metrics $M3_{Gain}$ (reflecting the strength of the microhabitat selection) and $M2_{Proportion}$ (reflecting the share of the average M2 model) between the four hydraulic variables, including all modelled taxa with significant LRT for M3 and $M3_{Gain}$ ≥0.05. In addition, we compared $M3_{Gain}$ and $M2_{Proportion}$ between the three hydraulic variables HFST, V40, and Fr, including only the taxa with significant microhabitat selection for these three hydraulic variables. To assess whether responses to HFST and V40 were less similar in alpine streams due to complex vertical velocity profiles, we compared AVG_HFST and AVG_V40 with RMA regression.

To assess the consistency of macroinvertebrate response to hydraulics between lowland and alpine streams for common taxa, we compared our results with those of Forcellini et al. (2022). Thus, for taxa with significant microhabitat selection (significant LRT for M3 and $M3_{Gain}$ ≥0.05), we compared the AVG_HFST between lowland and alpine streams using RMA regression. This test was made using AVG_HFST only to reduce the number of analyses, and because we obtained higher $M3_{Gain}$ for HFST in both studies.

3 | RESULTS

3.1 | Dataset characteristics

In total, our dataset was composed by 31 130 macroinvertebrate individuals, belonging to 114 taxa from 12 different orders. Taxonomic richness varied between 33 and 85 taxa in the five study sites, with 16 taxa occurring in all sites, and 37 occurring at a single site. Among the 14 *per site* dominant taxa (with relative abundance >5% in a specific site) only Orthocladiinae was dominant in all sites, *Baetis alpinus/melanonyx*, *Rhithrogena* spp. and Diamesinae were dominant in three sites (not the same), and the others in one or two sites. After selection and grouping, we considered 41 taxa among which 10 were clustered taxa either at the family or the genus level (see Methods). Diptera were predominant in the final dataset (26% of the total abundance, of which 48% were Chironomidae). Ephemeroptera was the second more abundant order (18%), followed by Plecoptera (8%), Tricladida (3%) and Trichoptera (2%).

Our dataset covered a large range of hydraulic conditions (Table 1), with HFST values ranging from 0 to 20, V40 from 0 to 1.8 m s^{-1}, Fr from 0 to 1.5, and D from 0.06 to 0.47 m. We observed significant correlations between HFST, V40, and Fr (RMA, R^2 between 0.72 and 0.92, $p < 10^{-3}$, Appendix S4), but not with D (RMA, R^2 below 0.03).

3.2 | Microhabitat selection models in alpine streams

3.2.1 | Macroinvertebrate responses to hydraulics (based on M2 and M3)

Among the 41 modelled taxa, 18, 20, 21 and 11 taxa had significant microhabitat selection (significant LRT for M3 and $M3_{Gain}$ ≥0.05) for HFST, V40, Fr, and D, respectively. For HFST, $M3_{Gain}$ ranged from 0.07 to 0.52, with an average of 0.25 (± 0.12), and 10/18 values of $M2_{Proportion}$ reached 1, for an average of 0.85 (±0.23). For V40, $M3_{Gain}$ ranged from 0.07 to 0.59, with an average of 0.23 (±0.13), and 16/20 values of $M2_{Proportion}$ reached 1, for an average of 0.93 (±0.23). Most taxa exhibiting a significant microhabitat selection also presented a comparable response to hydraulics across sites (Table 2). Indeed, 17/18, 19/20, 20/21 and 6/11 taxa had a relevant M2 (significant LRT for M2 and $M2_{Proportion}$ ≥0.5) for HFST, V40, Fr and D,

TABLE 2 Summary of modelling results for the 41 taxon models that converged for each hydraulic variable (except Limnephilinae for D) and comparison with lowland streams (Forcellini et al., 2022). Grey: relevant M3 (significant LRT for M3 and M3$_{Gain}$ ≥0.5); light grey: relevant M2 (significant LRT for M2 and M2$_{Proportion}$ ≥0.5); dark grey: improvement by M2g (significant LRT for M2g, M2g$_{Proportion}$ ≥0.5, and M2g$_{Proportion}$ > M2$_{Proportion}$); blank: no significant M3; "-": no model; "↗": positive relation; "↘": negative relation; "∩": bell shape

Stream type	Taxa	HFST				V40				Fr				D			
		M3	M2	M2g	Low land	M3	M2	M2g	Low land	M3	M2	M2g	Low land	M3	M2	M2g	Low land
Glacial	Diamesinae		↗		-		↗		-		↗		-				-
No glacial	Rhithrogena delphinensis		↗		-		↗		-		↗		-				-
	Ceratopogoninae				-				-				-				-
	Crenobia alpina				-				-				-				-
	Drusinae		↗		↗		↗		-		↗		-				-
	Ecdyonurus spp.				-		∩		∩				∩		-		-
	Epeorus alpicola		↗		↘		↗		-		↗		-				-
	Isoperla spp.				-				-				-				-
	Isoperla spp. tot				-				-				-				-
	Limnephilinae				-				-				-				-
	Nemoura mortoni				-				-				-				-
	Nemoura spp.		↗		↗		↗		-		↗		↗				-
	Nemoura spp. tot				-				-				-				-
	Philopotamus spp.				-				-		↗		-				-
	Philopotamus spp. tot				-				-				-				-
	Protonemura nitida				-				-				-				-
	Rhyacophila tristis		↗		↗		↗		↗		↗		↗		↗		-
	Tanytarsini		↗		-		∩		-		↗		-		↗		-
Both	Baetis alpinus				-		∩		-		↗		-				-
	Baetis alpinus/melanonyx				-		∩		-		↗		-				-
	Baetis spp. juv		↗		-		∩		-		↗		-				-
	Baetis spp. tot		↗		-				↗		↗		↗				-
	Brachyptera/Rhabdiopteryx				-				-				-				-
	Capniidae/Leuctridae				-				-				-				-
	Clinocerinae				-				-				-				-
	Corynoneura spp.				-				∩				-				-
	Dicranota spp.		↗		-		↗		↗		↗		-		↗		-
	Ecdyonurus spp. tot		↗		↗		↗		↗		↗		↗				↗
	Leuctra spp.				-				-				-				-
	Leuctra spp. tot				-				-				-				-
	Limnephilidae tot		↗		↗		↗		-		↗		-				-

(Continues)

TABLE 2 (Continued)

respectively. The abundance of these taxa increased with HFST for 11/17 taxa and decreased for 6/17. For V40, the abundance increased for 8/19 taxa, decreased for 5/19, and had a bell-shaped response for 6/19. For Fr, the abundance increased for 15/20 taxa and decreased for 5/20. Finally, the abundance of the six taxa with relevant M2 decreased with D. Our results showed that macroinvertebrate responses to hydraulics varied greatly across taxa (results detailed in Appendices S2 and S3). For example, we found that HFST had no effect on *Baetis* spp. juv, a negative effect on Limnephilidae tot, and a positive effect on Diamesinae and *Baetis alpinus* (Pictet, 1843) (Figure 1). For few taxa, the response to hydraulics was significant but varied across sites (no significant LRT for M2 and/or M2$_{Proportion}$ <0.5; Table 2). For example, Orthocladiinae had a significant response to hydraulic but exhibited different responses across sites for HFST, Fr and D (Table 2). The same was observed for *Corynoneura* spp. with V40 and D and for Clinocerinae, *Dicranota* spp., and Tanytarsini with D.

3.2.2 | Improved predictions by including stream type

A total of 18 taxa were present in a single stream type, of which two exclusively in glacier-influenced streams (Diamesinae and *Rhithrogena delphinensis*) (Degrange & Sowa, 1988). For the 23 other taxa, all M2g models numerically converged for HFST, V40, and Fr, except two for D (Table 2). For HFST, M2g improved the preference models of only 2/23 taxa: M2g$_{Gain}$ was 50% higher than M2$_{Gain}$ for *Ecdyonurus* spp. tot and 7% higher for Limnephilidae tot (Figure 1). Similarly, for Fr, M2g improved the model of 2/23 taxa, *Rhyacophila* spp. tot and *Liponeura* spp., with M2g$_{Gain}$ 20% and 8% higher than M2$_{Gain}$, respectively. In addition, for V40, M2g was relevant for *Corynoneura* spp unlike M2, as well as for Orthocladiinae for *Fr*. For D, M2g did not improve any model. For taxa with relevant M2g (significant LRT for M2g and M2g$_{Proportion}$ ≥0.5), the shape of the preference model remained comparable between M2 and M2g (Appendix S3).

3.3 | Comparisons of responses to hydraulics

3.3.1 | Between hydraulic variables in alpine streams

Results described above indicate that the number of significant microhabitat selection models (significant LRT for M3 and M3$_{Gain}$ ≥0.05) were high and comparable for HFST, V40 and Fr, while lower for D (Table 2). In addition, when considering all taxa with significant microhabitat selection, M3$_{Gain}$ and M2$_{Proportion}$ were higher for HFST, V40 and Fr than for D (Figure 2). The highest median of M3$_{Gain}$ was for HFST (0.24), followed by V40 (0.22), Fr (0.20) and D (0.13). Taking into account only the 15 common taxa in HFST, V40 and Fr models, the highest median of M3$_{Gain}$ was also for HFST (0.26), followed by V40 and Fr (0.23; Figure 2, blue dots). Finally, for the 16 common taxa
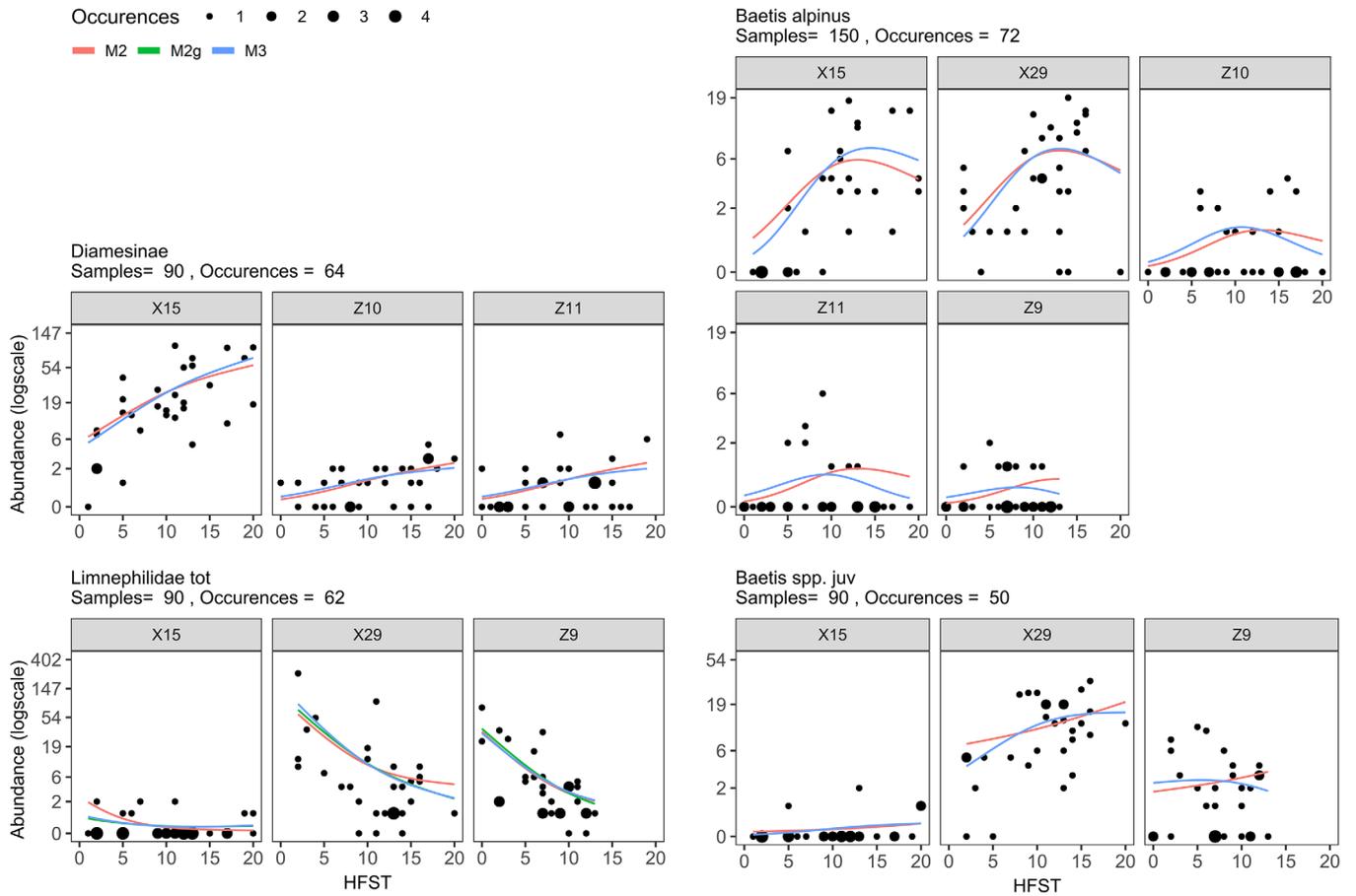
FIGURE 1 Examples of M2, M2g (for Limnephilidae only) and M3 fits with shear stress (HFST) to the observed abundances, for four taxa sampled in different sites. Diamesinae, *Baetis alpinus* and Limnephilidae have significant microhabitat selection (significant LRT for M3 and M3$_{Gain}$ ≥0.05) and relevant M2 (significant LRT for M2 and M2$_{Proportion}$ ≥0.5). *Baetis* spp. juv do not have significant microhabitat selection for HFST.
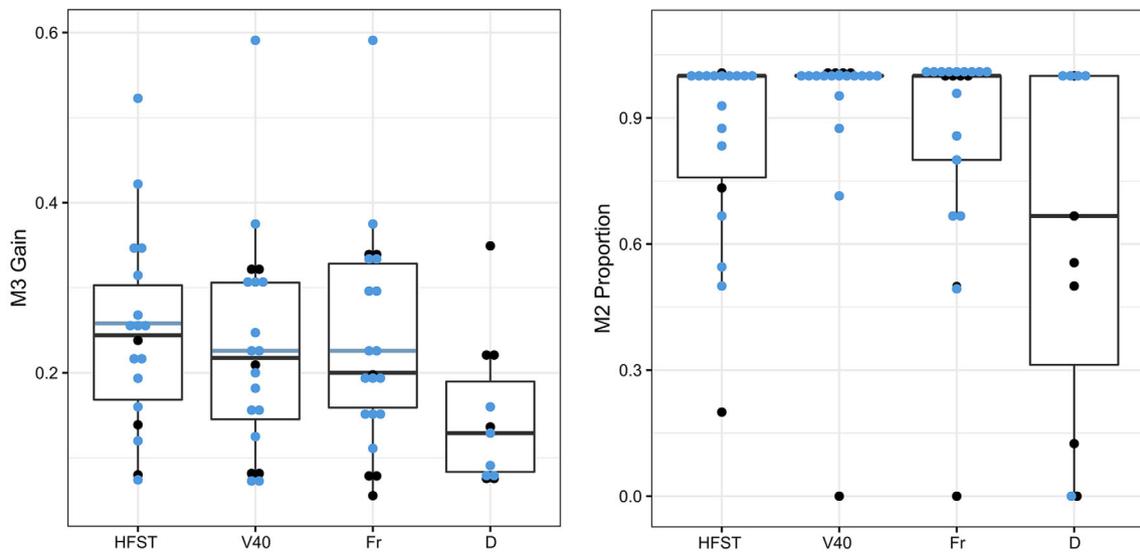

FIGURE 2 Comparison of median and quantiles (25% and 75%) of M3$_{Gain}$ and M2$_{Proportion}$ values among taxa with significant microhabitat selection (significant LRT for M3 and M3$_{Gain}$ ≥0.05), for the four predictors HFST ($n = 18$), V40 ($n = 20$), Fr ($n = 21$), and D ($n = 11$). Blue dots correspond to the 15 common taxa between HFST, V40 and Fr.

in HFST and V40 models, we observed a significant correlation between AVG_HFST and AVG_V40 (RMA, $R^2 = 0.86$, $p < 10^{-3}$, Appendix S5).

3.3.2 | Between lowland and alpine streams for HFST

As we obtained the highest M3$_{Gain}$ for HFST (Figure 2), we detailed the comparison between the results of Forcellini et al. (2022) and of our study for HFST only. Among the 41 models converging for HFST in this study, 22 taxa were common with Forcellini et al. (2022). Among them, 9/22 presented significant microhabitat selection (significant LRT for M3 and M3$_{Gain}$ ≥0.05) in lowland streams only, while 1/22, Limnephilinae, in alpine streams only. Clinocerinae had no significant microhabitat selection (no significant LRT for M3 and/or M3$_{Gain}$ <0.05) in both studies (Table 2). The remaining 11/22 taxa had significant microhabitat selection in both studies, among which eight presented a relevant M2 (significant LRT for M2 and M2$_{Proportion}$ ≥0.5) in both studies and three in only one study, (Table 2). The AVG_HFST of the 11 common taxa were significantly correlated between lowland and alpine streams, although slightly but systematically lower in alpine streams (RMA, $R^2 = 0.89$, $p < 10^{-3}$, Figure 3a). The magnitude of the average preference model M2, reflected by M2$_{Gain}$, were higher in lowland streams except for three taxa (Figure 3b). For the eight common taxa with significant microhabitat selection and relevant M2 in both studies, taxon responses to HFST had comparable shapes between both studies (Figure 4), except for *Baetis alpinus* whose

hydraulic preference curve reached a maximum at intermediate HFST values in alpine streams but high HFST values in lowland streams.

4 | DISCUSSION

4.1 | A significant selection of microhabitat hydraulics

In this study, based on five stream sites in the Arve and Arvan catchments, 63% of the modelled taxa (26/41) exhibited significant microhabitat selection for at least one of the four hydraulic variables tested. As Forcellini et al. (2022), we obtained comparable explanatory powers for models with shear stress, flow velocity, and Froude number (Figure 2), although we expected stronger responses to benthic shear stress than average water column velocity for benthic species (our hypothesis H2; Statzner & Müller, 1989). This result could be explained by the high correlation obtained between the three hydraulic variables (Appendix S4). Indeed, although we expected that these hydraulic variables would be less correlated in torrential alpine streams due to their complex morphologies (Statzner et al., 1988), this was not observed here. A possible explanation is that vertical velocity profiles in our alpine study sites did not differ strongly from those observed in lowland streams, due to moderate slopes, grain sizes, and consequently low Fr values (generally below 1) indicating tranquil flows (Table 1).

For 44% (18/41) of modelled taxa, we obtained a significant microhabitat selection to shear stress, among which most (17/18)
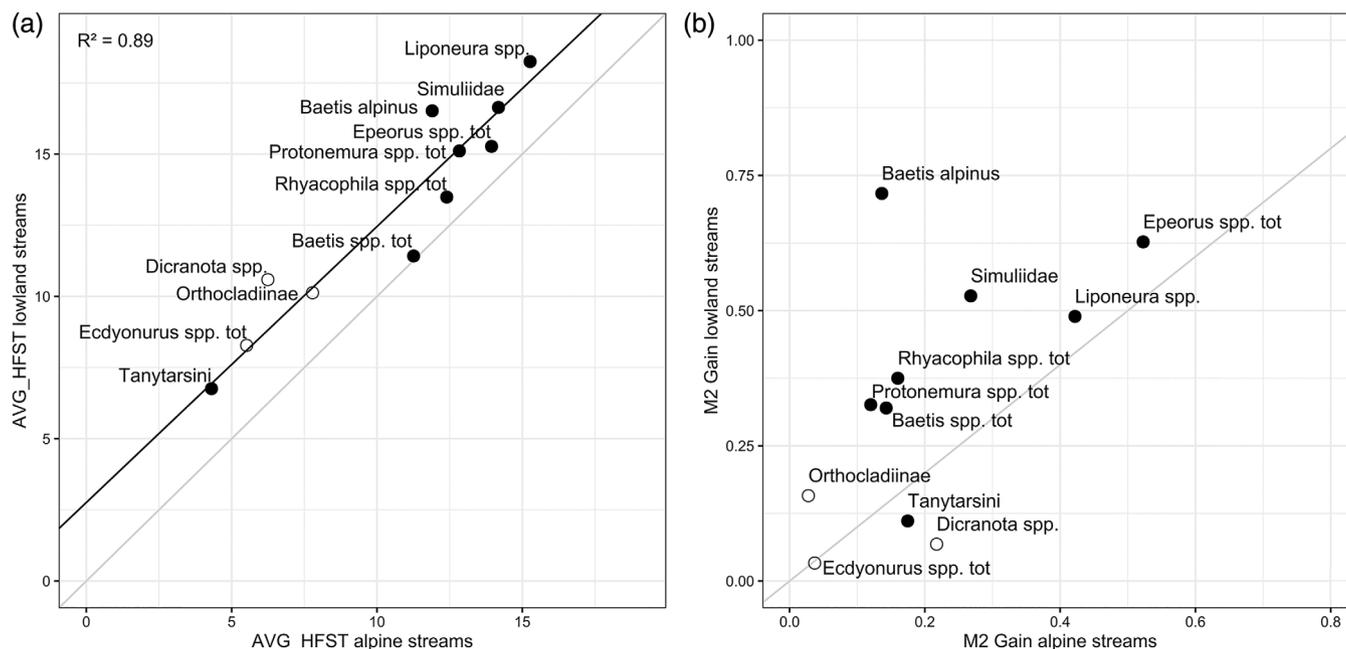

FIGURE 3 (a) Ranged Major Axis regression ($p < 10^{-3}$; black line) of the average preferred hemisphere number AVG_HFST (corresponding to model M2) of 11 common taxa between lowland (Forcellini et al., 2022) and alpine streams (this study) presenting significant microhabitat selection (significant LRT for M3 and M3$_{Gain}$ ≥0.05), (b) Corresponding M2$_{Gain}$. Grey lines correspond to the y = x lines. Empty dots correspond to taxa for which M3 was relevant but not M2 (M2$_{Proportion}$ <0.5) in one of the two studies.
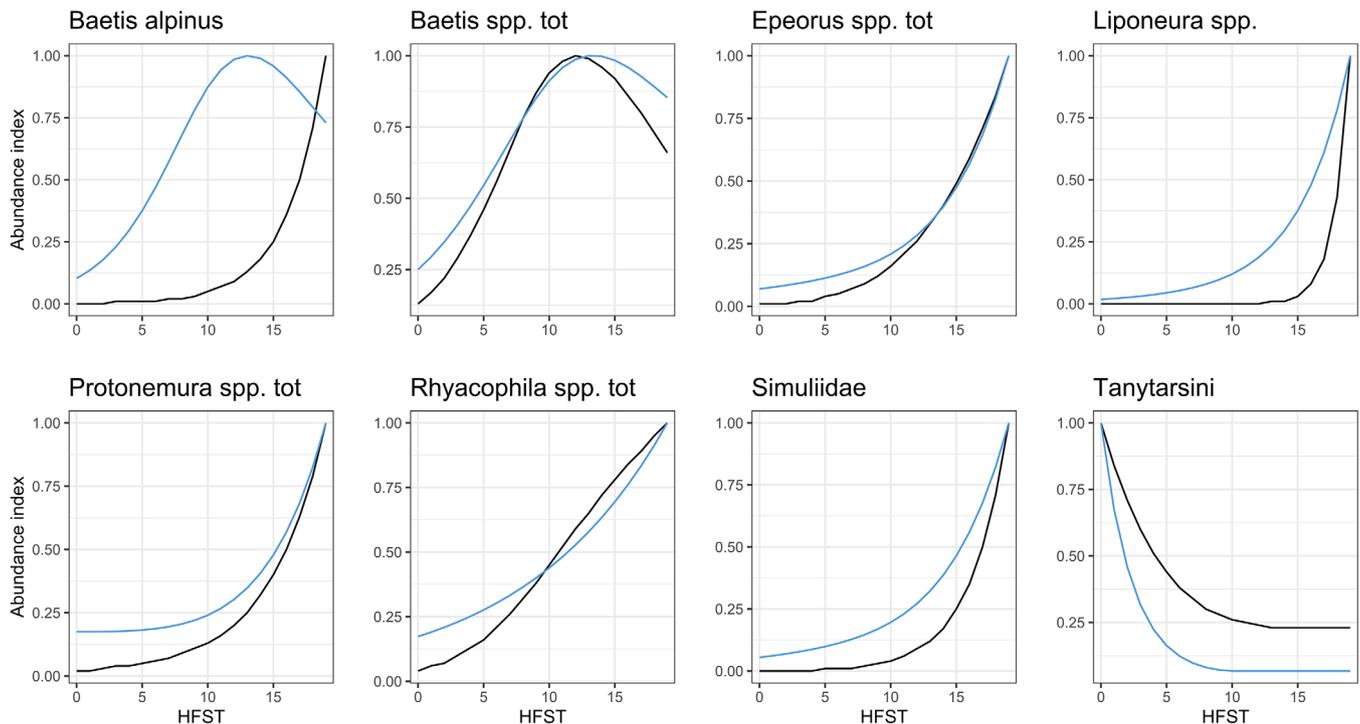
FIGURE 4 Hydraulic preference models (M2 fits rescaled between 0 and 1) for shear stress (HFST) and for eight common taxa with a relevant M2 in lowland (Forcellini et al., 2022; black line) and alpine streams (this study; blue line).

presented a consistent response across sites, indicating a high degree of transferability of microhabitat selection to shear stress among alpine streams (Lamouroux et al., 2013). However, our hypothesis H1 was only partly validated because for most taxa, the integration of the glacial influence did not improve the prediction of the models. In addition, 8 taxa with consistent microhabitat selection to shear stress had a similar response between our alpine study sites and the lowland sites studied by Forcellini et al. (2022) among the 11 taxa in common (with significant microhabitat selection), indicating a good degree of transferability of microhabitat selection to hydraulics among all types of streams.

Finally, only 27% (11/41) of modelled taxa presented a significant response to depth, among which six had a consistent response across sites. Depth models also had a lower explanatory power (Figure 2) than models for other variables. This might be because benthic macroinvertebrates make little use of the entire water column (Fenoglio et al., 2004; Walton, 1980) and because water depths were too shallow to exert hydrostatic pressure affecting biological functions (e.g., rate of CO_2 elimination; Miron, 1973). Nevertheless, *Rhyacophila tristis* (Pictet, 1834) was exclusively affected by water depth in our study, as well as Clinocerinae in both our and Forcellini et al. (2022) studies. The predation efficiency of these two predator taxa (Tachet et al., 2010) may be affected by water depth, changing their behaviour. In the same vein, Meissner et al. (2009) observed an adaptation of *Rhyacophila* predation at different flow velocities.

However, 37% (15/41) of modelled taxa showed no significant microhabitat selection for hydraulics. This result could be first partly explained by variations in hydraulic preferences during the life cycle,

as demonstrated for fish species (Capra et al., 2017; Plichard et al., 2020), because most of our modelled taxa included multiple instars (except *Baetis* spp. juv). For example, we observed that the first instar of *Baetis* (*Baetis* spp. juv), probably mostly composed by *Baetis alpinus* species, did not have significant microhabitat selection for hydraulics, contrary to the taxon *Baetis alpinus* including only advanced instar larvae (Figure 1). Indeed, first instar larvae of benthic macroinvertebrates generally use the hyporheic zone for growing (Bruno et al., 2020), as their small size allows them to penetrate further down into the substrate (Jacobi & Cary, 1996). Furthermore, for taxa identified at either genus or family level (e.g., Ceratopogoninae), detection of hydraulic preferences could also be blurred by the low taxonomic resolution (Monk et al., 2012) as biological traits might differ among species within genus and family (Gayraud et al., 2003). On the contrary, for some taxa, hydraulic preferences could be shared within the family. For example, at least seven species of Simuliidae exhibit a preference for high shear stresses (Dolédec et al., 2007) mainly linked to their feeding habit (filter feeders; Consoli et al., 2021). Finally, the reduced number of taxa with significant microhabitat selection in our study might also be linked to our limited number of samples (150 vs. 2158 in Forcellini et al., 2022), reducing statistical power (Vaudor et al., 2015).

4.2 | Specificities of alpine streams

Although we validated a good degree of transferability of hydraulic microhabitat selection among all types of streams for eight taxa

(Figure 3), our results also highlighted specific macroinvertebrate responses in alpine streams, confirming our hypothesis H3. Unlike Forcellini et al. (2022), we observed that Limnephilinae selected low shear stress, flow velocity and Froude number, significantly and consistently across sites. This might be because this Trichoptera subfamily does not include the same species in lowland and alpine streams (Graf et al., 2022). Conversely, Forcellini et al. (2022) reported a significant shear stress selection of nine taxa, including four Plecoptera (*Isoperla* spp. tot, *Nemoura* spp. tot, *Protonemura nitida* (Pictet, 1835), and *Leuctra* spp. tot), two Trichoptera (*Philopotamus* spp. tot and *Rhyacophila tristis*), two Diptera (Ceratopogoninae and Psychodidae), and *Rhithrogena* spp. tot., while we did not. This could be related to the particular environmental conditions of alpine streams. First, macroinvertebrate microhabitat selection may be explained by other variables correlated with hydraulics. For example, *Rhithrogena* spp., requiring highly oxygenated conditions (Lorenz & Wolter, 2019), might select turbulent microhabitats in warmer lowland streams for finding higher dissolved oxygen concentration (Rajwa-Kuligiewicz et al., 2015), while oxygen concentration did not appear as a limiting factor in our streams (average of 9.8 mg L^{-1} ± 0.8 mg L^{-1}; Davis, 1975) and generally in cold and fast flowing streams (Hynes, 1970). Second, macroinvertebrate microhabitat selection might be affected by more important covariables. In particular, taxa feeding on autochthonous organic matter such as *Isoperla* spp. tot, *Nemoura* spp. tot, *Protonemura nitida*, and *Leuctra* spp. tot (Tachet et al., 2010), may select less turbulent microhabitats with stable substrate in alpine streams, where biofilm can grow (Lorenz & Wolter, 2019) and the abrasion risk associated with the high concentration in fine sediments is reduced (Francoeur & Biggs, 2006).

The glacial influence improved the abundance prediction, although with minor effects on response shapes, for a few taxa; *Ecdyonurus* spp. tot and Limnephilidae tot for shear stress, *Corynoneura* spp. for flow velocity, and *Liponeura* spp., Orthocladiinae, and *Rhyacophila* spp. tot for Froude number. For the taxa feeding on autochthonous organic matter (e.g., *Ecdyonurus* spp. tot and Orthocladiinae, Tachet et al., 2010), this effect may be due to the specific environmental conditions of glacier-fed streams (i.e., low temperatures, high turbidity; Milner & Petts, 1994), as primary production is reduced in cold (Hall et al., 2015) and turbid waters that diminishes light penetration through the water column (Bilotta & Brazier, 2008). In addition, turbidity may influence the behaviour of predator taxa (limiting visual predation), thereby their microhabitat selection (Cauvy-Fraunié & Dangles, 2019).

Finally, the slightly lower average shear stress preference systematically observed in our alpine streams compared to lowland streams for common taxa (Figure 3a) may also be explained by the environmental characteristics of alpine streams, including the extreme conditions of glacier-fed streams (e.g., turbidity up to 2842 NTU in our streams, high variability in discharge; Becquet et al., 2022; Cauvy-Fraunié et al., 2015; Milner et al., 2001). In particular, in alpine streams, risks associated with high concentrations of fine sediments (i.e., abrasion, drift, clogging of filtering apparatus or gills; Cauvy-Fraunié & Dangles, 2019; Gibbins et al., 2010) may explain that rheophilic species select slower microhabitats, where they still find high oxygen concentrations. In addition, although unlikely due to the high velocity and shear stress values observed in alpine streams, it is possible that the clogging of interstitial spaces due to high concentrations of fine sediments impacts macroinvertebrate habitat preferences (Bo et al., 2007).

4.3 | Impacts of hydrological alterations and model applications

Our models allowed detecting a significant selection of microhabitats with high shear stress in alpine streams, independently of the study sites, for 11 taxa, including four Ephemeroptera (*Rhithrogena delphinensis*, *Epeorus alpicola* (Eaton, 1871), *Baetis alpinus*, *Baetis* spp. tot), three Diptera (Diamesinae, *Liponeura* spp., and Simuliidae), two Plecoptera of *Protonemura* genus, and two Trichoptera of *Rhyacophila* genus. These results support the study by Consoli et al. (2021) who showed higher abundances of *Baetis alpinus*, *Protonemura* spp., *Rhyacophila* spp., and Simuliidae at high shear stress, and Snook and Milner (2002) who showed that temporally attached macroinvertebrates (such as Simuliidae) persisted in high shear stress conditions. Consequently, stream flow reduction due to both water abstraction and glacier retreat (Milner et al., 2009) will, by reducing velocities and water depths in microhabitats (Dewson et al., 2007), undoubtedly impact these rheophilic taxa (Cauvy-Fraunié et al., 2016). These 11 taxa represent 25% of the total abundance of alpine macroinvertebrate community observed in 66 alpine stream sites by Becquet et al. (2022). In particular, specialist taxa such as Diamesinae or *Rhithrogena delphinensis*, exclusively observed in glacier-influenced streams in our study and once in a snowmelt stream (Degrange & Sowa, 1988; Launay et al., 2021), would be even more impacted by these changes and deserve special attention for biodiversity conservation purposes. On the contrary, flow reduction in alpine streams could favour six limnophilic taxa that preferred lower shear stress, such as Limnephilinae and *Ecdyonurus* spp. tot (Consoli et al., 2021; Dolédec et al., 2007).

When combined with available hydraulic models that predict changes in microhabitat hydraulics with discharge (e.g., Lamouroux et al., 1992, for shear stress or Girard et al., 2014, for velocity and depth), our biological models would be an effective tool to assess e-flows in alpine regions. Among the dominant taxa in alpine community (i.e., 39 taxa with total abundance higher than 100 individuals in Becquet et al., 2022), 21% exhibit no significant microhabitat selection for hydraulics and should therefore not be used for e-flow assessment in alpine streams. On the contrary, 31% present a significant microhabitat selection for at least one of the four hydraulic variables tested, and 23% present rheophilic response to at least one of the three velocity-related variables. 8% of the dominant taxa in alpine community also occur in lowland streams and exhibit significant shear stress microhabitat selection with consistent response among sites in both our alpine streams and lowland streams (Forcellini et al., 2022). For these taxa the lowland models can thus be used for e-flow assessment. Finally, 15% of the dominant taxa in alpine community present

significant microhabitat selection with consistent response among alpine streams but were not modelled in lowland streams (Forcellini et al., 2022). Thus, for these taxa, our models should be used for e-flow assessment in alpine catchments. Our new models will enable robust assessment of e-flow requirements and an improved management of water resources in alpine regions.

DATA AVAILABILITY STATEMENT

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

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