AGU ADVANCING EARTH AND SPACE SCIENCE

Water Resources Research

RESEARCH ARTICLE
10.1029/2020WR028496

Combining Hydrologic Simulations and Stream-network Models to Reveal Flow-ecology Relationships in a Large Alpine Catchment

Stefano Larsen[1,2], Bruno Majone[2], Patrick Zulian[2], Elisa Stella[3], Alberto Bellin[2], Maria Cristina Bruno[1], and Guido Zolezzi[2]

[1]Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy, [2]Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy, [3]Institute of Polar Sciences - Consiglio Nazionale delle Ricerche, Mestre-Venice, Italy

Key Points:

- The hydrological model HYPERstreamHS was used to simulate natural streamflow series at 100 bio-assessment sites across a large Alpine basin
- Three flow-regime classes were identified, representing typical nivo-glacial, nivo-pluvial, and pluvial streams
- Spatial stream-network models identified distinct flow-ecology relationships and relevant spatial autocorrelation across classified regimes, which can aid in the implementation of targeted water management schemes

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

S. Larsen,
stefano.larsen@fmach.it

Citation:

Larsen, S., Majone, B., Zulian, P., Stella, E., Bellin, A., Bruno, M. C., & Zolezzi, G. (2021). Combining hydrologic simulations and stream-network models to reveal flow-ecology relationships in a large Alpine catchment. *Water Resources Research*, *57*, e2020WR028496. https://doi.org/10.1029/2020WR028496

Received 28 JUL 2020
Accepted 22 FEB 2021

Abstract Flow regimes profoundly influence river organisms and ecosystem functions, but regulatory approaches often lack the scientific basis to support sustainable water allocation. In part, this reflects the challenge of understanding the ecological effects of flow variability over different temporal and spatial domains. Here, we use a process-based distributed hydrological model to simulate 23 years of natural flow regime in 100 bioassessment sites across the Adige River network (NE Italy), and to identify typical nivo-glacial, nivo-pluvial, and pluvial reaches. We then applied spatial stream-network models (SSN) to investigate the relationships between hydrologic and macroinvertebrate metrics while accounting for network spatial autocorrelation and local habitat conditions. Macroinvertebrate metrics correlated most strongly with summer, winter, and temporal variation in streamflow, but effects varied across flow regime types. For example (i) taxon richness appeared limited by high summer flows and high winter flows in nivo-glacial and pluvial streams, respectively; (ii) invertebrate grazers increased proportionally with the annual coefficient of flow variation in nivo-glacial streams but tended to decline with flow variation in pluvial streams. Although local land-use and water quality also affected benthic communities, most variation in macroinvertebrate metrics was associated with spatial autocorrelation. These findings highlight the importance of developing environmental flow management policies in ways that reflect specific hydro-ecological and land use contexts. Our analyses also illustrate the importance of spatially-explicit approaches that account for auto-correlation when quantifying flow-ecology relationships.

1. Introduction

The flow regime of streams and rivers has been modified by human activities at a global scale (Grill et al., 2019; Tonkin et al., 2019). As the human population continues to grow, the increasing demand for water supply, flood protection, and energy production has prompted the widespread adoption of engineering solutions such as the construction of dams, levees, and other hydraulic infrastructures (Couto & Olden, 2018; Shumilova et al., 2018; Zarfl et al., 2015). As a result, streams and rivers are under increasing anthropogenic pressure and are among the most threatened ecosystems worldwide, with particularly high rates of species extinctions (Tickner et al., 2020). The ongoing global climate change is expected to further exacerbate this situation by increasing the frequency of extreme hydrologic events such as floods and droughts that act synergistically with other stressors affecting aquatic ecosystems (e.g. Navarro-Ortega et al., 2015). This is of particular concern since freshwater ecosystems support about 10% of all known species (Strayer & Dudgeon, 2010) and are essential for human well-being, providing a wealth of ecosystem services (Green et al., 2015). Understanding and limiting the ecological effects of flow alteration is therefore fundamental for sustainable use of water resources.

The Natural Flow Regime Paradigm (Poff et al., 1997) is at the heart of the environmental flow definition and specifically acknowledges that river biota is adapted to seasonal and interannual variations of river flow. In order to mitigate the environmental impacts associated with infrastructures while maintaining their functioning, environmental flows (termed *e-flows* hereafter) should mimic the natural streamflow variability in terms of magnitude, frequency, duration, timing, and rate of change (Arthington et al., 2018). However, given the limits in the ability to mimic natural regimes in regulated rivers, *e-flows* policy must be informed by a clear understanding of the relation between river ecology and flow characteristics (i.e.,

flow-ecology relationships), which is, however, hampered by several practical challenges. These include, among others: (i) the paucity of the stream and river locations for which ecological information can be paired with long term hydrologic records (e.g. Patrick & Yuan, 2017); (ii) the natural variation in flow regime among rivers and sub-catchments, whereby ecological responses could vary significantly among individual flow regime types (Poff et al., 2010); and (iii) the spatial configuration of river ecosystems, which requires statistical approaches able to account for the complex autocorrelation associated with network topology and flow directionality (Peterson et al., 2013).

Several approaches have been used to address these challenges. Matching flow and ecological data is a prerequisite for quantifying flow-ecology relationships, and yet the spatial and temporal overlap between observed hydrologic and biological data is often poor (e.g. Mazor et al., 2018). To mitigate such limitations, either statistical or process-based hydrological models have been used. Statistical hydrological models aim to predict flow metrics at ungauged locations from the observed relation between available streamflow series and catchment characteristics (Booker et al., 2015; Patrick & Yuan, 2017), or by means of geostatistical interpolation (Skøien et al., 2006). Process-based hydrologic models, on the other hand, directly simulate streamflow time series at specific network locations by integrating the hydrological processes acting within the drainage area: i.e., precipitation, snowmelt, interception, evapotranspiration, infiltration, surface, and sub-surface flow, as well as their interactions (see e.g., Beven, 2012).

The second challenge is related to the heterogeneity of river basins where the natural streamflow regime and river biota differ markedly across the network. Therefore, it is necessary to classify flow regimes into distinct and easily interpretable classes in order to define reference flow conditions and implement targeted *e-flows* schemes, while also minimizing the effects of other co-varying environmental factors (Belmar et al., 2011; Booker et al., 2015). As a result, *e-flows* can be transferred among similar flow regimes at regional scales. For instance, the identification and classification of reference hydrographs are two key steps (i.e., "Hydrological foundation" and "River classification") in the assessment of the "Ecological Limits of Hydrologic Alteration" (ELOHA), the holistic framework increasingly adopted to define regional flow standards (Poff et al., 2010).

The third challenge is not strictly associated with flow-ecology research, but it is related to the spatial structure of river networks. The topology of branching river networks implies that classical statistical methods are unable to account for the spatial autocorrelation due to the connectivity and directionality of water flow within the network. Failing to account for such spatial patterns may lead to spurious correlations (Isaak et al., 2014). However, recent advances in the field of fluvial variography (i.e., spatial statistics applied to river networks) have provided the tools to model these spatial dependencies over the Euclidean and watercourse dimension, while also accounting for flow directionality (Carrara et al., 2012; Ver Hoef & Peterson, 2010; Zimmerman & Ver Hoef, 2017). Such stream-network models have been used to derive spatially explicit estimates of water quality and population abundance across river basins (Isaak et al., 2017; McGuire et al., 2014), but applications to flow-ecology research are surprisingly scarce (Bruckerhoff et al., 2019).

In this paper, we develop and discuss a framework that addresses these challenges using the Adige River basin (northeastern Italy) as a case study. In doing so, we aim to contribute to the understanding of flow-ecology relationships at the regional scale and evaluate potential flow-sensitive indicators, since recent works in the Italian Alps have shown the poor sensitivity of some of the current Water Framework Directive (WFD) biological indicators (e.g., Star_ICMi) to flow parameters (Larsen et al., 2019; Quadroni et al., 2017). Specifically, we focused on benthic macroinvertebrates as model organisms because of their essential role in the functioning of lotic systems, their widespread use as biological indicators, and the availability of monitoring data in the region (De Pauw et al., 2006; Friberg, 2014; Larsen et al., 2019). We included both taxonomic and functional (traits-based) metrics, as these provide independent and complementary information that could be valid across biogeographic zones (Heino et al., 2013).

To achieve the above-mentioned goals, first, we used the process-based HYPERstreamHS hydrological model (Avesani et al., 2021) to simulate the natural streamflow series of one-hundred stream reaches throughout the Adige River basin where biological information was available. Then, we classified distinct flow regimes representing the natural hydrological conditions of the streams in the basin. Subsequently, we used spatial stream-network models (SSN) to correlate the macroinvertebrate taxonomic and functional metrics

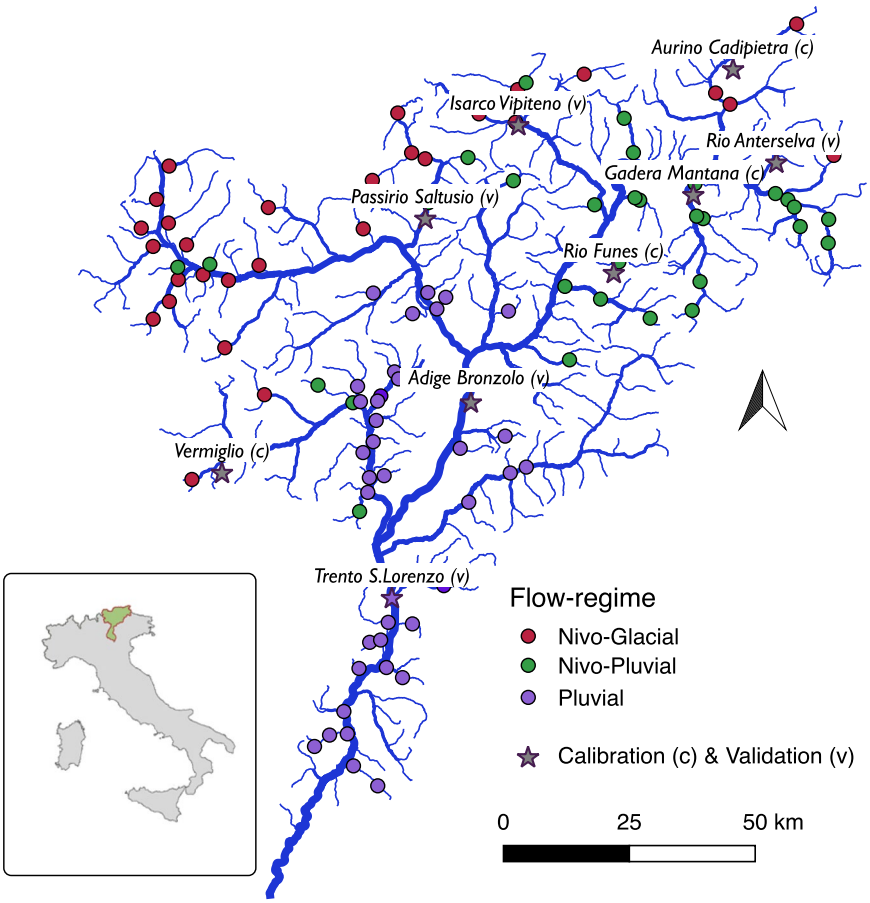

Figure 1. Map of the Adige River network (northeast Italy) showing the locations of the 100 biological monitoring sites for which 23 years of natural streamflow time series were simulated. Colors define the distribution of the three identified flow regime classes (see Section 2.4). The location of the gauging stations providing observed streamflow series is also shown, including those used for calibration (c) and validation (d) of the hydrological model.

with the streamflow characteristics and habitat conditions within each flow regime, while also accounting for spatial autocorrelation.

2. Data and Methods

2.1. Study Area

The study area is the Adige River basin, an Alpine catchment in northeastern Italy (Figure 1), closed at "Vo Destro" gauging station (drainage area 10,600 km^2). The Adige River is the second-longest Italian river, with the typical natural streamflow regime of the Alpine region showing two seasonal maxima, one occurring in spring-summer due to snow and glacial melt, and the other in autumn triggered by cyclonic storms (Chiogna et al., 2016; Mallucci et al., 2019). Recent analyses of historical hydro-climatic trends revealed that the basin is sensitive to climate change with the ongoing reduction of winter snowfall and anticipation of the snow-melting season (Diamantini et al., 2018; Lutz et al., 2016; Mallucci et al., 2019), which are likely to alter its flow regime by the second half of 21st century (Majone et al., 2016). Such modifications may have relevant socio-economic consequences in the catchment, where more than 80% of licensed withdrawn water is allocated to large hydropower plants, and about 6% to agriculture (Bellin et al., 2016; Zolezzi et al., 2009).

We selected 100 headwater stream reaches (Figure 1) throughout the catchment for which biological information was available and with an almost pristine streamflow regime (i.e., no major in-stream hydraulic infrastructure or impoundments upstream). The selected reaches were mostly first and second order streams, with elevation and drainage area ranging from 170 to 1900 m a.s.l. and from 10 to 434 km^2, respectively.

2.2. Observational Datasets

2.2.1. Streamflow data

The regional precipitation and temperature data set ADIGE (Mallucci et al., 2019) was used as meteorological forcing for hydrological modeling. This data set provides daily precipitations and temperatures for the time interval 1956–2013 at the spatial resolution of 1 km. The data set was developed by interpolating the measurements available at the meteorological stations within and nearby the river basin by means of kriging with external drift (Goovaerts, 1997; Mallucci et al., 2019). To comply with the computational grid adopted in the hydrologic modeling, the ADIGE data set was aggregated to the 5-km grid spacing.

Daily streamflow data collected at nine gauging stations (Figure 1) were provided by the Hydrological Office of the Autonomous Provinces of Trento (www.floods.it) and Bolzano (www.provincia.bz.it/hydro). Stations were selected according to the following criteria: i) observational period including the 1989–2013 timeframe used for calibration and validation of the hydrological model; ii) limited gaps in records; iii) large distance from upstream reservoirs if present; and, iv) broad spatial coverage including the major tributaries of the Adige River. The gauging stations were distributed in sub-catchments of different sizes, elevation, geology, and land-cover, and were, therefore, representative of the hydrological regimes of the Adige basin.

2.2.2. Macroinvertebrate Data

Macroinvertebrate data were collected by the Environmental Protection Agencies of the Provinces of Trento and Bolzano as part of their institutional monitoring programs (Larsen et al., 2019). Sampling was performed according to the multi-habitat sampling approach defined in the AQEM (http://www.aqem.de/) protocol: 10-replicate Surber samples were collected within a 20–50 m reach in proportion to the micro-habitats present (Hering et al., 2004). Samples were collected in the period 2009–2015, and sites were visited several times per year (median = 3), primarily in spring and autumn. Macroinvertebrate densities were averaged over all samples to remove seasonal effects, thereby obtaining a representative community composition of each site.

2.2.3. Reach-scale Environmental Data

Two additional reach-scale environmental variables were included in the analyses besides streamflow regime: the proportion of agricultural land-use ("Agr.landuse"), calculated within a 1-km buffer around each sampling location, and the physico-chemical water quality, as expressed by the "LIMeco" index (Livello di Inquinamento da Macrodescrittori per lo stato ecologico), one of the official WFD water quality indicators used to assess the ecological status of running water in Italy (European Commission, 2000). This is a multi-metric indicator assigning quality scores based on threshold levels for the concentration of oxygen, ammonia, nitrate and total phosphorus in freshwater (see Azzellino et al., 2015). These two environmental descriptors were included as covariates in the quantification of the flow-ecology relationship because of their proven influence on the composition of benthic invertebrates in the area (Larsen et al., 2019).

2.3. Hydrologic Simulations

Hydrological simulations were performed at the daily time scale with the HYPERstreamHS model (Avesani et al., 2021; Laiti et al., 2018), which couples the HYPERstream routing scheme (recently proposed by Piccolroaz et al., 2016) with a continuous Soil Conservation Service (SCS) module for surface flow generation (Michel et al., 2005). Subsurface return flow was modeled by a nonlinear reservoir (Majone et al., 2010). The HYPERstream routing scheme is specifically designed to couple with climate models and, in general, with gridded meteorological datasets. HYPERstream inherits the computational grid of the climatic model, or of the gridded product providing the meteorological forcing, and preserves geomorphological dispersion due to the structure of the river network (Rinaldo et al., 1991), regardless of grid resolution. In previous studies, the SCS runoff module was successfully applied to two tributaries of the Adige River (Bellin et al., 2016; Piccolroaz et al., 2016). For a detailed description of the hydrologic modeling framework see Laiti et al., (2018) and Avesani et al. (2021).

The hydrological model was calibrated against daily streamflow observations in the time window 1989–2013 using the ADIGE dataset as input meteorological forcing. The parameter space was explored for optimality,

according to the Nash-Sutcliffe efficiency index (NSE; Nash & Sutcliffe, 1970), by using the Particle Swarming Optimization algorithm (Kennedy & Eberhart, 1995). NSE was selected because of its effectiveness in assessing the performance of hydrologic models in reproducing observed streamflows. NSE is satisfactory when larger than 0.5 (Moriasi et al., 2007). Because hydrologic modeling was tailored to reproduce streamflow at unimpacted headwater locations (see Sect. Study area), four headwater gauging stations (Vermiglio, Rio Funes, Aurino, and Gadera in Figure 1) were calibrated simultaneously (i.e. NSE was defined as the average of individual efficiencies from the four stations). Subsequently, five other stations distributed across the basin (Saltusio, Vipiteno, Anterselva, Trento, and Bronzolo in Figure 1; drainage area ranging from 60 to 9000 km^2) were used for validation, in order to assess how the model reproduced streamflow at all the relevant scales. The first two years of the time series, i.e., 1989 and 1990, were used as spin-up for the simulations and therefore were excluded from the computation of NSE. Finally, we used the calibrated hydrologic model to simulate streamflow time series (1991–2013) at the 100 gauged and ungauged locations where biological data were available.

As additional validation of the hydrologic model, we further compared the response of taxon richness to the observed and simulated flow metrics using nine locations for which measured streamflow time series were also available.

2.4. Hydrologic Classification

Simulated streamflow time series at the 100 locations were first normalized by their mean annual discharge (MAD) to allow comparison across streams and develop flow-ecology relationships independent of stream size (e.g., Rosenfeld, 2017). In the following step, streamflow regimes were classified according to their typical seasonality as follows: first, we calculated the mean monthly hydrographs for each location from the MAD-normalised daily streamflow time series (Figure S1 in SM); then we performed a principal component analysis (PCA) on the resulting hydrographs to synthesize similarities among locations using the first two PC axes. Location scores on the two axes were then weighted by the proportion of variance explained in the PCs and used as synthetic variables in order to cluster the locations based on their flow regime (see e.g., Belmar et al., 2011). A flexible-beta hierarchical clustering approach was used, with the recommended value of beta = −0.25 (Belmar et al., 2011; Legendre & Legendre, 2012; Mazor et al., 2018), which provides an intermediate solution between chaining obtained via single linkage, and space dilation deriving from complete linkage. To further validate the degree of separation among the classified regimes, we ran a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2017) based on the Euclidean distance matrix of the weighted PCA scores.

2.5. Hydrologic Metrics

We used the 23 years MAD-normalised daily streamflow values to calculate 34 hydrologic metrics following the indicator of hydrologic alteration (IHA; Richter et al., 1997) approach (Table 1), implemented in R software with the "IHA" package (R Core Team, 2019). These metrics were averaged over the years to quantify ecologically relevant components of the long-term flow regime related to magnitude, duration, frequency, timing, and rate of change. As an exploratory step, and to visualize and further validate the separation of the hydrologic classes in the multidimensional space defined by the hydrologic metrics, we plotted the streams on the first two PCA axes derived from the correlation matrix of the IHA metrics. However, our main interest was to quantify flow-ecology relationships within the distinct hydrologic regimes considered as management units. Therefore, we ran additional PCA analyses for each classified regime to identify the most relevant metrics in each group. We then selected a set of non-redundant flow metrics showing high correlation (>0.8) with the first or second PC axes (see Table S1 and Section 3), which reflected the key flow components. These flow metrics were subsequently used as predictors in stream-network models for quantifying interpretable flow-ecology relationships.

2.6. Data Analysis

We derived a set of taxonomic and functional metrics from the macroinvertebrate community data. Our aim was to examine the sensitivity of different metrics to streamflow conditions to derive valid alternatives to

Table 1
List of the IHA Flow Metrics Computed From the 23 Years Simulated Streamflow Time Series

Flow component	IHA flow metric name	Description
1 - Magnitude of monthly flow conditions (12 parameters)	January, **February,** March, April, May June, **July**, August, September, October, November, December	Mean flow for January, ..., December
2 - Magnitude and duration of extreme conditions (11 parameters)	1, 3, 7, 30, 90 Day Min	Minimum flow, 1, 3, 7, 30, 90 days mean
	1, 3, 7, 30, 90 Day Max	Maximum flow, 1, 3, 7, 30, 90 days mean
	Base index	7 days minimum/mean flow
3 - Timing of extreme flow conditions (2 parameters)	min Julian	Mean Julian date of annual 1-day minimum
	max Julian	Mean Julian date of annual 1-day maximum
4 - Frequency and duration of high and low pulses (4 parameters)	**Low pulse number**	Number of flow events below 25thpercentile
	High pulse number	Number of flow events above 75th percentile
	Low pulse length	Number of days below 25th percentile
	High pulse length	Number of days above 75th percentile
5 – Rate of change and variation (5 parameters)	Rise rate	Median of all positive differences between consecutive values
	Fall rate	Median of all negative differences between consecutive values
	Reversals	Number of times flow period switches from rising to falling and vice-versa
	y.CV	Average annual coefficient of variation (SD/mean)
	m.CV	Average monthly coefficient of variation (SD/mean)

Note. **Metrics** in bold Were Selected for the Examination of Flow-ecology Relationship in the SSN Models.
Abbreviations: IHA, indicator of hydrological alterations. SSN, spatial stream-network models.

those currently implemented under the WFD. We included metrics related to the diversity of the community, such as taxonomic richness, Shannon diversity (as effective number of species of order $q = 1$; Jost, 2006), Functional Dispersion (FDis, which is minimally influenced by taxonomic richness), as these have been shown to reflect flow alterations elsewhere (e.g., Kennedy et al., 2016). We additionally included metrics describing the proportion of different feeding groups (i.e., grazers, shredders, gatherers, filterers, and predators) and the proportion of relatively small and large sized (range 0.25–0.5 mm and 20–40 mm, respectively) invertebrates. We focused on feeding traits as they convey information about the functional role of organisms in the ecosystems and on size traits that are a proxy of multiple life-history characteristics like e.g. life cycle duration, longevity (Poff et al., 2006) and may respond to variation in shear stress (e.g., Merigoux & Doledec, 2004). Finally, we also examined how the WFD Star_ICMi index responded to flow characteristics. The Star_ICMi is the official Biological Quality Element used in Italy to classify the status of running water in line with the WFD requirements (Buffagni & Erba, 2007; Buffagni et al., 2006). The index is formulated combining six normalized and weighted metrics, including richness, diversity, and taxa sensitivity to organic pollution (Buffagni et al., 2006).

Information for functional traits of the taxa was gathered from the online database of freshwater ecology (www.freshwaterecology.info; Schmidt-Kloiber & Hering, 2015). For the calculation of FDis, we included 13 traits (Tab. S2) in order to provide an inclusive measure of functional diversity. Feeding information was available for all taxa included in the analysis, whereas size traits were available for about 50% of the taxa. As such, taxa with no information for a given trait were not considered in the analyses.

2.6.1. Flow-ecology Relationships

Spatial stream-network models (SSN; Ver Hoef et al., 2014; Ver Hoef & Peterson, 2010) were run separately for each flow regime to quantify the relation between the biotic and hydrologic metrics while accounting for the autocorrelation structures of the dendritic network. The LIMeco index and Agr.landuse indicator

were included as additional covariates in the models. ArcMap 10.5 and the STARS toolset (Peterson & Hoef, 2014) were used to generate the spatial data necessary to analyze stream-network models. The full set of autocovariance functions were used to model spatial autocorrelation, including Euclidean, in-stream flow-connected (locations in which water flows from one to the other) and flow-unconnected (connected within the network, but not reflecting the directionality of the water flow) functions. This approach allows accounting simultaneously for the along-channel and across-basin (flow-unconnected and Euclidean, respectively) patterns of autocorrelation, while also distinguishing locations linked by direct water flow (i.e., flow-connected). In particular, SSN models take the form:

$$y = X\beta + z_{TU} + z_{TD} + z_{EU} + \varepsilon \quad (1)$$

where y is the response variable (i.e., macroinvertebrate metrics in this study), X is the matrix of predictors (flow metrics, LIMeco, and Agr.landuse) with associated β regression parameters, while $z_{TU} + z_{TD} + z_{EU}$ are zero-mean random variables with autocorrelation structure based on tail-up (TU), tail-down (TD) and Euclidean (EU) functions, respectively, and ε is the random independent error. The TU and TD functions are moving-averages functions autocorrelated in an upstream and downstream direction, respectively. The tail-up function assigns different weights to locations upstream of a given site according to the catchment area, used here as a proxy of streamflow. In this way, the moving-average autocorrelation is split at confluences so that upstream locations with larger catchments have a stronger influence on downstream communities. The reader can refer to Peterson et al. (2013) and Ver Hoef and Peterson (2010) for a detailed description of the SSN framework.

Biotic metrics expressed as proportions (i.e., feeding and size traits) were logit-transformed as recommended (Warton & Hui, 2011), and maximum-likelihood was used for parameter estimation in all SSN models. For each biotic metric, the most supported model was selected based on the root-mean-square prediction errors (RMSPE), which focus on model predictive power (Ver Hoef et al., 2014). The model was developed in a stepwise fashion, following guidelines provided in Ver Hoef et al. (2014). We first included all predictors (the selected flow metrics, LIMeco, Agr.landuse), and the full set of autocovariance functions (i.e., tail-up, tail-down, and Euclidean). Then we manually removed non-significant predictors and subsequently refined the spatial components. These can be defined by considering different autocovariance functions, including e.g., exponential, Mariah, spherical, linear-with sill, though spatial stream-network models appear little influenced by their mis-specification (Garreta et al., 2009; Isaak et al., 2014). We compared or removed different functions for the Euclidean, tail-up, and tail-down components and selected the final model with the lowest RMSPE. If different models had identical RMPSE values, the most parsimonious solution was selected based on Akaike Information Criterion (AIC). The spatial autocovariance functions were refined after the selection of the model predictors since the model accounts for spatial correlation in the error term after the effects of the covariates are removed (Frieden et al., 2014).

The SSN package (Ver Hoef et al., 2014) for R software (R Core Team, 2019) was used to run the stream-network models.

3. Results

3.1. Hydrologic Simulations and Classification

The capability of HYPERstreamHS hydrological model to reproduce the observed daily streamflow time series in the Adige River was validated in the period 1991–2013 by computing NSE at the nine gauging stations described in Section 2.4 (Figure 1). The parameters of the hydrologic model were inferred by maximizing the average NSE at Vermiglio, Rio Funes, Aurino, and Gadera gauging stations. Calibration produced a satisfactory mean NSE of 0.623 (range: 0.58–0.70; Figures S2 and S3). At the validation stations, mean NSE was 0.620 (range: 0.48–0.79), with lower values in the smaller subcatchments (Saltusio, Isarco, and Anterselva; Figure S2), and higher values at the larger downstream subcatchments of Trento and Bronzolo (0.74 and 0.79, respectively; Figures S2 and S3). The limited reduction of NSE efficiency at Saltusio, Vipiteno, and Anterselva gauging stations is in line with the general understanding that accurate reproduction of observed streamflows in small catchments would require accurate and spatially well-resolved precipitation and temperature fields at small spatial scales (e.g., Heisterman & Kneis, 2011). A further validation of the hydrologic

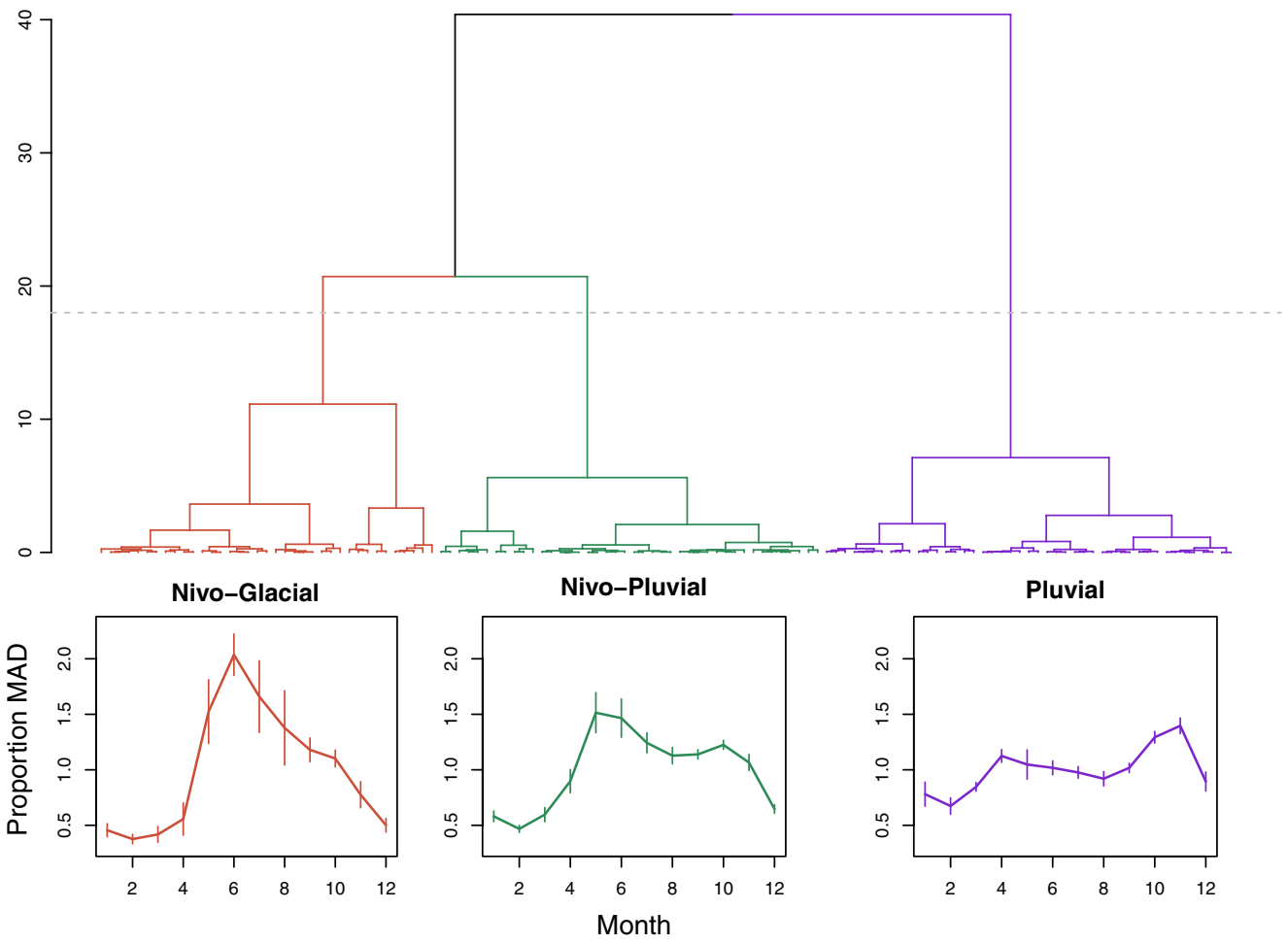

Figure 2. Dendrogram of the study reaches based on flexible beta-clustering of the first two weighted principal components (explaining 92% of variation) of the MAD-normalised monthly hydrography (expressed as the proportion of mean annual discharge). Lower panels show the mean across sites (±SD) of MAD-normalised hydrographs for each identified streamflow regime. MAD, mean annual discharge.

model emerged from the consistent response of taxon richness to the IHA flow metrics across observed and simulated flow data, with qualitatively similar patterns for 25 out of 30 flow metrics (Figure S4).

The calibrated model was subsequently used to simulate flow time series for the period 1991–2013 in the 100 reference locations for which biological data were available, and to perform the flow regime classification. Three hydrologic classes with distinct flow regimes were identified by the flexible beta-clustering of the first two weighted PC scores (explaining 92% of the variation) derived from the scaled monthly hydrographs (Figure 2). The first hierarchical division separated typically "pluvial" streams ($n = 38$), with peak flow in autumn, from those with spring and summer peaks. The second division further distinguished streams with "nivo-glacial" regime ($n = 30$) with summer peak flows and winter low flows, from intermediate "nivo-pluvial" streams ($n = 32$), with earlier spring peak flows and relatively higher autumn flows. A PERMANOVA based on Euclidean distances further validated the separation among the three groups with $R^2 = 0.85$. Figure 1 shows the distribution of the flow regime classes in the Adige River network. The three flow regimes were distributed along an altitudinal gradient, which reflects also the gradient of anthropogenic influence in the catchment (Figure 3). Indeed, pluvial streams at lower altitudes were characterized by more eutrophic (higher LIMeco scores) waters and a higher proportion of agricultural land-use in the adjacent area.

The three hydrologic classes identified in the previous step formed three groups in the first PCA factorial plane (i.e., the first two PCs) derived from IHA metrics, explaining about 80% of the total variation

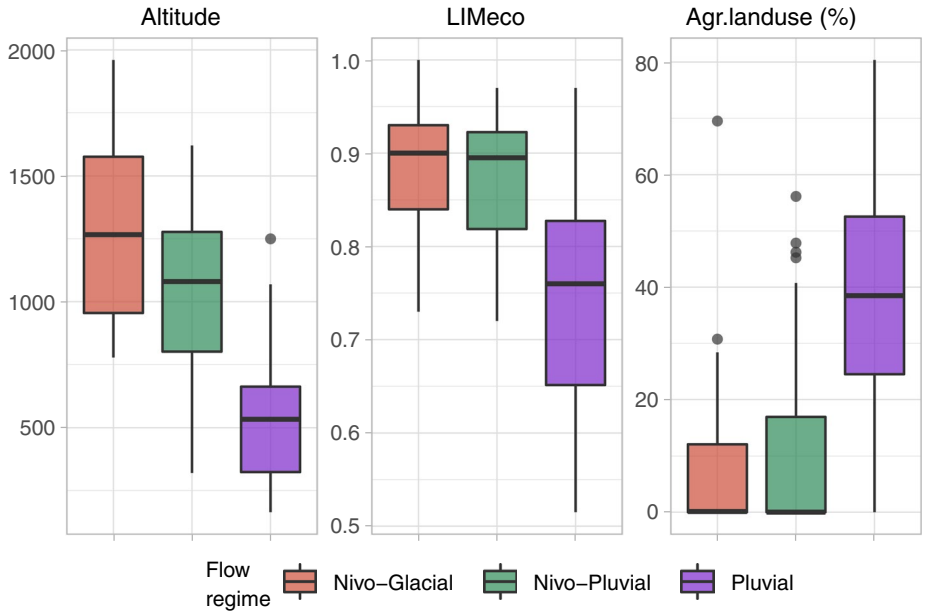

Figure 3. Boxplot of selected environmental descriptors for each identified streamflow regime. The following boxplot representation is adopted: horizontal line for median; a box for the inter-quartile range; whiskers for 1.5 times the inter-quartile range; dots for outliers. The LIMeco index and the percentage of local agricultural land-use (Agr.landuse) were included as covariates in the SSN models. SSN, spatial stream-network models.

(Figure 4). This analysis provided additional evidence of the separation among the flow regimes and allowed identifying the metrics that differed the most among them. For instance, as also evident from the annual hydrographs shown in Figure 2, nivo-glacial streams displayed higher flow maxima during summer months (June, July; Figures 4 and S5) as well as faster fall and rise rates. Conversely, streams with pluvial regimes showed higher flow minima (e.g., 30 Day Min) and Base index, but more frequent low flow events (Figure S5). Nivo-pluvial streams systematically showed flow metrics that were intermediate between the nivo-glacial and pluvial regimes.

The first two PCA axes extracted separately within each flow regime accounted for 75%, 81%, and 76% of variation in IHA metrics across the nivo-glacial, nivo-pluvial and pluvial regime, respectively. The loadings of the IHA metrics on the PC axes are shown in Table S1, and were used for a parsimonious selection of non-redundant flow metrics to include in the SSN models. After removing correlated metrics, the selection included: February and July streamflow, low pulse number, fall rate, and annual CV (y.CV). These metrics represent the magnitude, frequency, and rate of change of streamflow according to the IHA classification, respectively (Tab. 1). However, February and July flow magnitude were strongly correlated with minimum and maximum flows as well as with the Base index, and thus represented a proxy for the Magnitude and Duration of extreme flow conditions in the IHA classification.

3.2. Flow-ecology Relationship

A total of 64 invertebrate taxa were identified, mostly at the family and genus level (see Table S3). The SSN models identified several significant relationships between biotic and hydrologic metrics and the covariates related to water quality and land-use (Figure 5; Table S4). The relations differed among the flow regimes both in terms of explained variance and selected covariates. Overall, the influence of water quality (LIMeco index) and land-use on macroinvertebrate communities was consistent among flow regimes, with a positive effect of LIMeco and a negative effect of local agricultural land-use.

Conversely, few response variables responded consistently to the hydrological metrics across flow regimes, and rather, flow-ecology relationships often displayed divergent patterns (Figure 6). For instance, while the magnitude of February flows appeared important for most biotic metrics, the strength and pattern of

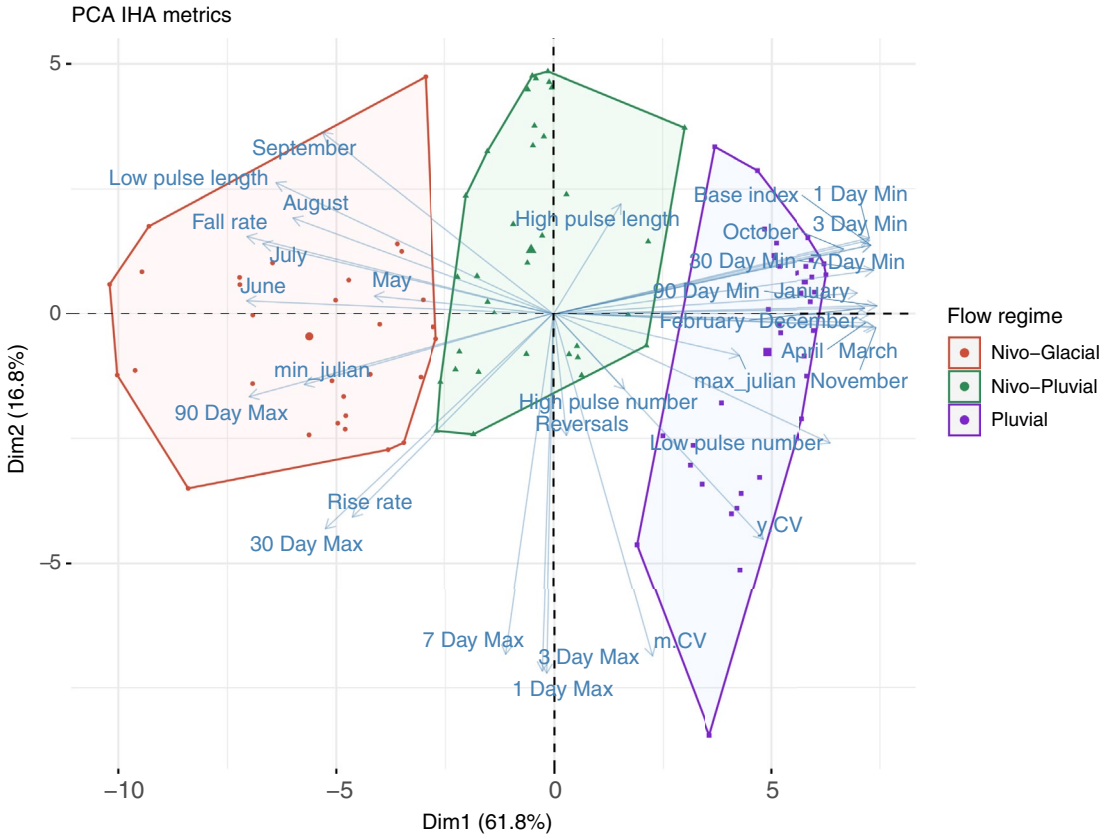

Figure 4. Biplot of the PCA based on 34 IHA flow metrics (direction and loading indicated by the blue arrows) derived from the 23 years streamflow series for the 100 investigated study sites. The sites are grouped according to the streamflow regime previously determined by the flexible beta-clustering approach. IHA, indicator of hydrologic alternations; PCA, principal component analysis.

responses varied. Taxon richness declined significantly with February flow magnitude in pluvial streams, but it tended to increase in the nivo-glacial streams, where instead it declined significantly with increasing July flow. Similarly, while Shannon diversity increased with the LIMeco index consistently across flow regimes, it showed a positive association with the number of low pulses, but only in the pluvial streams. Trait-based metrics also displayed rather unique patterns for each flow regime. The proportion of grazers displayed different relations with February flows across the three regimes. In addition, grazers increased significantly with annual flow variation (y.CV) only in nivo-glacial streams, while the proportion of filter feeders declined with increasing February flow, but only in the pluvial streams (Figure 6).

Overall, spatial autocorrelation, considering the flow-connected, flow-unconnected and Euclidean dimensions (i.e. z_{TU}, z_{TD}, z_{EU} in Equation 1), explained a larger proportion of variance (respectively 50%, 77%, and 44% in the nivo-glacial, nivo-pluvial and pluvial streams) than the model predictors ($X\beta$ in Equation 1), which explained 13%–26% of the variance (Figure 7). The tail-up and tail-down components (reflecting autocorrelation along the watercourse dimension) explained more residual variance (mean across flow regime: 35.3%) than the Euclidean spatial component (mean: 21.5%).

4. Discussion

In this study, we developed and applied a framework to assess the relationship between river ecology and flow characteristics while overcoming some of the challenges typically associated with flow-ecology research. By employing the HYPERSstreamHS hydrological model, we were able to reproduce natural streamflow time series at 100 ungauged biological sampling stations throughout the Adige River basin. Remarkably, the average value and range of variation of NSE efficiency did not deteriorate from calibration to validation sites, suggesting that the model parameters are representative of the entire river basin. An important val-

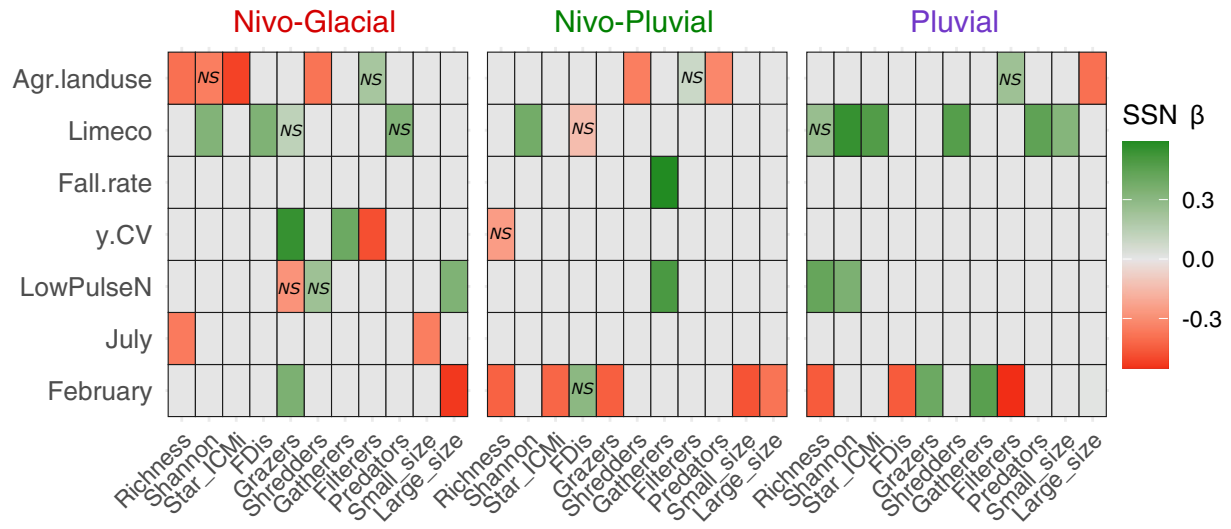

Figure 5. Heatmap showing the standardized SSN coefficients (β) of the covariates included in the most supported models for each biotic metric in the three flow regimes, according to the RMSPE. "*NS*" indicates a non-significant predictor ($p > 0.05$). RMSPE, root mean squared prediction error; SSN, spatial stream-network models.

idation of the model also stems from the consistent relationship between taxon richness and flow metrics obtained from the observed and simulated streamflow. This is key when hydrological models are used to investigate ecological responses (Kiesel et al., 2020), as the uncertainty associated with modeled streamflow is a fundamental limitation hampering the study of the flow-ecology relationship at the pan-European scale (Vigiak et al., 2018). We subsequently identified three distinct flow regime classes within which flow-ecology relationships were examined using spatially explicit geostatistical approaches. This allowed us to account for the natural variability of flow regimes, while also controlling for the spatial autocorrelation patterns of dendritic river networks.

The three identified flow regimes represent typical hydrologic patterns of the Alpine region. Low-order streams at higher elevation are fed primarily by glacial melt, snowmelt, and associated groundwater flow; streams at intermediate elevations by snowmelt and rain, and those at lower elevation mirror rainfall timing. While realistically representing a gradient of conditions, the three regimes were distinct enough to form separate groups according to both mean annual flow series and flow metrics. As such, they showed distinct flow-ecology relationships, especially dependent on high and low streamflow conditions and interannual variability in discharge. The three flow regimes were also separated along a gradient of anthropogenic influence represented by water quality and riparian land-use. This further highlights how classifying regimes can help minimize the effect of confounding factors in flow-ecology research: as streams with different flow regimes often occupy separate sections of the catchment, systematic differences in elevation, anthropogenic land-use, and underlying geology may confound the influence of streamflow characteristics, hindering the robust identification of flow-ecology relationships.

The distinct responses to flow metrics among the stream types indeed represent a key finding of the present work; had we combined all streams in the same analysis, we would have drawn different conclusions regarding the response of some biotic metrics, such as taxon richness and the proportion of grazers (*cfr* gray dashed line with individual fits in Figure 6). The few studies that have compared flow-ecology relations across classified flow regimes (e.g., Bruckerhoff et al., 2019; Mims & Olden, 2012), also showed that ecological responses can often diverge. Yet, while the classification of flow regimes is a common endeavor in hydrologic research (e.g., Belmar et al., 2011; Di Prinzio et al., 2011; McManamay et al., 2012; Snelder & Booker, 2013), its applications in flow-ecology studies remain surprisingly rare.

Besides the range of anthropogenic influence, the three streamflow types analyzed here are characterized by different levels of environmental severity, which declines with decreasing glacial influence (Brighenti et al., 2021). This could explain some of the specific flow-ecology patterns. Richness, for instance, de-

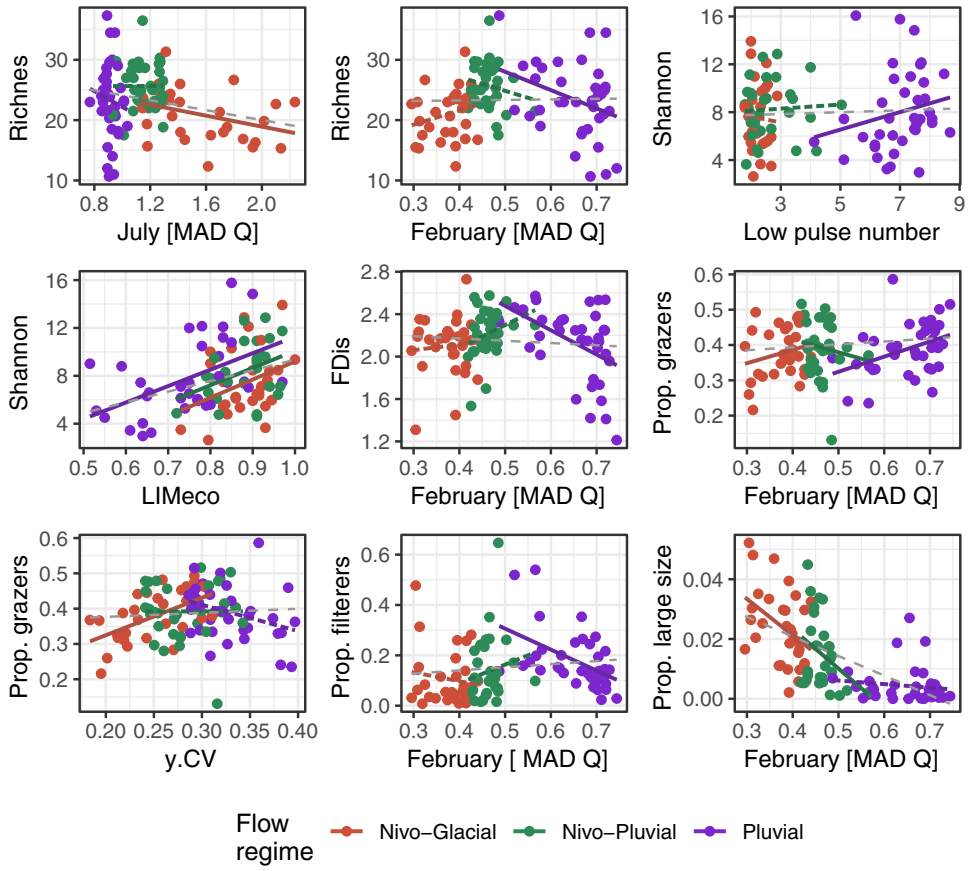

Figure 6. Scatterplot of selected flow-ecology relationships within each flow regime. Solid and dashed fit lines, respectively, indicate significant and non-significant relationships according to the SSN models. Gray dashed line indicates the overall relationship observed combining all three flow regimes. SSN, spatial stream-network models.

clined with increasing July flows in the nivo-glacial streams (representing the summer peak of snow- and glacial-melt), while in the pluvial regime, richness declined with increasing February flows (representing the winter low rainfall periods). Summer discharge is high in nivo-glacial streams, where increasing flows could cause higher drift rates and thus lower the observed benthic richness (e.g., Brittain & Eikeland, 1988). Conversely, in temperate streams characterized by pluvial regimes, minimum densities often occur in winter (Brittain & Eikeland, 1988; Naman et al., 2016), when higher-than-average flows could further decrease benthic richness. In the nivo-pluvial and pluvial streams, in fact, the magnitude of February flows appeared to limit the biotic metrics mainly related to community diversity (i.e., richness, Star_ICMi, Fdis). Overall, the magnitude of February discharge appeared to be the most influential flow metric, with mostly negative effects. On the other hand, the number of low flow pulses displayed a mainly positive association with both diversity and trait-based metrics across flow regimes. Low flow pulses can increase local diversity by preventing excessive drift while also favoring the deposition of fine organic matter, as suggested by the positive response of gatherers. Together with the positive association of both grazers and gatherers with the annual coefficient of variation in nivo-glacial streams, these results indicate how natural flow variation is fundamental for sustaining aquatic biodiversity.

The SSN models revealed how the STAR_ICMi index mostly responded to streams' physico-chemical parameters and riparian land-use. In agreement with recent investigations (Larsen et al., 2019; Quadroni et al., 2017), these results provide additional evidence of the limited sensitivity of WFD biological quality indicators, such as the Star_ICMi index, to stream hydrologic conditions. Like most present bioindicators (Friberg, 2014), the Star_ICMi is designed to reflect organic pollution and habitat degradation and should be used for hydrologic assessment or guide *e-flows* with great caution. Indeed, one of the aims of the present study was to evaluate alternative metrics that could serve as flow-sensitive indicators to be included in as-

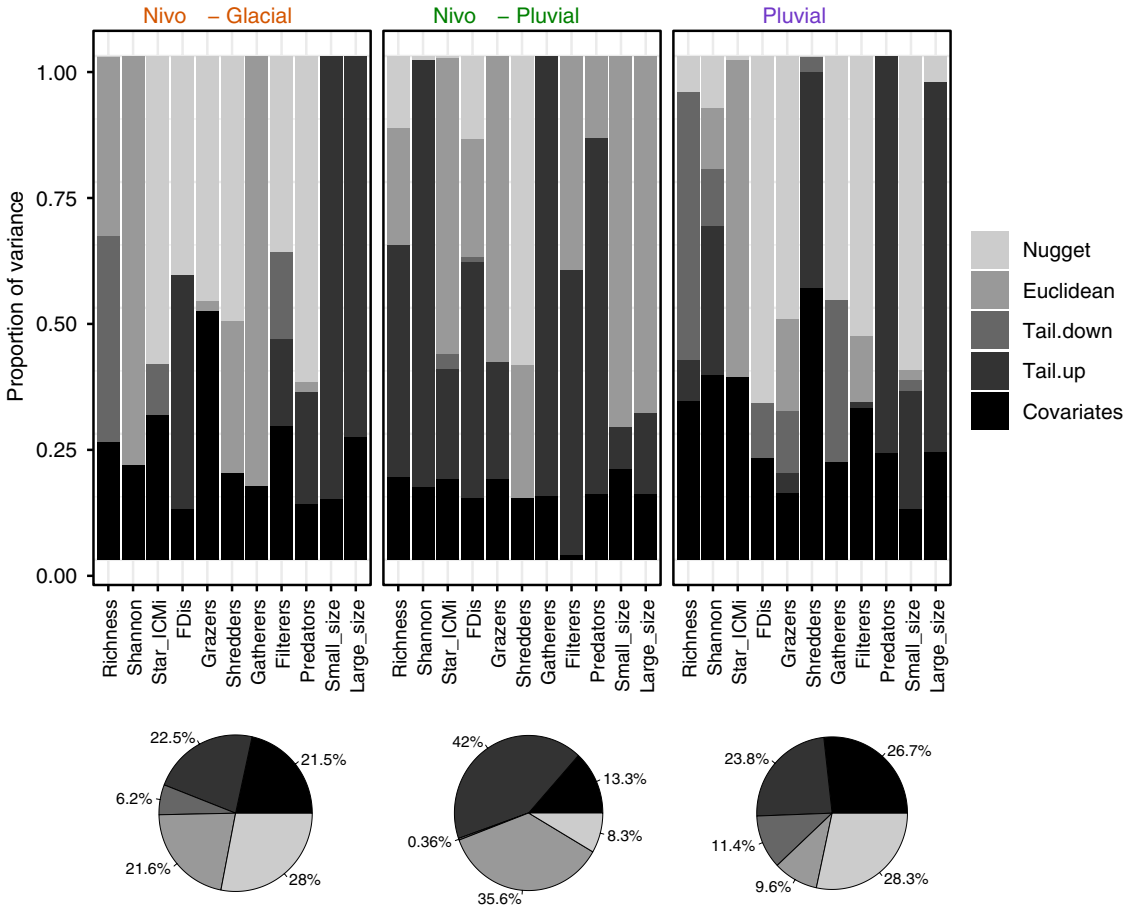

Figure 7. Proportion of variance of each biotic metric explained by the covariates (i.e. flow metrics, water quality, and local land-use) and by the spatial components modeled with tail-up, tail-down and Euclidean autocovariance functions across the three flow regimes. The nugget represents the residual variance.

sessment schemes like the one of the European WFD. To this end, species life-history traits can provide the mechanistic link between river biota and flow conditions that could be valid across large spatial scales (Heino et al., 2013; Mims & Olden, 2012). In the Adige River basin, the relative proportion of different feeding habits and body size structure appeared relatively sensitive to hydrologic conditions across flow regimes and thus deserve further investigation. The sensitivity of grazers to flow conditions, for example, can derive from their reliance on attached algae, which can be scoured during high flows or buried by fines during low flows (Buchanan et al., 2013; Doretto et al., 2020; Kennen et al., 2010). Nonetheless, our results suggest that their response to flow conditions can differ substantially across flow regimes. The response of body size structure to the magnitude of high and low flows may reflect the sensitivity of different developmental stages to shear stress, especially for insect larvae (e.g., Merigoux & Doledec, 2004), but detailed information on body size was not available for many taxa, and this response requires further examination.

While the SSN modeling revealed idiosyncratic responses of the biotic metrics to flow conditions, the effect of water quality (LIMeco) and the extent of local agricultural land-use appeared generally consistent with a positive and negative effect, respectively. This has both practical and fundamental implications. From an applied perspective, it implies that ecological responses to flow alterations can be contingent on local eco-hydrologic conditions, a caveat that must be considered when setting regional flow standards. In the Adige Basin, for instance, sustaining invertebrate richness, or specific feeding groups would require distinct management of high and low flows among the identified flow regimes. On a more fundamental level, it indicates that the often-observed nonlinear flow-ecology relationships (Rosenfeld, 2017) can reflect the distinct response of multiple flow regimes in the basin. More generally, the "shape" of flow-ecology relation-

ships is likely to be scale-dependent and determined by the range of hydrologic conditions in the region and the size of the species pool included.

The three identified flow regimes formed geographically separated clusters along a north-south axis, reflecting the orography of the basin. While this further validated our flow regime classification, it also introduced possible autocorrelation issues. The SSN models revealed that most variation in macroinvertebrate metrics was in fact associated with spatial patterns. This is typical for communities dwelling in complex habitats, such as river networks, whose geometry and flow directionality influence environmental and eco-evolutionary dynamics (Frieden et al., 2014; Isaak et al., 2014; Larsen et al., 2019). For some biotic metrics, the spatial autocorrelation was by far the most important component, explaining more than 80% of the variation (e.g., Shannon diversity and gatherers in both nivo-glacial and nivo-pluvial streams). Not surprisingly, given the dendritic configuration of river networks and the directionality of water flow, autocorrelation along the watercourse dimension (i.e., tail-up and tail-down) appeared stronger than over the isometric Euclidean dimension. However, the influence of autocorrelation differed across regimes, being particularly large in the nivo-pluvial streams, where the tail-up flow-connected component accounted for more than 40% of the residual variance. This could be due to the distribution of multiple sampling sites along the same river segments, as occurred in the eastern section of the basin. However, the Euclidean component, which reflects large scale variability across the basin, also accounted for more than 35% of the variance in nivo-pluvial streams. This may be due to the fact that streams with nivo-pluvial regimes were relatively more widely distributed throughout the basin. These findings are in line with a recent study from the US where SSN models were used to examine variation in fish community traits (Bruckerhoff et al., 2019). However, comparison across studies is challenging as the effects of spatial autocorrelation in a given model depend on the response variable and the covariates included, as well as on the spatial relationship of samples. Therefore, spatial effects may vary substantially across regions, but they are likely relevant for flow-ecology studies when these are paralleled with flow regime classification in which sites might be spatially structured (e.g., Bruckerhoff et al., 2019; Snelder & Booker, 2013). Ignoring such spatial dependency could lead to increased Type I error rates ("false positive"; Legendre & Legendre, 2012), with important implications for the success of *e-flows* design.

An additional issue to consider is that, although we selected streams with no evident alteration of flow regime, the influence of other factors on stream invertebrates was evident. The negative effect of agricultural land-use on multiple biotic metrics was evident (e.g., richness, Star_ICMi), especially in the nivo-glacial and nivo-pluvial streams, while water quality had the strongest (positive) influence on the lower gradient pluvial streams (e.g., increasing diversity, shredders, predators). These results are not surprising and in line with a recent study that included a larger sample of locations throughout the basin (Larsen et al., 2019). However, this highlights how defining a baseline flow-ecology relationship under natural conditions might become increasingly difficult as river catchments are modified globally (Tickner et al., 2020). In addition, alteration of flow regimes is often accompanied by changes in water temperature and in-stream habitat structure (e.g., Zolezzi et al., 2009). Therefore, non-hydrologic factors must be incorporated in *e-flow* frameworks to identify circumstances that might limit the desired outcome of flow management (Poff, 2018).

At the management level of *e-flows* setting, the present work represents the first data-driven classification of natural flow regimes in Italy that is paralleled by an ecological assessment. Previous catchment regionalization schemes were produced at the national scale (Di Prinzio et al., 2011), but they focused primarily on estimating streamflow at ungauged sites. Results demonstrated that flow-ecology relationships can substantially vary among flow regimes, highlighting the importance of developing *e-flows* tailored to specific eco-hydrologic contexts. Moreover, although analyses were conducted within a single river basin, and thus minimized the influence of larger-scale confounding factors, spatial patterns accounted for most of the variance in the data. The importance of using spatially explicit approaches to model empirical data in river networks is increasingly recognized (Frieden et al., 2014; Isaak et al., 2017; Larsen et al., 2019), and our results further support their application in flow-ecology research (Bruckerhoff et al., 2019).

In conclusion, we addressed three main challenges of flow-ecology research derived from (i) the limited availability of streamflow time series at sampling sites, (ii) the natural variability of flow regimes, and (iii) the spatial autocorrelation unique to dendritic river networks. In doing so we also completed the first two steps of the ELOHA framework (Poff et al., 2010), namely developing the hydrological foundation and clas-

sifying natural flow regimes across the catchment; to our knowledge, it is the first time that this is applied to a very heterogeneous Alpine river catchment.

Future developments should address the challenge of incorporating hydrologic variability when setting environmental flows, and of assessing the ecological effects of specific flow events or sequence of events without relying on stationary long-term flow records as baseline reference (Horne et al., 2019; Poff, 2018). The framework presented in this paper could thus be extended to include future climate scenarios to feed the hydrologic model. Simulated projections of streamflow could then be used to estimate future ecological responses to flow alteration.

Data Availability Statement

Data supporting this research are archived in the Dryad and are publicly available at: https://doi.org/10.5061/dryad.vdncjsxt1.

Acknowledgments
This project has received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie Grant Agreement No. 748969, awarded to SL. Further financial support was received by the Italian Ministry of Education, University and Research (MIUR) under the Departments of Excellence, grant L.232/2016, and by the Energy oriented Center of Excellence (EoCoE-II), GA number 824158, funded within the Horizon 2020 framework of the European Union. Bruno Majone also acknowledges support by the project "Seasonal Hydrological-Econometric forecasting for hydropower optimization (SHE)" funded within the Call for projects "Research Südtirol/Alto Adige" 2019 Autonomous Province of Bozen/Bolzano – South Tyrol. Streamflow data were provided by the Hydrographic Office of the Autonomous Province of Bolzano (www.provincia.bz.it/hydro) and by the Service for Hydraulic Works of the Autonomous Province of Trento (www.floods.it). We are grateful to Jay Ver Hoef for advice on the SSN models. Comments from three anonymous reviewers greatly improved the quality of the manuscript.

References

Anderson, M. J. (2017). Permutational multivariate analysis of variance (PERMANOVA). In *Wiley StatsRef: Statistics reference online* (pp. 1–15). American Cancer Society. https://doi.org/10.1002/9781118445112.stat07841

Arthington, A. H., Bhaduri, A., Bunn, S. E., Jackson, S. E., Tharme, R. E., Tickner, D., et al. (2018). The Brisbane Declaration and global action agenda on environmental flows. *Frontiers in Environmental Science*, *6*. https://doi.org/10.3389/fenvs.2018.00045

Avesani, D., Galletti, A., Piccolroaz, S., Bellin, A., & Majone, B. (2021). A dual-layer MPI continuous large-scale hydrological model including human systems. *Environmental Modelling & Software*. *139*, https://doi.org/10.1016/j.envsoft.2021.105003

Azzellino, A., Canobbio, S., Çervigen, S., Marchesi, V., & Piana, A. (2015). Disentangling the multiple stressors acting on stream ecosystems to support restoration priorities. *Water Science and Technology*, *72*(2), 293. https://doi.org/10.2166/wst.2015.177

Bellin, A., Majone, B., Cainelli, O., Alberici, D., & Villa, F. (2016). A continuous coupled hydrological and water resources management model. *Environmental Modelling & Software*, *75*, 176–192. https://doi.org/10.1016/j.envsoft.2015.10.013

Belmar, Velasco, J., & Martinez-Capel, F. (2011). Hydrological classification of natural flow regimes to support environmental flow assessments in intensively regulated Mediterranean rivers, Segura River Basin (Spain). *Environmental Management*, *47*(5), 992. https://doi.org/10.1007/s00267-011-9661-0

Beven, K. (2012). *Rainfall-runoff modeling: The primer*. Wiley-Blackwell.

Booker, D. J., Snelder, T. H., Greenwood, M. J., & Crow, S. K. (2015). Relationships between invertebrate communities and both hydrological regime and other environmental factors across New Zealand's rivers. *Ecohydrology*, *8*(1), 13–32. https://doi.org/10.1002/eco.1481ù

Brighenti, S., Tolotti, M., Bertoldi, W., Wharton, G., & Bruno, M. C. (2021). Rock glaciers and paraglacial features influence stream invertebrates in a deglaciating Alpine area. *Freshwater Biology*, *66*, 535–548. https://doi.org/10.1111/fwb.13658

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift — A review. *Hydrobiologia*, *166*(1), 77–93. https://doi.org/10.1007/BF00017485

Bruckerhoff, L. A., Leasure, D. R., & Magoulick, D. D. (2019). Flow–ecology relationships are spatially structured and differ among flow regimes. *Journal of Applied Ecology*, *56*(2), 398–412. https://doi.org/10.1111/1365-2664.13297

Buchanan, C., Moltz, H. L. N., Haywood, H. C., Palmer, J. B., & Griggs, A. N. (2013). A test of The Ecological Limits of Hydrologic Alteration (ELOHA) method for determining environmental flows in the Potomac River basin. *U.S.A. Freshwater Biology*, *58*(12), 2632–2647. https://doi.org/10.1111/fwb.12240

Buffagni, A., & Erba, S. (2007). Macroinvertebrati acquatici e direttiva 200/60/EC (WFD). *Notiziario Dei Metodi Analitici*, *1*, 94–100.

Buffagni, A., Erba, S., Cazzola, M., Murray-Bligh, J., Soszka, H., & Genoni, P. (2006). The STAR common metrics approach to the WFD intercalibration process: Full application for small, lowland rivers in three European countries. *Hydrobiologia*, *566*(1), 379. https://doi.org/10.1007/s10750-006-0082-7

Carrara, F., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences*, *109*(15), 5761–5766. https://doi.org/10.1073/pnas.1119651109

Chiogna, G., Majone, B., Cano Paoli, K., Diamantini, E., Stella, E., Mallucci, S., et al. (2016). A review of hydrological and chemical stressors in the Adige catchment and its ecological status. *The Science of the Total Environment*, *540*, 429–443. https://doi.org/10.1016/j.scitotenv.2015.06.149

Couto, T. B., & Olden, J. D. (2018). Global proliferation of small hydropower plants – science and policy. *Frontiers in Ecology and the Environment*, *16*(2), 91–100. https://doi.org/10.1002/fee.1746

De Pauw, N., Gabriels, W., & Goethals, P. L. M. (2006). River monitoring and assessment methods based on macroinvertebrates. In *Biological monitoring of rivers* (pp. 111–134). Wiley-Blackwell. https://doi.org/10.1002/0470863781.ch7

Diamantini, E., Lutz, S. R., Mallucci, S., Majone, B., Merz, R., & Bellin, A. (2018). Driver detection of water quality trends in three large European river basins. *The Science of the Total Environment*, *612*, 49–62. https://doi.org/10.1016/j.scitotenv.2017.08.172

Di Prinzio, M., Castellarin, A., & Toth, E. (2011). Data-driven catchment classification: Application to the pub problem. *Hydrology and Earth System Sciences*, *15*(6), 1921–1935. https://doi.org/10.5194/hess-15-1921-2011

Doretto, A., Bona, F., Falasco, E., Morandini, D., Piano, E., & Fenoglio, S. (2020). Stay with the flow: How macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought. *River Research and Applications*, *36*(1), 91–101. https://doi.org/10.1002/rra.3563

European Commission. (2000). *Directive 2000/60/EC of 20 December 2000 of the European Union and of the Council establishing a framework for community action in the field of water policy*. Official Journal of the European Communities.

Friberg, N. (2014). Impacts and indicators of change in lotic ecosystems. *Wiley Interdisciplinary Reviews: Water*, *1*(6), 513–531. https://doi.org/10.1002/wat2.1040

Frieden, J. C., Peterson, E. E., Angus Webb, J., & Negus, P. M. (2014). Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. *Environmental Modelling & Software*, *60*, 320–330. https://doi.org/10.1016/j.envsoft.2014.06.019

Garreta, V., Monestiez, P., & Ver Hoef, J. M. (2009). Spatial modeling and prediction on river networks: Up model, down model or hybrid? *Environmetrics*, *21*, 439–456. https://doi.org/10.1002/env.995

Goovaerts, P. (1997). *Geostatistics for natural resources evaluation*. Oxford University Press. https://link.springer.com/article/10.1023%2FA%3A1007530422454

Green, P. A., Vörösmarty, C. J., Harrison, I., Farrell, T., Sáenz, L., & Fekete, B. M. (2015). Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change*, *34*, 108–118. https://doi.org/10.1016/j.gloenvcha.2015.06.007

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., et al. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*(7755), 215–221. https://doi.org/10.1038/s41586-019-1111-9

Heino, J., Schmera, D., & Erős, T. (2013). A macroecological perspective of trait patterns in stream communities. *Freshwater Biology*, *58*(8), 1539–1555. https://doi.org/10.1111/fwb.12164

Heisterman, M., & Kneis, D. (2011). Benchmarking quantitative precipitation estimation by conceptual rainfall-runoff modeling. *Water Resources Research*, *47*(6). https://doi.org/10.1029/2010WR009153

Hering, D., Moog, O., Sandin, L., & Verdonschot, P. F. M. (2004). Overview and application of the AQEM assessment system. *Hydrobiologia*, *516*(1–3), 1–20. https://doi.org/10.1023/B:HYDR.0000025255.70009.a5

Horne, A. C., Nathan, R., Poff, N. L., Bond, N. R., Webb, J. A., Wang, J., & John, A. (2019). Modeling Flow-Ecology Responses in the Anthropocene: Challenges for Sustainable Riverine Management. *BioScience*, *69*(10), 789–799. https://doi.org/10.1093/biosci/biz087

Isaak, D. J., Peterson, E. E., Ver Hoef, J. M., Wenger, S. J., Falke, J. A., Torgersen, C. E., et al. (2014). Applications of spatial statistical network models to stream data: Spatial statistical network models for stream data. *Wiley Interdisciplinary Reviews: Water*, *1*(3), 277–294. https://doi.org/10.1002/wat2.1023

Isaak, D. J., Ver Hoef, J. M., Peterson, E. E., Horan, D. L., & Nagel, D. E. (2017). Scalable population estimates using spatial-stream-network (SSN) models, fish density surveys, and national geospatial database frameworks for streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(2), 147–156. https://doi.org/10.1139/cjfas-2016-0247

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kennedy, J., & Eberhart, R. (1995). Particle swarm optimization. In *Proceedings of ICNN'95*.

Kennedy, T. A., Muehlbauer, J. D., Yackulic, C. B., Lytle, D. A., Miller, S. W., Dibble, K. L., et al. (2016). Flow management for hydropower extirpates aquatic insects, undermining river food webs. *BioScience*, *66*, 561–575. https://doi.org/10.1093/biosci/biw059

Kennen, J. G., Riva-Murray, K., & Beaulieu, K. M. (2010). Determining hydrologic factors that influence stream macroinvertebrate assemblages in the northeastern US. *Ecohydrology*, *3*(1), 88–106. https://doi.org/10.1002/eco.99

Kiesel, J., Kakouei, K., Guse, B., Fohrer, N., & Jähnig, S. C. (2020). When is a hydrological model sufficiently calibrated to depict flow preferences of riverine species? *Ecohydrology*, *13*(3), e2193. https://doi.org/10.1002/eco.2193

Laiti, L., Mallucci, S., Piccolroaz, S., Bellin, A., Zardi, D., Fiori, A., et al. (2018). Testing the hydrological coherence of high-resolution gridded precipitation and temperature data sets. *Water Resources Research*, *54*(3), 1999–2016. https://doi.org/10.1002/2017WR021633

Larsen, S., Bruno, M. C., Vaughan, I. P., & Zolezzi, G. (2019a). Testing the River Continuum Concept with geostatistical stream-network models. *Ecological Complexity*, *39*, 100773. https://doi.org/10.1016/j.ecocom.2019.100773

Larsen, S., Bruno, M. C., & Zolezzi, G. (2019b). WFD ecological status indicator shows poor correlation with flow parameters in a large Alpine catchment. *Ecological Indicators*, *98*, 704–711. https://doi.org/10.1016/j.ecolind.2018.11.047

Legendre, P., & Legendre, L. (2012). Numerical Ecology (3rd ed., Vol. 24). Elsevier. Retrieved from https://www.elsevier.com/books/numerical-ecology/legendre/978-0-444-53868-0

Lutz, S. R., Mallucci, S., Diamantini, E., Majone, B., Bellin, A., & Merz, R. (2016). Hydroclimatic and water quality trends across three Mediterranean river basins. *The Science of the Total Environment*, *571*, 1392–1406. https://doi.org/10.1016/j.scitotenv.2016.07.102

Majone, B., Bertagnoli, A., & Bellin, A. (2010). A non-linear runoff generation model in small Alpine catchments. *Journal of Hydrology*, *385*(1), 300–312. https://doi.org/10.1016/j.jhydrol.2010.02.033

Majone, B., Villa, F., Deidda, R., & Bellin, A. (2016). Impact of climate change and water use policies on hydropower potential in the south-eastern Alpine region. *The Science of the Total Environment*, *543*, 965–980. https://doi.org/10.1016/j.scitotenv.2015.05.009

Mallucci, S., Majone, B., & Bellin, A. (2019). Detection and attribution of hydrological changes in a large Alpine river basin. *Journal of Hydrology*, *575*, 1214–1229. https://doi.org/10.1016/j.jhydrol.2019.06.020

Mazor, R. D., May, J. T., Sengupta, A., McCune, K. S., Bledsoe, B. P., & Stein, E. D. (2018). Tools for managing hydrologic alteration on a regional scale: Setting targets to protect stream health. *Freshwater Biology*. https://doi.org/10.1111/fwb.13062

McGuire, K. J., Torgersen, C. E., Likens, G. E., Buso, D. C., Lowe, W. H., & Bailey, S. W. (2014). Network analysis reveals multiscale controls on streamwater chemistry. *Proceedings of the National Academy of Sciences*, *111*(19), 7030–7035. https://doi.org/10.1073/pnas.1404820111

McManamay, R. A., Orth, D. J., Dolloff, C. A., & Frimpong, E. A. (2012). A Regionla classification of unregulated stream flows: Spatial resolution and hierarchical frameworks. *River Research and Applications*, *28*, 1019–1033.

Merigoux, S., & Doledec, S. (2004). Hydraulic requirements of stream communities: A case study on invertebrates. *Freshwater Biology*, *49*(5), 600–613. https://doi.org/10.1111/j.1365-2427.2004.01214.x

Michel, C., Andréassian, V., & Perrin, C. (2005). Soil Conservation Service Curve Number method: How to mend a wrong soil moisture accounting procedure? *Water Resources Research*, *41*(2). https://doi.org/10.1029/2004WR003191

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*(1), 35–45. https://doi.org/10.1890/11-0370.1

Moriasi, D. N., Arnold, J. G., Van Liew, M. W., Bingner, R. L., Harmel, R. D., & Veith, T. L. (2007). Model Evaluation Guidelines for Systematic Quantification of Accuracy in Watershed Simulations Transactions of the ASABE (Vol. 50 pp. 885–900). American Society of Agricultural and Biological Engineers, 3. https://doi.org/10.13031/2013.23153

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1292–1305. https://doi.org/10.1139/cjfas-2015-0363

Nash, J. E., & Sutcliffe, J. V. (1970). River flow forecasting through conceptual model. Part 1—A discussion of principles. *Journal of Hydrology*, *10*, 282–290. http://dx.doi.org/10.1016/0022-1694(70)90255-6

Navarro-Ortega, A., Acuña, V., Bellin, A., Burek, P., Cassiani, G., Choukr-Allah, R., et al. (2015). Managing the effects of multiple stressors on aquatic ecosystems under water scarcity: The GLOBAQUA project. *The Science of the Total Environment*, *503–504*, 3–9. https://doi.org/10.1016/j.scitotenv.2014.06.081

Patrick, C. J., & Yuan, L. L. (2017). Modeled hydrologic metrics show links between hydrology and the functional composition of stream assemblages. *Ecological Applications*, *27*(5), 1605–1617. https://doi.org/10.1002/eap.1554

Peterson, E. E., & Hoef, J. M. V. (2014). STARS: An ArcGIS Toolset used to calculate the spatial information needed to fit spatial statistical models to stream network data. *Journal of Statistical Software*, *56*(2). https://doi.org/10.18637/jss.v056.i02

Peterson, E. E., Ver Hoef, J. M., Isaak, D. J., Falke, J. A., Fortin, M.-J., Jordan, C. E., et al. (2013). Modeling dendritic ecological networks in space: An integrated network perspective. *Ecology Letters*, *16*(5), 707–719. https://doi.org/10.1111/ele.12084

Piccolroaz, S., Lazzaro, M. D., Zarlenga, A., Majone, B., Bellin, A., & Fiori, A. (2016). HYPERstream: A multi-scale framework for stream-flow routing in large-scale hydrological model. *Hydrology and Earth System Sciences*, *20*(5), 2047–2061. https://doi.org/10.5194/hess-20-2047-2016

Poff, N. L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biology*, *63*(8), 1011–1021. https://doi.org/10.1111/fwb.13038

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., et al. (1997). The natural flow regime. *BioScience*, *47*(11), 769–784. https://doi.org/10.2307/1313099

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: Traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*(4), 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., et al. (2010). The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards: Ecological limits of hydrologic alteration. *Freshwater Biology*, *55*(1), 147–170. https://doi.org/10.1111/j.1365-2427.2009.02204.x

Quadroni, S., Crosa, G., Gentili, G., & Espa, P. (2017). Response of stream benthic macroinvertebrates to current water management in Alpine catchments massively developed for hydropower. *The Science of the Total Environment*, *609*, 484–496. https://doi.org/10.1016/j.scitotenv.2017.07.099

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna.

Richter, B., Baumgartner, J., Wigington, R., & Braun, D. (1997). How much water does a river need? *Freshwater Biology*, *37*(1), 231–249. https://doi.org/10.1046/j.1365-2427.1997.00153.x

Rinaldo, A., Marani, A., & Rigon, R. (1991). Geomorphological dispersion. *Water Resources Research*, *27*(4), 513–525. https://doi.org/10.1029/90WR02501

Rosenfeld, J. S. (2017). Developing flow–ecology relationships: Implications of nonlinear biological responses for water management. *Freshwater Biology*, *62*(8), 1305–1324. https://doi.org/10.1111/fwb.12948

Schmidt-Kloiber, A., & Hering, D. (2015). *53*, 271–282. www.freshwaterecology.info – An online tool that unifies, standardizes and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2015.02.007

Shumilova, O., Tockner, K., Thieme, M., Koska, A., & Zarfl, C. (2018). Global water transfer megaprojects: A potential solution for the water-food-energy nexus? *Frontiers in Environmental Science*, *6*. https://doi.org/10.3389/fenvs.2018.00150

Skøien, J. O., Merz, R., & Blöschl, G. (2006). Top-kriging - geostatistics on stream networks. *Hydrology and Earth System Sciences*, *10*(2), 277–287. https://doi.org/10.5194/hess-10-277-2006

Snelder, T. H., & Booker, D. J. (2013). Natural flow regime classifications are sensitive to definition procedures. *River Research and Applications*, *29*(7), 822–838. https://doi.org/10.1002/rra.2581

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358. https://doi.org/10.1899/08-171.1

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., et al. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *BioScience*, *70*(4), 330–342. https://doi.org/10.1093/biosci/biaa002

Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., et al. (2019). Prepare river ecosystems for an uncertain future. *Nature*, *570*(7761), 301–303. https://doi.org/10.1038/d41586-019-01877-1

Ver Hoef, J. M., & Peterson, E. E. (2010). A moving average approach for spatial statistical models of stream networks. *Journal of the American Statistical Association*, *105*(489), 6–18. https://doi.org/10.1198/jasa.2009.ap08248

Ver Hoef, J. M., Peterson, E. E., Clifford, D., & Shah, R. (2014). SSN: An R package for spatial statistical modeling on stream networks. *Journal of Statistical Software*, *56*(3). https://doi.org/10.18637/jss.v056.i03

Vigiak, O., Lutz, S., Mentzafou, A., Chiogna, G., Tuo, Y., Majone, B., et al. (2018). Uncertainty of modeled flow regime for flow-ecological assessment in Southern Europe. *The Science of the Total Environment*, *615*, 1028–1047. https://doi.org/10.1016/j.scitotenv.2017.09.295

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, *92*(1), 3–10. https://doi.org/10.1890/10-0340.1

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*(1), 161–170. https://doi.org/10.1007/s00027-014-0377-0

Zimmerman, D. L., & Ver Hoef, J. M. (2017). The torgegram for fluvial variography: Characterizing spatial dependence on stream networks. *Journal of Computational & Graphical Statistics*, *26*(2), 253–264. https://doi.org/10.1080/10618600.2016.1247006

Zolezzi, G., Bellin, A., Bruno, M. C., Maiolini, B., & Siviglia, A. (2009). Assessing hydrological alterations at multiple temporal scales: Adige River, Italy. *Water Resources Research*, *45*(12). https://doi.org/10.1029/2008WR007266