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Nested analysis of macroinvertebrate diversity along a river continuum: Identifying relevant spatial scales for stream communities

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Abstract

Benthic macroinvertebrates are important for stream ecosystem function and are considerable food resources for vertebrate consumers such as fish. The diversity, composition, and distribution of stream macroinvertebrate taxa are affected by factors that act at different spatial scales, from microhabitat to watershed-level effects. While comparative studies of watershed-level and between stream influences on benthic diversity are common, the effects of scale are less investigated within individual river segments. Benthic macroinvertebrates were systematically sampled across nested spatial scales along a 2.2-km near-pristine stretch of the Upper Black River (MI, USA), and analyzed in relation to near-bed flow and substrate features. Responses of community diversity metrics to near-bed conditions were quantified, and diversity was modeled to determine the contribution of each spatial scale to total diversity. Near-bed conditions, especially Froude number and substrate size, were positively associated with macroinvertebrate diversity and abundance. Larger (e.g., 100 m stream reach) and finer scales (e.g., individual samples) accounted for a greater proportion of variation in taxon richness and abundance, respectively. Longitudinal variation in environmental conditions was an important driver of macroinvertebrate diversity, with replacement between sites (i.e., turnover) contributing a considerably greater proportion of variation in total diversity than nestedness. Results demonstrate that macroinvertebrate communities were shaped by both local flow and substrate conditions as well as taxa replacement over larger spatial scales. This emphasizes the importance of maintaining the hydro-morphological integrity along stream courses as a requisite condition to further watershed and fisheries conservation and management.

KEYWORDS
diversity, macroinvertebrates, near-bed conditions, nestedness, river continuum, spatial scale, turnover

1 | INTRODUCTION

Rivers are hierarchically structured systems (Durance, Lepichon, & Ormerod, 2006; Grant, Lowe, & Fagan, 2007) that exhibit differences in diversity, community composition, and ecological function across nested spatial scales (Frissell, Liss, Warren, & Hurley, 1986; Ward & Tockner, 2001). The relative scales can range from microhabitats of centimeters and meters, to stream reaches of tens to hundreds of meters, and watersheds encompassing tens to hundreds of kilometers (Altermatt, 2013; Blanchet, Legendre, Maranger, Monti, & Pepin, 2011; Tornwall, Sokol, Skelton, & Brown, 2015). Benthic macroinvertebrates are affected by in-stream conditions that themselves vary across different spatial scales (Batalla Salvarrey, Kotzian, Spies, & Braun, 2014; Heino et al., 2015). In addition to their direct effects on ecosystem function (e.g., nutrient cycling, decomposition), macroinvertebrates occupy similar niches as numerous fish and provide important food resources for resident and migratory fish populations (e.g., Wallace & Webster, 1996; Waraniak, Valentine, & Scribner, 2017).

Understanding the relative importance of physical factors that affect macroinvertebrates along the longitudinal continuum of rivers can guide watershed and fisheries management (Dovciak & Perry, 2002; Flinders, Horwitz, & Belton, 2008). However, identifying the appropriate scale at which such factors exert influence has been limited by challenges associated with logistical, financial and technical limitations. There is a need for studies that evaluate multi-scale changes in macroinvertebrate community metrics in relation to habitat variables. Information needs are especially important in rivers inhabited by threatened or endangered fish species that depend on macroinvertebrates as a food source or as an alternative prey resource for predators during vulnerable early life stages, such as the Upper Black River (MI, USA) which hosts an important population of Lake Sturgeon (*Acipenser fulvescens*; Waraniak, Baker, & Scribner, 2018).

Near-bed conditions (e.g., hydraulic forces and substrate characteristics) have been widely shown to affect microhabitat selection by benthic macroinvertebrates (Lamouroux, Mérigoux, Dolédec, & Snelder, 2013; Mérigoux & Dolédec, 2004; Rempel, Richardson, & Healey, 2000). For instance, water velocity affects respiration and feeding strategies of benthic taxa (Bouckaert & Davis, 1998). Medium to large substrate elements provide a wide array of interstitial spaces that support richer and more diverse benthic communities, while fine sediment tends to homogenize habitats and reduce overall diversity (Bona et al., 2016; Doretto et al., 2016, 2017; Jähnig & Lorenz, 2008). Given the importance of abiotic and biotic factors to the assembly of communities along watershed continua, and their nonrandom distribution, spatial scale is important to consider in community ecology studies.

To better understand the effects of spatial scale, it is particularly advantageous to adopt sampling approaches that survey sites juxtaposed across fine and coarse spatial levels simultaneously (Lamouroux, Dolédec, & Gayraud, 2004; Larsen, Vaughan, & Ormerod, 2009). Most existing studies include multiple sampling units as separate replicates across stream reaches and watersheds, but not as part of a systematic hierarchical design. Quantification of changes in diversity of macroinvertebrate communities across continuous and nested spatial scales, especially within the same river, is relatively under-studied (e.g., Ligeiro, Melo, & Callisto, 2010). Quantifying the importance of factors underlying macroinvertebrate community diversity and abundance at nested scales within individual watersheds is critical to understanding trophic dynamics and community assembly across trophic levels.

Measures of diversity can be partitioned into three components: alpha (α) is the local diversity, beta diversity (β) represents the change in composition among sites, while gamma diversity (γ) represents the total diversity of a system. Under the additive definition of diversity (sensu Baselga, 2010), beta diversity can be further partitioned into diversity due to two underlying processes, turnover and nestedness; species replacement and species gain/loss, respectively. Differentiating between turnover and nestedness and determining which has a greater importance in a given system is critical for making conservation decisions and the distinction between these processes has previously been investigated for benthic macroinvertebrates at differing hierarchical scales (Costa & Melo, 2008; Hawkins, Mykrä, Oksanen, & Vander, 2015).

The overall goal of this study was to quantify relationships between stream physical features and macroinvertebrate α diversity, relative abundance, and taxonomic composition in the Upper Black River (MI, USA). The intensive sampling design of our study allowed for a unique investigation of patterns in macroinvertebrate diversity within a single river. Specific study goals were to: (a) quantify associations between the near-bed conditions (stream flow and substrate) and macroinvertebrate α and β diversity; (b) assess variation in macroinvertebrate α and β diversity across multiple, nested spatial scales, elucidating the contributions of each scale to total diversity; and (c) determine the relative contribution of nestedness and turnover to overall beta diversity for each spatial scale of this study.

2 | MATERIALS AND METHODS

2.1 | Study location

The study was conducted along a 2.2 km stretch of the Upper Black River (UBR), a fourth order river in the upper Great Lakes basin, in Cheboygan County, MI (Figure 1a,b). This river segment was chosen for several reasons: in addition to differing substrate and flow conditions within a relatively short river reach, the whole section was wadable and thus accessible for in-stream sampling. Moreover, no relevant changes in the surrounding land use and riparian vegetation type occur along the selected river segment. The segment is also regularly monitored to quantify predator–prey dynamics and larval fish recruitment (Waraniak et al., 2018) including threatened Lake Sturgeon (*A. fulvescens*). Sampling was conducted from July 15 to August 8, 2014 to characterize physical and biotic stream features and to quantify relationships between stream features and macroinvertebrate communities. This short sampling period allowed us to sample when benthic macroinvertebrate communities were expected to be compositionally and numerically stable, thereby avoiding temporal changes due to the phenology of individual species. Transects ($N = 110$) were established every 20 m covering a 2.2 km stream reach. Transects were placed perpendicular to mid-channel (i.e., the thalweg) river flow. A random number generator was used to select two sample points on the transect at random distances from the left bank. Sampling points were assigned to a transect group

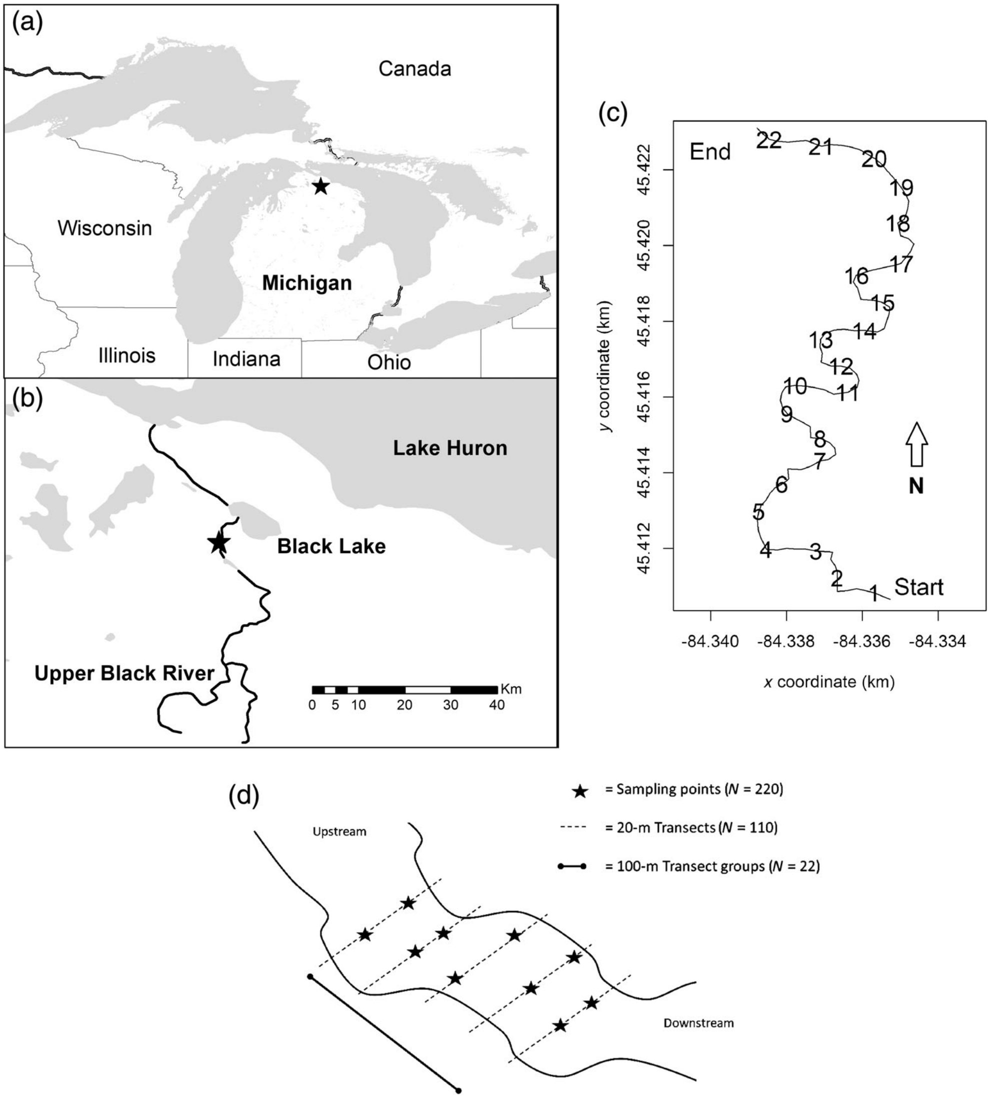

FIGURE 1 Area of study: (a) study site is indicated by star, (b) location of sampling along the Upper Black River. (c) Numbers is the locations of transect groups, colored (either black or grey) according to their clustering as shown in Figure 2. (d) Example of sampling design within one 100-m transect group (solid line): dashed lines represent the five 20-m transects, while the stars represent the two sample points on the transect at random distances from the left bank

(*N* = 22), each representing a 100 m length of stream and contained ten points, two samples from each of five consecutive transects (Figure 1c,d).

2.2 | Field collections and spatial scales

Four spatial scales were considered including the sample, transect, transect group, and the entire sampled reach. At each sampling point (*N* = 220) macroinvertebrates were collected within a 0.50 m^2 area using two adjoined 0.25 m^2 Surber samplers with 500 μm mesh. The substrate within the square was agitated for 10 s and collected macroinvertebrates were stored in 70% EtOH and identified to family using dichotomous keys for North America (Merritt, Cummins, & Berg, 2008). Such a taxonomic resolution is commonly used in biomonitoring programs worldwide (Buss et al., 2015). At each point, depth (m) was measured using a stadia rod and water velocity (m/s) was recorded using a flow meter at a depth of 15 cm (Marsh McBirney Flo-Mate Model 2000; Hach, Loveland, CO). A digital photograph was taken of each 0.50 m^2 area at a distance of 30 cm from the stream bottom and ImageJ software (Schindelin, Rueden, Hiner, & Eliceiri, 2015) was used to measure substrate size (diameter at widest point or coarse woody debris), median substrate size, and proportion of each USGS substrate type (Fitzpatrick et al., 1998).

2.3 | Statistical analyses

2.3.1 | Evaluating spatial impacts on community structure

Taxa accumulation curves were initially used to check the completeness of the sampled community at each spatial level using the function "specaccum" in the R package *vegan* (v. 2.5-2—Oksanen et al., 2015). Non-Metric Multidimensional Scaling ordination was used to evaluate upstream to downstream changes in macroinvertebrate community composition among the 22 consecutive stream sections (transect groups) by means of the "metaMDS" function in the *vegan* package (Oksanen et al., 2015). The total abundance of each taxon was calculated for each transect group and the Bray–Curtis index was used as measure of dissimilarity among transect groups. Moreover, the effect of near-bed conditions (i.e., Froude number, water velocity, depth, substrate size, percentage of fine sediment, and the coefficient of variation in median substrate size) on the composition of macroinvertebrate communities was quantified by adding the vectors of these environmental variables onto the NMDS plot using the function "envfit" in the vegan package (Oksanen et al., 2015). The statistical significance for each environmental variable was calculated by means of 999 permutations and *p* values were obtained as the proportional rank of the observed statistic among the statistics calculated in permutations (Oksanen et al., 2015). To determine if individual taxa were indicators of the groupings obtained from the NMDS ordination, an Indicator Species Analysis (Dufrêne & Legendre, 1997) was performed using the function "multipatt" in the R package *indicspecies* (v. 1.7.6—Caceres & Legendre, 2009).

2.3.2 | Effects of the near-bed conditions on community metrics

The effects of near-bed conditions on the α diversity of macroinvertebrate communities were assessed using Generalized Linear Mixed Models. This category of regression models was chosen over other approaches due to the nested experimental design with both transect and transect group included in the models as random factors. For each benthic sample ($N = 220$) the following metrics were calculated: total macroinvertebrate richness, total abundance, Ephemeroptera, Plecoptera, and Trichoptera (EPT) abundance, EPT richness, Shannon-Weiner, and Simpson's diversity and used as dependent variables in the models. Among the six environmental variables (i.e., water velocity, depth, Froude number, median substrate size, the coefficient of variation in median substrate size, and the percentage of fine sediment) only Froude number, median substrate size (cm) and their interaction were included in the initial models as independent variables because of low collinearity (Pearson's $r = .153$; Figure S1). Selecting only these two variables allowed us to reduce the number of explanatory variables in our models, avoiding collinearity, but at the same time keep at least one variable for the hydraulic and one for the substrate. Models were run for all the community metrics listed above with the lme4 R package (v. 1.1-17—Bates, Mächler, & Bolker, 2011). For count data a Poisson distribution was used, while a negative binomial distribution was used in case of overdispersion. Model selection was performed using Akaike's information criterion (AIC).

Prior to construction of regression models, semivariograms were used to investigate the spatial dependence of macroinvertebrate community diversity metrics ($\log[x + 1]$ transformed). Semivariograms were performed using the function "variogram" in the *gstat* package (v. 2.02—Pebesma, 2004). In addition, two observations were removed as outliers according to the protocol proposed by Zuur, Ieno, and Elphick (2010) for data exploration (dataset for statistical analyses: $N = 218$).

2.3.3 | Diversity across spatial scales

We quantified macroinvertebrate community diversity at several nested spatial scales using Additive Diversity Partitioning (Crist, Veech, Gering, & Summerville, 2003; Veech, Summerville, Crist, & Gering, 2002), which measures contributions of each scale to total macroinvertebrate diversity. This analysis was performed by using the function "adipart" in the R package *vegan* (v. 2.5-2—Oksanen et al., 2015), which allows the calculation of predicted values for a given metric for each scale assuming diversity is independent of scale and compares these with observed diversity to determine statistical significance. According to our sampling scheme, Alpha diversity was within sample diversity (individual samples), Beta1 was the mean diversity among samples in a transect, Beta2 was the mean diversity among transects in a transect group, and Beta3 was the among transect group component of variance. Gamma constituted the total diversity of the entire river section. To avoid redundancy in our analyses, two community diversity metrics were investigated in the Additive Diversity Partitioning: total taxa richness and Shannon-Wiener diversity index (H′).

2.3.4 | Contributions of nestedness and turnover to beta diversity

The contributions of the nestedness and turnover components (species gain/loss and replacement, respectively, sensu Baselga, 2010) of beta diversity were quantified, following the approach of Baselga, Orme, Villeger, Bortoli, and Leprieur (2013), that decomposes the Bray–Curtis dissimilarity index (*BC*) into two additive components: the balanced variation in abundances (*BC_bal*, substitution by individual of different species), and abundance gradients (*BC_gra*, gain/loss of species from one site without substitution), respectively. The former (*BC_bal*) is an indicator of taxa turnover, whereas the latter (*BC_gra*) is an indicator of nestedness. This analysis was performed with the function "beta.multi.abund" in the *betapart* package (v. 1.5.1—Baselga et al., 2013). Specifically, this analysis was carried out separately for each of the spatial scales: sample, transect, and transect group. For the latter two scales (i.e., transect and transect group) an overall macroinvertebrate community was obtained by summing all macroinvertebrate abundances of the samples belonging to each transect or transect group. All analyses were performed in R (v. 3.5.0—R Core Team, 2018).

3 | RESULTS

A total of 38 macroinvertebrate families were collected (Table S1) and the taxa accumulation curves (Figure S2) indicated that sampling was adequate to obtain a representative characterization of the macroinvertebrate family diversity at all the spatial scales investigated and according to the sampling procedure. The mean number of families per sample was 7.0 ± 3.2 (*M* ± *SD*). Trichoptera had the highest richness, followed respectively by Diptera and Ephemeroptera, while only two families of Plecoptera were collected. Mean abundance of macroinvertebrates per sample was 20.0 ± 15.6 (*M* ± *SD*). The four most abundant families were Ephemerellidae, Elmidae, Heptageniidae, and Hydropsychidae comprising 21, 11, 11, and 7% of all macroinvertebrates collected, respectively.

3.1 | Spatial heterogeneity of macroinvertebrate communities

NMDS ordination (stress = 0.113) of the sampled macroinvertebrates resulted in two distinct separations of transect groups: one represented by the upstream sections (US; transect groups 1–13) and the other (DS; transect groups 14–22) composed of downstream sections (Figures 1c and 2). This gradient in the community composition reflected a significant longitudinal variation in the near-bed conditions (Vegan: Envfit, *p* values < .01 for each environmental variable). US transect groups plotted on the left-side of the NMDS and were associated with higher water velocity, Froude number and substrate size and heterogeneity (i.e., coefficient of variation in mean substrate size). By contrast, DS transect groups plotted on the right-side of the NMDS and were associated with higher water depth and percentage of fine sediment (Figure 2). Indicator Species Analysis identified seven macroinvertebrate families which occurred in significantly different abundances between these two groups (Table S2). While the abundances of Hydropsychidae, Isonychiidae, Perlidae and Pyralidae were higher among the US group, Lepidostomatidae, Leptoceridae and Odontoceridae showed an inverse trend, occurring in higher abundance in the DS group (Figure 3 and Table S2).

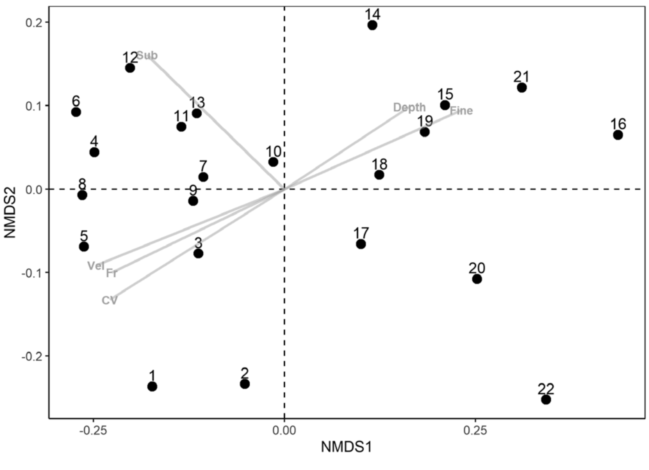

FIGURE 2 Ordination of the macroinvertebrate communities according to the first two NMDS axes. Dots represent the macroinvertebrate community of transect groups, numbered from 1 (the most upstream one) to 22 (the most downstream one). Grey segments represent six environmental variables associated with each macroinvertebrate sample and fitted to the NMDS ordination by using the "envfit" function. The direction of segments indicates the increasing gradient of each variable, while and their length is proportional to their correlation with the ordination. CV, coefficient of variation of the substrate size; Depth, water depth; Fine, percentage of fine sediment; Fr, Froude number; Sub, mean substrate size; Vel, water velocity

3.2 | Environmental effects on macroinvertebrate diversity

Models were run for the six community metrics listed in the previous section (i.e., total richness, total abundance, EPT abundance, EPT richness, Shannon-Weiner, and Simpson's diversity) but to avoid redundancy in our analyses, since several diversity metrics were strongly correlated (Pearson's $r > .6$; Figure S3), only the results for the total taxon richness and total abundance are presented, while those for the other metrics are available in supporting information section (Figure S4 and Table S3). Semivariograms did not indicate spatial autocorrelation in the selected diversity metrics (Figure S5).

In general, richness and diversity metrics significantly increased with higher Froude number and larger substrate size (Figure 4 and Table 1). Froude number had a larger effect on total richness ($Z = 4.03$), and abundance ($Z = 5.31$) than substrate size ($Z = 2.43$ and 2.03 respectively), while substrate size had a relatively stronger effect on Simpson's index ($F = 2.70$) than Froude number ($F = 2.40$). The interaction between Froude number and substrate size was never significant and removed after the model selection (Tables 1 and S3).

3.3 | Macroinvertebrate diversity partitioning across scales

Larger spatial scales explained a greater proportion of variance in taxa richness (Figure 5). The observed variance accounted for by diversity among transects (Beta2) and among transect groups (Beta3) were significantly higher (28.3 and 43.7%, respectively, $p < .05$) than predicted (26.6 and 37%). In contrast, the variance accounted for by finer spatial scales (i.e., Alpha and Beta1) was 18.5 and 9.5%, respectively, and were lower than predicted (25.1 and 11.3% respectively).

For Shannon-Wiener index, the within sample component contributed the greatest proportion of overall diversity. Though the observed variance explained by the within sample component was lower than predicted (70.6%, Alpha), it accounted for 58.5% of total diversity (Figure 5b). The proportion of variance among samples within a transect (13.6%, Beta1), among transects within a transect group (18.4%, Beta2) and between transect groups (9.4%, Beta3) were significantly higher than predicted ($p < .05$, 12.3, 13.1, and 3.4%, respectively).

Beta diversity attributed to taxa turnover contributed the largest proportion of overall beta diversity at both the sample (98.6%) and transect scale (97.1%) (Figure 6). The highest relative contribution of

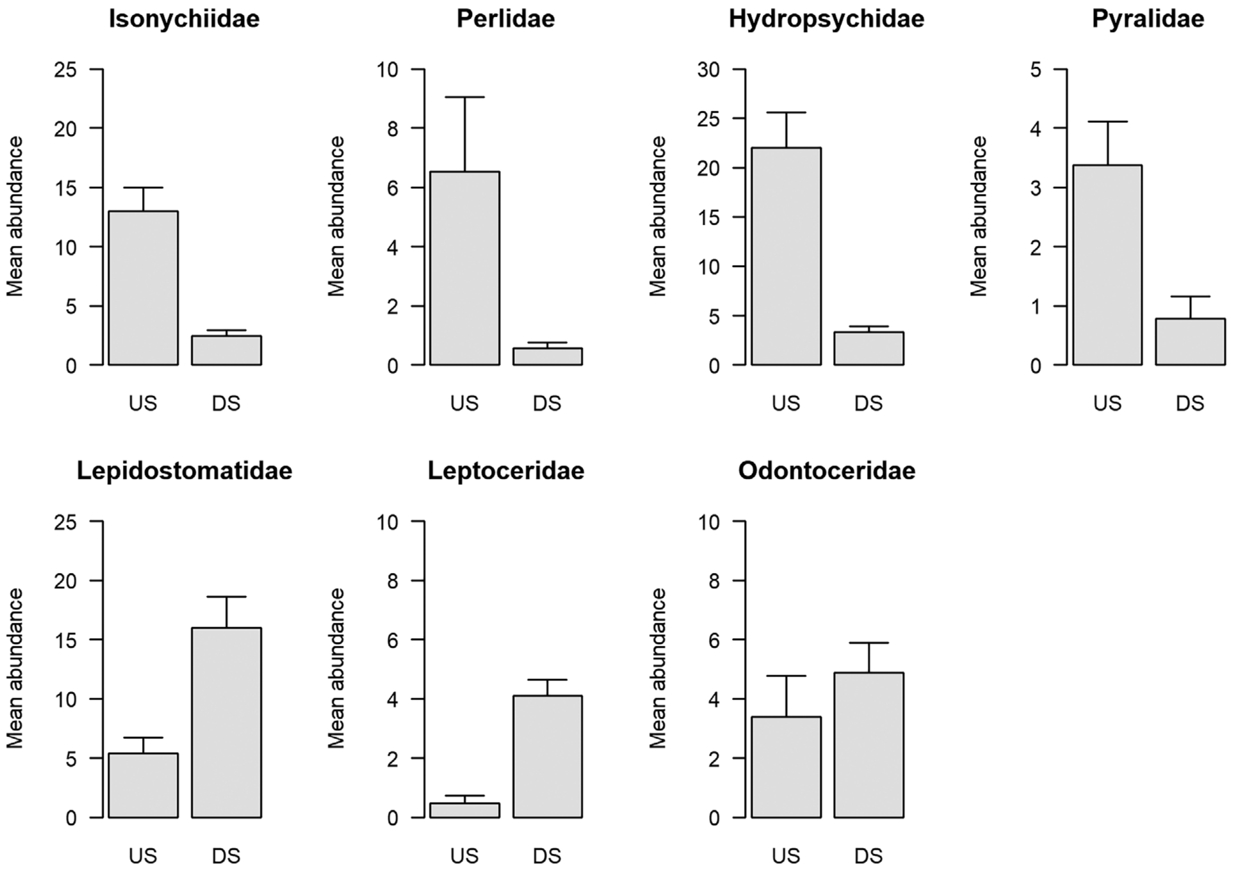

FIGURE 3 Macroinvertebrate indicator taxa for each group based on the NMDS ordination. Error bars are + Standard Error (*SE*). US, upstream; DS, downstream

nestedness was found between transect groups (15.8%), but even at this scale the differences in the total beta diversity of macroinvertebrate communities were mainly explained by taxa turnover (84.2%).

4 | DISCUSSION

A goal of this paper was to assess the relationship between macroinvertebrate community composition and α diversity and near-bed conditions along a stream continuum. Also, the present study was aimed at quantifying sources of variation in macroinvertebrate diversity and composition across nested spatial scales in a river where macroinvertebrate compositional heterogeneity has been documented to influence predation levels for larval life stages of fishes (Waraniak et al., 2017, 2018). We found that longitudinal variation in near-bed conditions and taxa turnover were important factors affecting macroinvertebrate communities along the continuum, providing evidence that near-bed conditions are strong predictors of macroinvertebrate richness and abundance at local scale, but at the same time the highest contribution to the total macroinvertebrate diversity was observed by taxa replacement over larger spatial scales.

4.1 | Effects of flow and substrate

Increasing Froude number and substrate size had positive effects on the total macroinvertebrate abundance and diversity. Froude number varied from 0 to 0.66, and no measures exceeded the critical value (Froude number ≥ 1) which is typically indicative of very turbulent flow (Hauer & Lamberti, 2017), while the substrate size ranged from fine sediment (<2 mm) to 26.8 cm. These results concur with previous findings on stream macroinvertebrates (Brooks & Haeusler, 2016; Dolédec, Lamouroux, Fuchs, & Merigoux, 2007; Jowett, 2003).

Yet, these variables, along with the other near-bed variables, shaped the composition of macroinvertebrate communities beyond the local scale with a clear up to downstream gradient, as highlighted by the multivariate analysis. This longitudinal variation was evident when looking at the taxon-specific distribution: four families (i.e., Hydropsychidae, Isonychiidae, Perlidae, and Pyralidae) were mostly associated with the erosive upstream sections, while three families (i.e., Lepidostomatidae, Leptoceridae, and Odontoceridae) preferred the depositional downstream sections. These results agree with the habitat categories defined by Merritt et al. (2008) for the aquatic insects of North America: Hydropsychidae, Isonichiidae, and Perlidae are classified as taxa preferring lotic-erosional habitats, while

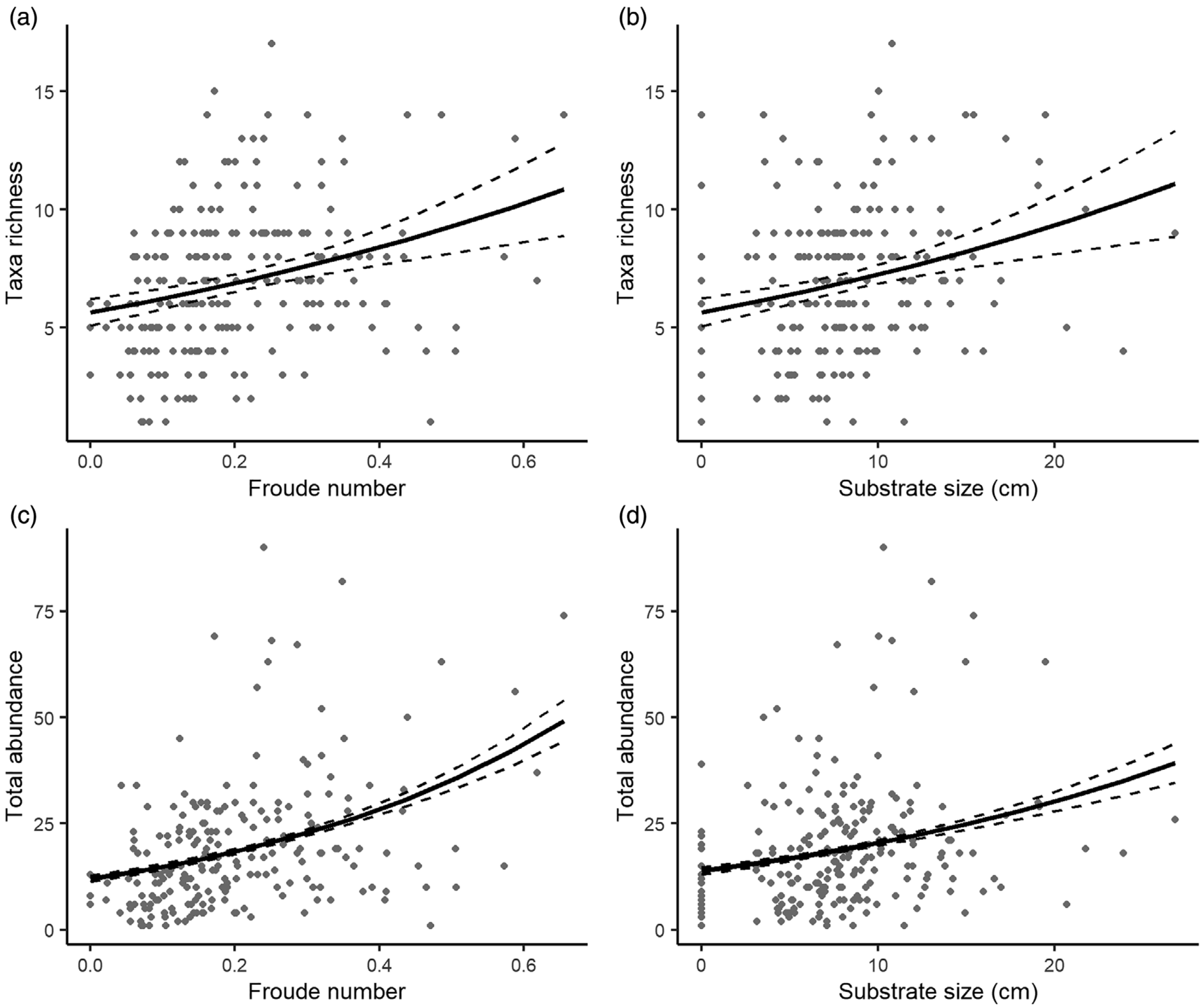

FIGURE 4 Relationships between taxon richness (a, b) and total abundance (c, d) to Froude number and median substrate size. Grey dots = observed values; black line = predicted values; dashed lines = 95% confidence intervals

TABLE 1 Results of mixed models for the total taxon richness and total abundance

Metric	i-AIC	Final model	f-AIC	Variable	*Z* value	*p* value
Richness	1,066.7	Froude + substrate size + (1| transect) + (1| transect group), family = poisson	1,065.6	Froude	4.026	<.001
				Substrate size	2.426	.015
Total abundance	1,644.7	Froude + substrate size + (1| transect) + (1| transect group), family = negative binomial	1,643.2	Froude	5.313	<.001
				Substrate size	2.025	.043

Note: For all the community metrics the initial model included: Froud number, substrate size and the interaction between these two variables.
Abbreviations: f-AIC, AIC of the final model; Final Model, select model after model selection; i-AIC, initial AIC.

Lepidostomatidae, Leptoceridae, and Odontoceridae are associated to both erosional and depositional habitats. The only exception is represented by Pyralidae, which in our study was more abundant in the upstream erosive sections of the Upper Black River, while according to the literature this family generally prefers lentic habitats with macrophytes (Merritt et al., 2008).

4.2 | Macroinvertebrate diversity across spatial scales

We found that larger spatial scales explained a higher proportion of variance in taxon richness than the finer scales. Results agree with those found in other studies (Karaus, Larsen, Guillong, & Tockner, 2013; Ligeiro

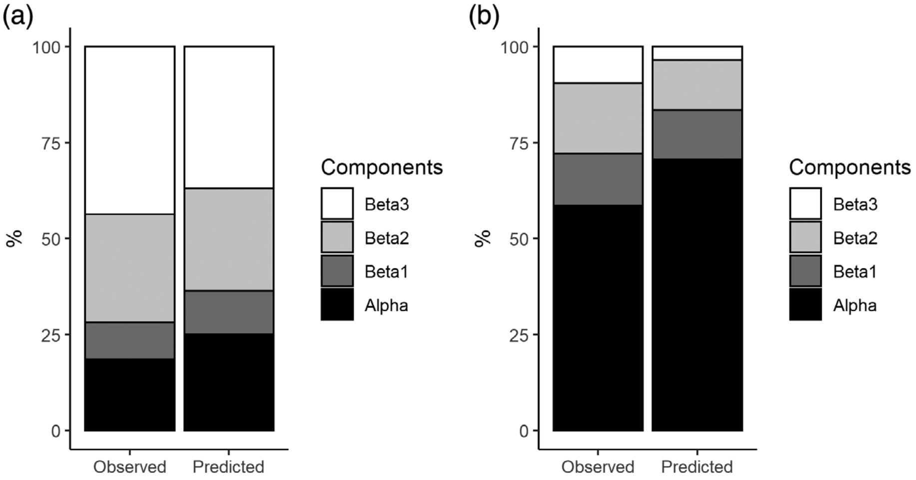

FIGURE 5 Results of Additive Diversity Partitioning for: (a) taxon richness, (b) Shannon diversity. Alpha, diversity within a sample; Beta1, diversity within a transect; Beta2, diversity between transects; Beta3, diversity between transect groups

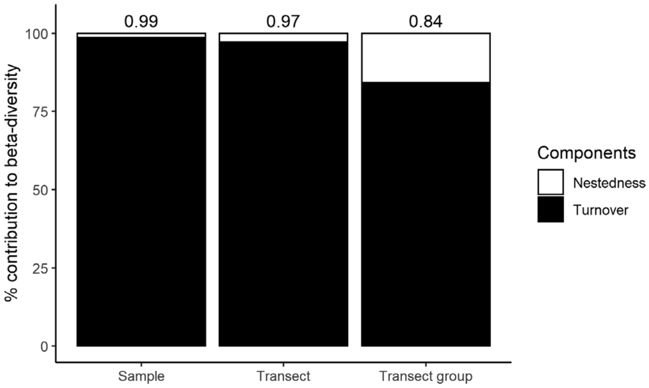

FIGURE 6 Stacked bars indicate the relative contribution of nestedness and turnover to total beta-diversity (numbers above bars) for each scale

et al., 2010), and support the conclusion that transects or transect groups (i.e., 100 m stream stretch) are the spatial scales that best describe macroinvertebrate community richness along river courses compared to the sampling points, probably because of the enhanced provision of ecological niches due to their habitat heterogeneity. When diversity was quantified using the Shannon-Weiner index, the individual sample component (Alpha) accounted for the highest proportion of total diversity likely due to a patchy distribution of macroinvertebrates in lotic ecosystems (which our hierarchical collection regime was able to capture), where fewer generalist taxa can dominate at local scales (Burgazzi, Guareschi, & Laini, 2018; Lake, 2000). At larger scales, each 100-m transect group contained different assemblages of macroinvertebrates, likely dependent on substrate conditions, and increased overall community diversity. Findings support previous work showing that natural longitudinal gradient and habitat variability enhance ecosystem diversity (Mesa, 2010; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980).

4.3 | Management applications

Although there are limitations to using family-level taxonomic resolution, analyses conducted at this level afford greater technical and financial flexibility for long-term monitoring by managers (Bo, Doretto, Laini, Bona, & Fenoglio, 2017; Doretto, Piano, Bona, & Fenoglio, 2018; Slimani et al., 2019). Thus, our coarser resolution of macroinvertebrate community identification works well for the goals of the study and has broader relevance to applied areas of watershed management.

Strong upstream to downstream changes in the composition of benthic macroinvertebrate communities was documented. Communities of most upper sections and the farthest downstream segments clustered separately, associated with the local substrate and flow conditions that mediated the richness, abundance and distribution of individual aquatic taxa. The analysis of the contribution of nestedness and turnover to beta diversity further corroborated this evidence. Turnover in family level macroinvertebrate communities explained substantial portions of overall community diversity up- to downstream, even at coarse levels of taxonomic resolution, emphasizing a similar importance of the longitudinal dimension in watershed diversity at our observed scale as found at other spatial scales (Grubaugh, Wallace, & Houston, 1996; Rosi-Marshall & Wallace, 2002). For instance, in a comparable study Burgazzi, Laini, Racchetti, and Viaroli (2017) quantified the relative contributions of nestedness and turnover among meso-habitats within the same river reach and found a greater contribution of taxa turnover, confirming the importance of varied habitats in increasing the local riverine biodiversity.

Based on findings presented here elucidated based on a detailed sampling regime, management can focus more effectively on sampling designs, studying, and managing macroinvertebrate communities. Specifically, the spatial hierarchical structuring of riverine macroinvertebrate community composition demonstrated in this study speaks to the need for management of rivers and river flows to maintain diverse habitats to maintain the diversity of macroinvertebrates as a functional component of a diverse and resilient stream community.

In this study, family turnover contributed almost entirely to beta diversity at the finer spatial scales, such as sample and transect, likely because of the strong influence of the near-bed conditions on the taxon-specific ecological preferences. Yet, the average contribution of nestedness at transect group scale increased to 15.8%, indicating that beta diversity at larger scales was at least affected also by the gain/loss of taxa. These findings suggest that macroinvertebrates communities in the Upper Black River are simultaneously shaped by local near-bed conditions and large-scale variation, emphasizing the importance of preserving the hydro-morphological integrity at different spatial scales of riverine systems against anthropogenic pressures such as damming, water abstraction and flow regulation (Dewson, James, & Death, 2007; Doretto et al., 2019; Perkin & Gido, 2012; Piano et al., 2019a, 2019b).

Moreover, such information can be used to identify quality stretches of river courses that provide the macroinvertebrate resources important to fisheries management because they are in agreement with the historical distribution of fish (Lake Sturgeon) spawning sites previously identified in this river reach. In fact, in a previous study, Waraniak, Marsh, and Scribner (2019) found that during 2–4 week periods when larval fish and macroinvertebrate "drift" passively in the water column at night, predatory fishes upstream will be exposed to different prey communities than predatory fishes downstream. Insect taxa enter and leave the benthic drift over relatively short distances (Danehy, Langshaw, Duke, & Bilby, 2011) relative to larval fishes whose adults spawn in upstream sections of the stream (Forsythe, Crossman, Bello, Baker, & Scribner, 2012). Differences in the origin of larval fishes and different macroinvertebrate taxa spatially and temporally, documented previously (Waraniak et al., 2019), directed the timing of field collections in the present study to occur over a short period of time. Macroinvertebrate community metrics can be useful as inputs into modeling approaches predicting recruitment or how introduced (i.e., stocked) fish populations may behave when reintroduced into native rivers.

Considerable spatial overlap exists among stream fishes and aquatic invertebrates (Copp, Spathari, & Turmel, 2005; Worischka, Koebsch, Hellmann, & Winkelmann, 2012) that abundantly occupy substrates on which many fish species spawn, and that co-occurrence frequently coincides with larval fish dispersal. Such co-occurrence and dispersal of invertebrates with fish can provide a dilution effect of predation on drifting larval fish through predator preference, prey switching and predator swamping; therefore, having potential to inform management of stream and river habitats for threatened or endangered fish species (Murdoch, 1969). Distributional overlap of invertebrate communities and target fish species suggests that species interactions across trophic levels may be common, but identification of physical stream conditions for taxa co-occurrence and the associated fitness or population level outcomes of these interactions are poorly understood. To achieve stream and fisheries management objectives for resident and adfluvial species, including threatened lake sturgeon, resource managers need empirically derived models that can identify and utilize causal factors that predict natural population levels of recruitment. Identifying abiotic and biotic factors limiting survival during early life stages will help managers predict where suitable habitat exists, define predation risks, and where restoration actions should be most effective. Management efforts would be improved if models were produced that predicted larval fish survival using "multi-scale" data as we have presented here based on stream features like substrate conditions and macroinvertebrate community composition, diversity, abundance, and distribution.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

All the authors contributed to this work. Kim T. Scribner, Edward A. Baker, and M. Eric Benbow conceived this study, wrote, and edited the manuscript; Alberto Doretto and Joseph P. Receveur wrote and edited the manuscript and carried out the statistical analysis.

DATA AVAILABILITY STATEMENT

All data and code used in preparation of this manuscript is available at https://github.com/BenbowLab/Benthos2020.

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REFERENCES

Altermatt, F. (2013). Diversity in riverine metacommunities: A network perspective. *Aquatic Ecology*, *47*, 365–377. https://doi.org/10.1007/s10452-013-9450-3

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., Orme, D., Villeger, S., Bortoli, J. D., & Leprieur, F. (2013). *Betapart: partitioning beta diversity into turnover and nestedness components R package version 1.5*. Retrieved from http://CRAN.R-project.org/package=betapart.

Batalla Salvarrey, B., Kotzian, C. B., Spies, M. R., & Braun, B. (2014). The influence of natural and anthropic environmental variables on the structure and spatial distribution along longitudinal gradient of macroinvertebrate communities in southern Brazilian streams. *Journal of Insect Science*, *14*, 13. https://doi.org/10.1093/jis/14.1.13

Bates, D., Mächler, M., & Bolker, B. (2011). *Lme4: Linear mixed-effects models using S4 classes*. R Package Version 0.999375-42. Retrieved from http://CRAN.R-project.org/package=lme4

Blanchet, F. G., Legendre, P., Maranger, R., Monti, D., & Pepin, P. (2011). Modelling the effect of directional spatial ecological processes at different scales. *Oecologia*, *166*, 357–368. https://doi.org/10.1007/s00442-010-1867-y

Bo, T., Doretto, A., Laini, A., Bona, F., & Fenoglio, S. (2017). Biomonitoring with macroinvertebrate communities in Italy: What happened to our past and what is the future? *Journal of Limnology*, *76*, 21–28. https://doi.org/10.4081/jlimnol.2016.1584

Bona, F., Doretto, A., Falasco, E., La Morgia, V., Piano, E., Ajassa, R., & Fenoglio, S. (2016). Increased sediment loads in alpine streams: An integrated field study. *River Research and Applications*, *32*, 1316–1326. https://doi.org/10.1002/rra.2941

Bouckaert, F. W., & Davis, J. (1998). Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology*, *40*, 77–86. https://doi.org/10.1046/j.1365-2427.1998.00329.x

Brooks, A. J., & Haeusler, T. (2016). Invertebrate responses to flow: Trait-velocity relationships during low and moderate flows. *Hydrobiologia*, *773*, 23–34. https://doi.org/10.1007/s10750-016-2676-z

Burgazzi, G., Guareschi, S., & Laini, A. (2018). The role of small-scale spatial location on macroinvertebrate community in an intermittent stream. *Limnetica*, *37*(2), 319–340. https://doi.org/10.23818/limn.37.26

Burgazzi, G., Laini, A., Racchetti, E., & Viaroli, P. (2017). Mesohabitat mosaic in lowland braided rivers: Short-term variability of macroinvertebrate metacommunities. *Journal of Limnology*, *76*, 29–38. https://doi.org/10.4081/jlimnol.2017.1650

Buss, D. F., Carlisle, D. M., Chon, T. S., Culp, J., Harding, J. S., KeizerVlek, H. E., … Hughes, R. M. (2015). Stream biomonitoring using macroinvertebrates around the globe: A comparison of large-scale programs. *Environmental Monitoring and Assessment*, *187*, 1–21. https://doi.org/10.1007/s10661-014-4132-8

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566-3574. https://doi.org/10.1890/08-1823.1

Copp, G., Spathari, S., & Turmel, M. (2005). Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. *River Research and Applications*, *21*(1), 75–90.

Costa, S. S., & Melo, A. S. (2008). Beta diversity in stream macroinvertebrate assemblages: Among-site and among-microhabitat components. *Hydrobiologia*, *598*, 131–138. https://doi.org/10.1007/s10750-007-9145-7

Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: A hierarchical analysis of α, β, and γ diversity. *The American Naturalist*, *162*, 734–743. https://doi.org/10.1086/378901

Danehy, R. J., Langshaw, R. B., Duke, S. D., & Bilby, R. E. (2011). Drift distance of macroinvertebrates throughout summer in headwater tributaries of the Calapooia River. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, *178*(2), 111–120.

Dewson, Z. S., James, A. B., & Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, *26*(3), 401–415. https://doi.org/10.1899/06-110.1

Dolédec, S., Lamouroux, N., Fuchs, U., & Merigoux, S. (2007). Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. *Freshwater Biology*, *52*, 145–164. https://doi.org/10.1111/j.1365-2427.2006.01663.x

Doretto, A., Bo, T., Bona, F., Apostolo, M., Bonetto, D., & Fenoglio, S. (2019). Effectiveness of artificial floods for benthic community recovery after sediment flushing from a dam. *Environmental Monitoring and Assessment*, *191*(2), 88. https://doi.org/10.1007/s10661-019-7232-7

Doretto, A., Bona, F., Falasco, E., Piano, E., Tizzani, P., & Fenoglio, S. (2016). Fine sedimentation affects CPOM availability and shredder abundance in alpine streams. *Journal of Freshwater Ecology*, *31*(2), 299–302. https://doi.org/10.1080/02705060.2015.1124297

Doretto, A., Bona, F., Piano, E., Zanin, I., Eandi, A. C., & Fenoglio, S. (2017). Trophic availability buffers the detrimental effects of clogging in an alpine stream. *Science of the Total Environment*, *592*, 503–511. https://doi.org/10.1016/j.scitotenv.2017.03.108

Doretto, A., Piano, E., Bona, F., & Fenoglio, S. (2018). How to assess the impact of fine sediments on the macroinvertebrate communities of alpine streams? A selection of the best metrics. *Ecological Indicators*, *84*, 60–69. https://doi.org/10.1016/j.ecolind.2017.08.041

Dovciak, A., & Perry, J. A. (2002). In search of effective scales for stream management: Does agroecoregion, watershed, or their intersection best explain the variance in stream macroinvertebrate communities? *Environmental Management*, *30*(3), 365–377.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs*, *67*(3), 345-366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Durance, I., Lepichon, C., & Ormerod, S. J. (2006). Recognizing the importance of scale in the ecology and management of riverine fish. *River Research and Applications*, *22*, 1143–1152. https://doi.org/10.1002/rra.965

Fitzpatrick, F. A., Waite, I. R., D'Arconte, R. J., Meador, M. R., Maupin, M. A., Gurtz, M. E. (1998). *Revised methods for characterizing stream habitat in the National Water-Quality Assessment Program*. US Geological Survey Water-Resources Investigations Report 98. Retrieved from https://pubs.usgs.gov/wri/wri984052/

Flinders, C., Horwitz, R., & Belton, T. (2008). Relationship of fish and macroinvertebrate communities in the mid-Atlantic uplands: Implications for integrated assessments. *Ecological Indicators*, *8*(5), 588–598.

Forsythe, P. S., Crossman, J. A., Bello, N. M., Baker, E. A., & Scribner, K. T. (2012). Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 60–72.

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. J. E. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management*, *10*, 199–214. https://doi.org/10.1007/BF01867358

Grant, E. H. C., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: Population dynamics and ecological processes in dendritic networks. *Ecology Letters*, *10*, 165–175. https://doi.org/10.1111/j.1461-0248.2006.01007.x

Grubaugh, J. W., Wallace, J. B., & Houston, E. S. (1996). Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 896–909. https://doi.org/10.1139/f95-247

Hauer, F. R., & Lamberti, G. (2017). *Methods in stream ecology*. London, UK: Academic Press.

Hawkins, C. P., Mykrä, H., Oksanen, J., & Vander Laan, J. J. (2015). Environmental disturbance can increase beta diversity of stream macroinvertebrate assemblages. *Global Ecology and Biogeography*, *24*, 483–494. https://doi.org/10.1111/geb.12254

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, *60*, 845–869. https://doi.org/10.1111/fwb.12533

Jähnig, S. C., & Lorenz, A. W. (2008). Substrate-specific macroinvertebrate diversity patterns following stream restoration. *Aquatic Sciences*, *70*, 292–303. https://doi.org/10.1007/s00027-008-8042-0

Jowett, I. G. (2003). Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications*, *19*, 495–507. https://doi.org/10.1002/rra.734

Karaus, U., Larsen, S., Guillong, H., & Tockner, K. (2013). The contribution of lateral aquatic habitats to insect diversity along river corridors in the Alps. *Landscape Ecology*, *28*, 1755–1767. https://doi.org/10.1007/s10980-013-9918-5

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, *19*, 573–592. https://doi.org/10.2307/1468118

Lamouroux, N., Dolédec, S., & Gayraud, S. (2004). Biological traits of stream macroinvertebrate communities: Effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society*, *23*, 449–466.

Lamouroux, N., Mérigoux, S., Dolédec, S., & Snelder, T. H. (2013). Transferability of hydraulic preference models for aquatic macroinvertebrates. *River Research and Applications*, *29*, 933–937. https://doi.org/10.1002/rra.2578

Larsen, S., Vaughan, I. P., & Ormerod, S. J. (2009). Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater*

Biology, *54*, 203–219. https://doi.org/10.1111/j.1365-2427.2008.02093.x

Ligeiro, R., Melo, A. S., & Callisto, M. (2010). Spatial scale and the diversity of macroinvertebrates in a Neotropical catchment. *Freshwater Biology*, *55*, 424–435. https://doi.org/10.1111/j.1365-2427.2009.02291.x

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

Merritt, R. W., Cummins, K. W., & Berg, M. B. (2008). *An introduction to the aquatic insects of North America*. Dubuque, IA: Kendall/Hunt Publishing Company.

Mesa, L. M. (2010). Hydraulic parameters and longitudinal distribution of macroinvertebrates in a subtropical andean basin. *Interciencia*, *35*, 759–764.

Murdoch, W. W. (1969). Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs*, *39*(4), 335–354.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2015). *Vegan: Community ecology package*. R Package Version 2.2-1.

Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers and Geosciences*, *30*, 683–691. https://doi.org/10.1016/j.cageo.2004.03.012

Perkin, J. S., & Gido, K. B. (2012). Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications*, *22*, 2176–2187. https://doi.org/10.1890/12-0318.1

Piano, E., Doretto, A., Falasco, E., Fenoglio, S., Gruppuso, L., Nizzoli, D., … Bona, F. (2019a). If alpine streams run dry: The drought memory of benthic communities. *Aquatic Sciences*, *81*(2), 32. https://doi.org/10.1007/s00027-019-0629-0

Piano, E., Doretto, A., Falasco, E., Gruppuso, L., Fenoglio, S., & Bona, F. (2019b). The role of recurrent dewatering events in shaping ecological niches of scrapers in intermittent alpine streams. *Hydrobiologia*, *841*, 177–189. https://doi.org/10.1007/s10750-019-04021-2

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rempel, L. L., Richardson, J. S., & Healey, M. C. (2000). Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology*, *45*, 57–73. https://doi.org/10.1046/j.1365-2427.2000.00617.x

Rosi-Marshall, E. J., & Wallace, J. B. (2002). Invertebrate food webs along a stream resource gradient. *Freshwater Biology*, *47*, 129–141. https://doi.org/10.1046/j.1365-2427.2002.00786.x

Schindelin, J., Rueden, C. T., Hiner, M. C., & Eliceiri, K. W. (2015). The ImageJ ecosystem: An open platform for biomedical image analysis. *Molecular Reproduction and Development*, *82*, 518–529.

Slimani, N., Sánchez-Fernández, D., Guilbert, E., Boumaiza, M., Guareschi, S., & Thioulouse, J. (2019). Assessing potential surrogates of macroinvertebrate diversity in north-African Mediterranean aquatic ecosystems. *Ecological Indicators*, *101*, 324–329. https://doi.org/10.1016/j.ecolind.2019.01.017

Tornwall, B., Sokol, E., Skelton, J., & Brown, B. (2015). Trends in stream biodiversity research since the river continuum concept. *Diversity*, *7*, 16–35. https://doi.org/10.3390/d7010016

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 130–137.

Veech, J. A., Summerville, K. S., Crist, T. O., & Gering, J. C. (2002). The additive partitioning of species diversity: Recent revival of an old idea. *Oikos*, *99*, 3–9. https://doi.org/10.1034/j.1600-0706.2002.990101.x

Wallace, J. B., & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, *41*(1), 115–139.

Waraniak, J. M., Baker, E. A., & Scribner, K. T. (2018). Molecular diet analysis reveals predator-prey community dynamics and environmental factors affect predation of larval lake sturgeon (*Acipenser fulvescens*) in a natural system. *Journal of Fish Biology*, *93*(4), 616–629. https://doi.org/10.1111/jfb.13726

Waraniak, J. M., Marsh, T. L., & Scribner, K. T. (2019). 18S metabarcoding diet analysis of the predatory fish community in the Black River, Cheboygan County, MI, during and after the larval lake sturgeon drift period. *Ecology and Evolution*, *9*(3), 1410–1430. https://doi.org/10.1002/ece3.4857

Waraniak, J. M., Valentine, S., & Scribner, K. T. (2017). Effects of changes in alternative prey densities on predation of drifting lake sturgeon larvae (*Acipenser fulvescens*). *Journal of Freshwater Ecology*, *32*(1), 619–632.

Ward, J. V., & Tockner, K. (2001). Biodiversity: Towards a unifying theme for river ecology. *Freshwater Biology*, *46*, 807–819. https://doi.org/10.1046/j.1365-2427.2001.00713.x

Worischka, S., Koebsch, C., Hellmann, C., & Winkelmann, C. (2012). Habitat overlap between predatory benthic fish and their invertebrate prey in streams: The relative influence of spatial and temporal factors on predation risk. *Freshwater Biology*, *57*(11), 2247–2261.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

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