



Communities in high definition: spatial and environmental factors shape the microdistribution of aquatic invertebrates

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1 **Title**

2 Communities in high definition: spatial and environmental factors shape the microdistribution of
3 aquatic invertebrates

4
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19
20 **Running head**

21 Micro-scale drivers of macroinvertebrate communities

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17 **28 KEYWORDS**
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20 29 macroinvertebrates, benthic organic matter, community drivers, metacommunity, microdistribution
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26 **31 ABSTRACT**
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- 28 32 1. According to metacommunity theories, the structure of natural communities is the result of
29
30 33 both environmental filtering and spatial processes, with their relative importance depending
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32 34 on factors including local habitat characteristics, functional features of organisms and the
33
34 35 spatial scale considered. However, few studies have explored environmental and spatial
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36 36 processes in riverine systems at local scales, explicitly incorporating spatial coordinates into
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38 37 multi-taxa distribution models. To address this gap, we conducted a small-scale study to
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40 38 discriminate between abiotic and biotic factors affecting the distribution of aquatic
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42 39 macroinvertebrates, applying metacommunity concepts.
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46 41 2. We studied a mountain section in each of three perennial streams within the Po River Basin
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48 42 (Northern Italy). We sampled macroinvertebrates both in summer and winter, using specific
49
50 43 in-situ 50-point random sampling grids. Environmental factors, including benthic organic
51
52 44 matter (BOM), flow velocity, water depth and substrate were recorded together with spatial
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54 45 coordinates for each sampling point. The relationships between community metrics (taxon
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56 46 richness, abundance, biomass, biomass-abundance ratio and functional feeding groups) and
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58 47 explanatory variables (environmental and spatial) were assessed using generalized additive
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3 47 models (GAMs). The influence of the explanatory variables on community structure was
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5 48 analysed with joint species distribution models.
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8 49 3. Environmental variables – primarily BOM – were the main drivers affecting community
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10 50 metrics, whereas the effects of spatial variables varied among metrics, streams and seasons.
11
12 51 During summer, the community structure was strongly affected by BOM and spatial position
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14 52 within the riverbed, the latter probably being a proxy of mass effects mediated by biotic and
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16 53 stochastic processes. In contrast, community structure was mainly shaped by hydraulic
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18 54 variables in winter.
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21 55 4. Using macroinvertebrate communities as a model group, our results demonstrate that
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23 56 metacommunity concepts can explain small-scale variability in community structure. We
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25 57 found that both environmental filtering and biotic processes shape local communities, with
26
27 58 the strength of these drivers depending on the season. These insights provide baseline
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29 59 knowledge that informs our understanding of ecological responses to environmental
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31 60 variability in contexts including restoration ecology, habitat suitability modelling and
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33 61 biomonitoring.
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1 INTRODUCTION

The investigation of factors affecting organization and distribution of natural communities is a critical issue for ecologists (Johnson, Furse, Hering, & Sandin, 2007; Kuemmerlen et al., 2014), both in community ecology studies and in biomonitoring surveys (Laini, Vorti, Bolpagni, & Viaroli, 2014; Tolonen et al., 2017). Metacommunity theories suggest environmental filtering and biotic and spatial processes as the main drivers of community variability. The relative influence of these processes is highly variable, depending on the functional features of taxa (e.g. dispersal ability), the characteristics of the studied environments (Grönroos et al., 2013; Soininen, 2016), and the spatial scale considered. In particular, the role played by assembly processes strictly depends on the spatial extent of the study area (Heino et al., 2015). Consequently, studies exploring the relative importance of environmental, biotic and spatial processes need a scale-explicit context. In riverine systems, species sorting (Leibold et al., 2004) is typically the most suitable model to explain metacommunity patterns (Cottenie, 2005; Heino et al., 2015; Soininen, 2016), although dispersal limitation is also a key influence on community structure. However, little is known about the relative importance of metacommunity processes at small spatial scales (i.e. among microhabitats within the same river segment, hereafter referred as the micro scale) because most metacommunity studies are carried out at medium or large scales (Tolonen et al., 2017).

Several authors have reported high levels of variability in the micro-scale distribution of macroinvertebrates in river ecosystems (Costa & Melo, 2008; Downes, Lake, & Schreiber, 1993; Lamouroux, Dolédec, & Gayraud, 2004; Lancaster & Belyea, 2006; LeCraw & Mackereth, 2010), which is attributed to environmental filtering for microhabitats differentiation (Bo, Piano, Doretto, Bona, & Fenoglio, 2016; Braccia & Voshell, 2006). Water depth and flow velocity (Brooks, Haeusler, Reinfelds, & Williams, 2005), substrate composition and sediment size (Barnes, Vaughan, & Ormerod, 2013; Boyero, 2003), algal cover, organic matter characteristics and macrophytes (Downes & Hindell, 2000; Fenoglio, Bo, Agosta, & Malacarne, 2005; Heino & Korsu, 2008) are generally

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88 identified as the main environmental drivers of macroinvertebrate distribution at the micro scale.
89 However, the fit between communities composition and environmental variables is not always strong,
90 and the unexplained proportion of variation often remains high (Dormann, 2007; Lamouroux et al.,
91 2004).

92 Biotic interactions, especially at micro spatial scales, can exert a strong influence on
93 community dynamics (Patrick & Swan, 2011). Several studies have reported intra and interspecific
94 interactions, including both negative (competition, predation and parasitism) and positive (mutualism
95 and commensalism) associations, as crucial drivers of macroinvertebrate communities (Crowley &
96 Johnson, 1982; Holomuzki, Feminella, & Power, 2010; Lamouroux et al., 2004; Lancaster, Hildrew,
97 & Townsend, 1991; McIntosh & Peckarsky, 1999). For example, Creed, Cherry, Pflaum, and Wood
98 (2009) demonstrated the effect of competition between the limnephilid caddisfly *Pycnopsyche* and
99 other detritivorous taxa, and Presa Abós, Lepori, Mckie, and Malmqvist (2006) detected aggregation
100 of shredder species among resource patches, highlighting possible commensalism. Such biological
101 interactions may gain greater importance as environmental conditions become less limiting
102 (Peckarsky, 1983).

103 Dispersal dynamics also create spatial patterns in macroinvertebrate communities (Dray et al.,
104 2012). Dispersal dynamics are usually measured at regional or catchment scales, where the use of
105 spatial variables as explicit covariates in statistical models helped to explain macroinvertebrate
106 community organization (Johnson et al., 2007; Mykrä, Heino, & Muotka, 2007; Soininen, 2016). The
107 relative importance of spatial variables in structuring communities increases with geographical
108 distance due to dispersal limitation (Mykrä et al., 2007). Consequently, communities located at
109 increasing distances from one another become progressively more dissimilar (Heino et al., 2015;
110 Mykrä et al., 2007). Equally, at micro scales, organisms are generally assumed to disperse without
111 limitation, causing communities located closer to each other to be increasingly similar, because they

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3 112 can be homogenized (Heino et al., 2015; Heino & Peckarsky, 2014; Tolonen et al., 2017) according
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5 113 to the mass effects model (sensu Leibold et al., 2004).
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8 114 Most studies exploring the microdistribution of aquatic macroinvertebrates only consider
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10 115 environmental variables, whereas few studies have used coordinates as explicit covariates to
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12 116 discriminate environmental and spatial drivers (see Tolonen et al., 2017). However, spatial variables
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15 117 – as a proxy of dispersal dynamics and biotic processes – can exert a strong influence on local
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17 118 community structure, and their omission could limit and simplify our understanding of
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19 119 macroinvertebrate distributions (Burgazzi, Guareschi, & Laini, 2018; McLaughlin, Emmerson, &
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21 120 O’Gorman, 2013). Indeed, even excluding the effects of dispersal limitation, biotic interactions,
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23 121 which are otherwise difficult to model in species-rich communities, could be inferred from local-scale
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25 122 spatial factors. Moreover, spatial variables can also capture the effects of missing environmental
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27 123 covariates (Ovaskainen et al., 2017). Strong micro-scale variability has also been reported for other
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29 124 aquatic communities, with the spatial position within the channel affecting the distribution of benthic
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31 125 algae (Bolpagni & Laini, 2016), diatoms (Soininen, 2007), bacteria (Augspurger, Karwautz,
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33 126 Mußmann, Daims, & Battin, 2010), and phytoplankton (Moresco et al., 2017).
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39 127 The aim of this study was to: 1) assess the role of metacommunity concepts to explain micro-
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41 128 scale variability in aquatic macroinvertebrate community composition; and 2) identify the main
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43 129 factors shaping variability in the microdistribution of aquatic macroinvertebrates, distinguishing
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45 130 between spatial and environmental drivers. Based on previous findings (Braccia & Voshell, 2006;
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47 131 Brooks et al., 2005; Diggins & Newman, 2009; Graça et al., 2004; He, Soininen, Deng, & Wang,
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49 132 2020; Tolonen et al., 2018), we hypothesized a major role of environmental filtering in shaping
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51 133 macroinvertebrate communities at the micro scale, with a dominance of species sorting mechanisms.
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58 135 **2 METHODS**

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136 2.1 Study area

137 The study was performed in the Nure, Parma and Enza streams, three tributaries of the Po
138 River in the Apennines in Northern Italy (Figure 1a). All sites experience a warm-summer temperate
139 climate (Köppen-Geiger classification Csb). These streams are fed only by precipitation and have
140 seasonal flow regimes with two high-discharge periods, in autumn and spring, and a low-discharge
141 period in summer. Additional details about each stream are reported in Table 1 and in Table S1.

142 Three sampling stations, one per stream, were selected in the upstream mountainous sections.
143 Sampling stations had similar environmental characteristics including stream order, wetted width,
144 altitude and riparian vegetation, and belonged to similar national river typologies. Each station was
145 sampled twice, once in summer (July 2016) and once in winter (February 2017), making a total of six
146 sampling campaigns (i.e. Parma summer, Enza summer, Nure summer, Parma winter, Enza winter,
147 Nure winter). We sampled in these seasons for their greater climatic stability compared to spring and
148 autumn, when the northern Apennine region experiences frequent, sudden heavy rainfall events and
149 thus flash flooding.

151 2.2 Field and laboratory activities

152 Macroinvertebrates were sampled according to a specific in situ design. We created a 50-point
153 random sampling grid for each sampling campaign by randomly generating spatial coordinates
154 according to the width and the length of the stream sections. In the field, grid points were identified
155 by placing marked stones on the riverbed (Figure 1b). We collected one macroinvertebrate sample at
156 each grid point, just upstream of each marked stone, using a Surber net (0.05 m² frame area; 500 µm
157 mesh). Each sample was preserved with 90% ethanol for laboratory sorting. At each point, flow
158 velocity and water depth were measured and the dominant mineral substrate characterized according

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3 159 to the size categories described by Buffagni and Erba (2007). Substrate data were converted from
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5 160 categorical to numeric by assigning the mean value of the size range to each category.
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8 161 We determined the total amount of Benthic Organic Matter (BOM) collected within the frame
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10 162 area of each Surber sample, including both coarse particulate organic matter (CPOM) and benthic
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12 163 algae. After removing macroinvertebrates, BOM was obtained by elutriation (Boulton & Lake, 1992),
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14 164 separating the organic fraction from the inorganic material. BOM was then passed through a 1 mm
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16 165 mesh sieve to retain only coarse particles. The sieved fraction was oven dried at 105°C until it reached
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20 166 a constant weight (approx. 3 d), then weighed.

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23 167 Macroinvertebrates were identified to family or genus level using Tachet, Richoux, Bournaud,
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25 168 and Usseglio-Polatera (2010) and each taxon counted. Such a taxonomic resolution can identify
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27 169 robust relationships with environmental variables in ecohydrological and ecological studies in river
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29 170 ecosystems (Guareschi et al., 2014; Heino & Soininen, 2007). Each taxon was also assigned to a
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31 171 functional feeding group (FFG, i.e. collectors, filterers, predators, scrapers and shredders) according
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33 172 to Ghetti (1997) and the abundance of each FFG calculated for each sample. Macroinvertebrates were
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35 173 dried and weighed to estimate bulk biomass per sample, following the same procedure as for BOM.
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43 175 **2.3 Data analysis**

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45 176 We used nMDS to visually compare variability in community composition among streams
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47 177 and seasons. Community metrics (univariate) and the community matrices (multivariate) were used
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49 178 to analyse the effects of spatial and environmental variables on macroinvertebrates distribution.
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52 179 The effects of spatial coordinates within each grid (x, y) and environmental variables (BOM,
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54 180 flow velocity, water depth and substrate size) on community metrics (taxon richness, abundance,
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56 181 biomass, biomass-abundance ratio – as an index of body size – and FFGs) were modelled with
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58 182 generalized additive models (GAMs). The smoothing function was applied to coordinates, to model
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3 183 spatial autocorrelation together with environmental variables. *Sampling campaign* was used both in
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5 184 the parametric part of the models and as grouping factor in the “*by*” option of the smoothing function,
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8 185 allowing a different smooth to be applied to each level of the grouping factor (Wood, 2017). The
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10 186 Restricted Maximum Likelihood method was used to estimate the smoothing parameter. Gaussian
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12 187 distributions were used for log-transformed metrics in GAMs.
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15 188 We modelled community composition in relation to measured environmental and spatial
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18 189 variables. The Bayesian joint species distribution approach of Hierarchical Modelling of Species
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20 190 Communities (HMSC; Ovaskainen et al. 2017) was applied to each sampling campaign. This
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22 191 framework represents a multi-taxa hierarchical generalized linear mixed model in which
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25 192 environmental variables are implemented as fixed effects, whereas spatial variables are implemented
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27 193 as spatially structured random effects. HMSC models the response of each taxon simultaneously and
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29 194 then partitions the variance explained by all environmental and spatial variables. We sampled the
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31 195 posterior distributions using the R-package HMSC (Tikhonov et al., 2020), with four Markov chain
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34 196 Monte Carlo (MCMC) chains sampled for 150,000 iterations per chain. We dropped the first 50,000
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36 197 samples of each chain as potentially transient, and thinned the remaining by 100, yielding 1000
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38 198 posterior samples per chain and hence 4000 in total. Because we analysed count data (i.e. the
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41 199 abundance of each taxon), we used a lognormal Poisson distribution for all campaigns. Rare taxa (i.e.
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43 200 abundance < 0.5% of all individuals, Nijboer & Verdonschot, 2004) were excluded from the analysis
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45 201 to avoid convergence problems due to zero-inflation. Model convergence was estimated with the
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48 202 Gelman-Rubin diagnostic. Following Tikhonov et al. (2020), we evaluated model fit with the pseudo-
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50 203 R^2 and Area Under Curve (AUC) statistics, computing both explanatory power (based on models
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52 204 fitted to all data) and predictive power (based on five-fold cross validation). The relative importance
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54 205 of spatial and environmental variables was assessed by means of variance partitioning, in which the
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57 206 contribution of each predictor (flow velocity, water depth, substrate, BOM and coordinates) to the
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3 207 explanatory power was computed for each taxon. Finally, the effects of biotic interactions were
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5 208 evaluated using residual correlations between taxa, after accounting for explanatory variables.
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8 209 All analyses were performed with the mgcv (Wood, 2019), HMSC (Tikhonov et al., 2020) and
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11 210 vegan (Oksanen et al., 2019) packages of the statistical software R (R Core Team, 2019). Bathymetric
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13 211 profiles for each sampling campaign and correlation plots were created using the plot3D (Soetaert,
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15 212 2019) and corrplot (Wei et al., 2017) R packages, respectively.
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18 213 19 20 21 214 **3 RESULTS**

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24 215 The bathymetric profiles of the sampled areas of the Parma, Enza and Nure streams in summer
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26 216 and winter are presented in Figure S1. Mean values of environmental variables for each sampling
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29 217 campaign are reported in Table 1. Water depth (summer: 23 ± 14 cm; winter: 27 ± 15 cm) and BOM
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31 218 (summer: 2.84 ± 6.63 g/m²; winter: 3.97 ± 13.09 g/m²) were higher in winter, whereas values of flow
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33 219 velocity (summer: 1.03 ± 0.94 m/s; winter: 1.10 ± 0.85 m/s) and substrate size (summer: 18 ± 17 cm;
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36 220 winter: 19 ± 18 cm) were comparable.
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39 221 A total of 29,363 organisms, belonging to 77 taxa were found, with Diptera and
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41 222 Ephemeroptera being the most abundant (33.3% and 32.6% respectively) and frequent (26.0% and
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43 223 27.9% respectively) orders. Mean taxon richness, total abundance, biomass and FFG abundances
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46 224 were higher during summer (Table 1). In contrast, the biomass-abundance ratio was higher in winter
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48 225 (Table 1) indicating that body size was larger in this season. Within each season, values of all metrics
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50 226 were similar among streams. NMDS ordinations (Figure S2) highlighted seasonal differences in
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52 227 community composition, with winter samples showing much greater compositional variability.
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55 228 Among-stream (within season) differences were weaker, with wide overlaps of the points in the
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57 229 ordination.
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3 230 Sampling campaign and the amount of BOM were the strongest determinants of all
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5 231 community metrics (Table 2). Indeed, for most metrics, we found higher values matching higher
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8 232 quantities of BOM. Contrarily, BOM had a negative effect on the biomass-abundance ratio (Figure
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10 233 2). The effect of other explanatory variables varied among metrics. Flow velocity and water depth
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12 234 had a positive and negative effect on both abundance and biomass, respectively, but were not related
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15 235 to taxon richness. In contrast, decreasing substrate size was associated with an increase in taxon
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17 236 richness, but had no effect on abundance or biomass. Variability in the biomass-abundance ratio was
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19 237 mainly explained by sampling campaign. Water depth was associated with a decrease in collector
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22 238 abundance, and scraper and filterer abundances increased with flow velocity. The influence of
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24 239 coordinates on metrics varied among sampling campaigns, with stronger effects for the Enza stream
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26 240 during summer (Table 2).

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29 241 Pseudo-R² values varied between 0.23 and 0.72, and AUC varied from 0.76 to 0.91, with
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31 242 predictive power being lower than explanatory power in all cases, indicating good model performance
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34 243 (Table 3). Variance partitioning highlighted considerable variability in the main drivers of community
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36 244 composition among rivers, seasons and taxa (Figure 3). BOM was one of the most relevant
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38 245 environmental covariates, accounting up to 39% of the total mean explained variance (Figure 3a),
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41 246 increasing to over 80% for individual taxa (Orthocladinae; Figure 3a). However, its influence
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43 247 decreased to a minimum of 11% during winter (Figure 3d), when hydraulic variables (flow velocity,
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45 248 water depth and substrate size) became dominant, explaining up to 78% of variance. Spatial
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48 249 coordinates were also an important driver of community composition, accounting for up to 36% of
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50 250 the total explained variance (Figure 3a). The explanatory power of spatial coordinates was higher
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52 251 during summer (Figure 3a-c) than in winter (Figure 3d-f). Considering the explanatory power of
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54 252 covariates for each taxon among sampling campaigns, we found a good consistency of results,
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57 253 especially within seasons. For example, for the *Baetis* mayfly (Baetidae), spatial and hydraulic
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59 254 variables were the dominant influences during summer and winter, respectively. Residual correlation
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3 255 plots (Figure 4) showed mainly positive associations between taxa, with high levels of taxa co-
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5 256 occurrence, especially during summer campaigns (Figure 4a-c). During winter campaigns, co-
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7 257 occurrence among taxa was lower, absent, or even negative (Figure 4d-f).
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10 11 258 12 13 14 259 **4 DISCUSSION**

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17 260 Few studies to date have applied metacommunity theories to the microdistribution of aquatic
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19 261 macroinvertebrates, or quantified the relative roles of spatial and environmental drivers in structuring
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21 262 these communities (Tolonen et al., 2017). Our results highlight strong effects of both environmental
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23 263 and spatial variables on the micro-scale distribution of macroinvertebrates, with their relative
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25 264 importance varying among seasons and among taxa. We found that the microdistribution of
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27 265 macroinvertebrates is mainly driven by BOM and spatial variables during summer, and by hydraulic
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29 266 variables (flow velocity, water depth and substrate size) during winter. In the context of
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31 267 metacommunity dynamics, these results highlight that both species sorting and mass effects
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33 268 concurrently shape the micro-scale distribution of macroinvertebrate communities.
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38 269 39 40 41 270 **4.1 The role of environmental filtering**

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43 271 The amount of BOM had a strong effect on macroinvertebrate communities, with significant
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45 272 relationships highlighted both by GAMs and variance partitioning. Taxon richness, abundance,
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47 273 biomass and the abundance of each FFG were positively correlated with the quantity of BOM. These
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49 274 results are consistent with many previous studies (e.g. Fenoglio et al., 2005; Graça et al., 2004; Straka,
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51 275 Syrovátka, & Helešic, 2012), although relationships between assemblages and organic matter can be
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53 276 weaker than for physical habitat features (Braccia & Voshell 2006). Our results highlight that the
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55 277 BOM-macroinvertebrate relationship persists in both summer and winter and can be ascribed to two
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57 278 main functions of BOM: provision of food resources and of instream habitat.
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3 279 BOM is an established trophic resource in lotic ecosystems (e.g. Dudgeon & Wu, 1999; Graça
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5 280 et al., 2004; Richardson, 1992; Tank, Rosi-Marshall, Griffiths, Entekin, & Stephen, 2010), where its
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7 281 micro-scale distribution is driven by a combination of several factors, including the preceding
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10 282 hydrological conditions, velocity and turbulence of the flow, channel morphology and water depth
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12 283 (Bastias et al., 2020; Martinez, Velasco, Suarez, & Vidal-Abarca, 1998). Macroinvertebrates play a
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14 284 key role in decomposing allochthonous organic matter (Fenoglio et al., 2005) and their distribution
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17 285 is strictly related to BOM availability (Straka et al., 2012). The presence of BOM can also promote
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19 286 the retention of fine particulate organic matter (Eggert, Wallace, Meyer, & Webster, 2012) and can
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21 287 thus affect macroinvertebrates trophic habits. BOM, including algal mats and allochthonous detritus,
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24 288 can also support benthic invertebrate communities by providing habitat as well as a refuges from the
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26 289 current, predators and drying (Haapala, Muotka, & Laasonen, 2003; Merten, Snobl, & Wellnitz, 2014;
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28 290 Stubbington & Datry, 2013). Moreover, BOM can simultaneously act as a food resource and habitat
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31 291 (Straka et al., 2012). We found a strong correlation between almost all community metrics and BOM,
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33 292 including evidence that BOM functions both as a feeding and habitat resource. The amount of BOM
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35 293 was also a key determinant of community composition, explaining nearly all variance in the
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37 294 distribution of some taxa (e.g. Orthoclaadiinae and Chironominae in the Parma summer campaign,
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40 295 Hydroptilidae in the Nure summer campaign). Moreover, in our study, BOM included both algal mats
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42 296 and allochthonous detritus, the latter providing food for shredders while algal mats represent a habitat
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44 297 for macroinvertebrates in multiple FFGs (Hansen, Sagerman, & Wikström, 2010). The relationship
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47 298 between the biomass-abundance ratio and BOM suggests that BOM also acted as a refuge: we
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49 299 recorded high densities of small organisms including early instar insects in extensive BOM masses,
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51 300 potentially protecting them from predation and/or drift (Chester & Robson, 2011). Equally, the
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54 301 retention of more fine particulate organic matter by higher BOM quantities (Lepori, Palm, &
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56 302 Malmqvist, 2005) could provide feeding resources for higher densities of small individuals.
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3 303 Other environmental variables also affected macroinvertebrate patterns; however, these
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5 304 relationships were weaker and metric-dependent. Flow velocity, for instance, was a good predictor
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8 305 of total abundance, biomass and the abundance of some FFGs (collectors, scrapers and filterers).
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10 306 Variance partitioning highlighted the dominance of hydraulic variables (i.e. flow velocity, water
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12 307 depth and substrate size) in structuring community during winter. This could be the effect of winter
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14 308 high flows, during which velocity and depth peak, exceeding the niche breadth of some
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17 309 macroinvertebrate taxa, thus limiting their distribution (Lancaster, Buffin-Bélanger, Reid, & Rice,
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19 310 2006; Lancaster, Downes, & Glaister, 2009; Vilmi, Tolonen, Karjalainen, & Heino, 2019).
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22 311 Collectively, our results highlight the influence of species sorting mechanisms (sensu Leibold
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24 312 et al., 2004) on the microdistribution of aquatic macroinvertebrates. This influence may reflect
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27 313 environmental filtering processes (Tolonen et al., 2018), with instream variation in BOM, flow
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29 314 velocity, depth and substrate size affecting both taxonomic and functional metrics as well as
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31 315 community structure. Our results also suggest that the importance of species sorting mechanisms –
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34 316 and the variables triggering these mechanisms – vary seasonally. In summer, macroinvertebrate
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36 317 distributions are influenced by trophic variables, notably BOM, whereas in winter, species sorting is
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38 318 mediated by hydraulic variables such as flow velocity, water depth and substrate size. As well as this
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41 319 selection by environmental conditions, the observed patterns of species sorting may reflect complex
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43 320 interplay between microhabitat characteristics and biotic interactions (García-Girón, Heino,
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45 321 García-Criado, Fernández-Aláez, & Alahuhta, 2020). Regardless of the source of species sorting, the
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47 322 strong relationship observed between environmental variables and some community characteristics
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50 323 can be used to inform management actions that support communities by enhancing micro-scale
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52 324 habitat variability (Cadotte & Tucker, 2017).
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4.2 The role of space

Our results indicate that spatial variables are an important driver of macroinvertebrate microdistribution, with community composition varying depending on the position inside the riverbed. Similar results have been found for a large lake system in Finland, where macroinvertebrate communities were affected by micro-scale spatial variables (Vilmi, Karjalainen, Nokela, Tolonen, & Heino, 2016). Conversely, Rezende, Santos, Henke-Oliveira, and Gonçalves Jr (2014) suggested that spatial variables have little influence on local-scale community patterns, but the scale considered was larger than in our study, and encompassed both pristine and impacted areas.

In our study, variance partitioning highlighted a stronger effect of spatial variables on community structure in summer, when they explained up to 70% of the variance for taxa including the genera *Esolus* (Elmidae), *Ephemerella* (Ephemerellidae) and *Ecdyonurus* (Heptageniidae). Spatial variables had little explanatory power in winter, probably due to the increased influence of hydraulic variables, which drove environmental filtering of communities. The residual correlation among taxa indicated a strong co-occurrence in summer campaigns, with most taxa co-occurring at individual sampling points. This could indicate the aggregation of consumers (Lancaster et al., 2009) in resource-rich patches, that in our study included areas in which high amounts of BOM both provided food and acted as a habitat and refuge.

Habitat contraction could also be an influence for high taxa co-occurrence in the summer campaigns, in which riffle crests and near shoreline habitats were exposed during the summer low discharge period (Stubbington, Wood, & Reid, 2011). High levels of co-occurrence among taxa can also reflect low environmental heterogeneity (Heino, 2013). This could be influential in the Parma and Nure streams during the summer campaigns, for which bathymetric profiles show relatively low morphological heterogeneity and we found higher values of taxa co-occurrence. On the contrary, for the other sampling campaigns, the higher spatial heterogeneity of the riverbeds could hamper the movement of macroinvertebrates and thus increase taxa segregation (Heino, 2013; Lancaster et al.,

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3 351 2006). In addition, spatial patterns reflecting the position of oviposition sites such as emergent rocks
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5 352 can persist in larval stages, especially in early instars, generating clumped distributions of organisms
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8 353 (Lancaster & Downes, 2014). If these larvae attract predators, clumped distributions may span trophic
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10 354 levels, contributing to the community patterns observed in our summer campaigns (Muotka, 1993).
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12 355 Alternatively, the observed co-occurrence pattern could reflect a shared response to environmental
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14 356 variables not measured in this study (Ovaskainen et al., 2017). Co-occurrences could also be
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17 357 explained by our exclusion of rare taxa, whose distributions could be more stochastic (Roque et al.,
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19 358 2016), whereas common taxa may occur at most sampling points but at different abundances, which
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22 359 are modulated by habitat preferences (Burgazzi et al., 2018).

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24 360 From a metacommunity perspective, our results suggest that mass effects can also operate at
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27 361 micro scales, and that their importance varies seasonally. In summer, environmental conditions in
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29 362 mountain streams can be less limiting for macroinvertebrates and instream dispersal rates can be high
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31 363 (Vilmi et al., 2019), allowing organisms to coexist even in positions in which they are inferior
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34 364 competitors (Leibold & Chase, 2018). Organisms' presence and abundance in each habitat patch (i.e.
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36 365 sampling point) result from multiple interacting factors, including prior oviposition choices
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38 366 (Lancaster & Downes, 2014) and drift from upstream (Lancaster & Belyea, 2006). However,
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41 367 disregarding such colonization mechanisms, individual taxa may become locally abundant in habitats
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43 368 matching their environmental preferences, and then spread to nearby areas with sub-optimal
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45 369 conditions (He et al., 2020). Higher abundances recorded during summer may enhance organisms'
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48 370 spread, triggering such mass effects. In contrast, during winter, when hydraulic conditions can
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50 371 become harsher, organisms are less abundant and their distributions are more environmentally driven.
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52 372 Accordingly, residual correlation between taxa decreased, signifying reduced co-occurrence. As
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54 373 observed during the Parma stream winter campaign, negative co-occurrence can occur together with
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57 374 taxa coexistence. For example, *Leuctra* (Leuctridae), *Brachyptera* (Taeniopterygidae) and
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59 375 *Rhithrogena* (Heptageniidae) had similar distribution patterns which differed from those of
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3 376 Hydroptilidae. These contrasting distributions may reflect consumptive competition (sensu Schoener,
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5 377 1983), but could also be due to shared (or opposing) responses to unmeasured environmental variables
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8 378 (Ovaskainen et al., 2017) and/or to similar habitat requirements of different taxa (e.g. Lencioni &
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10 379 Rossaro, 2005; Puntí, Rieradevall, & Prat, 2009).
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16 381 **4.3 Transferability of results among streams and seasons**

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18 382 The influence of specific abiotic variables on individual taxa depended on factors including
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21 383 stream and season. This supports the idea that a system's local features alter the relative influence of
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23 384 spatial and environmental factors, and therefore of mass effects versus species sorting mechanisms.
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25 385 However, the ranges of variability in environmental factors also affect their relationships with both
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28 386 community composition and individual taxa. Abiotic variables that display strong gradients reaching
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30 387 values that exceed the tolerances of some taxa represent limiting factors. Equally, an environmental
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32 388 variable with a narrow range might not be tracked by biota if it does not represent a limiting factor
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34 389 (Lancaster et al., 2006, 2009). The divergence in organisms' responses (e.g. the *Baetis* mayfly) could
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37 390 reflect the taxonomic resolution studied; for example, different species within one genus could
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39 391 respond to different drivers (Jiang et al., 2013; Monk et al., 2012). Increasing the taxonomic
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41 392 resolution from family or genus to species could thus further advance our understanding of
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44 393 microdistribution patterns of macroinvertebrates.

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47 394 Community metrics and structure responded in different ways to the spatial and environmental
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49 395 drivers, with community structure being more dependent on spatial variables than single metrics. This
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51 396 can be explained by taxa replacement: comparable instream positions can be occupied by different
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53 397 taxa with comparable functional roles (Smith & Lundholm, 2010), influencing community
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56 398 composition but not the metrics we studied.

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5 CONCLUSIONS

Our study represents one of the first attempts to disentangle abiotic and biotic drivers regulating the microdistribution of aquatic macroinvertebrates, explicitly incorporating spatial variables as covariate. Based on our results, micro-scale macroinvertebrate distributions were mainly driven by BOM in summer and by hydraulic factors in winter, indicating that environmental variables exerted a strong control. However, environmental filtering was less dominant than expected in our initial hypothesis, and it ultimately depended on the features of the systems (Bond, Perry, & Downes, 2000; Lancaster & Belyea, 2006). The latter can affect microhabitat selection and the possible prevalence of biotic interactions and stochastic processes in shaping macroinvertebrate communities. In this regard, our work provides information about the relative role of spatial variables in shaping macroinvertebrates communities and potential underlying mechanisms, but additional research is needed about how community composition varies among habitat patches at the micro spatial scale and how these changes relates with spatial distance.

Regarding our first aim, we verified that metacommunity concepts are relevant even at micro spatial scales. We showed that community processes including environmental filtering, dispersal limitation and biotic interactions shape the distribution of organisms at the patch level. Since the introduction of the metacommunity framework (Leibold et al., 2004), several studies have analysed communities from the perspective of metacommunity paradigms (e.g. Diggins & Newman, 2009; Rezende et al., 2014; Vilmi et al., 2016), by investigating the roles of environmental conditions and dispersal/spatial processes. Some of these studies have recognized that metacommunity paradigms are not mutually exclusive (Cottenie, 2005; Rocha et al., 2018; Tolonen et al., 2018). Our findings support this perspective, demonstrating that both species sorting and mass effects can describe the micro-scale organization of communities, with seasonal changes in their relative importance. Our results provide insight into ecological dynamics in rivers, which may be useful beyond ecological

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424 research in applied contexts including restoration ecology, habitat suitability modelling and
425 biomonitoring.

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436 **DATA AVAILABILITY STATEMENT**

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

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716 TABLES

717

718 **TABLE 1** Mean \pm standard deviation of environmental variables (flow velocity, water depth,
 719 substrate size and BOM) and macroinvertebrate community metrics (taxon richness, abundance,
 720 biomass, biomass-abundance ratio and functional feeding groups) during the summer and winter
 721 sampling campaigns in the Parma, Enza and Nure streams.

	Summer			Winter		
	Parma	Enza	Nure	Parma	Enza	Nure
Flow velocity (<i>m/s</i>)	0.15 ± 0.14	0.45 ± 0.35	0.34 ± 0.25	0.23 ± 0.20	0.38 ± 0.30	0.38 ± 0.24
Water depth (<i>cm</i>)	20 ± 9	32 ± 18	17 ± 7	25 ± 16	26 ± 12	31 ± 18
Substrate size (<i>cm</i>)	15 ± 12	23 ± 22	16 ± 13	12 ± 13	33 ± 20	12 ± 12
BOM (<i>g/m²</i>)	2.04 ± 3.21	1.80 ± 1.87	4.68 ± 10.71	2.77 ± 6.46	6.36 ± 19.02	2.78 ± 10.44
Taxon richness (<i>taxa/m²</i>)	312 ± 94	300 ± 79	282 ± 68	150 ± 60	142 ± 83	96 ± 54
Abundance (<i>ind./m²</i>)	2868 ± 2478	3364 ± 2788	3306 ± 3024	498 ± 555	1493 ± 1801	215 ± 155
Biomass (<i>g/m²</i>)	0.81 ± 0.61	0.72 ± 0.61	0.83 ± 0.40	0.50 ± 0.25	0.70 ± 1.05	0.38 ± 0.16
Biomass-abundance ratio (<i>mg per ind.</i>)	0.45 ± 0.46	0.28 ± 0.18	0.35 ± 0.19	1.38 ± 0.66	0.63 ± 0.45	2.55 ± 1.90
Collectors (<i>ind./m²</i>)	1322 ± 1240	1852 ± 2123	1853 ± 1534	31 ± 45	137 ± 195	27 ± 41
Filterers (<i>ind./m²</i>)	168 ± 154	258 ± 299	524 ± 612	18 ± 40	171 ± 439	24 ± 44
Predators (<i>ind./m²</i>)	561 ± 513	686 ± 534	172 ± 209	70 ± 63	58 ± 92	88 ± 91
Scrapers (<i>ind./m²</i>)	455 ± 564	359 ± 359	564 ± 938	288 ± 457	1088 ± 1355	70 ± 61
Shredders (<i>ind./m²</i>)	340 ± 359	178 ± 217	184 ± 399	93 ± 114	30 ± 75	6 ± 14

722 *Abbreviation:* BOM, benthic organic matter.

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724 **TABLE 2** Results (expressed as F-values) of generalized additive models (GAMs), testing the effect of sampling campaign, environmental
 725 variables (flow velocity, water dept, substrate size and BOM) and spatial coordinates (x and y within each grid) on macroinvertebrate community
 726 metrics (taxon richness, abundance, biomass, biomass/abundance ratio and functional feeding groups). Significant results are indicated in bold.
 727 Community metrics were log-transformed using the natural logarithm.

	Residual degrees of freedom	Sampling campaign	Flow velocity		Water depth		Substrate size		BOM			s(x,y)				
		F-value	sign	F-value	sign	F-value	sign	F-value	sign	F-value	P_s	E_s	N_s	P_w	E_w	N_w
<i>Taxon richness</i>	267.49	51.87	+	1.10	-	3.66	-	10.19	+	41.65	1.13	1.56	0.45	1.51	7.38	1.59
<i>Abundance</i>	262.76	52.59	+	14.20	-	9.00	+	0.27	+	34.24	2.48	4.55	0.55	1.13	3.98	0.25
<i>Biomass</i>	264.70	7.09	+	20.48	-	6.30	-	0.42	+	51.61	2.48	7.49	0.74	1.04	3.32	2.63
<i>Biomass/abundance</i>	265.27	62.88	-	1.03	+	3.02	-	2.20	-	3.50	2.16	2.81	0.42	2.23	1.93	1.31
<i>Shredders</i>	262.17	40.32	-	0.14	-	0.17	-	7.64	+	46.82	0.90	3.21	0.21	1.35	3.34	2.26
<i>Collectors</i>	266.18	97.50	+	8.55	-	12.08	-	0.56	+	15.67	1.38	2.50	0.21	1.36	1.55	1.51
<i>Scrapers</i>	258.59	27.81	+	11.03	-	0.30	+	0.15	+	17.24	2.07	2.01	0.37	1.85	1.60	2.73
<i>Filterers</i>	263.96	36.90	+	12.01	-	0.39	-	0.57	+	21.15	0.27	2.18	1.22	14.54	2.26	3.00
<i>Predators</i>	260.53	31.03	-	2.22	+	1.15	-	0.76	+	26.04	6.35	3.20	0.00	1.75	1.86	1.59

728 *Abbreviations:* BOM, benthic organic matter; E_s, Enza stream summer campaign; E_w, Enza stream winter campaign; N_s, Nure stream summer campaign;
 729 N_w, Nure stream winter campaign; P_s, Parma stream summer campaign; P_w, Parma stream winter campaign; s(x,y), coordinates with smoothing function.

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730 **TABLE 3** Explanatory and predictive power of the HMSC model fitted for each sampling campaign,
731 measured as pseudo-R² and AUC. Explanatory power is based on a model fitted to all data, and
732 predictive power is based on five-fold cross validation.

Season	Stream	Explanatory power		Predictive power	
		pseudo-R ²	AUC	pseudo-R ²	AUC
Summer	Parma	0.72	0.91	0.42	0.83
	Enza	0.68	0.89	0.50	0.81
	Nure	0.70	0.87	0.50	0.79
Winter	Parma	0.35	0.86	0.23	0.76
	Enza	0.58	0.88	0.41	0.80
	Nure	0.35	0.87	0.25	0.81

733 *Abbreviations:* AUC, area under curve; HMSC, hierarchical modelling of species communities

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3 **735 FIGURE CAPTIONS**

6 **736 FIGURE 1** (a) The Nure, Parma and Enza stream basins; black dots indicate sampling stations; the
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8 **737** inset shows the location of the study area in Italy; (b) Scheme of the sampling design; black dots
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11 **738** represent 50 randomly generated sampling points within a grid, with positions varying depending on
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13 **739** sampling campaign. The x-axis is parallel to the stream and the y-axis crosses the stream.

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16 **740**
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18 **741 FIGURE 2** Relationship between the biomass-abundance ratio, an indicator of body size in which
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20 **742** higher values indicate larger body sizes and the amount of benthic organic matter (BOM). All values
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23 **743** were log-transformed using the natural logarithm.

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26 **744**
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28 **745 FIGURE 3** Variance partitioning bar plots for taxa recorded in each sampling campaign. Each bar
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30 **746** corresponds to a single taxon, and different colours within the bars correspond to the proportion of
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32 **747** variation explained by different environmental and spatial variables. Vel = flow velocity (m/s), depth
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35 **748** = water depth (cm), sub = mean substrate size (cm), BOM = dry weight of benthic organic matter
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37 **749** (g/m²), space = spatial coordinates (included as a spatially structured random effect).

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40 **750**
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43 **751 FIGURE 4** Association plots for residual correlations among common taxa after accounting for the
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45 **752** effect of measured explanatory variables, for each sampling campaign. The chromatic scale
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48 **753** represents pairwise residual correlation values between taxa, with dark red and dark blue indicating
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50 **754** correlation values of -1, and +1, respectively. Only those residual correlations that are positive or
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52 **755** negative with at least 0.90 posterior probability are shown.

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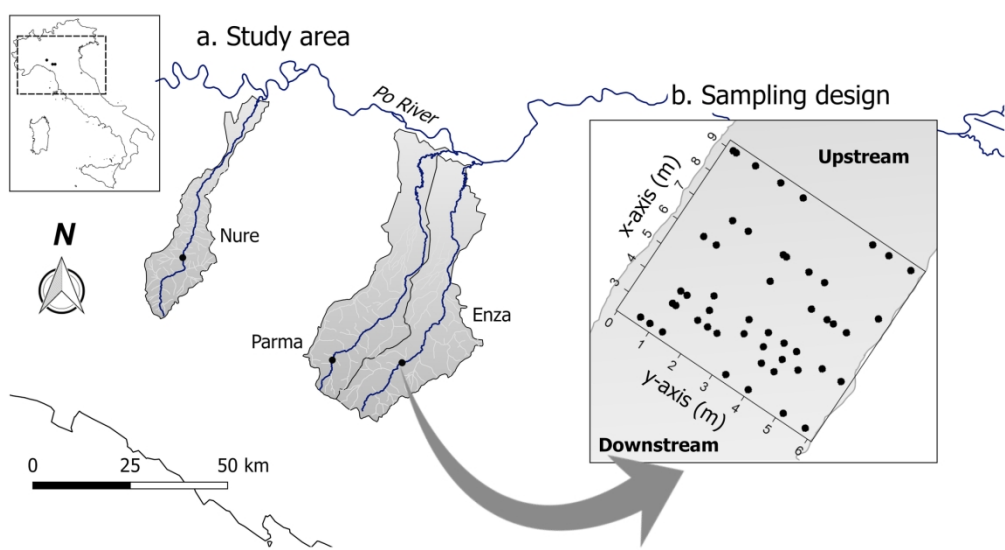


FIGURE 1 (a) The Nure, Parma and Enza stream basins; black dots indicate sampling stations; the inset shows the location of the study area in Italy; (b) Scheme of the sampling design; black dots represent 50 randomly generated sampling points within a grid, with positions varying depending on sampling campaign. The x-axis is parallel to the stream and the y-axis crosses the stream.

180x127mm (300 x 300 DPI)

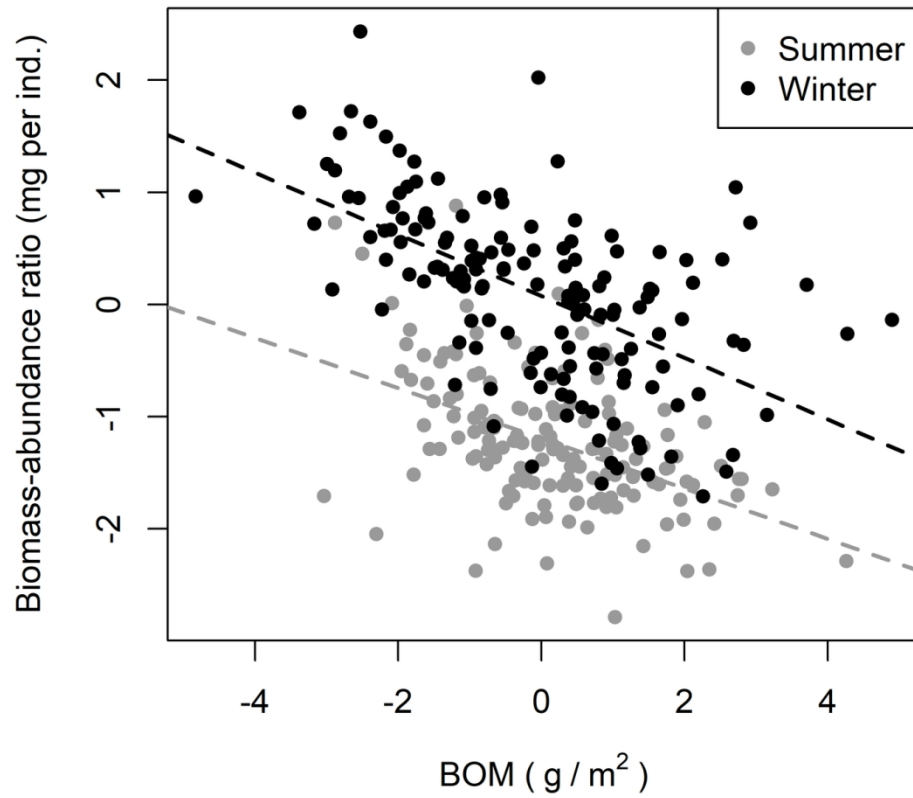


FIGURE 2 Relationship between the biomass-abundance ratio, an indicator of body size in which higher values indicate larger body sizes and the amount of benthic organic matter (BOM). All values were log-transformed using the natural logarithm.

127x127mm (300 x 300 DPI)

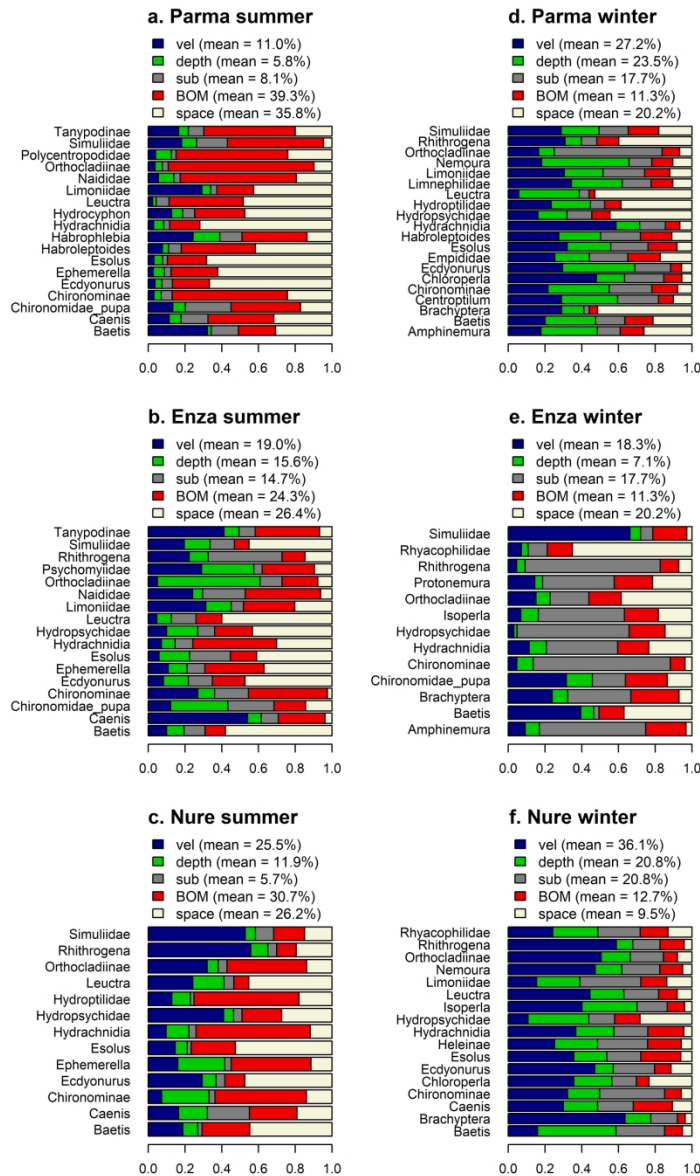


FIGURE 3 Variance partitioning bar plots for taxa recorded in each sampling campaign. Each bar corresponds to a single taxon, and different colours within the bars correspond to the proportion of variation explained by different environmental and spatial variables. Vel = flow velocity (m/s), depth = water depth (cm), sub = mean substrate size (cm), BOM = dry weight of benthic organic matter (g/m²), space = spatial coordinates (included as a spatially structured random effect).

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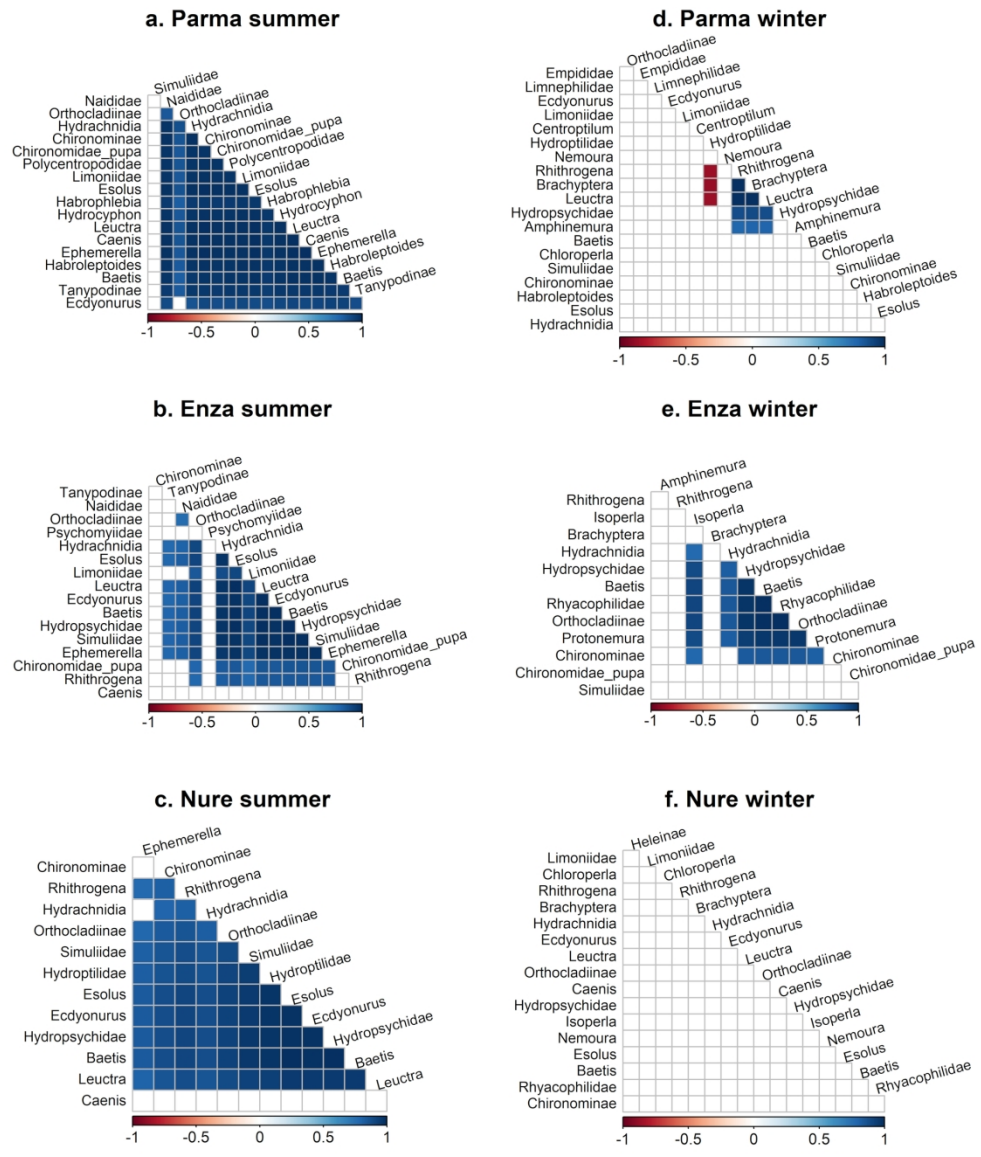


FIGURE 4 Association plots for residual correlations among common taxa after accounting for the effect of measured explanatory variables, for each sampling campaign. The chromatic scale represents pairwise residual correlation values between taxa, with dark red and dark blue indicating correlation values of -1, and +1, respectively. Only those residual correlations that are positive or negative with at least 0.90 posterior probability are shown.

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1 SUPPORTING INFORMATION

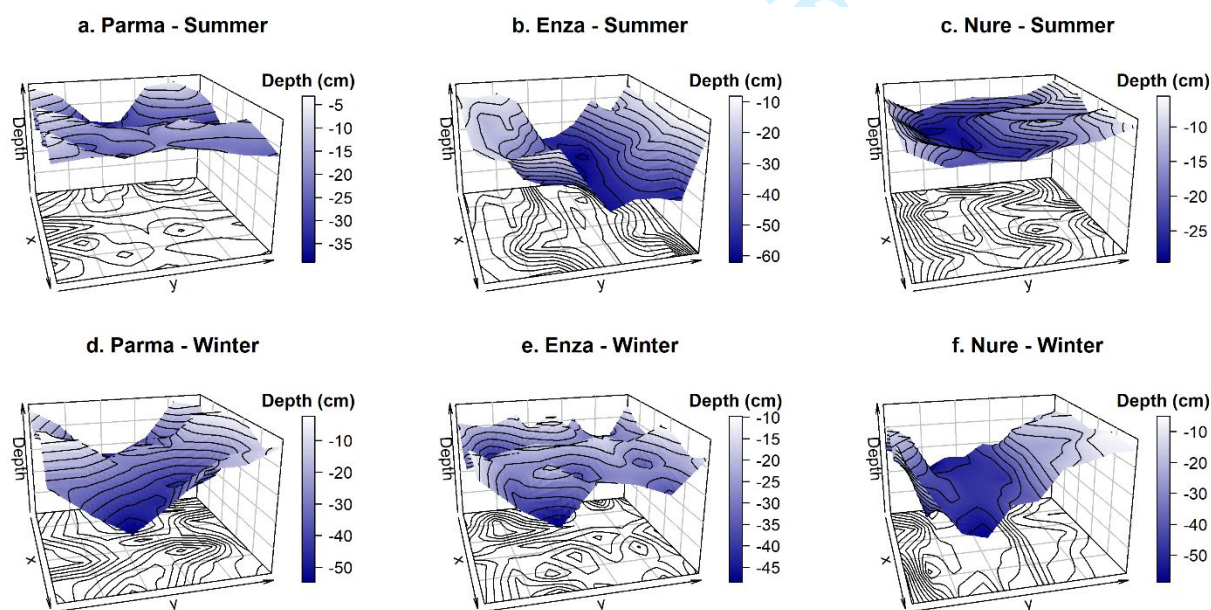
2 Additional supporting information may be found online in the Supporting Information section at the end of
3 this article.

6 **TABLE S1** Main features of the Parma, Nure and Enza streams.

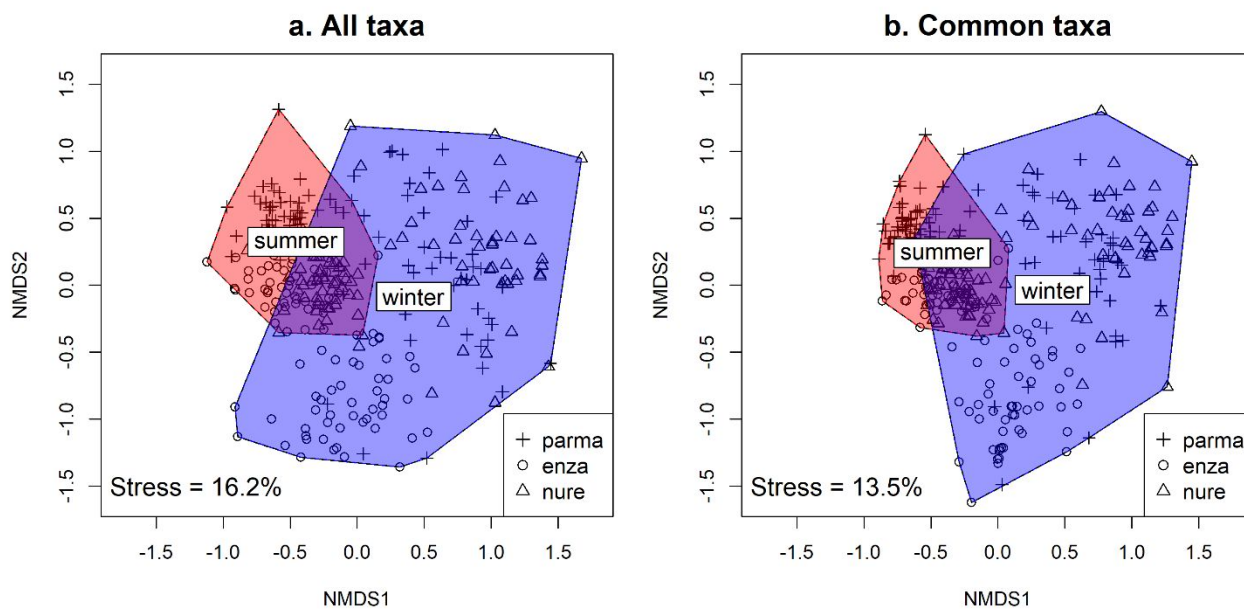
Stream	L	D	A	t	h
<i>Parma</i>	104	11	815	10SS2N	661
<i>Enza</i>	97	12	890	10SS2N	409
<i>Nure</i>	77	15	431	10SS3N	440

7 *Abbreviations:* A, basin area (km²); D, mean annual discharge (m³/s); h, station altitude (m a.s.l.); L, total
8 length (km); t, Italian river typology (according to Ministerial Decree 260/2010).

10 **FIGURE S1** Bathymetric profiles of the sampled sections of Parma, Enza and Nure Streams during
11 summer (a-c) and winter (d-f). Darker blue colours indicate greater depths.



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3 14 **FIGURE S2** Non-metric multidimensional scaling (nMDS) ordinations of communities, including
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5 15 (a) all taxa and (b) only common taxa (i.e. abundance > 0.5%). Sampling season (summer, winter) is
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7 16 represented by red and blue polygons, respectively. Streams are marked with plotting symbols. Stress
8
9 17 values are also reported.



Review