

Effect of microhabitats, mesohabitats and spatial position on macroinvertebrate communities of a braided river

Original

Effect of microhabitats, mesohabitats and spatial position on macroinvertebrate communities of a braided river / Burgazzi, G., Vezza, P., Negro, G., Astegiano, L., Pellicanó, R., Pinna, B., Viaroli, P., Laini, A.. - In: JOURNAL OF ECOHYDRAULICS. - ISSN 2470-5365. - STAMPA. - 6:2(2021), pp. 95-104. [10.1080/24705357.2021.1938254]

Availability:

This version is available at: 11583/2924802 since: 2021-09-20T17:39:17Z

Publisher:

Taylor & Francis

Published

DOI:10.1080/24705357.2021.1938254

Terms of use:

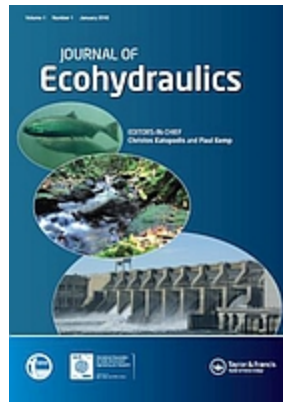
This article is made available under terms and conditions as specified in the corresponding bibliographic description in the repository

Publisher copyright

Taylor and Francis postprint/Author's Accepted Manuscript con licenza CC by-nc-nd

This is an Accepted Manuscript version of the following article: Effect of microhabitats, mesohabitats and spatial position on macroinvertebrate communities of a braided river / Burgazzi, G., Vezza, P., Negro, G., Astegiano, L., Pellicanó, R., Pinna, B., Viaroli, P., Laini, A.. - In: JOURNAL OF ECOHYDRAULICS. - ISSN 2470-5365. - STAMPA. - 6:2(2021), pp. 95-104. [10.1080/24705357.2021.1938254]. It is deposited under the

(Article begins on next page)



Exploring the role of microhabitat and mesohabitat in structuring macroinvertebrate communities

Journal:	<i>Journal of Ecohydraulics</i>
Manuscript ID	TJoE-2020-0035
Manuscript Type:	Short Communication
Date Submitted by the Author:	30-Jun-2020
Complete List of Authors:	Burgazzi, Gemma; University of Parma, Department of Chemistry, Life Sciences and Environmental Sustainability Veza, Paolo; Politecnico di Torino, Department of Environment, Land and Infrastructure Engineering Negro, Giovanni; Politecnico di Torino, Department of Environment, Land and Infrastructure Engineering Astegiano, Luca; Politecnico di Torino, Department of Environment, Land and Infrastructure Engineering Pellicanó, Riccardo; Politecnico di Torino, Department of Environment, Land and Infrastructure Engineering Pinna, Beatrice; Politecnico di Torino, Department of Environment, Land and Infrastructure Engineering Viaroli, Pierluigi; University of Parma, Department of Chemistry, Life Sciences and Environmental Sustainability Laini, Alex; University of Parma, Department of Chemistry, Life Sciences and Environmental Sustainability
Keywords:	mesohabitat, microhabitat, habitat suitability models, braided rivers, variance partitioning, habitat filtering
Abstract:	Habitat modelling aims to predict changes in the structure of aquatic communities as a function of habitat availability. It is a primary tool to inform management actions and to search for the best compromise between biodiversity conservation and water supply. The construction of these models requires in-depth knowledge of the main hydrological and geomorphological drivers affecting local communities. However, determining which investigation scale is the best trade-off between model accuracy and model transferability is also a top priority. The present work aims at establishing the basis for the application of mesoscale habitat modelling for aquatic macroinvertebrates, through testing the effect of microhabitat (flow velocity, water depth and

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

	<p>substrate), mesohabitat (riffles, glides, backwaters and isolated ponds) and spatial position on macroinvertebrate community variability. Multivariate spatial analyses have been used to analyze macroinvertebrate data collected in a braided reach of Trebbia River (Northern Italy). Mesohabitat resulted a good predictor for macroinvertebrate distribution, with a clear differentiation in community composition. However, also microhabitat and spatial position exerted a non-negligible effect on macroinvertebrates metrics and community structure. Collectively, the outcomes of the present work highlight a transferability of results across mesohabitats, supporting the use of mesoscale modelling for macroinvertebrate distribution in braided rivers.</p>



1
2
3 1 **Exploring the role of microhabitat and mesohabitat in structuring**
4
5
6 2 **macroinvertebrate communities**
7

8
9 3 Gemma Burgazzi^{*}, Paolo Vezza^b, Giovanni Negro^b, Luca Astegiano^b, Riccardo Pellicanó^b, Beatrice
10
11 4 Pinna^b, Pierluigi Viaroli^a and Alex Laini^a
12

13
14 5 *^aDepartment of Chemistry, Life Sciences and Environmental Sustainability, University of Parma,*
15
16 6 *Parma, Italy; ^bDepartment of Environment, Land and Infrastructure Engineering, Polytechnic*
17
18 7 *University of Turin, Turin, Italy*
19
20

21
22 8
23
24
25 9 *corresponding author
26

27
28 10 Gemma Burgazzi, Department of Chemistry, Life Sciences and Environmental Sustainability,
29
30 11 University of Parma, Parco Area delle Scienze 33/A, 43124, Parma, Italy.
31

32
33 12 gemma.burgazzi@unipr.it
34
35

36 13
37
38
39 14 **Abstract**
40

41
42 15 Habitat modelling aims to predict changes in the structure of aquatic communities as a function of
43
44 16 habitat availability. It is a primary tool to inform management actions and to search for the best
45
46 17 compromise between biodiversity conservation and water supply. The construction of these models
47
48 18 requires in-depth knowledge of the main hydrological and geomorphological drivers affecting local
49
50 19 communities. However, determining which investigation scale is the best trade-off between model
51
52 20 accuracy and model transferability is also a top priority. The present work aims at establishing the
53
54 21 basis for the application of mesoscale habitat modelling for aquatic macroinvertebrates, through
55
56 22 testing the effect of microhabitat (flow velocity, water depth and substrate), mesohabitat (riffles,
57
58 23 glides, backwaters and isolated ponds) and spatial position on macroinvertebrate community
59
60

1
2
3 24 variability. Multivariate spatial analyses have been used to analyze macroinvertebrate data collected
4
5 25 in a braided reach of Trebbia River (Northern Italy). Mesohabitat resulted a good predictor for
6
7 26 macroinvertebrate distribution, with a clear differentiation in community composition. However, also
8
9
10 27 microhabitat and spatial position exerted a non-negligible effect on macroinvertebrates metrics and
11
12 28 community structure. Collectively, the outcomes of the present work highlight a transferability of
13
14 29 results across mesohabitats, supporting the use of mesoscale modelling for macroinvertebrate
15
16
17 30 distribution in braided rivers.
18
19

20 31
21
22
23 32 **Keywords:** mesohabitat, microhabitat, habitat suitability models, braided rivers, variance
24
25 33 partitioning, habitat filtering.
26
27
28 34
29
30
31 35

34 36 **Introduction**

37 37 Developing tools for predicting spatial variability in distribution and abundance of organisms based
38
39 38 on their habitat requirement is of primary importance in ecology (Lancaster et al. 2009), both to
40
41 39 develop the best conservation strategies and to support streams ecological management (Dolédec et
42
43 40 al. 2007). Physical habitat models have been largely used to predict changes in aquatic communities
44
45 41 (fish and macroinvertebrates) as a consequence of changes in habitat availability (Dolédec et al. 2007)
46
47 42 and therefore to assess environmental flow requirements (Shearer et al. 2015). The construction of
48
49 43 these models requires to deeply understand which are the main hydrological and geomorphological
50
51 44 drivers affecting local communities. However, also determining which is the investigation scale
52
53 45 representing the best trade-off between model accuracy and model transferability is top priority
54
55 46 (Radinger et al. 2015), as this can affect sampling effort in terms of time- and resource-consumption.
56
57
58
59
60

1
2
3 47 Hydraulic microhabitat and substrate have been widely recognised as key drivers for aquatic
4
5 48 macroinvertebrates (Lancaster & Hildrew 1993; Rempel et al. 2000; Mérioux & Dolédec 2004;
6
7 49 Brooks et al. 2005). Flow velocity, water depth and substrate size can be highly variable over space
8
9
10 50 and time, thus creating a dynamic mosaic of different habitat patches. This is especially true in braided
11
12 51 rivers, where the high hydrological variability and sediment transport promotes local heterogeneity.
13
14 52 In a single river reach different hydro-morphological units occur together, covering the whole range
15
16
17 53 from lotic to lentic habitats (Gray & Harding 2009). Given their peculiar characteristics, braided
18
19 54 rivers can represent a unique model system to investigate the relationships occurring between
20
21 55 hydromorphology and macroinvertebrate communities. Indeed, their complexity allow the co-
22
23
24 56 occurrence of organisms with very different niche requirements (Robinson et al. 2002; Gray et al.
25
26 57 2006; Burgazzi et al. 2017).

27
28
29 58 This work aims at: 1) evaluate macroinvertebrate community variability (for composition and
30
31 59 structure) in different mesohabitats; and 2) quantify the relative role of the hydraulic microhabitats,
32
33
34 60 hydromorphological mesohabitats and spatial position in shaping communities. We predict a relevant
35
36 61 role of mesohabitats in shaping the distribution of aquatic macroinvertebrates in braided rivers.
37
38 62 Indeed, despite the strongly supported role of hydraulic microhabitat, some authors pointed out that
39
40 63 species can be present in places not predicted by their own auto-ecological requirements (e.g. Jowett
41
42 64 2003). In this perspective, mesohabitats allow to encompass larger ecological patterns, thus
43
44
45 65 improving the reliability of predictions (Parasiewicz & Walker 2007; Vezza et al. 2012).

46
47
48 66 The present work is done in the framework of the BENTHAB project, funded by the River Po Basin
49
50 67 Authority. The project aims to model the spatio-temporal habitat availability for aquatic
51
52 68 macroinvertebrates in large braided rivers, using the mesohabitat modelling approach MesoHABSIM
53
54
55 69 (Parasiewicz 2007; Parasiewicz et al. 2013). This methodology describes habitat availability for a
56
57 70 target species or community as a function of particular environmental features such as the river
58
59
60 71 discharge and hydro-morphological river characteristics.

72

73 **Materials and Methods**

74 ***Study area***

75 This study was performed in the Trebbia River, a right-side tributary of the Po River, in Northern
76 Italy (Figure 1). The climate of the Po plain is classified as temperate (Köppen Cfa/Cfb), with mean
77 annual precipitation of ~800 mm and mean temperature of 13 °C (Peel et al. 2007). Trebbia River
78 flows from the Northern Apennine to the Po River, for a total length of 118 km. Its annual discharge
79 is 21.2 m³/s (www.arpae.it), and it is characterized by periods of high discharge in spring and autumn
80 and low discharge (often with total dry out in the last section) in summer. After the Apennines-
81 lowland margin, the Trebbia riverbed widens, becoming multi-thread river system and creating a
82 mosaic of different hydro-morphological units in the main and secondary channels. The study site
83 (Canneto Sotto, 44°58'13.8"N 9°35'34.0"E, 102 m a.s.l.) is located within a lowland braided river
84 reach. Sampling have been performed over an area of approximately 0.75 km² (500 m wide and
85 1500 m long, Figure 1) in June 2019.

86 ***Field and laboratory protocol***

87 The river reach has been divided into several hydro-morphological units (i.e. mesohabitats),
88 belonging to the categories: riffle, glide, backwater and isolated pond. These mesohabitats are
89 characterized by a gradient of hydraulic conditions (from lotic to lentic) and connectivity. Sampling
90 points (154 in total) have been distributed in the different mesohabitats proportionally to their
91 occurrence in the river reach (49 in riffles, 60 in glides, 13 in backwaters and 32 in isolated ponds,
92 Figure 1). Each point has been georeferenced and has been sampled for macroinvertebrate
93 community, also recording flow velocity (mean and at the bottom of the water column), water depth
94 and dominant substrate (according to the categories in Buffagni & Erba 2007). Macroinvertebrates
95 have been collected with a surber net (frame area 0.05 m², mesh size 500 µm) and preserved in ethanol

1
2
3 96 for laboratory sorting. Organisms have been counted and identified to the finest possible taxonomical
4
5 97 level (mainly genus) according to Campaioli et al. (1994) and Tachet et al. (2010).
6
7

8 98 ***Data analysis***

9
10
11 99 The effect of mesohabitats on macroinvertebrate community structure was visually assessed with
12
13 100 non-Metric Multidimensional Scaling (nMDS) and tested with permutational multivariate analysis of
14
15 variance (PERMANOVA, Anderson 2001). Bray-Curtis distance was used as dissimilarity measure
16 101
17 in nMDS and stress was computed to evaluate the goodness of ordination. PERMANOVA was run
18 102
19 with 9999 permutations and using Bray-Curtis distance between samples. The indicator value analysis
20 103
21 (IndVal, Dufrêne & Legendre 1997) was performed in order to detect taxa significantly associated
22 104
23 with particular mesohabitats. For this test, macroinvertebrate taxa have been aggregated at family
24 105
25 level.
26 106
27

28
29
30 107 The relative importance of microhabitat (i.e. mean and bottom velocity, depth and substrate),
31
32 mesohabitats and spatial position on community composition was assessed with variance partitioning
33 108
34 on Hellinger-transformed data. This method allow to assess the contribution of explanatory variables
35 109
36 by the decomposition of R-squared as described in (Peres-Neto et al. 2006). Spatial structure was
37 110
38 modelled by using principal coordinates of neighbour matrices (Borcard & Legendre 2002; Dray et
39 111
40 al. 2006). PCNM method produces orthogonal spatial variables from broad to fine scale that allow to
41 112
42 take into account spatial patterns among the samples. In order to construct these spatial variables, the
43 113
44 procedure proposed by Borcard et al. (2011) was followed. To detect significant PCNM and
45 114
46 environmental variables for community structure a forward stepwise selection procedure was
47 115
48 performed.
49 116
50
51

52
53
54 117 All analyses were performed and plots realized with the packages vegan (Oksanen et al. 2019),
55
56 packfor (Dray et al. 2016), indicpecies (Cáceres et al. 2020) and biomonitoR
57 118
58 (https://github.com/alexology/biomonitoR) of the R statistical software (R Core Team 2019).
59 119
60

1
2
3 120
4
5
6 121
7
8
9 122
10
11 123
12
13 124
14
15
16 125
17
18 126
19
20
21 127
22
23 128
24
25
26 129
27
28 130
29
30
31 131
32
33 132
34
35
36 133
37
38 134
39
40 135
41
42 136
43
44
45 137
46
47 138
48
49 139
50
51
52 140
53
54 141
55
56 142
57
58
59 143
60

Results

Flow velocity (both mean and bottom) and water depth varied greatly among mesohabitats (Table 1).

In particular, the mean flow velocity varied from a maximum of 1.9 m/s in riffle to a minimum of 0.0 m/s in backwaters and pools. The maximum depth (0.84 m) has been recorded for glide mesohabitats.

Substrate resulted less variable among mesohabitats and mainly dominated by mesolithal (diameter 6-20 cm).

The macroinvertebrate community resulted mainly dominated by Diptera and Ephemeroptera (representing the 36% and 32% of the total abundance respectively). Among these orders, the most representative taxa were the non-biting midges Chironominae and Orthocladiinae and the mayflies *Baetis* and *Oligoneuriella*.

Mesohabitats were highly variable in terms of community composition (Figure 2), with points in nMDS ordination grouped in two clusters corresponding to lotic (riffles and glides) and lentic (backwaters and ponds) mesohabitats. Based on PERMANOVA (Figure 2), mesohabitats resulted a good driver for macroinvertebrate distribution, significantly affecting the variability in community composition ($R^2 = 0.20$, $p = 0.001$). The indicator value analysis pointed out 7 indicator families for riffles, 7 for backwaters and 11 for isolated ponds, whereas no families were found to be indicative for glides (Table 2). Regarding the relative role of the microhabitats, mesohabitats and spatial position, variance partitioning results (Figure 3) highlight that the largest contribution to explained variance is given by mesohabitats (22%), considering pure and shared fractions together. However, this contribution is substantially lower when considering only the pure mesohabitat fraction (3%). Also, microhabitat variables and PCNMs explained the variability in community composition, both individually (5% of explained variance each one) and jointly with mesohabitats (7% and 4% respectively).

1
2
3 144
4
56 145 **Discussion and Conclusions**
7
8

9 146 Community composition resulted influenced by the mesohabitats hydro-morphological
10
11 147 characteristics, with macroinvertebrates showing a compositional shift moving from lotic to lentic
12
13 148 conditions. Such findings support the presence of a strong habitat filtering effect at the mesoscale
14
15
16 149 level. Some taxa have been also highlighted as indicative of particular mesohabitats. For example,
17
18 150 the family Oligoneuriidae (Ephemeroptera) was found to be associated with riffle habitats, whereas
19
20 151 Potamanthidae (Ephemeroptera) has been found almost exclusively in backwaters. These associations
21
22
23 152 are particularly important in the context of habitat suitability modelling, as these taxa may be highly
24
25 153 sensitive to changes in river discharge. Moreover, the associations persist even at the family level,
26
27 154 reinforcing the strength of mesoscale habitat filtering on macroinvertebrates. Interestingly, no
28
29
30 155 indicator taxa were found for glide mesohabitats. This could be due to the intermediate features of
31
32 156 glides, that can host both rheophilic and lentic taxa (Leung et al. 2009). Also, variance partitioning
33
34 157 highlighted mesohabitat as influential for community composition, pointing out their role in
35
36
37 158 explaining variations in community composition. These outcomes are consistent with previous
38
39 159 findings (Gray & Harding 2009; Starr et al. 2014) that described a differentiation in macroinvertebrate
40
41 160 communities among mesohabitats.
42

43
44 161 However, based on our results, also microhabitats are important for macroinvertebrate community
45
46 162 composition. Indeed, even within mesohabitat units, a certain degree of heterogeneity may trigger the
47
48
49 163 co-occurrence of organisms with different niche requirements. For example, near-shore microhabitats
50
51 164 in riffles can host taxa that are absent from the centre of the channel, representing a flow refuge
52
53 165 (Lancaster 1999). On the other hand, rheophilous taxa may be abundant in the centre of the channel
54
55
56 166 and absent from the banks (Dudgeon 1997).
57

58
59 167 Our results highlight that also the spatial position (here implemented as coordinates) can affect both
60
168 macroinvertebrate metrics and community. In rivers and streams, spatial arrangement of habitat

1
2
3 169 patches can deeply affect macroinvertebrate distribution (Mykrä et al. 2007; Zilli & Marchese 2011).
4
5 170 Indeed, along highly connected mesohabitats like the ones in the main channel, organisms can easily
6
7
8 171 disperse, especially through drift phenomena (Brown et al. 2011). In this case, the community
9
10 172 inhabiting a certain mesohabitat can be affected by the community of mesohabitats located just
11
12 173 upstream, with a sink-source mass-effect mechanism (Leibold et al. 2004). The importance of these
13
14
15 174 mechanisms may be enhanced in case of high abundance taxa (Tonkin & Death 2013). This can be
16
17 175 the case of glides, where the intermediate environmental conditions allow the co-occurrence of taxa
18
19 176 with different niche requirements. This is supported by the lack of indicator taxa for these
20
21
22 177 mesohabitats.

23
24 178 Collectively, our findings support the use of mesoscale habitat modelling for aquatic
25
26
27 179 macroinvertebrates. Indeed, as macroinvertebrates may persist in different hydraulic microhabitats
28
29 180 (Jowett 2003), mesohabitats represent a grouping factor spanning different combinations of flow
30
31 181 velocity, water depth and substrate. Thus, they can be a proxy for macroinvertebrates distribution,
32
33
34 182 tracking their environmental preferences without being too much specific. This sets the conditions
35
36 183 for result transferability and consequently for a good predictive power of mesoscale models.

37
38
39 184

40 41 42 185 **Disclosure statement**

43
44
45 186 No potential conflict of interest was reported by the authors.

46
47
48 187

49 50 51 188 **Funding**

52
53
54 189 This work was supported by the River Po Basin Authority.

55
56
57 190

58 59 60 191 **Data Availability Statement**

1
2
3 192 Due to the nature of this research, participants of this study did not agree for their data to be shared
4
5 193 publicly, so supporting data is not available.
6
7

8 194

9
10
11 195 **References**
12

13
14 196 Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. Austral
15
16 197 Ecol. 26(1):32–46.
17
18

19
20 198 Borcard D, Legendre P. 2002. All-scale spatial analysis of ecological data by means of principal
21
22 199 coordinates of neighbour matrices. Ecol Model. 153(1):51–68.
23
24

25 200 Brooks AJ, Haeusler T, Reinfelds I, Williams S. 2005. Hydraulic microhabitats and the distribution
26
27 of macroinvertebrate assemblages in riffles. Freshwater Biol. 50(2):331–344.
28 201
29

30
31 202 Brown BL, Swan CM, Auerbach DA, Campbell Grant EH, Hitt NP, Maloney KO, Patrick C. 2011.
32
33 203 Metacommunity theory as a multispecies, multiscale framework for studying the influence of river
34
35 204 network structure on riverine communities and ecosystems. J N Am Benthol Soc. 30(1):310–327.
36
37

38
39 205 Buffagni A, Erba S. 2007. Intercalibrazione e classificazione di qualità ecologica dei fiumi per la
40
41 206 2000/60/EC (WFD): L'indice STAR. ICMi IRSA-CNR Notiziario Dei Metodi Analitici. 1:94–100.
42
43

44
45 207 Burgazzi G, Laini A, Racchetti E, Viaroli P. 2017. Mesohabitat mosaic in lowland braided rivers:
46
47 208 Short-term variability of macroinvertebrate metacommunities. J Limnol. 76(s1):29–38.
48
49

50 209 Cáceres MD, Jansen F, Dell N. 2020. indicpecies: Relationship Between Species and Groups of
51
52 210 Sites. <https://CRAN.R-project.org/package=indicpecies>
53
54

55
56 211 Campaioli S, Ghetti PF, Minelli A, Ruffo S. 1994. Manuale per il riconoscimento dei
57
58 212 macroinvertebrati delle acque dolci italiane. Edizione del Museo di Storia Naturale di Trento.
59
60 213 Provincia Autonoma di Trento.

- 1
2
3 214 Dolédec S, Lamouroux N, Fuchs U, Méricoux S. 2007. Modelling the hydraulic preferences of
4
5 215 benthic macroinvertebrates in small European streams. *Freshwater Biol.* 52(1):145–164.
6
7
8
9 216 Dray S, Legendre P, Blanchet G. 2016. packfor: Forward Selection with permutation (Canoco p.46)
10
11 217 version 0.0-8 from R-Forge. <https://rdrr.io/rforge/packfor/>
12
13
14 218 Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: a comprehensive framework for
15
16 219 principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model.* 196(3):483–493.
17
18
19
20 220 Dudgeon D. 1997. Life histories, secondary production and microdistribution of hydropsychid
21
22 221 caddisflies (Trichoptera) in a tropical forest stream. *J Zool.* 243(1):191–210.
23
24
25
26 222 Dufrière M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible
27
28 223 asymmetrical approach. *Ecol Monogr.*:345–366.
29
30
31 224 Gray D, Harding JS. 2009. Braided river benthic diversity at multiple spatial scales: a hierarchical
32
33 225 analysis of β diversity in complex floodplain systems. *J N Am Benthol Soc.* 28(3):537–551.
34
35
36
37 226 Gray D, Scarsbrook MR, Harding JS. 2006. Spatial biodiversity patterns in a large New Zealand
38
39 227 braided river. *New Zeal J Mar Fresh.* 40(4):631–642.
40
41
42 228 Jowett IG. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed
43
44 229 rivers. *River Res Appl.* 19(5–6):495–507.
45
46
47
48 230 Lancaster J. 1999. Small-scale movements of lotic macroinvertebrates with variations in flow.
49
50 231 *Freshwater Biol.* 41(3):605–619.
51
52
53
54 232 Lancaster J, Downes BJ, Glaister A. 2009. Interacting environmental gradients, trade-offs and
55
56 233 reversals in the abundance–environment relationships of stream insects: when flow is unimportant.
57
58 234 *Mar Freshwater Res.* 60(3):259–270.
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 235 Lancaster J, Hildrew AG. 1993. Flow Refugia and the Microdistribution of Lotic Macroinvertebrates.
236 J N Am Benthol Soc. 12(4):385–393.
- 237 Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB,
238 Law R, Tilman D, et al. 2004. The metacommunity concept: a framework for multi-scale community
239 ecology. *Ecol Lett.* 7(7):601–613.
- 240 Leung ES, Rosenfeld JS, Bernhardt JR. 2009. Habitat effects on invertebrate drift in a small trout
241 stream: implications for prey availability to drift-feeding fish. *Hydrobiologia.* 623(1):113–125.
- 242 Méricoux S, Dolédec S. 2004. Hydraulic requirements of stream communities: a case study on
243 invertebrates. *Freshwater Biol.* 49(5):600–613.
- 244 Mykrä H, Heino J, Muotka T. 2007. Scale-related patterns in the spatial and environmental
245 components of stream macroinvertebrate assemblage variation. *Global Ecol Biogeogr.* 16(2):149–
246 159.
- 247 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB,
248 Simpson GL, Solymos P, et al. 2019. *vegan: Community Ecology Package.* [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)
249 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan)
- 250 Parasiewicz P. 2007. The MesoHABSIM model revisited. *River Res Appl.* 23(8):893–903.
- 251 Parasiewicz P, Rogers JN, Vezza P, Gortázar J, Seager T, Pegg M, Wiśniewolski W, Comoglio C.
252 2013. Applications of the MesoHABSIM Simulation Model. In: *Ecohydraulics: John Wiley & Sons,*
253 *Ltd; p. 109–124.* <https://onlinelibrary.wiley.com/doi/abs/10.1002/9781118526576.ch6>
- 254 Parasiewicz P, Walker JD. 2007. Comparison of MesoHABSIM with two microhabitat models
255 (PHABSIM and HARPHA). *River Res Appl.* 23(8):904–923.

- 1
2
3 256 Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate
4
5 257 classification. *Hydrol. Earth Syst. Sci. Discuss.* 4(2):439–473.
6
7
8
9 258 Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation Partitioning of Species Data
10
11 259 Matrices: Estimation and Comparison of Fractions. *Ecology.* 87(10):2614–2625.
12
13
14 260 R Core Team. 2019. R: The R Project for Statistical Computing. Vienna, Austria: R Foundation for
15
16 261 Statistical Computing. <https://www.r-project.org/>
17
18
19
20 262 Radinger J, Wolter C, Kail J. 2015. Spatial Scaling of Environmental Variables Improves Species-
21
22 263 Habitat Models of Fishes in a Small, Sand-Bed Lowland River. *PLOS ONE.* 10(11):e0142813.
23
24
25 264 Rempel LL, Richardson JS, Healey MC. 2000. Macroinvertebrate community structure along
26
27 gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biol.*
28 265 45(1):57–73.
29
30 266
31
32
33 267 Robinson CT, Tockner K, Ward JV. 2002. The fauna of dynamic riverine landscapes. *Freshwater*
34
35 268 *Biol.* 47(4):661–677.
36
37
38
39 269 Shearer KA, Hayes JW, Jowett IG, Olsen DA. 2015. Habitat suitability curves for benthic
40
41 270 macroinvertebrates from a small New Zealand river. *New Zeal J Mar Fresh.* 49(2):178–191.
42
43
44
45 271 Starr SM, Benstead JP, Sponseller RA. 2014. Spatial and temporal organization of macroinvertebrate
46
47 272 assemblages in a lowland floodplain ecosystem. *Landscape Ecol.* 29(6):1017–1031.
48
49
50 273 Tachet H, Richoux P, Bournaud M, Usseglio-Polatera P. 2010. *Invertébrés d’eau douce -*
51
52 274 *systematique, biologie, écologie - CNRS Editions. Paris: CNRS EDITIONS.*
53
54
55 275 <https://www.cnrseditions.fr/catalogue/ecologie-environnement-sciences-de-la-terre/invertebres-d->
56
57 276 [eau-douce-henri-tachet/](https://www.cnrseditions.fr/catalogue/ecologie-environnement-sciences-de-la-terre/invertebres-d-eau-douce-henri-tachet/)
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 277 Tonkin JD, Death RG. 2013. Macroinvertebrate drift-benthos trends in a regulated river. *Fund Appl*
278 *Limnol.* 231–245.
- 279 Vezza P, Parasiewicz P, Rosso M, Comoglio C. 2012. Defining Minimum Environmental Flows at
280 Regional Scale: Application of Mesoscale Habitat Models and Catchments Classification. *River Res*
281 *Appl.* 28(6):717–730.
- 282 Zilli FL, Marchese MR. 2011. Patterns in macroinvertebrate assemblages at different spatial scales.
283 Implications of hydrological connectivity in a large floodplain river. *Hydrobiologia.* 663(1):245–257.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60285 **Tables**

286

287 **Table 1.** Mean (\pm SD) values of hydraulic variables and dominant substrate for each mesohabitat.

	Mean flow velocity (m/s)	Bottom flow velocity (m/s)	Water depth (m)	Dominant substrate
<i>Riffle</i>	0.71 \pm 0.47	0.43 \pm 0.30	0.22 \pm 0.16	Mesolithal
<i>Glide</i>	0.39 \pm 0.35	0.20 \pm 0.21	0.31 \pm 0.22	Mesolithal
<i>Backwater</i>	0.01 \pm 0.02	0.01 \pm 0.02	0.22 \pm 0.09	Silt
<i>Pond</i>	0.03 \pm 0.10	0.03 \pm 0.10	0.16 \pm 0.11	Mesolithal

288

1
2
3 289 **Table 2.** Indicator families found with the indicator species analysis for each mesohabitat. “Stat”
4
5 290 represents the indicator value of each family.
6
7

8 291
9

Class/Order	Family	Stat	p-value	
RIFFLE				
Ephemeroptera	Oligoneuriidae	0.792	0.001	***
Diptera	Simuliidae	0.767	0.001	***
Trichoptera	Hydropsychidae	0.643	0.002	**
Ephemeroptera	Baetidae	0.619	0.026	*
Ephemeroptera	Heptageniidae	0.591	0.034	*
Coleoptera	Scirtidae	0.407	0.013	*
Trichoptera	Rhyacophilidae	0.401	0.021	*
GLIDE				
No indicator taxa found for glide				
BACKWATER				
Ephemeroptera	Caenidae	0.708	0.002	**
Coleoptera	Elmidae	0.684	0.001	***
Ephemeroptera	Potamanthidae	0.651	0.002	**
Trombidiformes	NA	0.630	0.007	**
Diptera	Ceratopogonidae	0.606	0.002	**
Ephemeroptera	Leptophlebiidae	0.505	0.003	**
Amphipoda	Gammaridae	0.404	0.012	*
POND				
Haplotaxida	Naididae	0.780	0.001	***
Diptera	Chironomidae	0.695	0.004	**
Trichoptera	Hydrophilidae	0.679	0.001	***
Coleoptera	Dytiscidae	0.678	0.001	***
Coleoptera	Hydraenidae	0.468	0.001	***
Coleoptera	Haliplidae	0.449	0.008	**
Odonata	Lestidae	0.433	0.003	**
Gastropoda	Physidae	0.433	0.004	**
Diptera	Culicidae	0.431	0.012	*
Coleoptera	Dryopidae	0.428	0.011	*
Diptera	Tipulidae	0.412	0.028	*

55 292
56

58 293
59

60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

294 **Figure captions**

295

296 **Figure 1.** Orthophoto of the study area and its location in the Trebbia Basin (Northern Italy).

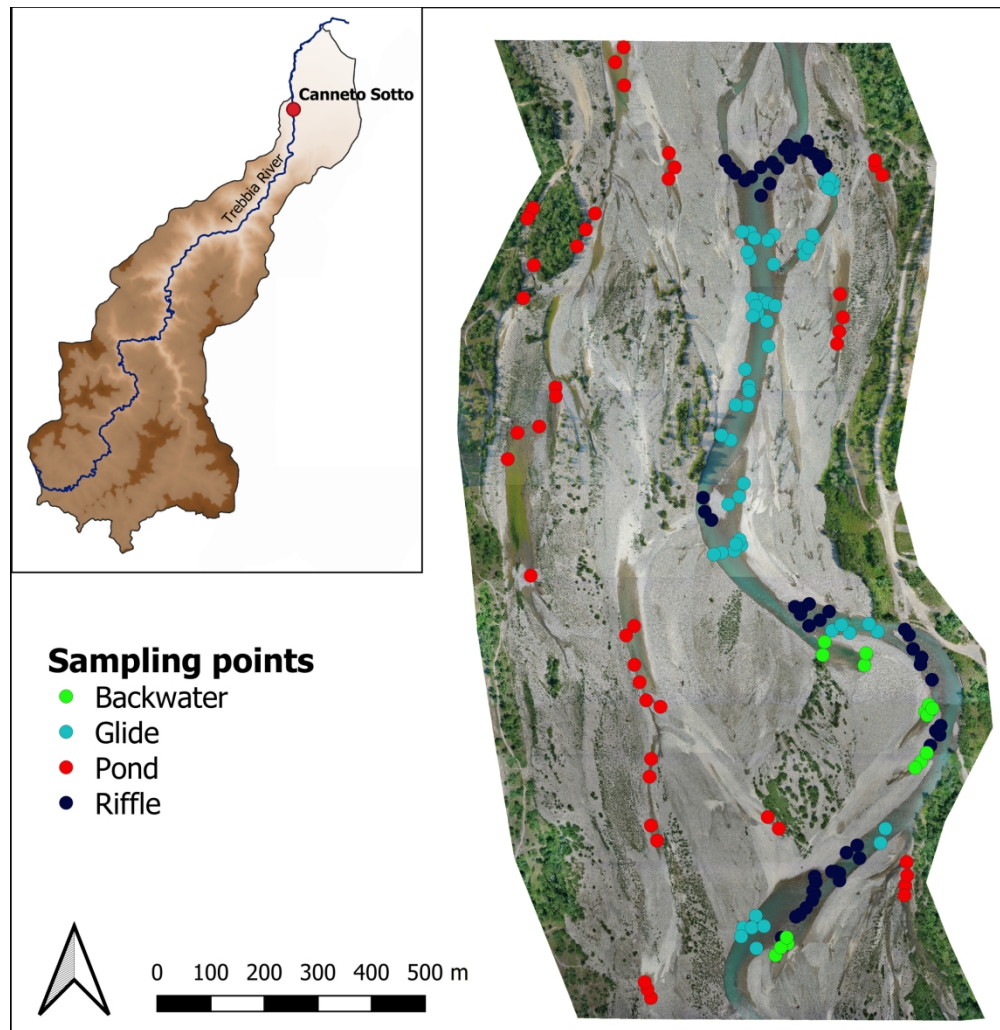
297 Sampling points are represented with full dots, with a colour classification based on the mesohabitats.

298

299 **Figure 2.** Non-Metric Multidimensional Scaling (nMDS) ordination output for community
300 composition data. Ellipsoids correspond to the mesohabitats. 3D stress value is reported as measure
301 of goodness of ordination.

302

303 **Figure 3.** The variance partitioning results (represented with a Venn diagram) for community
304 composition among the components of mesohabitats, microhabitat variables (flow velocity, water
305 depth and substrate size) and the significant PCNM variables (labelled as space in the diagram and
306 computed from spatial coordinates). The numbers represent the proportion of variance explained by
307 each component. Residual values are also displayed.



39
40
41
42

Figure 1. Orthophoto of the study area and its location in the Trebbia Basin (Northern Italy). Sampling points are represented with full dots, with a colour classification based on the mesohabitats.

43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

191x196mm (300 x 300 DPI)

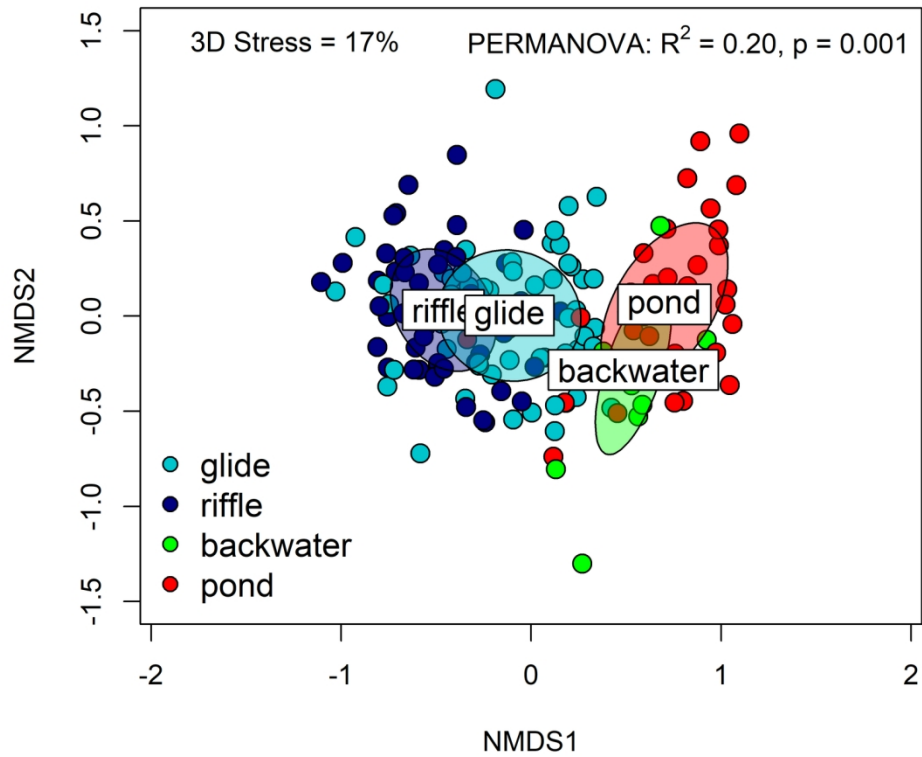


Figure 2. Non-Metric Multidimensional Scaling (nMDS) ordination output for community composition data. Ellipsoids correspond to the mesohabitats. 3D stress value is reported as measure of goodness of ordination.

152x127mm (300 x 300 DPI)

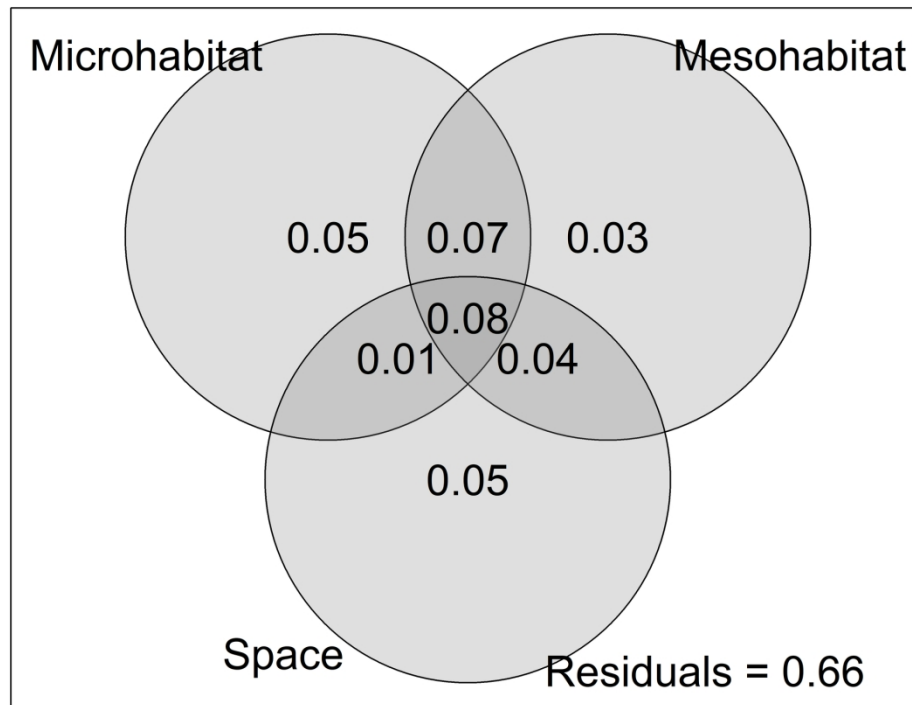


Figure 3. The variance partitioning results (represented with a Venn diagram) for community composition among the components of mesohabitats, microhabitat variables (flow velocity, water depth and substrate size) and the significant PCNM variables (labelled as space in the diagram and computed from spatial coordinates). The numbers represent the proportion of variance explained by each component. Residual values are also displayed.

177x139mm (300 x 300 DPI)