



BRIEF REPORT



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

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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 about the main hydrological and geomorphological drivers that affect local communities. However, these drivers act at different spatial scales and determining which investigation scale is the best trade-off between model accuracy and model transferability is crucial. The present work aims to evaluate the mesoscale for habitat modelling of aquatic macroinvertebrates, by testing the effect of microhabitat (flow velocity, water depth, substrate), mesohabitat (riffles, glides, backwaters, isolated ponds) and spatial position (coordinates and derived spatial variables) on macroinvertebrate community variability. Multivariate spatial analyses were used to analyse the macroinvertebrate data collected in a braided reach of the Trebbia River (N Italy). Mesohabitat was a good predictor of macroinvertebrate community composition, although both microhabitat and space also showed a significant effect. The outcome of this work highlights the transferability of the results across mesohabitats, which supports the use of mesoscale modelling for macroinvertebrate distribution in braided rivers.

ARTICLE HISTORY

Received 30 June 2020
Accepted 15 March 2021

KEYWORDS

Mesohabitat; microhabitat; habitat suitability models; braided rivers; variance partitioning; habitat filtering

Introduction

Developing tools for predicting the spatial distribution of organisms, based on their habitat requirement, is of primary importance in ecology (Lancaster et al. 2009), to both conceive the best conservation strategies and to support stream ecological management (Dolédec et al. 2007). Physical habitat models aim to predict the suitability of a habitat for a target species or community by quantifying the relationship between stream biota and physical habitat (Conallin et al. 2010). Flow velocity, water depth, substrate size and composition are among the most commonly used physical parameters (Jowett et al. 2008), but other parameters can also be included (e.g. water temperature and near-bed shear stress, Mériçoux and Dolédec 2004; Grand et al. 2006). Physical habitat models have been largely employed to predict changes in aquatic communities (fish and macroinvertebrates) resulting from changes in habitat availability (Dolédec et al. 2007) and, therefore, to assess environmental flow requirements (Shearer et al. 2015). The construction

of these models requires an in-depth understanding of the main hydrological and geomorphological drivers that affect local communities. However, determining the investigation spatial scale, which represents the best trade-off between model accuracy (i.e. the model's ability to correctly predict) and model transferability (i.e. the model's validity under different environmental conditions) is crucial (Lamouroux et al. 2013; Radinger et al. 2015; Paton and Matthiopoulos 2016) because it can affect sampling efforts in terms of time and resources.

Hydraulic microhabitat patterns can be highly variable in space and time, which creates a dynamic mosaic of different habitat patches. This is particularly true in braided rivers, where the high hydrological variability and sediment transport promote high spatio-temporal heterogeneity in hydraulic and geomorphological features (Gray and Harding 2009; Singh et al. 2017). In these systems, different geomorphic units (*sensu* Gurnell et al. 2016; hereafter referred to as mesohabitats) occur in a single river reach, covering the whole range from lotic to lentic habitats (Gray and Harding 2009). Mesohabitats are

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Supplemental data for this article can be accessed <https://doi.org/10.1080/24705357.2021.1938254>.

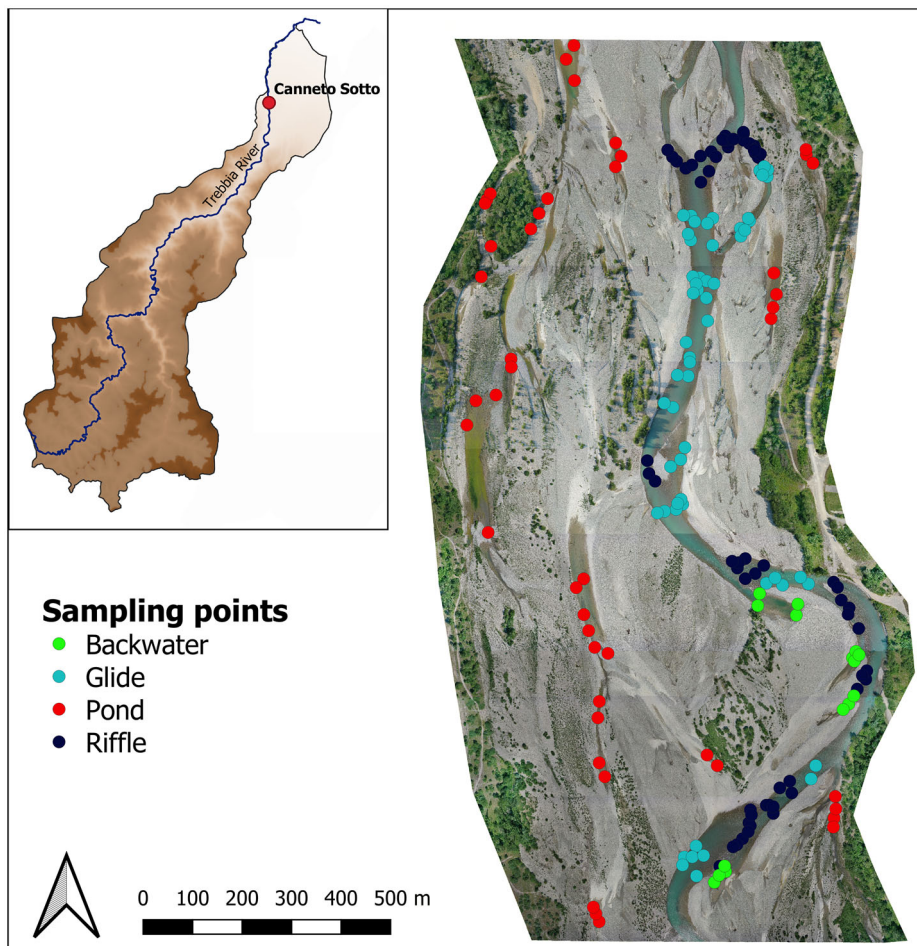


Figure 1. Orthophoto of the study area and its location in the Trebbia Basin (N Italy). Sampling points are represented by full dots, with colour classification based on mesohabitats.

defined as medium-scale habitats within a river reach (like riffles, pools etc.) which arise through the interactions of erosion and deposition. The mesohabitat scale size is generally 10^{-1} – 10^3 m (Gurnell et al. 2016; Belletti et al. 2017), whereas our definition of the microhabitat scale coincide with smaller spatial scales (i.e. river elements, ~ 1 – 50 cm; Gurnell et al. 2016; Belletti et al. 2017). Given their peculiar characteristics, braided rivers can represent a unique model system to investigate the relationships between hydromorphology and macroinvertebrate communities. Indeed, their complexity promotes the co-occurrence of organisms with very different niche requirements (Robinson et al. 2002; Gray et al. 2006; Burgazzi et al. 2017). For example, mesohabitats with higher flow velocities, like riffles and glides, can host rheophilic taxa (e.g. some Plecoptera and Ephemeroptera), whereas isolated ponds or instream pools are colonized by lentic taxa (e.g. Heteroptera and Odonata).

Spatial position (i.e. coordinates or derived spatial variables, accounting for spatial patterns) can also affect macroinvertebrate community composition by acting as a proxy for dispersal dynamics and biotic processes (Burgazzi et al. 2020). For example, the closer the communities are located, the more similar

they are, due to higher dispersion rates (via mass effect mechanisms; Heino et al. 2015), with a gradual distance-decay of community similarity (Soininen et al. 2007). Spatial variables can also summarize the effect of biotic interactions like competition and predation, which can strongly influence community dynamics (Lamouroux et al. 2004; Holomuzki et al. 2010; Patrick and Swan 2011; Morales-Castilla et al. 2015).

The general goal of our work was to evaluate the mesoscale for habitat modelling of aquatic invertebrates. More specifically, our aims were to: 1) quantify the role of hydraulic microhabitats, mesohabitats and spatial variables in shaping macroinvertebrate communities, 2) identify indicator taxa for each mesohabitat. We predicted a relevant role of mesohabitats in shaping the distribution of aquatic macroinvertebrates in braided rivers. Despite the strongly supported role of hydraulic variables on the microhabitat scale, some authors have pointed out that species can be present in places not predicted by their own auto-ecological requirements (e.g. Jowett 2003). For example, in the near-shore area of riffles and glides, where lentic conditions are often present, it is possible to find rheophilic taxa under environmental conditions different from their

expected requirements (Burgazzi et al. 2018; He et al. 2020). From this perspective, mesohabitats may reflect larger ecological patterns and, thus, improve the reliability of predictions (Parasiewicz and Walker 2007; Vezza et al. 2012). We also predicted a relevant role of spatial processes (e.g. dispersal) in shaping macroinvertebrate communities, as mesohabitat distance and isolation can enhance community dissimilarity (Karaus et al. 2005; 2013).

Materials and methods

Study area

This study was performed in the Trebbia River, a right-side tributary of the Po River in Northern Italy (Figure 1). The climate of the Po plain is classified as temperate (Köppen Cfa/Cfb), with mean annual precipitation of ~ 800 mm and a mean annual temperature of 13°C (Peel et al. 2007). The Trebbia River flows from the Northern Apennine to the Po River over a total length of 118 km. Its mean annual discharge is $21.2\text{ m}^3/\text{s}$ (www.arpae.it), with high flow periods in spring and autumn, and low flows (often drying out completely in the downstream section) in summer. Downstream the Apennines, the Trebbia riverbed widens, becoming a multi-thread river system that creates a mosaic of different mesohabitats in main and secondary channels. The study site (Canneto Sotto, $44^\circ 58' 13.8''\text{N}$ $9^\circ 35' 34.0''\text{E}$, 102 m a.s.l.) is located within a lowland braided river reach. The study was conducted over an area covering approximately 0.75 km^2 (500 m wide, 1500 m long; Figure 1) in June 2019. Sampling activity lasted one week (from 5 to 12 June), with narrow variability of discharge, water level and connectivity during the sampling period.

Field and laboratory protocol

The river reach was divided into several geomorphic units (i.e. mesohabitats) and they belonged to these categories: riffles, glides, backwaters, isolated ponds. These mesohabitats are characterized by a gradient of hydraulic conditions (from lotic to lentic) and connectivity. Sampling points (154 in total) were distributed into the different mesohabitats proportionally to their occurrence in the river reach (49 in riffles, 60 in glides, 13 in backwaters, 32 in isolated ponds; Figure 1). The column and bottom flow velocity (i.e. water velocity at a 60% depth and 2.5 cm above the bottom respectively; measured with OTT MF pro electromagnetic current meter), water depth, dominant substrate (according to the categories in Buffagni and Erba 2007) and spatial coordinates were recorded at each sampling point prior to sampling. Macroinvertebrates were collected at each

point with a Surber net (0.05 m^2 frame area, $500\ \mu\text{m}$ mesh size) and preserved in 90% ethanol for laboratory sorting. Organisms were counted and identified to the family level (except for Hydracarina) according to Campaioli et al. (1994) and Tachet et al. (2010). This taxonomic level is used for ecological status quantification *sensu* WFD in Italy and other European Countries (e.g. Laini et al. 2019). This level also prevents major taxonomic inconsistencies, while maintaining a good relationship with environmental variables in ecohydrological and ecological studies (Heino and Soininen 2007; Bruno et al. 2014).

Data analysis

Differences in the hydraulic microhabitat variables among mesohabitats were tested for significance by Generalised Additive Models (GAMs) to correct for spatial autocorrelation. The mesohabitat (*riffle*, *glide*, *backwater*, *isolated pond*) was entered into each model as the non-smooth term, while the smoothing function was applied to spatial coordinates.

The effect of mesohabitats on the macroinvertebrate community structure was visually evaluated by non-Metric Multidimensional Scaling (nMDS) and tested with a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). Bray-Curtis distance was used as the dissimilarity measure in nMDS, and stress was computed to evaluate the goodness of fit. The PERMANOVA was run with 9,999 permutations and using Bray-Curtis distance on previously Hellinger-transformed data. An Indicator Value analysis (IndVal, Dufrene and Legendre 1997) was run to detect the taxa that were significantly associated with particular mesohabitats.

Variance partitioning on the Hellinger-transformed data was used to assess the single and joint effect of the explanatory variables by the decomposition of R-squared, as described in Peres-Neto et al. (2006). Three sets of explanatory variables were employed, namely hydraulic variables on the microhabitat scale (i.e. column and bottom flow velocity, water depth, substrate size), mesohabitat category (a categorical variable with *riffle*, *glide*, *backwater* and *isolated pond* as levels) and spatial variables (derived from the spatial coordinates of each sampling point). Spatial coordinates were not used directly in variance partitioning, but modelled with Principal Coordinates of Neighbour Matrices (PCNM, Borcard and Legendre 2002; Dray et al. 2006). The procedure proposed by Borcard et al. (2011) was followed to construct these spatial variables. Briefly, the PCNM method produces a new set of spatial variables (i.e. PCNM variables) that are the positive eigenvectors obtained by a Principal Coordinates Analysis on a truncated Euclidean-distance matrix

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

	Column 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	Microolithal/Clay
<i>Isolated pond</i>	0.03 \pm 0.10	0.03 \pm 0.10	0.16 \pm 0.11	Mesolithal

(computed from the coordinates). PCNM variables map neighbourhood relationships on different scales onto orthogonal and linearly uncorrelated components, and allow spatial patterns to be detected among sampling points (Borcard et al. 2004; Alahuhta et al. 2013). A forward stepwise selection procedure was followed separately for the two sets of PCNM and microhabitat variables. The variables provided by the forward selection were used in variance partitioning.

The effect of microhabitats, mesohabitats and spatial coordinates was also tested for the log-transformed abundance of the ten dominant taxa (i.e. the ten taxa with highest abundance) using GAMs. Substrate and mesohabitat were used as the parametric terms, whereas the smoothing function was applied to the continuous microhabitat variables (column and bottom flow velocity and water depth) and to coordinates. The restricted maximum likelihood method was used to estimate the smoothing parameter. Variables selection was done according to the double penalty approach (Marra and Wood 2011).

All the analyses were performed with the packages *vegan* (Oksanen et al. 2019), *packfor* (Dray et al. 2016), *mgcv* (Wood 2019), *indicspecies* (Cáceres et al. 2020), *ggplot2* (Wickham et al. 2019) and *biomonitoR* (<https://github.com/alexology/biomonitoR>) of the R statistical software (R Core Team 2019).

Results

Flow velocity (both column and bottom) and water depth varied among mesohabitats (Table 1, Figure S1), with a significant decrease in both the column and bottom flow velocities from riffles to isolated ponds (Table S1). In particular, the column flow velocity ranged from a maximum of 1.9 m/s in riffles to a minimum of 0.0 m/s in backwaters and ponds. Both column and bottom flow velocity varied greatly even within mesohabitats, especially for riffles and glides (Figure S1). The maximum depth (0.84 m) was recorded for glides, with significant differences among mesohabitats (Table S1). Both flow velocity (column and bottom) and water depth exhibited high within-mesohabitat variability, especially in riffles and glides (Figure S1). Mesolithal (diameter 6–20 cm) was the most frequent substrate for riffles (55% of the samples), glides (58%) and ponds (44%), whereas microlithal (diameter 2–6 cm)

and clay (diameter $<6 \mu\text{m}$) were dominant in backwaters (31% of the samples for both). Organic substrates (i.e. CPOM, algae, macrophytes) were recorded only in backwaters and ponds (Figure S1).

In the studied river reach, 13,130 individuals from 44 families were recorded. Macroinvertebrate communities were composed mainly of Diptera and Ephemeroptera (representing 36% and 32% of total abundance, respectively). Within these orders, the most representative taxa were the non-biting midges Chironomidae and mayflies Baetidae and Oligoneuriidae. The family richness of each sample varied slightly among mesohabitats, with mean values of 9 (SD \pm 4) taxa in riffles, 10 (SD \pm 3) taxa in glides, 12 (SD \pm 3) taxa in backwaters and 11 (SD \pm 3) taxa in isolated ponds. On the contrary, macroinvertebrate density widely varied among mesohabitats, with mean values of 1,336 (SD \pm 1,342) ind./m² in riffles, 1,186 (SD \pm 901) ind./m² in glides, 2,557 (SD \pm 1,941) ind./m² in backwaters and 2,898 (SD \pm 2,288) ind./m² in isolated ponds. Some taxa were found exclusively in one mesohabitat. We found 5 exclusive taxa in the isolated ponds: Hydraenidae (Coleoptera), Lestidae (Odonata), Nepidae (Heteroptera), Physidae (Gasteropoda) and Sialidae (Megaloptera), one exclusive taxon in both backwaters (the Diptera Dolichopodidae) and glides (the Diptera Empididae), and none for riffles.

Mesohabitats were widely variable in community composition terms (Figure 2), with samples in the nMDS ordination grouped into two clusters corresponding to the lotic (riffles and glides) and lentic (backwaters and ponds) mesohabitats. According to the PERMANOVA, macroinvertebrate communities significantly varied among mesohabitats ($R^2 = 0.26$, $p < 0.001$). The Indicator Value analysis identified seven indicator families for riffles, seven for backwaters and 11 for isolated ponds, but no families were indicative for glides (Table 2).

Variance partitioning (Figure 3) showed that the effect of the three sets of explanatory variables on macroinvertebrates was similar, with the microhabitat, mesohabitat and spatial variables respectively explaining 21%, 21% and 20% of community variability (considering pure and shared fractions together). However, relative contributions widely varied when considering only pure fractions, with 5% explained by microhabitats, 3% by mesohabitats and 7% by spatial variables. A large fraction of variance (66%) remained unexplained.

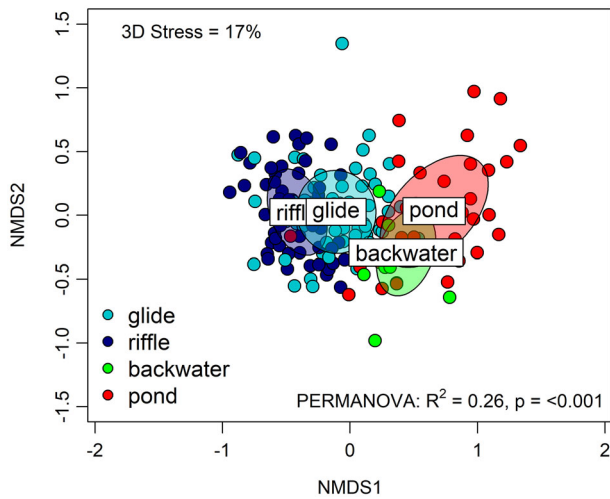


Figure 2. Non-Metric Multidimensional Scaling (nMDS) ordination output for the community composition data. Ellipsoids correspond to mesohabitats. The 3D stress value is reported as a measure of goodness of ordination.

Table 2. Indicator families found with the Indicator Value analysis for each mesohabitat. “Stat” represents the indicator value of each family.

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	*
ISOLATED POND				
Haptotaxida	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	*

For the dominant taxa (Figure S2, Table S2), mesohabitat was the most important determinant of taxa variability because it significantly affected nine of the ten tested taxa. The effect of the microhabitat variables varied among taxa, often with non-linear relationships showing optima at intermediate values. The column flow velocity significantly affected eight of the ten dominant taxa, with either non-linear (e.g. Baetidae, Hydropsychidae; optimum of approximately 0.4-0.5

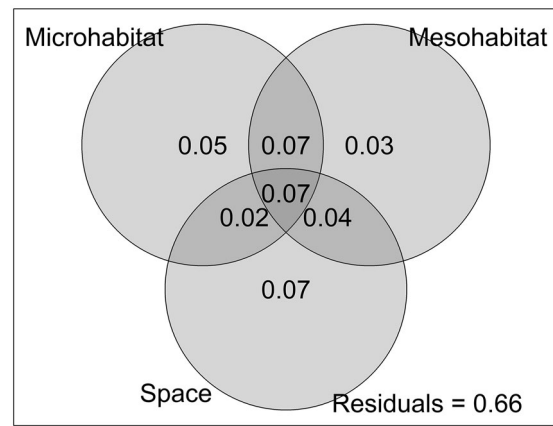


Figure 3. The variance partitioning results (represented by a Venn diagram) for community composition among the components of mesohabitats, microhabitat variables (column and bottom flow velocity, water depth, substrate size) and significant PCNM variables (labelled as space in the diagram and computed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

m/s) or negative (e.g. Chironomidae, Naididae) relationships. The bottom flow velocity was influential only for the Heptageniidae and Oligoneuriidae family (non-linear and positive relationships, respectively). Depth and substrate significantly affected nearly half of the ten dominant families (respectively Chironomidae, Baetidae, Naididae, Heptageniidae, Simuliidae, Caenidae, and Chironomidae, Naididae, Hydracnida, Caenidae, Leuctridae). The spatial coordinates also had a strong impact on explaining dominant taxa’s variability, with a significant effect on most tested taxa.

Discussion and conclusions

The distribution of aquatic macroinvertebrates in a single river reach is shaped by factors acting on different spatial scales (García-Roger et al. 2013; Manfrin et al. 2016; Krajenbrink et al. 2019). In this study, we examined the relative effect of hydraulic microhabitats, mesohabitats and spatial position on macroinvertebrate communities in a braided river.

Effect of mesohabitats on macroinvertebrate community composition

Community composition was influenced by mesohabitat hydromorphological characteristics, with macroinvertebrates showing a compositional shift from lotic to lentic conditions. Such findings support the presence of a habitat filtering effect on the meso-scale level. Our outcomes are consistent with previous findings (Pastuchová et al. 2008; Gray and Harding 2009; Karaus et al. 2013; Starr et al. 2014) that describe a differentiation in macroinvertebrate communities among mesohabitats. In most previous

works however, the examined mesohabitats were not classified as in the present study (see Belletti et al. 2017 for details). For example, Karaus et al. (2013) studied the EPT (Ephemeroptera, Plecoptera and Trichoptera) fauna of tributaries, backwaters and ponds, whereas Gray and Harding (2009) evaluated the variability of macroinvertebrate communities in main channels, side braids, spring creeks, spring sources and ponds. However, disregarding the classification system used, mesohabitats were good predictors of macroinvertebrate communities.

Variance partitioning also highlighted mesohabitats as being influential for community composition. However, the variance explained by mesohabitats sharply dropped when considering only the pure fraction. This could be due to the high correlation between microhabitats and mesohabitats. Mesohabitats are highly defined by flow velocity and water depth values. This supports the notion of a high level of variance explained by shared fractions. The large number of rare taxa in the dataset could also affect mesohabitats' explanatory power. Indeed, rare taxa were found to correlate less to environmental variables than common taxa (e.g. Šizling et al. 2009; Alahuhta et al. 2014). When we examined the dominant taxa, our results highlighted that mesohabitats could be better descriptors of density variability than microhabitat variables for certain taxa (e.g. Leuctridae, Hydropsychidae, Oligoneuriidae). Moreover, some taxa were indicative, or even exclusive, of particular mesohabitats. For example, the family Oligoneuriidae (Ephemeroptera) was associated with riffle habitats, whereas Potamanthidae (Ephemeroptera) was found almost exclusively in backwaters. Interestingly, no indicator taxa were found for glides, which could be due to their intermediate features, as they can host both rheophilic and lentic taxa (Leung et al. 2009). Considering exclusive taxa, isolated ponds were the most peculiar habitats. Here, we recorded five exclusive families, generally found in lentic waters. Backwaters can also be considered lentic environments, as supported by the presence of pool-like taxa (Bonada et al. 2007). However, their dissimilarity from lotic environments may be reduced by their greater connectivity, which allows exchanges of aquatic stages of organisms.

These relationships are particularly important in the habitat suitability modelling context, especially in braided rivers. Indeed, the taxa associated with specific mesohabitats can be extremely sensitive to changes in river discharge (as discharge affects the proportion of each type of mesohabitats), whereas the distribution of microhabitats may be less affected. For example, a low flow period may increase the relative spatial extension of backwaters and ponds through a lentication process (Falasco

et al. 2018), limiting the occurrence of rheophilic taxa, that are replaced by lentic ones (Datry et al. 2014). Conversely, flood events may lead to a higher proportion of riffles and lotic habitats, with changes in relative abundance in macroinvertebrates (e.g. decreased abundance of Gammaridae and Turbellaria and increase for Baetidae, Chironomidae and Simuliidae; Robinson et al. 2003).

Effect of microhabitat variables on macroinvertebrate community composition

Based on our results, microhabitats were also relevant for determining macroinvertebrate community composition, especially when the entire community is taken into account. Even within a mesohabitat, a certain degree of heterogeneity (as observed especially for riffles and glides) can trigger the co-occurrence of organisms with different niche requirements. For example, near-shore microhabitats in riffles can act as flow refuge by hosting both rheophilic taxa and more lentic taxa that are absent from the centre of the channel, representing a flow refugia (Lancaster 1999). Under such conditions, both mesohabitats and microhabitats would affect macroinvertebrate communities with different taxa responding to variables on distinct spatial scales (Boyer 2003; Gray and Harding 2011). At the same time, microhabitats cannot fully predict the distribution of all dominant taxa. For example, Hydropsychidae was affected only by column velocity, but not by the other microhabitat variables, whereas Leuctridae responded to depth and substrate but not to column or bottom flow velocity. Thus, the effect of microhabitat variables may depend on the taxa considered.

Column velocity and water depth were the most influential microhabitat variables for dominant taxa, as already found in previous studies (e.g. Méricoux and Dolédec 2004; Brooks et al. 2005). Our results show that these variables affect macroinvertebrate distribution with non-linear relationships, with optima at intermediate values for most taxa. Also substrate category (both organic and inorganic) was an important driver of macroinvertebrates distribution, as also reported in previous findings (Cummins and Lauff 1969; Braccia and Voshell 2006; Heino and Korsu 2008; Barnes et al. 2013), with some taxa, like Chironomidae and Naididae, showing preferences for organic or fine inorganic substrates.

Effect of spatial position on macroinvertebrate community composition

Our results highlight that spatial position can also affect macroinvertebrate communities. In rivers and streams, the spatial arrangement of habitat patches

can profoundly affect macroinvertebrate distribution (Mykrä et al. 2007; Zilli and Marchese 2011). Indeed, along highly connected mesohabitats like those in the main channel, organisms can easily disperse, especially through drift (Brown et al. 2011). In this case, the community that inhabits a certain mesohabitat can be affected by the community of mesohabitats located immediately upstream, with a sink-source mass effect mechanism (Leibold et al. 2004). The importance of these mechanisms can be enhanced with very abundant taxa (Tonkin and Death 2013). This can be the case of glides, for which intermediate environmental conditions allow the co-occurrence of taxa with different niche requirements. This is supported by the indicator taxa for these mesohabitats being absent. On the contrary, spatial disconnection can also profoundly affect macroinvertebrate communities by reducing the exchange of organisms and selecting taxa with aerial dispersal ability (Astorga et al. 2012; Karaus et al. 2013). In this context, the use of connectivity measures that account for network topography and patches arrangement can help to unravel patterns of macroinvertebrates distribution (Cañedo-Argüelles et al. 2015).

Concluding remarks

Based on our results, braided rivers are a good model system for building the relationships needed to apply mesoscale modelling for macroinvertebrates. In our studied reach, we found a wide range of different habitat conditions (high diversity of geomorphic features and units) that allowed the co-occurrence of taxa with various habitat requirements. Hence, the dynamism of these systems can be an added value for applying mesoscale modelling methods, as long as these methods are calibrated with data collected from different seasons and flow conditions. Taxonomic resolution resulted sufficient for detecting the effect of the studied variables. However, improving taxonomic resolution from family to genus or species level could further improve the observed relationships, taking into account the within-family variability in habitat preferences that exists for some families (for example the genera *Baetis* and *Cloeon* within the family Baetidae; Schmidt-Kloiber and Hering 2015).

Collectively, our findings support the use of mesoscale habitat modelling for aquatic macroinvertebrates. In fact, as macroinvertebrates may persist in different hydraulic microhabitats (Jowett 2003), mesohabitats represent a grouping factor that spans distinct combinations of flow velocity, water depth and substrate. This means they can act as a proxy for macroinvertebrates distribution by tracking the

processes that act on different spatial scales. This sets the conditions for result transferability and, consequently, for a good predictive power of meso-scale models.

Acknowledgements

Authors wish to thank Dr. Rossano Bolpagni for his support during project writing and field activity and Giulia Costa and Stefano Ippoltoni that helped during samples collection and analysis.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was carried out in the framework of the BentHab Project (mesoscale habitat modelling of macroinvertebrate communities with the MesoHABitat SIMulation model - MesoHABSIM), supported by the River Po Basin Authority, Emilia-Romagna region and ANBI (Associazione Nazionale Consorzi di gestione e tutela del territorio e acque irrigue).

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Data availability statement

Due to the nature of this research, participants of this study did not agree for their data to be shared publicly, so supporting data is not available.

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