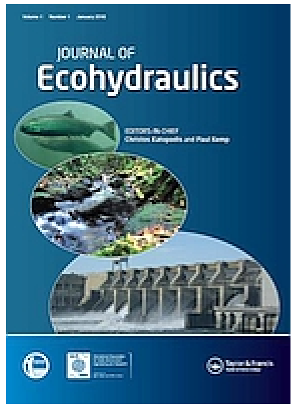
Effect of microhabitats, mesohabitats and spatial position on macroinvertebrate communities of a braided river



Exploring the role of microhabitat and mesohabitat in structuring macroinvertebrate communities

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Keywords:	mesohabitat, microhabitat, habitat suitability models, braided rivers, variance partitioning, habitat filtering
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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.

Exploring the role of microhabitat and mesohabitat in structuring macroinvertebrate communities

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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 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 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.

Keywords: mesohabitat, microhabitat, habitat suitability models, braided rivers, variance partitioning, habitat filtering.

Introduction

Developing tools for predicting spatial variability in distribution and abundance of organisms based on their habitat requirement is of primary importance in ecology (Lancaster et al. 2009), both to develop the best conservation strategies and to support streams ecological management (Dolédec et al. 2007). Physical habitat models have been largely used to predict changes in aquatic communities (fish and macroinvertebrates) as a consequence of 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 to deeply understand which are the main hydrological and geomorphological drivers affecting local communities. However, also determining which is the investigation scale representing the best trade-off between model accuracy and model transferability is top priority (Radinger et al. 2015), as this can affect sampling effort in terms of time- and resource-consumption.

Hydraulic microhabitat and substrate have been widely recognised as key drivers for aquatic macroinvertebrates (Lancaster & Hildrew 1993; Rempel et al. 2000; Mérigoux & Dolédec 2004; Brooks et al. 2005). Flow velocity, water depth and substrate size can be highly variable over space and time, thus creating a dynamic mosaic of different habitat patches. This is especially true in braided rivers, where the high hydrological variability and sediment transport promotes local heterogeneity. In a single river reach different hydro-morphological units occur together, covering the whole range from lotic to lentic habitats (Gray & Harding 2009). Given their peculiar characteristics, braided rivers can represent a unique model system to investigate the relationships occurring between hydromorphology and macroinvertebrate communities. Indeed, their complexity allow the co-occurrence of organisms with very different niche requirements (Robinson et al. 2002; Gray et al. 2006; Burgazzi et al. 2017).

This work aims at: 1) evaluate macroinvertebrate community variability (for composition and structure) in different mesohabitats; and 2) quantify the relative role of the hydraulic microhabitats, hydromorphological mesohabitats and spatial position in shaping communities. We predict a relevant role of mesohabitats in shaping the distribution of aquatic macroinvertebrates in braided rivers. Indeed, despite the strongly supported role of hydraulic microhabitat, some authors pointed out that species can be present in places not predicted by their own auto-ecological requirements (e.g. Jowett 2003). In this perspective, mesohabitats allow to encompass larger ecological patterns, thus improving the reliability of predictions (Parasiewicz & Walker 2007; Vezza et al. 2012).

The present work is done in the framework of the BENTHAB project, funded by the River Po Basin Authority. The project aims to model the spatio-temporal habitat availability for aquatic macroinvertebrates in large braided rivers, using the mesohabitat modelling approach MesoHABSIM (Parasiewicz 2007; Parasiewicz et al. 2013). This methodology describes habitat availability for a target species or community as a function of particular environmental features such as the river discharge and hydro-morphological river characteristics.

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 mean temperature of 13 °C (Peel et al. 2007). Trebbia River flows from the Northern Apennine to the Po River, for a total length of 118 km. Its annual discharge is 21.2 m^3/s (www.arpae.it), and it is characterized by periods of high discharge in spring and autumn and low discharge (often with total dry out in the last section) in summer. After the Apennines-lowland margin, the Trebbia riverbed widens, becoming multi-thread river system and creating a mosaic of different hydro-morphological units in the main and secondary channels. The study site (Canneto Sotto, 44°58'13.8"N 9°35'34.0"E, 102 m a.s.l.) is located within a lowland braided river reach. Sampling have been performed over an area of approximatively 0.75 km^2 (500 m wide and 1500 m long, Figure 1) in June 2019.

Field and laboratory protocol

The river reach has been divided into several hydro-morphological units (i.e. mesohabitats), belonging to the categories: riffle, glide, backwater and isolated pond. These mesohabitats are characterized by a gradient of hydraulic conditions (from lotic to lentic) and connectivity. Sampling points (154 in total) have been distributed in the different mesohabitats proportionally to their occurrence in the river reach (49 in riffles, 60 in glides, 13 in backwaters and 32 in isolated ponds, Figure 1). Each point has been georeferenced and has been sampled for macroinvertebrate community, also recording flow velocity (mean and at the bottom of the water column), water depth and dominant substrate (according to the categories in Buffagni & Erba 2007). Macroinvertebrates have been collected with a surber net (frame area 0.05 m^2, mesh size 500 μm) and preserved in ethanol for laboratory sorting. Organisms have been counted and identified to the finest possible taxonomical level (mainly genus) according to Campaioli et al. (1994) and Tachet et al. (2010).

Data analysis

The effect of mesohabitats on macroinvertebrate community structure was visually assessed with non-Metric Multidimensional Scaling (nMDS) and tested with permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). Bray-Curtis distance was used as dissimilarity measure in nMDS and stress was computed to evaluate the goodness of ordination. PERMANOVA was run with 9999 permutations and using Bray-Curtis distance between samples. The indicator value analysis (IndVal, Dufrêne & Legendre 1997) was performed in order to detect taxa significantly associated with particular mesohabitats. For this test, macroinvertebrate taxa have been aggregated at family level.

The relative importance of microhabitat (i.e. mean and bottom velocity, depth and substrate), mesohabitats and spatial position on community composition was assessed with variance partitioning on Hellinger-transformed data. This method allow to assess the contribution of explanatory variables by the decomposition of R-squared as described in (Peres-Neto et al. 2006). Spatial structure was modelled by using principal coordinates of neighbour matrices (Borcard & Legendre 2002; Dray et al. 2006). PCNM method produces orthogonal spatial variables from broad to fine scale that allow to take into account spatial patterns among the samples. In order to construct these spatial variables, the procedure proposed by Borcard et al. (2011) was followed. To detect significant PCNM and environmental variables for community structure a forward stepwise selection procedure was performed.

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

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 manly 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).

Discussion and Conclusions

Community composition resulted influenced by the mesohabitats hydro-morphological characteristics, with macroinvertebrates showing a compositional shift moving from lotic to lentic conditions. Such findings support the presence of a strong habitat filtering effect at the mesoscale level. Some taxa have been also highlighted as indicative of particular mesohabitats. For example, the family Oligoneuriidae (Ephemeroptera) was found to be associated with riffle habitats, whereas Potamanthidae (Ephemeroptera) has been found almost exclusively in backwaters. These associations are particularly important in the context of habitat suitability modelling, as these taxa may be highly sensitive to changes in river discharge. Moreover, the associations persist even at the family level, reinforcing the strength of mesoscale habitat filtering on macroinvertebrates. Interestingly, no indicator taxa were found for glide mesohabitats. This could be due to the intermediate features of glides, that can host both rheophilic and lentic taxa (Leung et al. 2009). Also, variance partitioning highlighted mesohabitat as influential for community composition, pointing out their role in explaining variations in community composition. These outcomes are consistent with previous findings (Gray & Harding 2009; Starr et al. 2014) that described a differentiation in macroinvertebrate communities among mesohabitats.

However, based on our results, also microhabitats are important for macroinvertebrate community composition. Indeed, even within mesohabitat units, a certain degree of heterogeneity may trigger the co-occurrence of organisms with different niche requirements. For example, near-shore microhabitats in riffles can host taxa that are absent from the centre of the channel, representing a flow refuge (Lancaster 1999). On the other hand, rheophilous taxa may be abundant in the centre of the channel and absent from the banks (Dudgeon 1997).

Our results highlight that also the spatial position (here implemented as coordinates) can affect both macroinvertebrate metrics and community. In rivers and streams, spatial arrangement of habitat patches can deeply affect macroinvertebrate distribution (Mykrä et al. 2007; Zilli & Marchese 2011). Indeed, along highly connected mesohabitats like the ones in the main channel, organisms can easily disperse, especially through drift phenomena (Brown et al. 2011). In this case, the community inhabiting a certain mesohabitat can be affected by the community of mesohabitats located just upstream, with a sink-source mass-effect mechanism (Leibold et al. 2004). The importance of these mechanisms may be enhanced in case of high abundance taxa (Tonkin & Death 2013). This can be the case of glides, where the intermediate environmental conditions allow the co-occurrence of taxa with different niche requirements. This is supported by the lack of indicator taxa for these mesohabitats.

Collectively, our findings support the use of mesoscale habitat modelling for aquatic macroinvertebrates. Indeed, as macroinvertebrates may persist in different hydraulic microhabitats (Jowett 2003), mesohabitats represent a grouping factor spanning different combinations of flow velocity, water depth and substrate. Thus, they can be a proxy for macroinvertebrates distribution, tracking their environmental preferences without being too much specific. This sets the conditions for result transferability and consequently for a good predictive power of mesoscale models.

Disclosure statement

No potential conflict of interest was reported by the authors.

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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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Tables

Table 1. Mean (±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**
Riffle	0.71 ± 0.47	0.43 ± 0.30	0.22 ± 0.16	Mesolithal
Glide	0.39 ± 0.35	0.20 ± 0.21	0.31 ± 0.22	Mesolithal
Backwater	0.01 ± 0.02	0.01 ± 0.02	0.22 ± 0.09	Silt
Pond	0.03 ± 0.10	0.03 ± 0.10	0.16 ± 0.11	Mesolithal

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

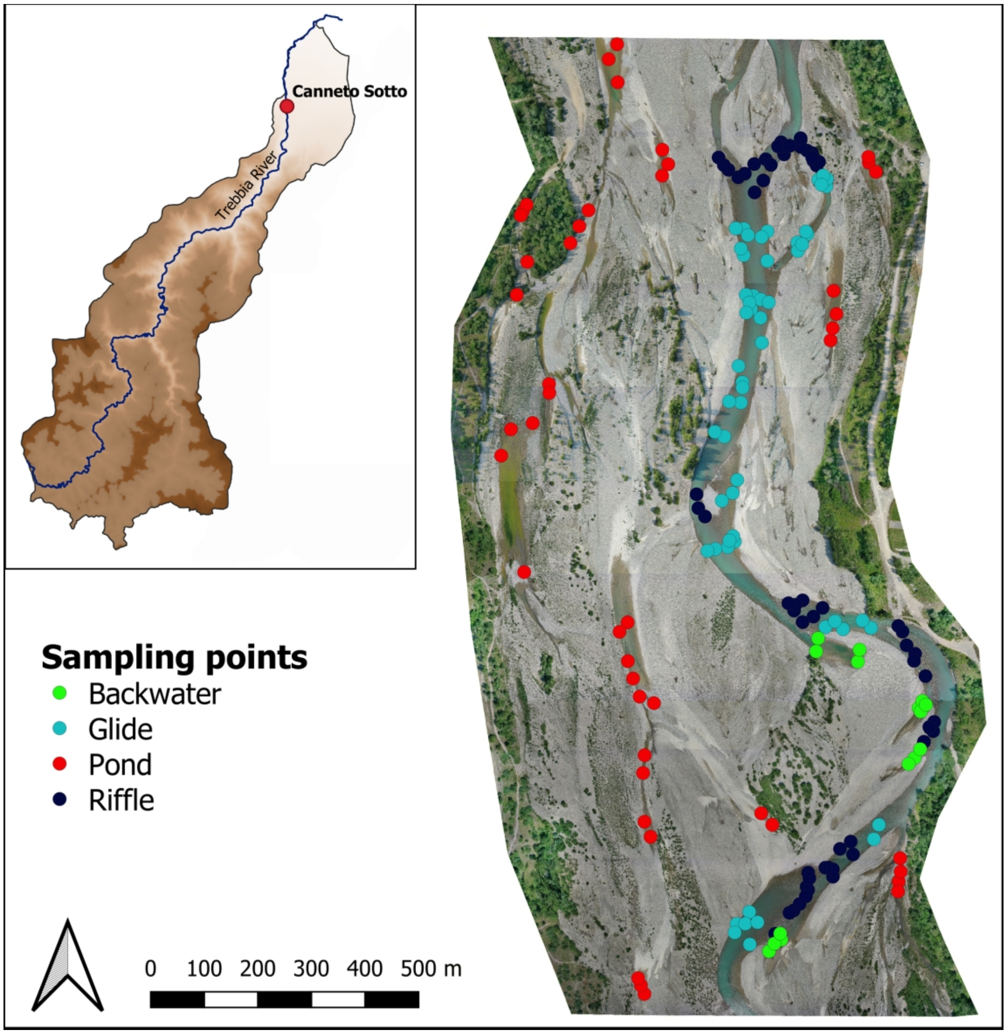
Class/Order	Family	Stat	p-value	
		RIFFLE		
Ephemeroptera	Oligoneuriidae	0.792	0.001	***
Diptera	Simuliidae	0.767	0.001	***
Trichoptera	Hydropsychidae	0.643	0.002	**
Ephemeroptera	Baetidae	0.619	0.026	*
Ephemeroptera	Heptageniidae	0.591	0.034	*
Coleoptera	Scirtidae	0.407	0.013	*
Trichoptera	Rhyacophilidae	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	*
		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	*

Figure captions

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.

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.

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.



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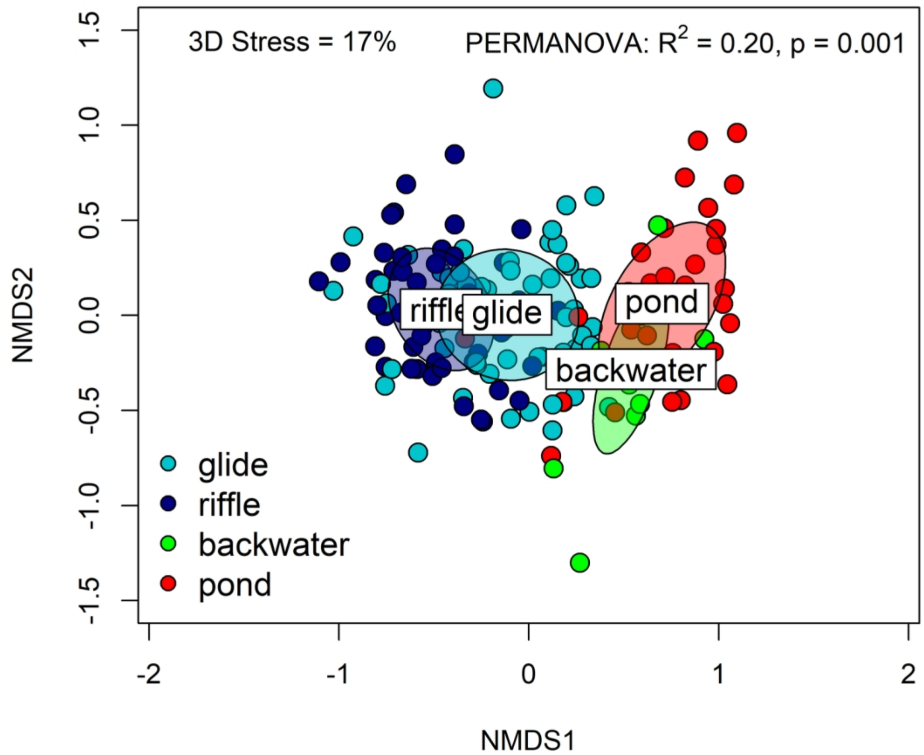

Figure 2. Non-Metric Multidimensional Scaling (nMDS) ordination output for community composition data. Ellipsoids correspond to the mesohabitats. 3D stress value is reported as measure of goodness of ordination.

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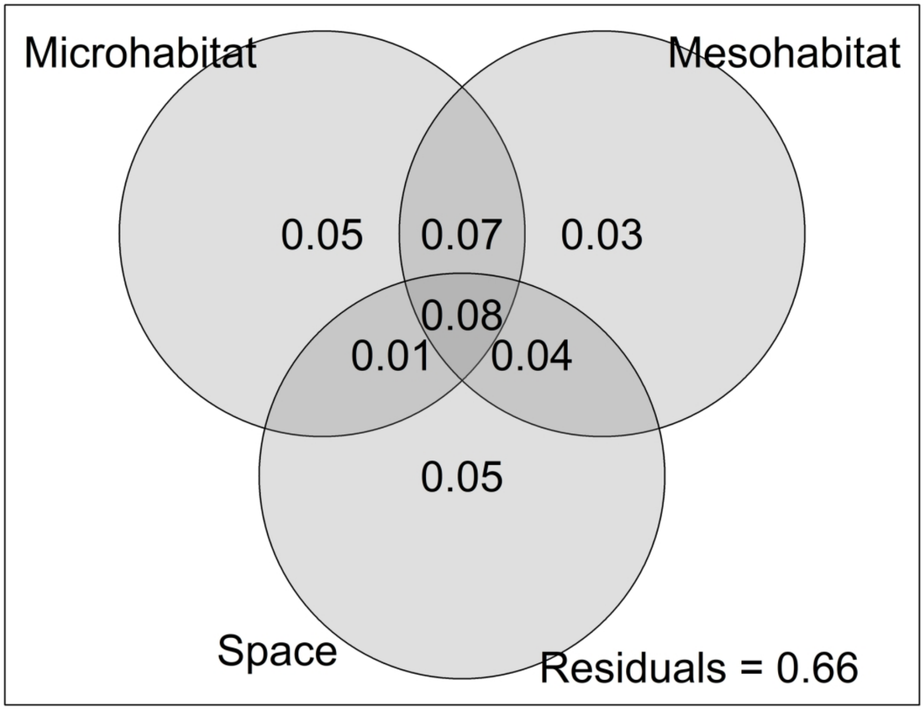

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