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Thermal regime, together with lateral connectivity, control aquatic invertebrate composition in river floodplains

Pierre Marle^{1,2}  | Jérémie Riquier³  | Pablo Timoner¹  | Hélène Mayor¹ | Vera I. Slaveykova¹  | Emmanuel Castella¹ 

¹Department F.A. Forel for Environmental and Aquatic Sciences, Section of Earth and Environmental Sciences and Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland

²CNRS, UMR 5023 - Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, University Claude Bernard, Villeurbanne, France

³UJM - Saint-Étienne, CNRS, EVS UMR 5600, University of Lyon, Saint-Étienne, France

Correspondence

Pierre Marle, Department F.A. Forel for Environmental and Aquatic Sciences, Section of Earth and Environmental Sciences and Institute for Environmental Sciences, University of Geneva, Carl-Vogt 66, Geneva, Switzerland.

Email: pierre.marle@unige.ch

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Abstract

1. Large river floodplains are dynamic environments, where alternating low and high flows are key ecological processes shaping aquatic biota. As a result of fluctuations in flow in floodplain channels, the diversity of benthic assemblages is assumed to result from the balance between surface flow connections, which are dominant during high flows, and groundwater inputs, which are dominant during low flows. However, the relative importance of these inputs in explaining aquatic invertebrate diversity has never been tested.
2. The response of aquatic invertebrates to hydrological changes of a river floodplain was investigated in seven braided and six braided–anastomosed floodplain channels of the French upper Rhône River that are fed by three different processes: groundwater supply (which controls the thermal inertia of the water bodies), surface slow flow connections (i.e. diffuse overbank flows; passive overflow), and surface shear stress-related connections (i.e. condensed flows; active overflow) during high flows.
3. Generalised dissimilarity models indicated that floodplain invertebrate composition had complex relationships with the three processes considered. The relative importance of the latter appeared dependent upon the morphology of the floodplain channels. In the braided channels, the effects of shear stress-related connections were more prominent than in the anastomosed ones, for which the effects of the three processes were more similar.
4. Overall, the diversity of flow connections, that is, lateral surface water connections (both shear stress-related and slow, as defined above) and vertical connection with groundwater (inferred through thermal inertia) enhanced the species turnover at the reach scale. Thermal inertia influenced invertebrate composition when, during low flow periods, surface flow connections had limited effect.
5. Our results highlighted that the role of hydrologic connectivity upon floodplain diversity cannot be reduced to a single process. They also indicate the

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importance of vertical connectivity for maintaining biodiversity in floodplain habitats where surface flow connectivity is neither frequent nor constant.

KEYWORDS

floodplain processes, generalised dissimilarity model, hydrological connectivity, Rhone River, species turnover

1 | INTRODUCTION

Riverine floodplains are commonly considered among the most species-rich and productive ecosystems (Amoros & Bornette, 2002; Naiman et al., 1993; Tockner & Stanford, 2002; Ward et al., 1999). The complex interaction between topography, sediment transport and flow variations control the biodiversity in inter-connected and dynamic habitats of large river floodplains. Since the second half of the 19th century, alteration of large rivers and their floodplains resulted in ecological discontinuities, habitat fragmentation, morphological alterations, changes in flow and thermal regimes, and sediment processes (Poole & Berman, 2001; Tockner et al., 2008). These alterations also led to large-scale losses of both natural habitats and biodiversity in these systems (Montoya et al., 2012) and to the establishment of novel biotic assemblages (Carling & Petts, 1992; Hobbs et al., 2006; Tockner et al., 2008; Ward, 1989; Ward & Stanford, 1995). As a consequence, floodplain restoration attempts emerged, aimed at achieving more *natural* geomorphic and hydrological processes according to the flood and flow pulse concepts (Junk et al., 1989; Junk & Wantzen, 2004; Poff et al., 1997; Puckridge et al., 1998; Tockner et al., 2000).

The flood pulse concept emphasises the importance of flooding for floodplain productivity and maintenance of biotic diversity (Junk et al., 1989). Since the application of this concept in large-scale restorations of river floodplains (Lamouroux et al., 2015; Tockner et al., 1999), important efforts to understand how hydrology influences floodplain biodiversity have been carried out. Evaluation of restoration through biological monitoring demonstrated that processes generated by flow increase and floods, such as the establishment of connections with floodplain water bodies (e.g. secondary channels, riverine wetlands, oxbow lakes) and the local increase in hydraulic shear stress, can influence invertebrate densities and species replacement (i.e. turnover; Dolédec et al., 2007; Rader et al., 2008; Wohl et al., 2015; Rolls et al., 2018). At low connectivity, species assemblages are dominated by lenitophilous taxa, such as the majority of Gastropoda. While rheophilous taxa as some mayflies (Ephemeroptera) and caddisflies (Trichoptera), more suited to hydraulic shear stress, increase as lateral connectivity increases (Castella et al., 2015; Marle et al., 2021; Paillex et al., 2007; Reckendorfer et al., 2006). A deeper knowledge of these processes remains necessary to understand the alterations of biodiversity induced by river regulations to improve conservation and restoration. A predictive understanding of hydro-ecological relationships can help mimic key aspects of the natural flow regime, or create

hydrological conditions that maximise restoration success within regulated rivers (Palmer & Ruhi, 2019).

A unique feature in semi-connected and disconnected floodplain channels (i.e. secondary channels adjacent to the main river channel) is the fact that the direction of surface water flow can reverse depending on the water level in the main channel and the relative altitude of the upstream and downstream alluvial plugs (i.e. sediment deposited in a neck-floodplain channel). Therefore, two types of connections with the main channel can occur in floodplains, with contrasted sedimentological and biotic consequences. A shear stress-related connection (i.e. condensed flow or active overflow) that usually occurs at the upstream channel entry and generates disturbances through scouring of bed material and biota (Bornette et al., 1994; Bornette et al., 1998). However, surface flow connections can also occur with no generation of shear stress (i.e. diffuse overbank flows or passive overflow, slow connection hereafter) in semi-connected floodplain channels or in disconnected water bodies distant from the river (Amoros & Roux, 1988; Citterio & Piégay, 2009). Slow connections create an entry of river water, suspended solids, and biological propagules in the floodplain channel. This process enhances fine sediment deposition, especially at the downstream parts of floodplain channels (Riquier et al., 2015; Riquier et al., 2017). Although recognised as critical in floodplain functions by Bornette and Amoros (1991) and Amoros (2001), accounting for slow connections remains rare in models of biodiversity changes in floodplains (but see Marle et al., 2021).

In addition to these two types of surface water connection, floodplain water bodies also differ in their degree of vertical connection with the floodplain aquifer. The relative contribution of surface vs. groundwater was shown to influence the function and biota particularly in semi-connected and disconnected floodplain channels (Amoros, 2001; Bornette et al., 1998; Boulton et al., 2008). Indeed, while surface waters generally provide turbid and oxygenated waters and warmer temperatures in summer, groundwater dominated channels are generally characterised by less turbid, more oligotrophic, often less oxygenated waters, buffered temperature variations (i.e. thermal inertia) and a higher yearly persistence of aquatic vegetation (Boulton et al., 2010; Kondolf et al., 2006; Wohl, 2017). Such floodplain channels were shown to maintain stenothermal (i.e. restricted to narrow temperature variations), oligotrophic (i.e. adapted to nutrient-poor waters) and hyporheobiont (i.e. adapted to living in the transitional zone between river and ground water) organisms (Boulton et al., 2008; Brunke & Gonser, 1997; Glanville et al., 2016; Trudgill et al., 2005). Floodplain channel restoration, not only modifies surface water connections, but

can also impinge upon groundwater–surface water interactions when lentic pools or channel stretches are deepened by mechanical means primarily to increase the duration of lateral connection with the river (Boulton et al., 2010). To improve models of floodplain biodiversity responses to hydrology and temperature changes under alternative restoration scenarios, it is therefore critical to integrate both types of surface connections as well as the contribution of groundwater. This could apply both at the level of individual channels and of entire floodplains.

We therefore aimed at assessing how lateral surface water connections (both shear stress-related and slow, as defined above) and vertical connection with groundwater (inferred through thermal inertia) contribute and interact to explain variations in aquatic invertebrate taxonomic composition and turnover at the floodplain scale. Aquatic invertebrate assemblages were chosen because: (1) their composition is known to change along the lateral hydrological connectivity gradient in floodplains (Gallardo et al., 2014; Marle et al., 2021; Paillex et al., 2007; Reckendorfer et al., 2006; Waringer et al., 2005); (2) the majority of species have short generation times (lifecycles are often less than 1 year); and (3) they are sensitive to flow variations (Dolédéc et al., 2007; Dolédéc & Statzner, 1994; Šporka & Nagy, 1998). We used a dataset on floodplain aquatic invertebrates sampled over 10 years (from 2007 to 2016) in 13 floodplain channels located in two bypassed sections of the Rhône River (France) that were subjected to restoration in 2005–2006 (Lamouroux et al., 2015). The two floodplains are adjacent but differ in general morphology, one being strictly braided, the other being wider and incorporating both anastomosed and braided channels. We hypothesised that these morphological differences may influence hydrological processes and therefore the invertebrate assemblages for which divergences in species composition between the two floodplains were already observed (Castella et al., 2021; Castella et al., 2022). We expected the shear stress-related connections to have a prevailing influence upon aquatic biodiversity in the braided floodplain that has a higher overall slope. In more anastomosing floodplains, the lower channel-flow capacity caused by in-channel fluvial deposition (Makaske, 2001) may cause slow connections and thermal inertia as the main drivers of floodplain biodiversity. To test these hypotheses, two biodiversity metrics were considered: (1) taxonomic richness was compared among the three channel types i.e. connected, semi-connected, and disconnected; (2) species turnover was modelled using generalised dissimilarity modelling (Ferrer et al., 2007; Timoner et al., 2020) along three environmental gradients referring to the three components of hydrologic connectivity mentioned above.

2 | MATERIAL AND METHODS

2.1 | Study sites

The study was carried out on the Upper Rhône River in France, between the cities of Geneva and Lyon. Data were collected after restoration between 2007 and 2016 in two adjacent reaches (Belley [BELL] and Brégnier-Cordon [BREG]; Figure 1) as part of the long-term

monitoring of river restoration (Lamouroux & Olivier, 2015). These bypassed sections of the river receive a minimum flow, except when they are used to evacuate floods that exceed the maximum operating flow of the plant. Such hydropower bypass schemes strongly modify flow characteristics (Klingeman et al., 1998) and result in an artificial regime with a base discharge maintained at 60 and 100 m³/s for BELL and 80 and 150 m³/s for BREG in winter and summer, respectively (Table S1). The mean annual discharge is 110 and 150 m³/s for BELL and BREG sections, respectively (calculated over the period 2006–2016).

The 13 floodplain channels (six in BELL and seven in BREG) included in the study were mostly restored in 2005 (BELL) and 2006 (BREG). The nine restored floodplain channels were dredged, with or without downstream plug removal (Table 2) and the groundwater–surface water exchanges were improved as a consequence (Riquier et al., 2015). In addition, the increase of the minimum regulated flows in the bypassed river channels also increased water levels in floodplain channels (Lamouroux et al., 2015). Of the 13 sampled channels, four (two in each floodplain) had an upstream plug at average level and permanent connections at their downstream ends, five were lentic channels (two in BELL and three in BREG) with an upstream and a downstream plug at average water level. Four channels (two in each floodplain) were permanently connected to the main channel. All channels differed in their connectivity level and distance from the main channel (Table 2).

2.2 | Overview of floodplain patterns

At the end of the last glaciation, the BREG floodplain was strongly influenced by a landslide that filled up the valley and forced alluviation of eroded material from a former glacier (Bethemont et al., 2016). The aggradation of the longitudinal profile in the glacial basin caused the riverbed to adopt an anastomosed pattern (Bravard, 2010). The anastomosed floodplain channels are currently sinuous, deep, and stable in location; their slope is low (except GRAN; Table 1) since their sinuosity compensates for the steeper gradient of the floodplain (see Table 1 for the general slope of the floodplain) (Bravard et al., 1986; Riquier, 2015). The BELL reach proved to be more hydrologically dynamic than the BREG reach. The braiding pattern of the BELL sector is associated with a steeper slope and a heavier load of coarse material drifting in the main channel (Olivier et al., 2009). In general, the braided channels carry substantial volume of bedload and are characterised by more unstable, shallower channels with marked flow variations (Bravard & Gilvear, 1996).

2.3 | Invertebrate data collection

In two of the channels, aquatic invertebrate sampling was limited to one site and extended to two (upstream and downstream parts of the channel) in the 11 others (Table 2). In each site, three samples were randomly distributed along a 30-m stretch. Invertebrates

FIGURE 1 The Rhône River and the studied reaches and sites: location in France and Switzerland, with the catchment (dashed lines), the main cities and tributaries (a) and the two reaches Belley (BELL) and Brégner-cordon (BREG) showing the studied channels and sampling sites (symbols) (b)

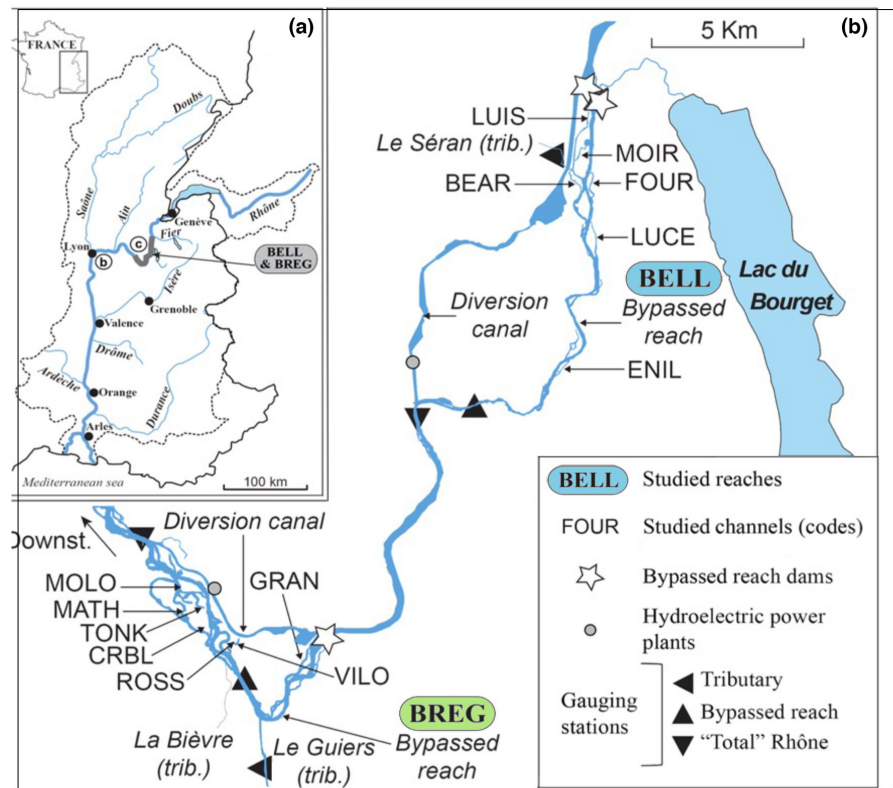


TABLE 1 Main characteristics of the two studied bypassed reaches. For shear stress values, medians are associated with the range in brackets

Study reach	Kilometric distance ^a	Slope (%)	Floodplain width (km) ^b	Number of studied channels	Number of studied sites	Range of connectivity Q_{up} Thresholds (m^3/s) ^c	Shear stress (N/m^2) ^c
BELL (Belley)	-131.6 to -114.6	0.8	0.2-0.7	6	10	$Q_{min} \rightarrow 982$	0 (0-42)
BREG (Brégner)	-102.9 to -91.6	0.6	0.4-1.6	7	10	$Q_{min} \rightarrow 1,380$	0 (0-37)

^aCurrent river kilometre (0 = Lyon, with negative distance upstream).

^bWidth measured on aerial photos from Géoportail (<https://geoportail.gouv.fr/>).

^cThe values concern the floodplain channels.

were sampled in a 0.5 × 0.5 m metal frame with a hand net. The material collected was fixed in ethanol and sorted in the laboratory. Sampling was repeated in spring (March–April) and summer (June–July) in 2007, 2009, 2011, 2013, 2015, and 2016 in BELL, and 2008, 2010, 2012, and 2016 in BREG. In total, 112 (for BELL) and 64 (for BREG) samples were used, and all analyses were based upon the sum of the three samples collected in a given site on the same date. Benthic invertebrates were identified to the lowest practical taxonomic level, usually species or genus, except for dipterans that were identified to family and hydracarina that were not identified further. The identification keys of various authors were used (as e.g. Studemann et al., 1992; Glöer, 1994; Tachet et al., 2010; Waringer & Graf, 2011).

2.4 | Environmental variables

Metrics related to flow connection were taken from Marle et al. (2021) where 14 hydrological variables were identified in

models of the distribution of Ephemeroptera, Plecoptera, and Trichoptera insects and gastropods. For each floodplain channel, overflow and backflow durations in days were quantified for a range of periods prior to each invertebrate sampling event. Seven periods were calculated, ranging from 1 month to 1 year. Of these 14 variables (seven periods for overflow and seven periods for backflow), we chose the two that most explained the occurrence of species: the upstream overflow and backflow connection durations calculated over 1 year prior to sampling. Following Marle et al. (2021), the flow connections calculated over 1 year had approximately twice as much contribution in predictive models than connections calculated over shorter durations. The duration of overflow connection was split according to the associated bed shear stress (i.e. magnitude of connections; see Section 2.4.2 below) leading to the distinction of: (1) shear stress-related (i.e. overflow connection with shear stress); and (2) slow (i.e. overflow connection without shear stress plus backflow connection) connection durations. Thermal inertia (see Section 2.4.3 below) was also estimated over 1 year prior to the sampling date. The three

TABLE 2 Characteristics of the floodplain channels. Reach codes are BELL: Belley and BREG: Brégnier-cordon (Figure 1). See the text for upstream overflow (Q_{up}) and backflow (Q_{down}) threshold calculations (from Riquier et al., 2015)

ID	Reach	Fluvial pattern	Thalweg length (km)	Nb of sites	Type	Q_{up} (m^3/s)	Q_{down} (m^3/s)	Maximum shear stress (N/m^2)	Type of restoration works			Minimal Q increased ^a	Method of Q_{up} And Q_{down} ^b Estimation
									Dredging	Reconnection			
										Up	Down		
BEAR	BELL	Braided	0.91	2	Disconnected	982	200	30	X	-	X	X	Riquier (2015)
FOUR	BELL	Braided	0.92	2	Semi-connected	167	0 ^b	42	X	-	-	X	Riquier (2015)
LUIS	BELL	Braided	2.51	2	Semi-connected	229	0 ^b	29	X	-	-	X	Riquier (2015)
MOIR	BELL	Braided	1.13	2	Disconnected	417	229	9	X	-	-	X	Riquier (2015)
ENIL	BELL	Braided	0.68	2	Connected	0 ^b	-	20.6	X	X	X	X	-
LUCE	BELL	Braided	1.51	2	Connected	0 ^b	-	26.5	-	-	-	X	-
CRBL	BREG	Anastomosed	0.4	1	Disconnected	0 ^b	596	0	-	-	-	-	Džubáková et al. (2015)
GRAN	BREG	Braided	1.31	2	Semi-connected	539	170	37	X	-	-	X	Riquier (2015)
MOLO	BREG	Anastomosed	1.66	2	Semi-connected	560	0 ^b	10	X	-	X	-	Riquier (2015)
ROSS	BREG	Anastomosed	0.95	2	Disconnected	1'100	627	0	-	-	-	-	Džubáková et al. (2015)
MATH	BREG	Anastomosed	1.71	2	Connected	0 ^b	-	27.7	X	X	X	-	-
TONK	BREG	Anastomosed	2.13	2	Connected	0 ^b	-	No values	-	-	-	-	-
VILO	BREG	Anastomosed	0.59	1	Disconnected	1'380	1'100	0	-	-	-	-	Džubáková et al. (2015)

^aMinimal discharge increased.

^bPermanently connected: a permanent flow-path links the floodplain channel to the main channel by its upstream or downstream connection.

explanatory variables were not significantly linearly correlated (Pearson $r < 0.14$ and $0.08 < p < 0.43$ for all pairs).

2.4.1 | Surface flow connections

For each floodplain channel, the river discharge thresholds (Q_{up} and Q_{down} ; Table 2), for which flow connections are initiated, were estimated combining field observations, topographic field measurements (DGPS), stage–discharge relationships for the more connected floodplain channels (as described in Riquier et al., 2015 and Marle et al., 2021) and a raster-based method developed on an airborne LiDAR DEM covering the floodplain for the more lentic channels (as described in Džubáková et al., 2015). The stage–discharge relationships and the DGPS method were mainly used to define the river discharge thresholds of the floodplain channel close to the main channel. The LiDAR method performed well in defining the river discharge thresholds for floodplain channels away from the main channel, where the stage–discharge relationships showed some limitations. Flow connection durations for each floodplain site as well as the mean and the median daily flows in the main channel were calculated using the hydrostats package (Bond, 2015) within the R statistical environment (R Core Team, 2016) according to the hourly discharge time series recorded in the bypassed sections from 2006 to 2016 and provided by the Compagnie Nationale du Rhône.

2.4.2 | Shear stress

Because a given flow connection does not entail the same level of shear stress in different channels, we associated each flow connection with a measure of shear stress. (Dépret et al., 2017; Džubáková et al., 2015; Riquier et al., 2015) Following Riquier et al. (2015), the total boundary shear stress (τ) was calculated hourly for a given main channel discharge (Q) as:

$$\tau = \rho g H s$$

where ρ is the water density (1000 kg/m^3), g the gravitational acceleration (9.8 m/s^2), H the average water depth (m; related to Q) along the floodplain channel, and s the average water–surface slope (detailed in Riquier et al., 2015). For each floodplain channel site, shear stress values were computed over a wide range of discharge in the main channel (Q) displaying in most of cases a logarithmic relation (except LUIS, where the shear stress–discharge relationship is more complex due to multiple connections to the main channel). These relations, specific for each channel, were used to convert hourly discharge in the main channel (Q) into hourly shear stress (τ) in the floodplain channel during connections.

In the studied floodplain channels, shear stress ranged from 0 to 42 N/m^2 (Tables 1 and 2). We postulated that the shear stress was a measure of the effect of flow connections on the habitat. In this

way, we referred to the shear stress to differentiate the slow from the shear stress-related connections. This requires defining a shear stress threshold that we defined as the minimum energy required to export the fine sediment particles (e.g. silt or clay) from the benthic habitat. From an ecological point of view, the export of sediment particles that occurs during shear stress-related connections is thought to be the trigger that initiates invertebrate drift. Due to the presence of silt and clay (i.e. cohesive sediments) in floodplain deposits, the behaviour of cohesive sediment mixture differs considerably from that of non-cohesive sediments. In the literature, most values of the minimum shear stress for the initiation of movement of cohesionless clay and silt sediments are below 0.5 N/m^2 (Hauer et al., 2007). In a cohesive mixture of clay–silt–gravel and clay–silt–sand–gravel (as observed in floodplain channel beds), the sediment transport mechanism, including incipient movement, requires a higher shear stress than in the case of cohesionless sediments. The critical bed-shear stress for mud–sand mixture is in the order of $1.2 \pm 0.5 \text{ N/m}^2$ (Table S2). Jacobs (2011) also reported a surface erosion for a shear stress of $1 \pm 0.4 \text{ N/m}^2$ and for a sediment composed of mud (at least 80%) and sand, a mixture representative of sediments observed in the Rhone River floodplain. Therefore, we set the shear stress-related connection above 1 N/m^2 , above which we assume that invertebrate drift increases significantly (see values from Gibbins et al., 2007). Subsequently, shear stress below this threshold was considered as slow connection. This relatively low threshold (compared to the observed shear-stress range) suggests that invertebrate drift in lentic floodplain channels (where fine particles constitute a significant proportion of the substrate) occurs regularly during lateral upstream connections, rather than being a rare phenomenon associated only with high flow events. Brittain and Eikeland (1988) also affirm that these invertebrate drifts are very common in freshwater ecosystems as they are linked to small hydrological variations and changing current velocity.

2.4.3 | Thermal inertia

The intensity of the vertical connection between surface and groundwater can be measured directly (e.g. measurement of the hydraulic head, Capderrey et al., 2013), but thermal variables, such as the surface water–air temperature relationship (Caissie, 2006; Webb et al., 2003; Webb & Walling, 1985; Wohl et al., 2015) was used as surrogate to infer groundwater contribution, offering a simple characterisation of thermal regime in water bodies. The slopes extracted from water–air temperature linear regression models were used as surrogates to estimate the groundwater importance in each site over one year preceding the benthic sampling date (Erickson & Stefan, 2000) to conform with the calculation of flow connection durations. Surface water and air temperatures used for calculation were recorded at hourly intervals using temperature data-loggers (Hobo Data logger, Onset) installed in the sites from 2006 to 2016. Missing values were estimated using non-parametric random forest algorithm from the R missForest package

(Stekhoven & Bühlmann, 2012) within the R statistical environment (R Development Core Team, 2016).

2.5 | Taxonomic richness

Taxonomic richness was calculated by channel types (i.e. connected, semi-connected and disconnected channels) through the construction of species accumulation curves based on 999 random permutations and using the `specaccum` function of the `vegan` package in R (Oksanen et al., 2018). Venn diagrams were used to assess the proportion of shared and unique taxa among channel types, using the `vennDiagram` function of the `VennDiagram` package in R (Chen & Boutros, 2011).

2.6 | Difference in invertebrate assemblages

Based on a Bray–Curtis distance for abundance data, we generated a non-metric multidimensional scaling plot to describe the dissimilarities between invertebrate assemblages of the two sectors. To help visualise the underlying explanatory variables potentially affecting the invertebrate distribution, we used the `metaMDS` and the `envfit` functions from the R package `vegan` (Oksanen et al., 2018). The function `envfit` calculates multiple regression of the variables with ordination axes. Significance of the variables is tested with a permutation test and the variables can be projected onto the non-metric multidimensional scaling ordination. We also used the function `anosim` from the `vegan` package to determine if the difference in assemblage composition between the two sectors was significant. The `anosim` function compared the mean dissimilarity between assemblages with the mean of dissimilarities within groups. A Bray–Curtis distance and 9999 permutations were used as settings of the `anosim` to determine an r value and its significance. An R value close to 1 suggests actual dissimilarity, while an r value close to 0 suggests homogeneity in species composition between groups. We used the R base (R Development Core Team, 2016) and `ggplot2` R packages (Wickham, 2009) for all graphics.

2.7 | Species turnover modelling

For the modelling of species turnover, permanently and fully connected channels were discarded because they lead to an overestimation of the influence of shear stress-related connections. This overestimation is explained by the fact that slow connections are lacking in lotic conditions (i.e. a permanently and fully connected channel is always lotic with a downstream flow direction) and because the thermal inertia does not vary from one connected channel to another (they share the same surface water source from the main channel). Therefore, we investigated the relative importance of thermal inertia, shear stress-related connections, and slow connections

as explanatory variables of species turnover in disconnected and semi-connected channels using general dissimilarity modelling (GDM, Fitzpatrick & Keller, 2015) as implemented in the R package `gdm` (Ferrier et al., 2007; Manion et al., 2017). GDM is an extension of matrix regression that relates the curvilinear relationship between increasing environmental distance (based on the three explanatory variables) and species turnover i.e. number of species eliminated and replaced from one site to another along a gradient. This is achieved using permutations on distance matrices to perform model and variable significance testing and to estimate the importance, i.e. the relative influence, of the explanatory variables on species turnover. Significance of the differences in relative influence between environmental variables was tested using unpaired Wilcoxon tests. For each sampling year, the species presence–absence matrix was used to derive Jaccard dissimilarities between sites as the biological response variable for the GDM. We started the modelling using the three explanatory variables and keeping the sampling season as a dummy variable (spring and summer). Geographic distance between sites was not incorporated in the models. The significance of the model and of each of the three variables were calculated by permutations ($n = 300$) of the site pairs (Table 2) using the R function `gdm.varImp`, which also gives the relative importance of each variable in the models.

3 | RESULTS

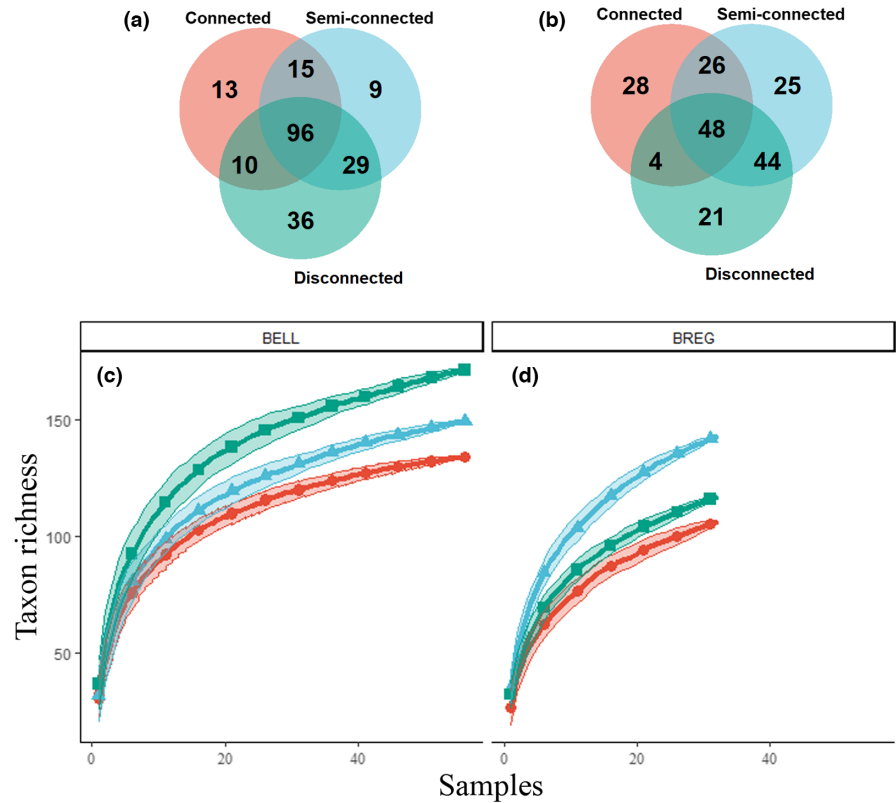
3.1 | Taxonomic richness

Aquatic invertebrate assemblages from the nine floodplain channels (including lotic ones) were composed of 236 taxa (from 528 individual samples). Among the three floodplain channel types, the cumulated species richness in semi-connected (143 taxa in BREG and 149 in BELL) and disconnected channels (117 taxa in BREG and 171 in BELL) were higher than in the connected channels that exhibited the lowest value with 103 taxa in BREG and 143 in BELL (Figure 2). Interestingly, over the 196 taxa recorded from BREG and 208 from BELL, a high proportion (>85%) were present in both semi-connected channels and disconnected channels (168 for BREG and 195 for BELL), while only 28 and 13 taxa were restricted to lotic channels (Figure 2).

3.2 | Composition of the invertebrate assemblages

The two sectors differed significantly in the composition of their invertebrate assemblages (Anosim $r = 0.15$ and $p < 0.001$; Figure 3). The thermal inertia and the shear stress connection durations appeared as the most influential variables explaining the variations in assemblage composition. Whereas the BELL sites show a relatively homogeneous spread around the ordination origin, the BREG sites appear divided in two groups, at low (samples from disconnected and semi-connected channels; Table 2) and high (samples from

FIGURE 2 Venn diagrams: Comparison of taxon richness between channel types showing the number of common and distinctive species for BELL (a) and BREG (b) floodplains. Sample-based species accumulation curves constructed for aquatic invertebrates from two connected (in red; for both floodplains), two semi-connected (in blue; for both floodplains), and two (for BELL) or three (for BREG) disconnected (in green) floodplain channels for BELL (c) and BREG floodplains (d). Solid line refers to the richness and the shaded area to the standard deviation of the richness. Characteristics of the studied floodplain channels are detailed in Table 2



connected channels; Table 2) values of shear-stress connection durations, respectively (Figure 3).

3.3 | General dissimilarity modelling: Community composition and environmental variable relationships

In total, 215 taxa (from 354 individual samples) were identified in the nine semi-connected and disconnected floodplain channels. Between 17.3% (BELL 2011) and 73.5% (BREG 2008) of the observed between-site variation in invertebrate composition was significantly accounted for by the three explanatory variables in the GDM models (Table 3). When the variation explained by the GDM was partitioned, the unique contributions of the shear stress-related connections (GDM permutation test p -value < 0.1 ; Table 3) was the most important (median = 36.4%; Figure 3a) for the BELL floodplain. The slow connections and thermal inertia contributions (median = 4.74% and 14.2%, respectively; Figure 3a) were considered to be at least twice less important in the same sector. For the BREG floodplain, the influence of the three variables was more similar with slightly higher contributions of the slow connections (median = 29.1%; Figure 3a). The relative importance of the thermal inertia and the shear stress-related connections were highly similar (median = 24.6% and 23.2%, respectively; Figure 3a).

The shape of all the fitted functions (GDM-fitted I-splines) for the variables associated with taxonomic turnover was consistently nonlinear suggesting a complex behaviour for the rate of turnover

along the gradient of the explanatory variables (Figure 4b–g). High rates of community changes were observed until a threshold value in the explanatory variable was exceeded, this was the case for thermal inertia in both BELL and BREG sectors (Figure 4d, g) and for the slow connections in BELL (Figure 4c, f). Turnover increased abruptly from 0 to 10 days of slow connections in the BELL sector (Figure 4c), suggesting that connection changes had a strong effect on community structure at low connectivity. Concerning the thermal inertia, turnover increased steeply from 1 to 2 for BELL and to 1.5 for BREG (Figure 4d, g). Meanwhile, in relation with the shear stress-related connections, turnover showed a non-asymptotic behaviour (Figure 4b, e). The concavity of the relation with shear stress connections in the BELL sector (Figure 4b) and the slow connections in the BREG sector (Figure 4e) means that species turnover increased quickly at low values of connectivity, but more slowly for longer connection durations. More generally, the models showed decreases of the flow connections relative importance (i.e. shear stress-related plus slow connections) as the relative importance of thermal inertia increased. As an example, during low water flows in BELL 2007 (mean daily flow = 74.7 m³/s; range: 65.8 m³/s in 2011–120.9 m³/s in 2015; Table S1), thermal inertia contributed 59.2% to the explanation of dissimilarity, while shear stress-related and slow connections contributed 10.1% and 1.7%, respectively. Conversely, during the year of highest flows in BREG 2012 (mean daily flow = 221.4 m³/s; range: 92 m³/s in 2010 to 221.4 m³/s in 2012; Table S1), shear stress-related and slow connections, contributed 49.1% and 30.6% respectively, while the contribution of thermal inertia reduced to zero (Table 3).

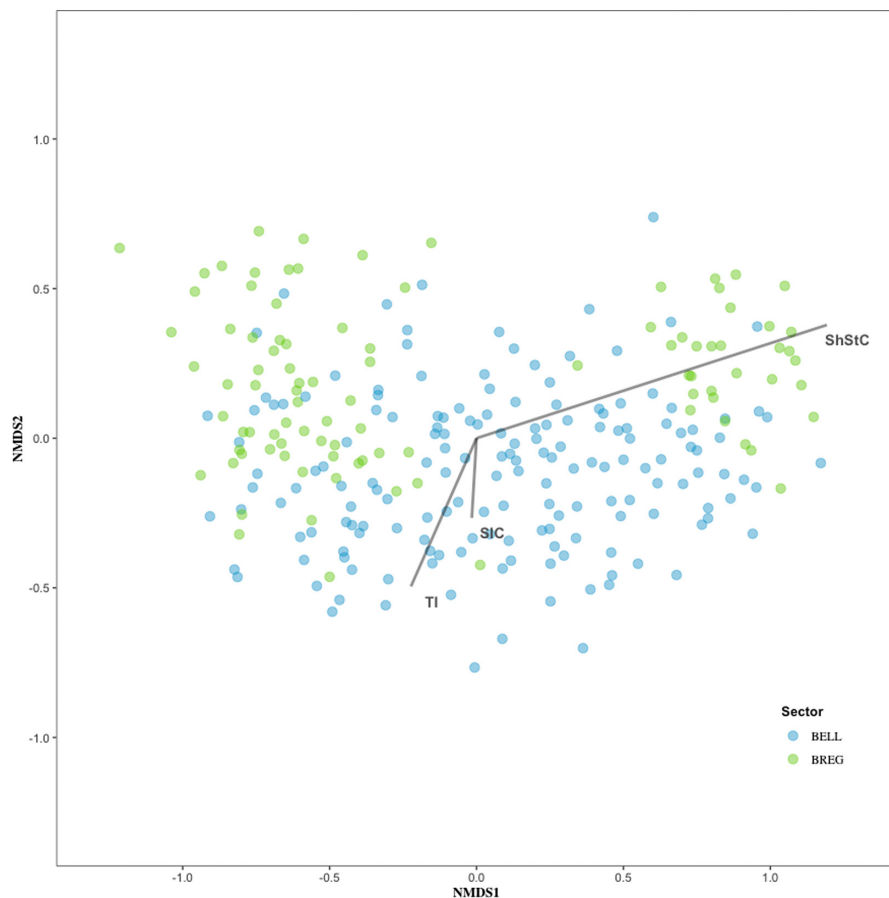


FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination of Bray-Curtis dissimilarities from untransformed species abundance data for 176 floodplain samples from 2006 to 2016 in the BELL (blue) and BREG (green) sectors. Envfit vectors (grey segments) are overlaid on the NMDS and represent the shear stress connection durations (ShStC), the slow connection duration (SIC), and the thermal inertia (TI). The three variables are significantly ($p < 0.05$) correlated with one of the two axes of the NMDS ordination

Sector/year	Shear stress connection	Slow connection	Thermal inertia	Explained variation of the full model (%)	p full model
BELL/2007	10.1**	1.7	59.2**	42.8	<0.01
BELL/2009	41.2**	1	35.1**	26.4	<0.05
BELL/2011	59.4*	7.7	19.1	17.3	<0.05
BELL/2013	62.8**	0.1	6.8	29.2	<0.05
BELL/2015	31.5**	51.8***	7	27	<0.01
BELL/2016	9.4*	45.9***	9.2	38.3	<0.01
BREG/2008	29.7***	18.9***	37.0***	73.5	<0.01
BREG/2010	1.8	27.6**	52.3**	41.5	<0.01
BREG/2012	49.1***	30.6*	0	28.8	<0.01
BREG/2016	16.6**	63.1***	12.3	37.4	<0.01

Note: Significance of each variable was tested using permutation tests. ***, $p < 0.01$; **, $p < 0.05$ and * $p < 0.1$.

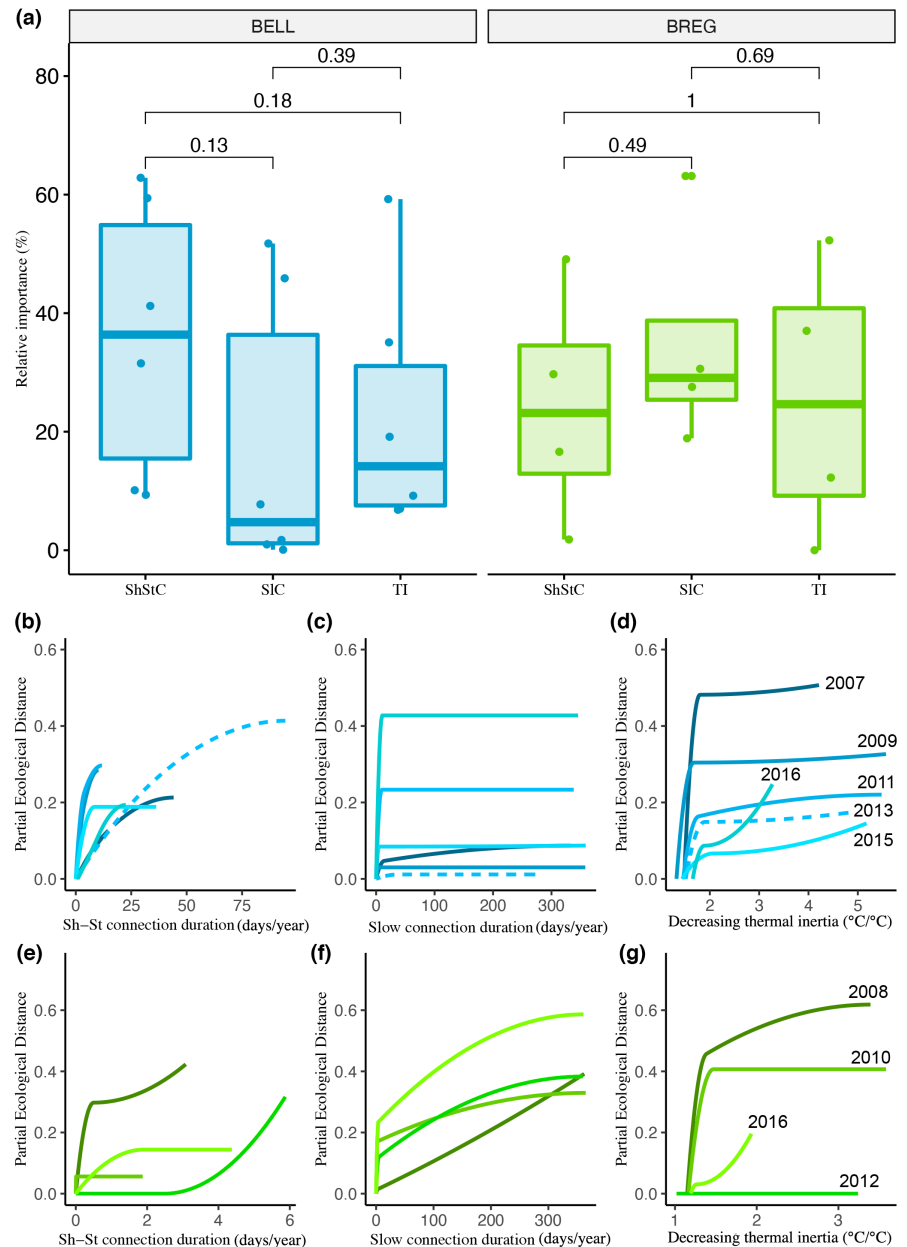
TABLE 3 Summary of the generalised dissimilarity models with the relative importance (%) of each variable. Each model was fitted using presence-absence dissimilarity matrices (Jaccard index) from nine semi-connected and disconnected floodplain channels

4 | DISCUSSION

Understanding how various patterns of hydrological connectivity interacts to shape biodiversity has been a key focus of floodplain research (Baumgartner et al., 2018; Leigh & Sheldon, 2009; Obolewski et al., 2015; Postma et al., 2010; Van den Brink et al., 1996). In our analysis, the disconnected and semi-connected channels were characterised by higher species richness than the

connected ones. This pattern was also mirrored by the GDM models indicating that the interaction of the two types of surface hydrological connectivity (generating bottom shear stress or not) is decisive for the turnover in invertebrate composition in the floodplain studied. Moreover, the heterogeneity of habitat conditions related to thermal inertia, was shown to have a significant effect on invertebrate composition when surface flow connections had limited effect.

FIGURE 4 (a) Percentage contribution of each environmental variables to the GDM total explained deviance in the two floodplains. Points are annual percentual contributions of each explanatory variable. ShStC, Shear stress-related connections; SIC, Slow connections; TI, Thermal inertia. Significance of the differences between environmental variables was tested using unpaired Wilcoxon tests. (b–g) Generalised dissimilarity models and fitting of explanatory variables. The curves indicate the variability explained by each driver for 1 year, while slopes relate to the rate of species turnover along each variable's range with (b and e) shear stress-related connections, (c and f), slow connections and (d and g) the decreasing thermal inertia (thermal inertia decreases when the values increase). Blue and green colours refer to the braided BELL and the braided-anastomosed BREG floodplains, respectively. Variations in blue and green colours refer to a given year (see panels d and g).



4.1 | Contribution of semi-connected and disconnected channels to the floodplain biodiversity

Semi-connected and disconnected channels together supported more than 80% of the taxa in the floodplain sectors considered, leading us to regard these lateral habitats as prominent reservoirs of floodplain biodiversity (see Karaus et al., 2013). This suggests that when hydraulic constraints generated by shear stress-related connections decrease (in space or time), a richer set of species can establish. A likely explanation is given by the fact that, especially in semi-connected channels, invertebrate assemblages are characterised by a mix of rheophilic taxa that can tolerate in relatively stagnant conditions and of lenitophilic taxa that can tolerate semi-lotic conditions. These results are in line with other studies (Gallardo et al., 2014; Paillex et al., 2007) that have also shown a replacement of the floodplain species assemblage between differently connected habitats of a large river floodplains. We also showed that in semi-connected or disconnected channels, thermal regime is a crucial

aspect contributing, among other factors, to between-channel biological heterogeneity. This is evidently associated with the proportion of groundwater supply in the waterbodies, an important driver of the thermal regime (Arrigoni et al., 2008). We supposed this mixing of surface waters and groundwaters increases the between-habitat heterogeneity of environmental conditions and subsequently maintains differences in species assemblages between sites. Such patterns have been observed elsewhere (e.g. Boulton & Lloyd, 1991; Simões et al., 2013).

4.2 | How is the diversity of invertebrate assemblages influenced by surface flow connections and the thermal inertia?

Changes in floodplain assemblages, described in this study as species turnover, were clearly linked to the flow variation in the main channel. The influence of thermal inertia on diversity was higher

during low flow conditions and decreased as the influence of flow connections increased. Specifically, the effects of the shear stress-related connections on compositional dissimilarity were stronger in the braided floodplain. However, in the anastomosed floodplain, the three types of connection contributed more equally. The inclusion of shear stress in the models provided additional insights into the function of each of the two types of surface connections and highlighted that the role of hydrologic connectivity upon floodplain diversity cannot be reduced to a single process (Amoros & Bornette, 2002; Marle et al., 2021).

Across the braided floodplain, species composition was associated primarily with shear stress-related connections. This corroborates findings on the Danube River, where hydrological connectivity was the main determinant explaining the distribution of aquatic invertebrates (Reckendorfer et al., 2005; Tockner et al., 1998) and supports the notion that most aquatic invertebrate taxa exhibit a preference for a specific degree of surface connectivity (Arcsott et al., 2003; Castella et al., 1991; Marle et al., 2021). The variation in species turnover with increasing shear stress-related connections implies that species turnover is a continuous process related to a continuous variation between floodplain habitats across the lateral dimension of the floodplain (Amoros & Roux, 1988; Bornette et al., 1998; Van den Brink et al., 1996; Ward, 1998). Indeed, the lateral continuum from semi-connected to disconnected channels provides a variety of habitats for aquatic invertebrates for which abiotic factors, such as local substrate composition and macrophyte cover, are effectively tied to the intensity of shear stress during flow connections. Moreover, we also observed a strong effect of shear stress-related connections from 0 to 15 days/year on species turnover. Accompanied by shear stress, these short events can change the structure of some disconnected habitats through, for example, the export of fine, organic sediments and aquatic vegetation by erosive forces. Because taxa that live in such conditions are more sensitive to scour and show a higher propensity to drift (Brittain & Eikeland, 1988; Cellot & Bournaud, 1988), shear stress-related connections can strongly affect species assemblages within disconnected channels, early during the connection process. In addition to changing substrate character, shear stress-related connections can also re-establish the vertical connections between surface and hyporheic habitats by reduction of the clogging of substrate interstices. Interstices and groundwater fluxes are important for invertebrate development in the floodplain hyporheic and benthic zones (Brunke & Gonser, 1997).

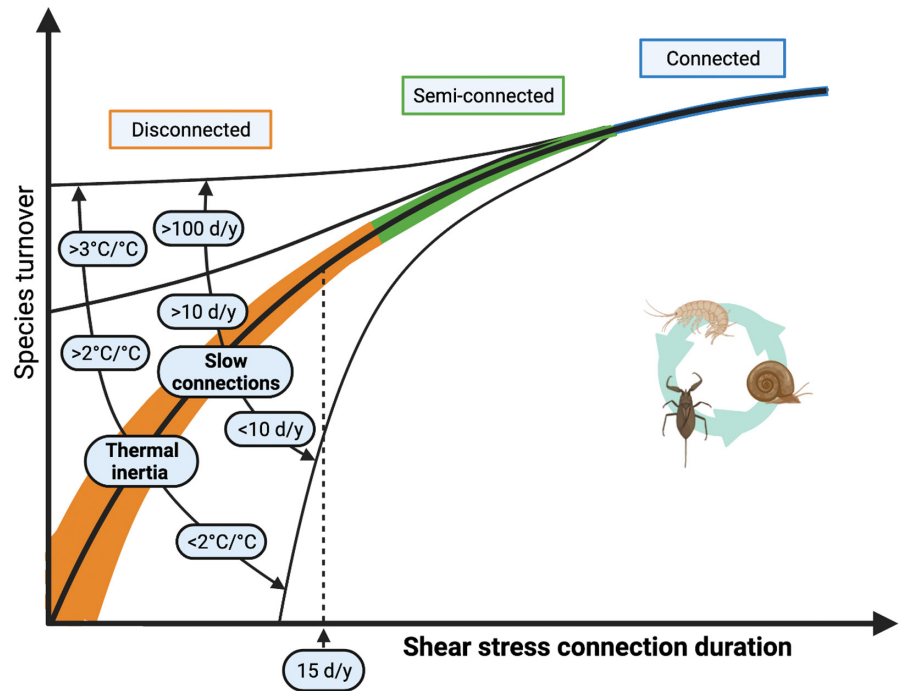
Similarly, variations in slow connections generate taxonomic turnover observed even for very short connection durations (from 0 to 15 days/year), even in that also concern highly disconnected sites. As opposed to the shear stress-related connections, the effect of slow connections on species turnover was effective in both floodplains studied. Slow connections in disconnected channels entail important and rapid water chemistry changes, enhanced oxygen or water temperature variations that can result locally in changes in taxonomic assemblage (Amoros & Petts, 1996). We hypothesised

that slow connections influence, via nutrient delivery, the onset of primary production and the development of functional groups such as grazers (gastropods) or active filterers (bivalves). These connections are also especially influencing groundwater supplied habitats (Brunke & Gonser, 1997; Caissie, 2006) where stenothermic coldwater species can disappear when temperature exceeds a critical value. Although species turnover mainly occurred below a thermal inertia value of 2°C/°C, this may be a threshold above which such stenothermic invertebrates are likely to disappear (Arrigoni et al., 2008). The low species turnover linked to thermal inertia, above a value of 2°C/°C, may be due to the dominance of more eurythermic species.

Inter-annual variations in flow regime appeared to have major implications for the response of taxonomic turnover to the three components of hydrological connectivity. As surface flow connectivity is a key variable that governs the occurrence of habitat types (Power et al., 1995) and aquatic invertebrate distribution in floodplains (Blettler et al., 2016; Gallardo et al., 2014; Marle et al., 2021), it is not surprising that the extension of the phenomenon increased the influence of shear stress-related connections on species turnover (Figure 5). Abundance of *Micronecta* sp., *Laccophilus* sp., *Caenis horaria*, *Theodoxus fluviatilis*, and *Goera pilosa* followed the increase in flow (years >2012). Conversely, a low inter-annual variability in flow regime appears as a condition increasing the influence of slow connections and thermal inertia on species turnover (Figure 5). The effect of thermal inertia is often much more important in drier years (from 2007 to 2011 in our case), during which the median daily flow was close to two thirds of the mean annual discharge. Under these conditions and despite very different ecological requirements, species such as *Ancylus fluviatilis*, *Dikerogammarus villosus*, *Silo nigricornis*, *Limnephilus lunatus*, *Psychomyia pusilla*, *Hippeutis complanatus*, and *Anisus vorticulus* were particularly abundant (years from 2007 to 2011). Even if other factors such as riparian shading and shelter from wind also modify thermal inertia in rivers (Stefan & Sinokrot, 1993; Erickson & Stefan, 2000), we argue that vertical connectivity can contribute significantly to taxonomic changes in floodplain landscapes.

Beyond the temporal and hydrological aspects, shear stress-related connections influenced species turnover, depending on floodplain morphology. Indeed, the two floodplains did not differ widely in the hydrological regime of their bypassed river section (characterised by a high discharge during spring and summer; Olivier et al. (2009)). This hydrological resemblance suggests that the morphology of the floodplain (especially its slope and width) but also the type of sediment (coarser and more mineral on average in BELL) could explain differences between floodplains in species assemblages and the relative influence of hydrological factors on taxonomic turnover. Because of a lower slope and a higher width of the floodplain, the assemblages in the BREG sector may also be more resilient to changes in flow conditions. Indeed, BREG-type floodplain morphology can play a large hydraulic role as an energy dissipator. This seems consistent with the weak influence of surface connections on species turnover observed in the wider BREG floodplain.

FIGURE 5 Between-channel and floodplain scale taxonomic turnover vary with shear stress connections. The top labels represent the three floodplain channel types. The bold solid line illustrates species turnover driven by shear stress, considered as the main factor. The two other factors, slow connections and thermal inertia (in bold) induce potential divergences (arrows between thin solid lines) of species turnover that may occur at low shear stress connection duration (potentially <15 days/year). The width of the coloured trend reflects the cumulated richness per channel type that decreases with increasing duration of shear stress connection



5 | CONCLUSION

Our analysis was based on two floodplain reaches only and, although BREG was wider, shallower and contained less dynamic anastomosed channels, it is obviously difficult to generalise beyond the two study cases. In any case, unexplained variations in taxonomic turnover suggests that additional variables (e.g. seasonality, species phenology), not accounted for in the current study, influenced invertebrate assemblage composition (see Larsen et al., 2019; Dong et al., 2021). In this sense, biogeochemical fluxes and food webs influenced by hydrological connectivity between the various types of surface and ground waters, could also potentially explain the variability in floodplain communities. In addition, on a more technical level, the adjustment of the shear stress threshold could lead to a more accurate characterisation of the two types of surface connections. Indeed, hydraulic models can help identify potential shear stress thresholds that may mark the onset of invertebrate drift or fine sediment scouring. Finally, we also believe that species interactions such as predation by fish or between invertebrates may modify floodplain assemblages.

Our findings have direct implications for the management of river flow regimes in anthropogenically-altered rivers and for the restoration of floodplain channels. To maximise spatial heterogeneity in floodplains, channels should differ in their connection thresholds (i.e. altitude of their upstream and downstream plugs). With the slope and the orientation of the floodplain channel, flow connections are also expected to differ in shear stress. This heterogeneity of flow connections sustains a mosaic of floodplain habitats with differing hydrological conditions, further enhancing the invertebrate diversity at the reach scale. Finally, restoring vertical connectivity can act

as an important driver enhancing biodiversity in floodplain habitats where surface flow connectivity is neither frequent nor constant. Future restoration and rehabilitation efforts should consider the role of flow processes in relation with floodplain morphology when deciding upon strategies to best improve floodplain habitat diversity for promoting biodiversity in large alluvial rivers.

AUTHOR CONTRIBUTIONS

Conceptualisation: P.M., J.R., E.C. Developing methods: P.M., J.R., P.T., H.M., E.C. Data analysis: P.M., P.T., E.C. Preparation of figures and tables: P.M. Conducting the research, data interpretation, writing: P.M., J.R., P.T., V.S., E.C.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Restrictions apply to the availability of discharge data, which were used under an agreement for this study. Floodplain invertebrate data are available from the authors upon reasonable request.

ORCID

Pierre Marle  <https://orcid.org/0000-0003-4464-9795>

Jérémie Riquier  <https://orcid.org/0000-0002-7008-7960>

Pablo Timoner  <https://orcid.org/0000-0003-4757-4928>

Vera I. Slaveykova  <https://orcid.org/0000-0002-8361-2509>

Emmanuel Castella  <https://orcid.org/0000-0002-4115-4124>

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SUPPORTING INFORMATION

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

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