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How to cite

PAILLEX, Amael et al. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. In: Journal of applied ecology, 2009, vol. 46, n° 1, p. 250–258. doi: 10.1111/j.1365-2664.2008.01593.x

This publication URL: https://archive-ouverte.unige.ch/unige:26772
Publication DOI: 10.1111/j.1365-2664.2008.01593.x

Journal of Applied Ecology

Journal of Applied Ecology 2009, **46**, 250–258 doi: 10.1111/j.1365-2664.2008.01593.x

Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity

Amael Paillex[1]*, Sylvain Dolédec[2], Emmanuel Castella[1] and Sylvie Mérigoux[2]

[1]Laboratory of Ecology and Aquatic Biology, University of Geneva, 18 chemin des Clochettes, 1206 Genève, Switzerland; and [2]UMR CNRS 5023, Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, Villeurbanne, F-69622, France

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Summary

1. Floodplains are species-rich environments often strongly impacted by human activities. In particular, the negative effects of progressive and rapid disconnection of secondary channels have led to restoration programmes and a growing interest in restoration ecology.

2. Current restoration strategies in large river floodplains focus on the macroinvertebrate response related to the increases in lateral connectivity of the secondary channels. We constructed a framework to assess a gradient of hydrological connectivity among 13 secondary channels and the main channel of a large river, and we modelled the response of a set of macroinvertebrate metrics to this gradient. Comparisons between predicted and observed metrics in restored channels allowed us to measure the effect of an increase in the hydrological connectivity on the biological characteristics of macroinvertebrate assemblages.

3. The pre-restoration framework enabled a clear ordering of channels into three types according to levels of hydrological connectivity. Rarefied richness and species traits, responding to the connectivity gradient, showed a net difference between disconnected channels and the main river channel. We were able to highlight a predation–colonization trade-off along the gradient of hydrological connectivity with a maximum colonization potential in the most connected channels.

4. Post-restoration sampling showed deviations of the restored channels from their expected ecological state. A large proportion of colonizers were favoured by the restoration operations and non-native species occurred in the restored channels.

5. *Synthesis and applications.* Macroinvertebrate biodiversity in large river floodplains is shaped by lateral hydrological connectivity. Increasing hydrological connectivity led to an increase in colonization rate. One year after restoration, the increase in lateral connectivity had shifted the restored sites away from the predicted state. This unpredictability is, in part, a consequence of the rapid colonization by non-native species of new habitats created by the restoration measures. We recommend that floodplain-scale restoration should focus on diversification of the hydrological connectivity of channels, thereby conserving a maximum of functional characteristics in macroinvertebrate communities.

Key-words: floodplain restoration, lateral connectivity, large river, macroinvertebrates, species traits, non-native species, Rhône River

Introduction

Riverine floodplains are among the most species-rich environments (e.g. Tockner & Standford 2002). Their fluvial dynamics create a complex mosaic of habitats and gradients of hydrological connectivity (e.g. Ward, Tockner & Schiemer 1999). Under natural conditions, large river floodplains contain secondary channels, permanently or temporarily connected to the main river channel. The resulting gradient of lateral connectivity refers to the degree of linkage between the various water bodies of the floodplain and the main river channel (Amoros & Bornette 2002). At the floodplain scale, this lateral hydrological connectivity is known to influence biogeochemical fluxes, food web-structure (Amoros & Bornette 2002), and biodiversity patterns of macroinvertebrate (Tockner *et al.* 1999; Reckendorfer *et al.* 2006; Paillex, Castella

*Correspondence author. E-mail: amael.paillex@unige.ch

& Carron 2007), macrophyte (Amoros & Bornette 2002), and fish assemblages (Aarts, Van den Brink & Nienhuis 2004; Lasne, Lek & Lafaille 2007).

European and North American riverine floodplains have been severely altered by the construction of embankments and hydroelectric power plants (Petts, Möller & Roux 1989; Nilsson *et al*. 2005). In Europe, low-fall hydroelectric power plants using part of the main flow were built on most large rivers after 1950 (e.g. Roux *et al*. 1989; Hohensinner *et al*. 2004). They disrupt the lateral connectivity and accelerate both the disconnection of the secondary channels and the terrestrialization of the floodplain (e.g. Henry, Amoros & Roset 2002; Amoros *et al*. 2005; Coops *et al*. 2006). The alterations led to important changes in the biota (Bornette, Amoros & Collilieux 1994; Dolédec, Dessaix & Tachet 1996; de Groot 2002).

Accumulating evidence of alteration of the hydrological and ecological functions induced by channel disconnection resulted in restoration programmes in various fluvial systems (e.g. Gore & Shields 1995; Hohensinner *et al*. 2004; Coops *et al*. 2006), and the need for clarification on what constitutes a successful restoration programme (Palmer *et al*. 2005; Jansson, Nilsson & Malmqvist 2007). However, many studies in floodplain restoration ecology have been performed on a small number of channels and with limited consideration of the main river channel (Merritt *et al*. 2002; Amoros *et al*. 2005). Indeed, they have mainly reported the effects of restoration measures on macrophyte and sediment composition, with less emphasis on aquatic macroinvertebrate assemblages in the lateral dimension (but see Gallardo *et al*. 2008). Consequently, little attention has been paid to predicting the effects of increasing the lateral connectivity and the minimum base flow, currently two crucial restoration strategies, on macroinvertebrate communities.

At present, a large-scale restoration project is in progress for the entire French Rhône River. The project aims to increase both the fluvial dynamics, by raising the minimal base flow in the by-passed sections of the river, and the lateral connectivity, through secondary-channel deepening or reconnection with the main river channel. In this context, the aims of this study were: (i) to model the relationships between lateral hydrological connectivity and a range of invertebrate-based metrics in 28 pre-restoration alluvial sites, and (ii) to assess the level of post-restoration hydrological connectivity in four sites in order to compare the expected and the actual richness and trait metrics of macroinvertebrate assemblages.

Hypotheses were developed in order to assess trends of macroinvertebrate metrics associated with the gradient of hydrological connectivity. We expected total taxonomic richness to peak at intermediate levels of hydrological connectivity (Connell 1978; Townsend, Scarsbrook & Dolédec 1997). However, components of the total species richness were expected to behave differently. For example, we predicted that the richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) would be maximal for channels with a high level of hydrological connectivity (Usseglio-Polatera 1994), whereas the richness of Coleoptera (Davis, Brown & Dinnin 2007), Odonata (Tockner *et al*. 1999) and Gastropoda (Reckendorfer *et al*. 2006) would be maximal in habitats with a low level of hydrological connectivity. Moreover, because non-native species are mostly rheophilic in the Rhône River and the flow facilitates their dispersion, we expected them to increase with increasing lateral connectivity. Because, isolated habitats tend to progressively disappear, species unique to those habitats are mostly listed as threatened. Therefore, we expected a maximum of those species in isolated habitats and a decrease in their numbers with increasing lateral connectivity. According to a set of hypotheses developed by Paillex *et al*. (2007), we predicted that an increase in connectivity with the main river channel would be detected by a decrease in shredders and predators (Mackay 1992), and an increase in deposit feeders, passive filter feeders, plurivoltine species (Connell 1978), benthic and drift prey availability (Merritt *et al*. 2002).

Considering the types of restoration work (dredging or reconnection), the two sites being deepened by dredging, and not directly reconnected to the main channel, were expected to experience the smaller increase in connectivity, caused by the increased discharge in the by-passed section of the river. In contrast, the two other sites being reconnected to the main channel would obviously experience a major increase in lateral connectivity. Therefore, we expected selected invertebrate-based metrics to change with increasing connectivity in the four sites. However, because reconnected sites are expected to receive an immediate supply of colonizers from the main river channel and because the founder effect should be prominent in small isolated water bodies, we predicted the post-restoration observed values of metrics to be closer to the predicted values in the reconnected sites than in the isolated ones.

Methods

STUDY SITES

The study was carried out in two sectors of the French Rhône River. A low-fall power plant was completed in each sector, in 1982 ('Belley') and in 1984 ('Brégnier-Cordon'), respectively. The main river channel of the two sectors and 13 secondary channels located along the two by-passed sections were studied before restoration. Two secondary channels permanently connected to the main channel presented a constant flow (eupotamal; Amoros, Richardot-Coulet & Pautou 1982). At average water levels, six secondary channels were only permanently connected with the main river channel at their downstream end with their upstream disconnected section composed of isolated pools (parapotamal; Amoros *et al*. 1982). Five further secondary channels were totally disconnected from the main river channel (plesiopotamal; Amoros *et al*. 1982). One year after restoration, we used four sites in two secondary channels located in the 'Belley' sector as test sites, taking into consideration the different types of restoration works. The first channel ('Béard', abbreviated BEAR) was dredged to enhance groundwater supply and several isolated pools were created in its upstream section. The upstream alluvial plug was preserved to avoid a direct input from the main river channel. The second channel ('En l'ile', abbreviated ENIL) was entirely dredged and the upstream alluvial plug was removed to provide a direct connection of the channel with the main river channel.

MACROINVERTEBRATE SAMPLING

The different physical condition of the main and secondary channels (especially depth and velocity) necessitated the use of two different sampling techniques (see Supporting Information, Appendix S1 for details).

Each sector comprised one sampling site in the main river channel represented by a reach length of 15 times the width of the channel. A total of 20 sampling points were randomly selected along the total reach length, in spring and summer 2002. For each sampling point, the organisms were collected with a Hess sampler.

Each secondary channels comprised two sampling sites, one at each extremity (UP, upstream; DO, downstream) to represent the diversity of habitats occurring in the parapotamal and plesiopotamal types. A 30-m long stretch was designated for each site, within which four sampling points were randomly selected. At each point, macroinvertebrates were collected with a hand net within a quadrat (area, 0·25 m^2). Sampling was repeated before restoration in summer 2003 and spring 2004 in the Belley floodplain, and in summer 2004 and spring 2005 in the Brégnier-Cordon floodplain.

One year after the restoration of BEAR and ENIL channels, and the increase of the minimum base flow in the by-passed section of the river, the macroinvertebrates in the two restored channels were sampled again (summer 2005 and spring 2006) using the previously described protocol for the secondary channels. Within each of the two channels, we sampled the upstream part (BEAR-UP and ENIL-UP) and a new downstream located site. These new and previously terrestrial sites were transformed into a permanent aquatic habitat after restoration (BEAR-DO-N and ENIL-DO-N; see Supporting Information, Table S1 for a summary).

MACROINVERTEBRATE METRICS

Macroinvertebrates were identified to the most accurate taxonomic resolution, usually species or genus. Four taxonomic richness indices were calculated at each site as the number of taxa for: (i) the total richness, and as the number of species for (ii) the Ephemeroptera, Plecoptera and Trichoptera (EPT) richness, (iii) the Coleoptera and Odonata richness, and (iv) the Gastropoda richness. Coleoptera and Odonata were summarized in a unique metric, because they were expected to have a similar response to the gradient of hydrological connectivity. A rarefaction procedure was performed for the four indices at each site to avoid biased comparisons due to sampling protocol differences. Moreover, two aspects of species status were considered: (i) whether it was native or not to the French Rhône River, and (ii) whether it could be regarded as 'threatened'.

Four biological traits derived from published sources (Colling 1996; Usseglio-Polatera *et al.* 2000; Gayraud *et al.* 2003) were used to compute different metrics: the percentages of deposit feeders, shredders, passive filter feeders, predators, plurivoltines and also the percentages of benthos and drift prey availability (Merritt *et al.* 2002). Technical details about macroinvertebrate metrics are given in the Supporting Information, Appendix S1. A summary of the rationale of predictions made on these metrics as well as associated references are provided in the Supporting Information (see Supporting Information, Table S2).

HABITAT DESCRIPTION

Habitat characteristics of the main and secondary channels were recorded at the site or the sampling point scale. Vegetation cover, diversity of mineral substrate, water conductivity, ammonia nitrogen concentration (NH_3-N) and organic matter in the sediment were assessed in the secondary channels, as described in Paillex *et al.* (2007) and similarly applied for the main river channel. Post-restoration habitat characteristics in BEAR and ENIL channels were recorded in summer 2005 and spring 2006, following the pre-restoration protocol. The measures of NH_3-N and the sampling of the organic matter content were made in winter 2005.

ASSESSMENT OF THE LATERAL CONNECTIVITY

Following Paillex *et al.* (2007), we computed an index of lateral hydrological connectivity for each site using six environmental variables known to integrate the level of connectivity of secondary channels to the main river channel. Four variables were expected to decrease with increasing lateral hydrological connectivity: (i) water conductivity (COND), (ii) organic content (OM) of the sediment upper layer, and aquatic vegetation density (iii) in the lower (VSUB) and (iv) the upper (VUP) halves of the water column. Two variables were expected to increase accordingly: (i) diversity of the mineral sediment grain size (DSUB) measured with a Simpson index, and (ii) NH_3-N concentration. The six connectivity variables were summarized with a principal component analysis (PCA) to produce synthetic variables (factorial axes) used as surrogates for the level of connectivity between the secondary channel sites and the main river channel. We investigated the relationships between hydrological connectivity (PCA axis score) and the macroinvertebrate metrics using linear regressions. Variables were appropriately (log or square-rooted) transformed to ensure normality. PCA and corresponding graphical outputs were computed with the ade4 library (Chessel, Dufour & Thioulouse 2004).

PREDICTIONS OF MACROINVERTEBRATE CHARACTERISTICS

The four restored sites were plotted as supplementary individuals on the above PCA ordination of the pre-restoration sites providing a value of hydrological connectivity for each restored site. From these values, we computed the predicted functional characteristics of the aquatic macroinvertebrate assemblages according to the pre-restoration regression models defined above. Finally, we compared the predicted characteristics of the aquatic macroinvertebrate assemblages, from the post-restoration habitat characteristics (i.e. using the pre-restoration regression models), with their observed post-restoration characteristics in the four restored sites (i.e. field sampling). We assessed this comparison with a 10% tolerance range around the predicted values.

Results

LATERAL CONNECTIVITY BEFORE AND AFTER RESTORATION

The first two axes of a PCA performed on the six connectivity variables, explained 73·6% of the total variability. All the variables were well correlated with the first axis (51·6% of the total variability), except water conductivity which was mostly correlated with the second PCA axis (22% of the total variability), and NH_3-N concentration which was equally correlated with the first and the second axes (Fig. 1a). Sites were ordered along the first PCA axis from the most disconnected sites (plesiopotamal) to the frequently and

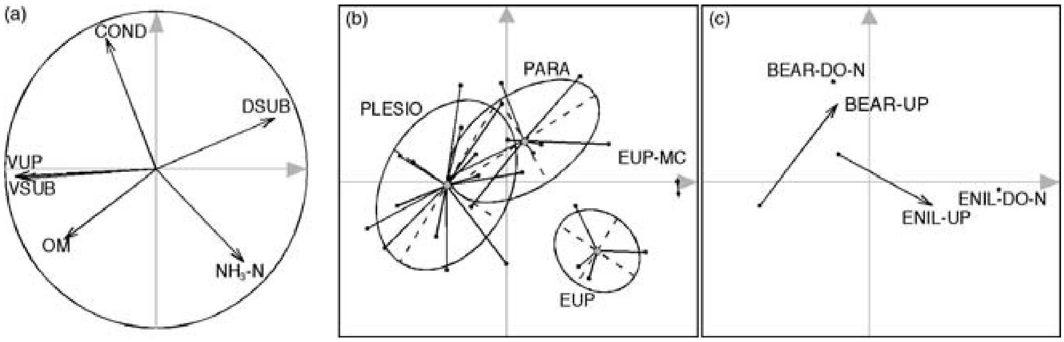

Fig. 1. Principal component analysis on the sites by environmental variable matrix. (a) Correlation plot of the variables, COND: water conductivity, DSUB: diversity of the mineral sediment grain size, NH_3-N: ammonia nitrogen concentration, OM: organic sediment content, VSUB and VUP: aquatic vegetation in the lower and the upper halves of the water column. (b) Ordination of the pre-restoration sites, regrouped by channel types (PLESIO, plesiopotamal; PARA, parapotamal; EUP, eupotamal; MC, main river channel). (c) Ordination of the post-restoration sites. The arrows denote the direction of the changes after restoration.

permanently connected sites (eupotamal) (Fig. 1b). Moreover, the two main river channel sites were plotted at the extreme right of the plot (Fig. 1b). Owing to the important part of the variability explained by the first PCA axis and the strong correlation of four of the variables, we used the first axis scores as a surrogate for lateral hydrological connectivity:

$$\text{First PCA axis score} = -0{\cdot}53 \ast \text{VUP} - 0{\cdot}51 \ast \text{VSUB} - 0{\cdot}35 \ast \text{OM} - 0{\cdot}19 \ast \text{COND} + 0{\cdot}33 \ast \text{NH3-N} + 0{\cdot}45 \ast \text{DSUB} \qquad \text{eqn 1}$$

The equation of the second PCA axis score was:

$$\text{Second PCA axis score} = -0{\cdot}04 \ast \text{VUP} - 0{\cdot}05 \ast \text{VSUB} - 0{\cdot}39 \ast \text{OM} + 0{\cdot}72 \ast \text{COND} - 0{\cdot}51 \ast \text{NH3-N} + 0{\cdot}28 \ast \text{DSUB} \qquad \text{eqn 2}$$

The four post-restoration sites were plotted on the first two PCA axes as supplementary individuals (Fig. 1c) using equations 1 and 2.

BEAR-UP post-restoration shifted along the first and the second axes of the PCA, whereas ENIL-UP post-restoration shifted mostly along the first PCA axis toward the main river channel (Fig. 1c). The two new sites (BEAR-DO-N and ENIL-DO-N, Fig. 1c) plotted respectively close to BEAR-UP and ENIL-UP.

SPECIES RICHNESS, STATUS AND TRAITS ALONG THE GRADIENT OF HYDROLOGICAL CONNECTIVITY

The total rarefied richness was stable along the gradient of connectivity with an average of 41 taxa per site. No quadratic relation was observed for the total rarefied richness with the gradient of connectivity ($R^2 = 0{\cdot}04$, $P = 0{\cdot}601$) and no linear relationship for the Gastropoda ($R^2 = 0{\cdot}06$, $P = 0{\cdot}478$). The EPT and the Coleoptera and Odonata rarefied richness showed a significant positive relationship with the gradient of connectivity ($R^2 = 0{\cdot}61$, $P < 0{\cdot}001$; $R^2 = 0{\cdot}18$, $P = 0{\cdot}026$, respectively, Fig. 2). We observed a post-restoration increase of the EPT taxa and a decrease of the Coleoptera and Odonata richness for the test sites (see Supporting Information, Table S3).

A total of 20 threatened species (11 insects and 9 molluscs) were identified prior to site restoration (see Supporting Information, Table S4). The number of threatened species per site was not related to the gradient of connectivity ($R^2 = 0{\cdot}09$, $P = 0{\cdot}126$). The threatened insect species significantly increased with hydrological connectivity ($R^2 = 0{\cdot}22$, $P = 0{\cdot}013$, Fig. 2), but the threatened mollusc species were not related to the connectivity gradient ($R^2 = 0{\cdot}01$, $P = 0{\cdot}549$). Two threatened species present only in BEAR-UP and ENIL-UP before restoration disappeared after restoration. Six new threatened species were found in BEAR-DO-N after restoration and only one in ENIL-DO-N. A total of five new threatened species were found in the channels after restoration (Table 1).

Before restoration, six non-native species were identified in the sites: four molluscs [*Corbicula fluminea* (O.F. Müller), *Dreissena polymorpha* (Pallas), *Physella acuta* (Draparnaud), *Potamopyrgus antipodarum* (Gray)], and two crustaceans [*Crangonyx pseudogracilis* Bousfield and *Orconectes limosus* (Rafinesque)]. The relative combined abundance of the non-native species was significantly, and positively, related to the gradient of connectivity ($R^2 = 0{\cdot}15$, $P = 0{\cdot}04$, Fig. 2). Before restoration, BEAR-UP was devoid of non-native species and ENIL-UP had only one non-native species: *Physella acuta* (Table 1). After restoration, *Physella acuta* was present in all the restored sites and four new non-native species appeared, especially in ENIL-UP (*Corbicula fluminea, Potamopyrgus antipodarum*, *Crangonyx pseudogracilis*, *Dikerogammarus villosus* Martynov).

Contrasting trait patterns occurred along the gradient of connectivity. The percentages of passive filter feeders and plurivoltine taxa significantly increased with connectivity ($R^2 = 0{\cdot}50$, $P < 0{\cdot}001$; $R^2 = 0{\cdot}42$, $P < 0{\cdot}001$, respectively, Fig. 2). The benthic and the drift prey availabilities showed a similar pattern (respectively, $R^2 = 0{\cdot}37$, $P < 0{\cdot}001$; $R^2 = 0{\cdot}46$, $P < 0{\cdot}001$, Fig. 2). By contrast, the percentage of predators significantly declined with connectivity ($R^2 = 0{\cdot}28$, $P = 0{\cdot}004$,

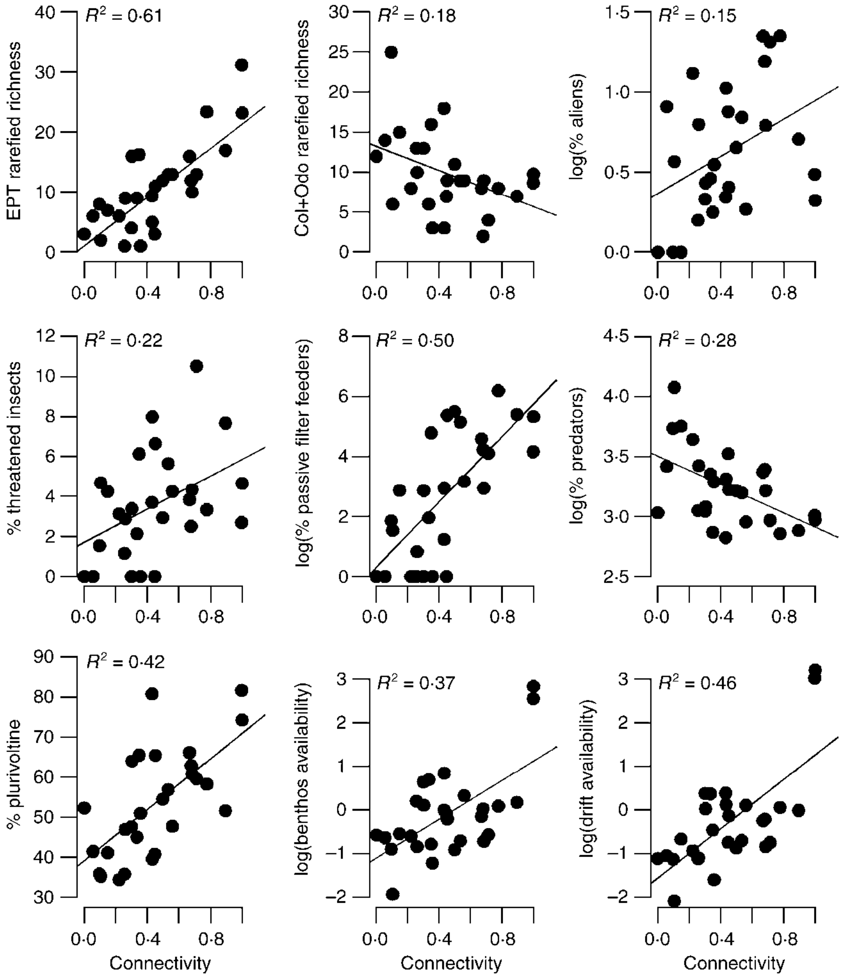

Fig. 2. Relationship between aquatic macroinvertebrate metrics and the gradient of hydrological connectivity (sites scores along the first axis of the PCA). Each point represents the combination of two seasons for one site (n = 28 for all relationships).

Table 1. Number of threatened and non-native aquatic macroinvertebrate species collected in the four restored sites before and after restoration. 'Pre', number of species present only before restoration and not found after. 'Pre + Post', number of species encountered before and after restoration. 'Post', number of species found only after restoration

		Threatened species			Non-native species		
Code	Restoration works	Pre	Pre + Post	Post	Pre	Pre + Post	Post
BEAR-UP	dredging	2	0	1	0	0	1
BEAR-DO-N	dredging	–*	–	6	–*	–	2
ENIL-UP	reconnection	2	3	2	0	1	4
ENIL-DO-N	reconnection	–*	–	1	–*	–	3
	TOTAL	2	3	5	0	1	4

*terrestrial before restoration.

Fig. 2). The percentages of shredders and deposit feeders were not related to the gradient of connectivity ($R^2 = 0{\cdot}11$, $P = 0{\cdot}085$, $R^2 = 0{\cdot}01$, $P = 0{\cdot}686$). Following restoration, the plurivoltine taxa increased to 95% in ENIL-DO-N and the drift prey availability also increased (see Supporting Information, Table S3).

PREDICTION OF MACROINVERTEBRATE METRICS IN THE RESTORED SITES

The nine significant relationships between metrics and connectivity were used to predict the metrics' values after restoration in the BEAR and ENIL sites. The observed metrics' values in BEAR-UP and ENIL-UP conformed better to the predictions than those in BEAR-DO-N and ENIL-DO-N (Table 2). The percentages of passive filter feeders and predators respectively conformed to predictions, whereas the less-conforming metrics included the number of threatened insect species and the rarefied richness. In general, observed values were higher than the predicted ones, ENIL-DO-N excepted (Table 2).

Discussion

THE SIGNIFICANCE OF HYDROLOGICAL CONNECTIVITY FOR AQUATIC MACROINVERTEBRATE DIVERSITY

The gradient used as a surrogate for the lateral hydrological connectivity, separated the channels according to type (eupotamal, parapotamal, plesiopotamal; Fig. 1b). Moreover, the predicted post-restoration increase in lateral connectivity was detected by six connectivity variables and resulted in a

Table 2. Comparisons between the predicted values of the metrics (exp.) with a confidence of ±10% (int.) and the post-restoration observations (obs.), with the difference between observed and predicted values (dif.). The observed values comprised into the confidence interval are in bold

Channels	BEAR								ENIL							
Sites	-UP				-DO-N				-UP				-DO-N			
Metrics	exp.	int.	obs.	dif.	exp.	int.	obs.	dif.	exp.	int.	obs.	dif.	exp.	int.	obs.	dif.
EPT rarefied richness	8·6 ±	0·9	12·0	3·4	8·4 ±	0·8	12·5	4·1	14·9 ±	1·5	20·0	5·1	19·2 ±	1·9	13·0	–6·2
Col+Odo rarefied richness	10·6 ±	1·1	14·0	3·4	10·7 ±	1·1	18·0	7·3	8·3 ±	0·8	11·0	2·7	6·8 ±	0·7	4·0	–2·8
% threatened insects species	3·2 ±	0·3	0·9	–2·3	3·1 ±	0·3	7·6	4·5	4·4 ±	0·4	5·7	1·3	5·3 ±	0·5	3·2	–2·1
% non-native individuals (log)	0·6 ±	0·1	0·8	0·2	0·6 ±	0·1	1·1	0·5	**0·7 ±**	**0·1**	**0·7**	**0·0**	0·9 ±	0·1	0·3	–0·5
% passive filter feeders (log)	2·2 ±	0·2	0·0	–2·2	**2·1 ±**	**0·2**	**2·1**	**–0·1**	**3·9 ±**	**0·4**	**4·1**	**0·3**	5·0 ±	0·5	6·1	1·1
% predators (log)	**3·3 ±**	**0·3**	**3·5**	**0·2**	**3·3 ±**	**0·3**	**3·1**	**–0·2**	**3·1 ±**	**0·3**	**3·3**	**0·1**	**3·0 ±**	**0·3**	**3·1**	**0·1**
% plurivoltine	**50·3 ±**	**5·0**	**50·9**	**0·6**	49·9 ±	5·0	63·7	13·7	60·0 ±	6·0	74·4	14·4	66·6 ±	6·7	95·0	28·3
Benthic prey availability (log)	–0·3 ±	0·0	0·1	0·4	–0·4 ±	0·0	0·5	0·9	0·3 ±	0·0	0·6	0·3	0·8 ±	0·1	–0·7	–1·5
Drift prey availability (log)	–0·6 ±	–0·1	–0·1	0·4	–0·6 ±	–0·1	0·5	1·1	0·3 ±	0·0	0·8	0·5	0·9 ±	0·1	0·3	–0·6

shift of the test sites along the first axis of a PCA (Fig. 1c). Direct reconnection (ENIL sites) led to a rapid establishment of typically eupotamic characteristics. Contrastingly, dredging operations (BEAR sites) resulted in an increase of the water conductivity, highlighting the improvement of groundwater seepage and the restoration of vertical connectivity (Cellot *et al.* 1994; Boulton 2007). The variables used to depict the lateral connectivity may be adapted locally to the floodplain context (Amoros *et al.* 2005; Reckendorfer *et al.* 2006; Lasne *et al.* 2007). However, the components of an index for hydrological connectivity in other floodplains may change and need testing prior to being computed in a composite variable. Nevertheless, the construction of a composite variable based on connectivity variables, is a promising tool for the evaluation of the effect of restoration on hydrological connectivity.

Regarding the pre-restoration framework, increases of EPT taxa and decreases of Coleoptera and Odonata were correlated with an increase in hydrological connectivity. Conversely to Usseglio-Polatera (1994), Ephemeroptera and Trichoptera were found to respond positively along the gradient of hydrological connectivity. However, in accordance with Usseglio-Polatera (1994), we found a maximum of Plecoptera in the main channel habitats of the Rhône River. EPT patterns along the gradient of hydrological connectivity may be explained by the sensitivity of these species to low oxygen levels. Indeed, the most disconnected sites showed high macrophyte densities, which can lead to an oxygen depletion during the night and limit EPT richness. Similarly to Davis *et al.* (2007), we found that aquatic Coleoptera richness was negatively related to the connectivity gradient, with a low species richness in sites of higher connectivity. Finally, we found no relationships between hydrological connectivity and total or Gastropoda rarefied richness. According to the link between hydrological connectivity and disturbance (high connectivity implies frequent and intense disturbance by floods, whereas low connectivity implies reduced or no flood disturbance), such absence of relationship confirms observations made by numerous other studies (Mackey & Currie 2001). Our results suggest that even if the total taxonomic richness does not respond to the gradient of connectivity, components of this richness can behave differently.

Besides richness metrics, five species traits out of seven were significantly related to the gradient of hydrological connectivity. Four traits had their maximum in the most connected sites and in the main river channel (plurivoltine taxa, passive filter feeders, benthic and drift prey availability), while predators tended to be less abundant in the main river channel. This supported the idea that predation (percentage of predators amongst invertebrates) is dominant in stagnant water bodies. Additionally, under high levels of connectivity, only those species that reach maturity quickly (percentage of plurivoltine taxa) can withstand frequent disturbances. This underlines a predation–colonization trade-off along the gradient of hydrological connectivity, and corroborates the idea that disturbance shapes the traits conferring high colonization potential for high level of disturbance (Haddad *et al.* 2008). These results demonstrated that species traits can improve classical biomonitoring tools for aquatic environment assessment based on richness and composition measures (e.g. Merritt *et al.* 2002; Gayraud *et al.* 2003; Dolédec & Statzner 2008). They provide a means of assessing functional community changes caused by restoration works when total richness is not expected to change drastically after restoration.

ARE THE CHARACTERISTICS OF THE MACROINVERTEBRATE COMMUNITIES PREDICTABLE?

Our pre-restoration models permitted the prediction of the functional characteristics of the macroinvertebrate communities after restoration. However, the post-restoration field observations demonstrated the difficulties in accurately predicting macroinvertebrate community responses only 1 year after changes in hydrological connectivity. Indeed, we observed several responses of the macroinvertebrate communities that were not supported by the pre-restoration model. The increase of EPT richness after restoration was higher than predicted, probably due to their short generation time and therefore high capacity to recolonize habitats (Wallace 1990). This trend was also supported by the plurivoltine taxa that were more abundant than predicted by the pre-restoration model. Indeed, the large presence of plurivoltine taxa, capable of rapidly reaching maturity, increased the colonization potential. This result confirms that pioneering species are more represented in disturbed environments and are favoured by disturbance (Connell 1978). Conversely, the decrease of Coleoptera and Odonata richness after restoration was less than predicted. High dispersal potential ensured by flying adults, may explain their good recolonization of post-restoration habitats with individuals originating from unrestored sites. Contrary to Mackay (1992), who stated that predators are late settlers after a disturbance, our observations revealed that the predators quickly reached their predicted percentages compared to the rest of the community, 1 year after restoration. This good correspondence might be explained by a sufficient availability of preys for macroinvertebrate predators.

Apart from the new site in ENIL, the availability of benthic and drift preys for higher trophic levels such as fish (Merritt *et al.* 2002) were above predictions, confirming that the increase of lateral connectivity has implication for food supply to upper consumers. These results reinforced the statement of Lasne *et al.* (2007) that an increase in the hydrological connectivity is an appropriate restoration measure for fish. Despite the good correspondence of certain metrics, the generally poor correspondence of the observations and the predictions for all the sites suggests that they were far from the ecological state expected from the pre-restoration model. The mechanical operations (dredging or reconnecting) may have prevented recolonization by taxa refuged in the hyporheic zone (Wallace 1990; Boulton 2007), which can act as sources of recolonization and natural refuges for macroinvertebrates during natural disturbance (e.g. floods). This potential lack of recolonization may explain the divergence between the predictions and the observations 1 year after restoration. Observations continued over the long term are needed to reveal whether the metrics (richness and traits) will reach the values predicted by the pre-restoration models. However, if the restoration measures are repeated several times within a short time period, the actual ecological states of the sites may be maintained far from their pre-restoration model predictions.

RESTORATION OF HYDROLOGICAL CONNECTIVITY AND NON-NATIVE SPECIES

As stated by Van Andel & Grootjans (2006), the restoration or the rehabilitation of an ecosystem may be interpreted as a disturbance to which the system responds through resistance, resilience or instability, shifting the system towards a new domain or a new steady state. Our study demonstrates the difficulties in predicting the macroinvertebrate communities' responses after the restoration of hydrological connectivity. The low level of concordance between the predictions and the post-restoration observations showed that the restoration pushed the system towards a mostly unpredictable state. A component of this unpredictability is the unexpected arrival of non-native species after restoration, an aspect that needs to be integrated into future restoration project plans (see e.g. Jansson *et al.* 2007). Our results show that the increase of the lateral hydrological connectivity by restoration increased both the richness and the relative abundance of non-native macroinvertebrate species. These species have rapidly occupied the restored sites and prevented the native species from inhabiting the new habitats provided by restoration. Indeed, most of the existing non-native species in the pre-restoration state were rheophilic and were constrained to the main river channel.

Conversely, Lasne *et al.* (2007) demonstrated that the richness of non-native fish decreased in connected areas of a large river floodplain. They underlined that non-native fish were mostly 'macrohabitat generalist', and suggested the maintenance of a high hydrological connectivity level to conserve native species, and to reduce non-native species. As shown by our results, this suggestion would lead to an increase of non-native macroinvertebrate species. Furthermore, the relative abundance of non-native species was higher than predicted in the stagnant sites and conversely, their relative abundance was equal or lower than predicted in the lotic sites. Similarly, Combroux, Bornette & Amoros (2002) showed that sediment dredging led to an increase in the abundance of a non-native aquatic macrophyte [*Elodea nuttallii* (Planchon) H. St. John]. They concluded that restoration will be successful when seed or vegetative propagules of unwanted species are not present or can be physically removed from sediment. This objective might be regarded as unrealistic and certainly in our case, the restoration measures did not remove the established non-native species, but on the contrary, created conditions favourable for the introduction and settlement of new ones. According to the results, it is not yet possible to know if the sites have enough resilience or if the restoration programme has shifted them towards a new domain. One measure of successful river restoration would be a reduction in the occurrence of non-native species (Palmer *et al.* 2005). As stated by Jansson *et al.* (2007), such a trend must be seriously surveyed in the future to assess the true success of restoration operations or to consider other types of operation.

IMPLICATIONS FOR FUTURE FLOODPLAIN RESTORATION

A holistic approach must be used to better understand floodplain systems and associated macroinvertebrate communities. The full lateral dimension should be taken into account to provide efficient restoration assessments and recommendations. Indeed, the main river channel has been the key focus of riverine research (e.g. Usseglio-Polatera & Beisel 2002; Lamouroux *et al.* 2007), while the lateral habitats of large rivers have been mostly ignored. By incorporating this lateral dimension here, we revealed that restoring the hydrological connectivity of floodplain channels modifies the predation–colonization trade-off among macroinvertebrates by shifting the trade-off towards less predation (percentage of predators within macroinvertebrates) and more colonization (percentage of plurivoltine). Secondly, our results confirm the establishment of non-native species in the restored sites. These species were mostly restricted to the main river channel before restoration. As a result, before restoration works are initiated, the probability of colonization by non-native species into the restored sites should be assessed (Jansson *et al.* 2007).

Additionally, restoration practitioners should measure the importance of restoring a given ecological function against the probability of non-native species colonization of newly created habitats. The introduction of non-native species as a side effect of restoration may cause more damage in a given site than the absence of restoration. Furthermore, our study emphasizes the importance of traits to supplement the classical approaches using richness metrics (Statzner *et al.* 2001; Gayraud *et al.* 2003). The use of biological traits and the different richness components enables us to avoid inconsistent results when relating total richness to disturbance (Mackey & Currie 2001). Certain traits and components of the total richness are related to the hydrological connectivity and each extreme of the gradient has its own characteristics. Indeed, isolated habitats included species characteristics drastically different from the connected habitats. The potential reduction of the spectrum of connectivity levels between channels at the scale of the floodplain may lead to a reduction or loss of the diversity of macroinvertebrate characteristics. As a result, during restoration works, we suggest diversifying the level of connectivity of the channels at the floodplain scale to preserve the diversity of biological characteristics (e.g. Amoros 2001). Finally, pre-restoration models of community metrics provide reference conditions against which post-restoration changes can be assessed. The post-restoration observations were made only 1 year after restoration, and thus, it remains to be seen over the long term if the restored habitats and their associated communities will reach the predicted state. Long-term monitoring must be undertaken to examine the resilience of the macroinvertebrate communities over time, especially in the presence of non-native species in the restored space.

Acknowledgements

We are grateful to J.M. Olivier and N. Lamouroux for the coordination of the restoration Rhône restoration project. We thank D. McCrae for editing the English, M. Fisher, his team, M. Cadotte and two anonymous referees for their useful suggestions on a previous version of the paper. We thank all the people who helped us during field work, sorting and identification. We thank G. Carron, J. Dessaix, A. Guenat and A.L. Montbertrand who contributed to invertebrate identification. This research was funded by the Agence de l'Eau Rhône Méditerrannée Corse, the Direction Régionale de l'Environnement, the Compagnie Nationale du Rhône, and the University of Geneva.

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Received 11 July 2008; accepted 27 October 2008
Handling Editor: Marc Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methods

Table S1. General information on the alluvial test sites

Table S2. General information on macroinvertebrate metrics

Table S3. Comparisons of the metrics before and after restoration

Table S4. List of the threatened species identified before and after site restoration