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The generality of changes in the trait composition of fish and invertebrate communities after flow restoration in a large river (French Rhône)

SYLVAIN DOLÉDEC*, EMMANUEL CASTELLA[†], MAXENCE FORCELLINI[‡], JEAN-MICHEL OLIVIER*, AMAEL PAILLEX^{†,§,¶} AND PIERRE SAGNES^{*,**}

*CNRS, UMR 5023, LEHNA, Biodiversité des Ecosystèmes Lotiques, Université Lyon 1, Villeurbanne, France

[†]Institute F.A. Forel and Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland

[‡]IRSTEA, UR MALY, Villeurbanne, France

[§]Aquatic Ecology Group, Department of Zoology, University of Cambridge, Cambridge, U.K.

[¶]EAWAG, Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

**ONEMA, Pôle écohydraulique, Institut de Mécanique des Fluides de Toulouse, Toulouse, France

SUMMARY

1. A multiple-trait-based approach can provide predictions and interpretations of the responses of freshwater communities to river restoration that apply in different taxonomic contexts. We compared the observed and predicted effects of restoration on sets of traits in fish and invertebrate communities in four reaches of the Rhône River. Restoration included minimum flow increases in three bypassed main channels and the reconnection of eight floodplain channels.

2. Predictions (described in detail in three other articles in this Special Issue) were based on habitat models that related the density of modelled taxa to their physical habitats. We used trait information extracted from the literature to translate predicted taxonomic changes into predicted changes in traits. Observed changes in traits calculated for modelled taxa and for all taxa in the community were both compared to predictions.

3. In 10 of 12 cases, observed changes in traits correlated with predicted ones. With few exceptions, the agreement was higher for fish and invertebrates in the main channels than for invertebrates in floodplain channels. Predictions translated to the trait category level improved those at the taxonomic level in 5/6 and 4/6 cases for modelled taxa and all taxa, respectively. However, the improvement was statistically significant according to a null model for 1/6 and 3/6 cases for modelled taxa and all taxa, respectively.

4. The validation of trait predictions suggested that traits related to locomotion and attachment, as well as general biology and physiology, were particularly suited to predicting and understanding the effects of physical restoration. For example, after restoration, clingers and passive filter feeders dominated invertebrate communities in the main channels, whereas invertebrate communities in the floodplain underwent a selection of traits frequent in running water (clingers, flattened shape and gill respiration). Within fish communities, the periodic life-history strategy that characterises fish species in downstream reaches (long life span, large body, late sexual maturity) increased with restoration, whereas the opportunistic strategy decreased.

5. Our results suggest that a better understanding of how hydraulics shapes traits in riverine systems is critically needed for assessing the effects of restoration measures impacting flow. In addition, existing trait databases (especially for fish) should be expanded to better reflect the energetic trade-offs that organisms must make in various flow contexts.

Keywords: benthic macroinvertebrates, fish, minimum flow increase, multiple-trait-based approach

Introduction

Rivers are among the most heavily impacted ecosystems on earth as a result of multiple human-caused stressors (Dudgeon *et al.*, 2006). In particular, stream regulation during the 19th and 20th centuries deeply transformed large rivers to allow navigation and power generation, resulting in habitat loss (Petts, Möller & Roux, 1993; Aarts, Van Den Brink & Nienhuis, 2004) and reduced connectivity between the main channel and adjacent floodplain channels (Ward *et al.*, 2001), and causing dramatic changes in freshwater biodiversity (see Ward & Tockner, 2001; de Nooij *et al.*, 2006; Poff *et al.*, 2007). The wide recognition of the importance of flow regimes on aquatic communities (Hart & Finelli, 1999) has led to calls for a quantitative understanding of the responses of macroinvertebrate and fish community composition to flow alterations; this information is critically needed for the efficient management of water resources (de Nooij *et al.*, 2006; Poff & Zimmerman, 2010).

Over the last two decades, restoring large rivers has become a challenging task in aiding in the recovery and managing the ecological integrity of damaged floodplain ecosystems (de Nooij *et al.*, 2006; Lamouroux *et al.*, 2015). This challenge has gained priority based on the need to achieve a 'good ecological status' in rivers by 2015, a goal instituted in Europe by the Water Framework Directive (European Commission, 2000). In a recent review, Palmer, Menninger & Bernhardt (2010) found that few stream restoration projects, which were mainly focused on physical channel characteristics, achieved the expected significant enhancement of species richness. However, species are not necessarily equivalent, and species richness may not be the appropriate end point for assessing stream restoration; instead, considering species traits may provide a higher degree of generalisation about the responses of communities to changing hydrodynamic gradients (see Statzner & Bêche, 2010).

Two decades ago, a Special Issue of *Freshwater Biology* was dedicated to establishing a framework that related the species traits of a wide range of riverine organisms to the environmental variability in a large river (Statzner, Resh & Dolédec, 1994). The study, embedded in a test of the habitat templet theory (Southwood, 1977; Townsend & Hildrew, 1994), demonstrated that any manipulation of the spatial heterogeneity of the physical habitat and its temporal variability (flow disturbance) would predictably change the biological characteristics of aquatic communities. Therefore, considering traits or trait combinations that confer on a given species the ability to deal with spatial and temporal variations

in its habitat may improve our understanding of flow effects as a selective pressure on species (Verberk, Van Noordwijk & Hildrew, 2013).

Restoration operations, such as floodplain channel reconnection and flow increases, should favour species adapted to higher hydraulic constraints (Lamouroux, Dolédec & Gayraud, 2004; Sagnes & Statzner, 2009; Statzner & Bêche, 2010; Gallardo *et al.*, 2014). Translated to species traits of macroinvertebrates, the increase in near-bed velocity and shear stress should favour small body size to reduce drag. This would have indirect consequences on invertebrate species' life histories including decreased longevity, increased reproduction frequency and/or a decrease in the frequency of predators (generally large species; see Statzner & Bêche, 2010). Flow increases should modify locomotion ability and select species with firm attachment to the substrate (clingers) and also involve a change from spherical to streamlined shape to reduce drag. In addition, with higher flows, one should expect an increase in passive filter feeders. Finally, higher flows should limit aerial respiration, thereby benefiting aquatic respiration (tegument and gill respiration; see Statzner & Bêche, 2010). For fish, flow increases should enhance water velocity and depth, favouring morphologies that minimise the swimming coefficient (low ratio of the minimum depth of the caudal peduncle to the maximum caudal fin depth, see Webb & Weihs, 1986), with a relatively high shape (5–6) coefficient (the ratio of total body length to maximum body depth; see Vogel, 1994) and a low (<0.3) drag coefficient (the resistance offered by a fish facing the flow, see Sagnes & Statzner, 2009). In addition, increasing hydraulic constraints should favour the proportion of periodic species (*sensu* Winemiller & Rose, 1992) with a long life, large body length, intermediate fecundity, large egg size, late maturation, high number of reproductive cycles and long travel distances per reproductive cycle (see Lamouroux *et al.*, 1999; Blanck, Tedesco & Lamouroux, 2007).

Restoration operations on the French Rhône River have involved four reaches. Their mean unregulated discharge ranged between 410 and 1030 m³ s⁻¹, but the reaches were bypassed by hydropower plants decades ago. Since 1999, a total of 47.3 km were restored along 165 km of river (see Lamouroux *et al.*, 2015; for details). Restoration increased minimum flows in the bypassed main channels and enhanced lateral connectivity between the main channel and 24 floodplain channels, among which six were directly reconnected with the main channel. Multiple surveys of fish and invertebrate taxa were conducted before and after restoration in the main channels of restored

reaches, and invertebrates were monitored in the floodplain channels. In addition, habitat models predicting changes in density after restoration (that is, after- minus before-restoration average values) of several fish and invertebrate taxa were detailed in three articles of this Special Issue (fish of the main channel, Lamouroux & Olivier, 2015; invertebrates of the main channel, Méri-goux *et al.*, 2015; invertebrates of reconnected floodplain channels, Castella *et al.*, 2015; hereafter called ‘taxonomic’ articles). These predictions involved a subset of modelled taxa, which occurred in reaches before restoration and for which preference models (relating taxon density to physical habitat) were available in the taxonomic articles. For modelled taxa, results obtained in the three articles suggested that changes in density after restoration were partly predictable.

In this article, we examine whether translating taxon-level predictions to the level of community traits can result in a more general interpretation of ecological responses to flow restoration across taxonomic groups (fish, invertebrates) and reaches (main and floodplain channels). We first provide a synthetic description of taxon-level predictions made in the three ‘taxonomic’ articles. Second, we translate predictions made for a subset of modelled taxa into predicted changes for community traits and compare them to observed changes (for modelled taxa and for the whole community). We then discuss which groups of traits are particularly relevant for understanding the observed taxonomic responses.

Methods

Study sites and taxonomic predictions

Three of the four reaches considered here are in the French Upper Rhône between Switzerland and Lyon

(Chautagne, Belley and Brégner-Cordon, restored between 2004 and 2006), and the last reach (Pierre-Bénite, restored in 1999) is downstream of Lyon and the confluence of the Rhône with its main tributary, the Saône River.

The two taxonomic articles concerning the main channels of bypassed reaches (datasets hereafter named CHAN INV and CHAN FISH for channel invertebrate and fish communities, respectively) involved three reaches with fish data (Chautagne, Belley, Pierre-Bénite; Lamouroux & Olivier, 2015) and two with invertebrate data (Chautagne and Pierre-Bénite; Méri-goux *et al.*, 2015). These reaches were subjected to an increase in the daily minimum flow after restoration (10-fold at Pierre-Bénite, fivefold at Chautagne and slightly more than twofold at Belley). Minimum flows occur during most of the year in bypassed reaches and their restoration generated large changes in in-stream velocities and depths; for example, the average current velocity at Pierre-Bénite increased fivefold after restoration (from 8 to 36 cm s⁻¹). The fish and invertebrate data collected in these reaches included repeated surveys made before and after restoration from 1995 to 2010 (see Table 1). Most surveys involved 100–200 electrofishing points (fish) or 8–40 samples (invertebrates) distributed at regular spatial intervals over the reaches. In the two articles concerning the main channels, predictions of changes in taxon density (log-transformed) were based on hydraulic habitat models. Such habitat models relate a hydraulic model at the reach scale with preference models of aquatic taxa for microhabitat hydraulics (point velocities and depths for fish and near-bed shear stresses for invertebrates). The habitat models used for predictions were mostly developed in rivers other than the Rhône (see e.g. Lamouroux *et al.*, 1999; Méri-goux *et al.*, 2009).

Table 1 Number of taxa (total considered and the number involved in the habitat models) and sampling periods (before and after restoration) for the three data sets used in this article

Channels/ reach	Taxonomic group	Total number of taxa	Number of modelled taxa	Sampling period (number of surveys)	
				Before	After
Main channels/					
Chautagne (CHAU)	Invertebrates	62	30	1997–2002 (7)	2006–10 (8)
	Fish	36	14	1996–2004 (17)	2004–10 (7)
Belley (BELL)	Fish	36	14	2003–04 (3)	2005–10 (6)
	Invertebrates	50	22	1995–99 (8)	2001–08 (8)
Pierre-Bénite (PBE)	Fish	36	14	1995–99 (7)	2001–10 (12)
	Invertebrates				
Floodplain channels/					
Belley & Brégner- Cordon	Invertebrates	145	54	2003–06 (2)	2007–10 (2)

The third taxonomic article (dataset hereafter named FLOODPL INV) involved invertebrate collections made in five floodplain channels that were fully reconnected to the main channel at the Belley and Brégner-Cordon reaches (Castella *et al.*, 2015; Table 1). We used only floodplain data from the reconnected channels because discharge increases at those localities should favour species with traits adapted to higher flow rates, as in the main channels. Therefore, analysing these reconnected channels together with main channel data provided a consistent comparison of responses observed at the community-trait level. A total of eight sites in the five reconnected channels were sampled (with 6–8 quadrats) on four occasions, corresponding to two seasons before and two seasons 4 years after restoration. We did not use samples taken 2 years after restoration (see Castella *et al.*, 2015) to allow sufficient time for floodplain channel invertebrate communities to demonstrate changes, as well as for simplicity. In this third article, predictions of changes in density of invertebrate taxa after restoration were based on regressive habitat models relating taxa density to an index of lateral connectivity across floodplain sites before restoration. This index of lateral connectivity was defined from environmental observations of water conductivity, vegetation cover, organic matter and substratum diversity and was related to the flooding frequency and magnitude at the sites (Riquier, Piégay & Šulc Michalkova, 2015).

In all three taxonomic articles, predictions were made only for a subset of the sampled taxa (modelled taxa; see numbers in Table 1) for which enough information on hydraulic preferences was available and significant habitat models could be computed. In addition, for invertebrates, difficulties in separating species with potentially different hydraulic preferences in some taxonomic groups (e.g. gammarids) also constrained the selection of modelled taxa. Therefore, predicted changes in taxa density were calculated for modelled taxa only, whereas observed changes in taxa density could be computed for all sampled taxa considered in the taxonomic articles (hereafter named ‘the whole community’).

Trait data

For each invertebrate taxon collected in the main channel and in floodplain channels, we documented 12 biological traits that were coded using 54 trait categories (e.g. for the maximum number of reproductive cycles per year: semivoltine, univoltine, plurivoltine; Table 2). Similarly, for each fish species, we documented 21 biological traits that were coded using 75 trait categories

Table 2 Traits and their categories that were available for the invertebrate taxa of the Rhône River

Biological trait	Code	Trait category
1. Life history		
Maximum potential size (mm)	s1	≤5
	s2	5–10
	s3	10–20
	s4	20–40
	s5	>40
Maximum number of descendants per reproductive cycle	nd1	<100
	nd2	100–1000
	nd3	1000–3000
	nd4	>3000
Maximum number of reproductive cycles per year	sem	Semivoltine
	uni	Univoltine
	plu	Plurivoltine
Life duration of adults (days)	ld1	≤1
	ld2	1–10
	ld3	10–30
	ld4	30–365
	ld5	>365
Reproductive technique	sin	Single individual
	bot	Hermaphroditism
	two	Male and female
Reproduction type	bud	Budding regeneration
	egf	Free eggs
	egv	Eggs in vegetation
	egt	Cemented terrestrial eggs
	ega	Cemented aquatic eggs
	egp	Ovoviviparity
2. Locomotion and dispersal		
Dissemination potential (in the water in m)	ds1	≤10
	ds2	10–100
	ds3	100–1000
	ds4	>1000
Locomotion and attachment to substrate of aquatic stages (excluding eggs)	swr	Swimmer rowing
	swo	Swimmer undulating
	clg	Clinger
	spr	Sprawler
	clb	Climber
bur	Burrower	
3. Morphology		
Body flexibility of aquatic stages	nof	None (<10°)
	lof	Low (>10–45°)
	hif	High (>45°)
Body form of aquatic stages (excluding eggs)	str	Streamlined
	fla	Flattened
	cyl	Cylindrical
	sph	Spherical
4. Biology and physiology		
Feeding habits	dep	Deposit-feeder
	shr	Shredder
	scr	Scraper
	ffa	Filter-feeder active
	ffp	Filter-feeder passive
	pie	Piercer
	pre	Predator
	teg	Tegument
Respiration type of aquatic stages (excluding eggs)	gil	Gills
	pla	Plastron
	aer	Aerial

(Table 3). For both fish and invertebrates, traits were grouped into four sets. The first set gathered those traits related to life history (e.g. size, number of descendants per reproductive cycle; see Table 2 for invertebrates and Table 3 for fish) with additional information for fish (e.g. relative fecundity, longevity, length at maturation; Table 3). The second set grouped those traits related to locomotion and dissemination in the water that confer resilience or resistance to disturbance (Tables 2 & 3). The third set included morphological features (e.g. body form, shape and swimming coefficients; Tables 2 & 3). The fourth set concerned more general biological and physiological features (e.g. feeding habits, respiration types; Tables 2 & 3). Trait information for invertebrates was obtained from data published by Statzner *et al.* (1994) for the Upper Rhône River species and the BIO-FUN project (Gayraud *et al.*, 2003) for species found in large European rivers and was supplemented by a literature search (Falkner *et al.*, 2001). For fish species, data were obtained from various sources in the literature (Persat, Olivier & Pont, 1994; Pont *et al.*, 1995; Mann, 1996; Blanck *et al.*, 2007; Sagnes & Statzner, 2009).

Because multiple sources of information were considered in establishing trait databases (data were derived from a review of existing literature as well as from expert knowledge), a fuzzy coding approach (*sensu* Chevenet, Dolédec & Chessel, 1994) helped to quantify the affinity of each taxon for each category within a trait. This established method of coding (Usseglio-Polatera *et al.*, 2000; Gayraud *et al.*, 2003; Bêche, McElravy & Resh, 2006) involves, for each taxon, the assignment of an affinity score to each category of a given trait. An affinity score of 0 indicates no association of the taxon with a trait category, whereas a score of 3 indicates a high affinity for a given trait category. The approach acknowledges the variability in traits that often occurs among different life stages or populations of an organism (Blanck & Lamouroux, 2007). Moreover, based on the taxonomic levels used by authors in this issue, especially for the identification of invertebrates (Castella *et al.*, 2015; Mérigoux *et al.*, 2015), fuzzy coding was the only way to account for within-species, within-genus or even within-family variation (especially for Diptera not identified beyond tribe level). As an example of the coding, *Caenis luctuosa* was given an affinity of 3 for the 'plurivoltine' category and 1 for the 'univoltine' category for the trait of the maximum number of reproductive cycles per year. As another example, *Helochaeres* sp., whose larvae are predators and adults are scrapers (feeding on algae), was given an affinity of 3 for the feeding-habit category 'predator' and 3 for the category

Table 3 Traits and their categories that were available for the fish species of the Rhône River

Biological trait	Code	Trait category
1. Life history		
Maximum potential size (mm)	s1	20–80
	s2	80–300
	s3	300–1000
	s4	>1000
Maximum number of descendants per reproductive cycle	nd1	100–2000
	nd2	2000–100 000
	nd3	>100 000
Maximum number of reproductive cycles per individual	rc1	1
	rc2	2
	rc3	2–6
	rc4	7–20
	rc5	>20
Relative fecundity*	rf1	2–3
	rf2	3–4
	rf3	>4
Egg size (mm)	es1	≤1
	es2	1–2
	es3	2–3
	es4	>3
Longevity (years)	ld1	<4
	ld2	4–7
	ld3	7–10
	ld4	>10
Length at maturity (mm)	sm1	≤100
	sm2	100–250
	sm3	250–350
	sm4	>350
Age at maturity (years)	am1	≤2
	am2	2–3
	am3	3–5
	am4	>5
Growth rate (year ⁻¹)	gr1	≤0.2
	gr2	0.2–0.4
	gr3	>0.4
Length of breeding season (months)	lb1	1–2
	lb2	2–3
	lb3	>3
Reproductive guild	lit	Lithophilous
	phy	Phytophilous
	ost	Ostracophilous
	ari	Ariadnophilous
	cat	Catadromous
Reproduction type	egf	Products released
	ega	Products deposited
	egp	Sheltered by parents
2. Locomotion and dispersal		
Drift dispersal by fry (km)	df1	<0.5
	df2	0.5–10
	df3	10–100
	df4	>100
Upstream migration of adults (km)	da1	<0.5
	da2	0.5–10
	da3	10–100
	da4	>100
Attachment to substrate	noa	Not in contact
	att	In contact

Table 3 (Continued)

Biological trait	Code	Trait category
	opa	Facultative
3. Morphology		
Body form	str	Streamlined
	fla	Flattened
	cyl	Cylindrical
Shape coefficient [†]	sh1	<4
	sh2	4–5
	sh3	5–6
	sh4	>6
Swimming coefficient [‡]	sw1	<0.4
	sw2	0.4–0.5
	sw3	>0.5
Minimum drag coefficient	cd1	<0.3
	cd2	≥0.3
4. Biology and physiology		
Feeding habits	in	Invertivore
	om	Omnivore
	hb	Herbivore
	pr	Piscivore
	pk	Planktivore
Respiration type	gil	Aquatic, ventilation
	aer	Aerial, no special organs

*Quantified as the number of eggs per 100 g body mass.

†Quantified as the ratio of the total body length to the maximum body depth.

‡Quantified as the ratio of the minimum depth of the caudal peduncle to the maximum caudal fin depth.

‘scraper’. Any category of a given trait for which information was not available was scored as 0. For invertebrates, 10.5, 6.7 and 0.4% of the total taxa lacked information about their dissemination potential in water, the maximum number of descendants per reproductive cycle and the life duration of adults, respectively. For fish species, three traits (longevity, egg size and length of the breeding season) lacked information for one species (2.8% of the total taxa), two traits (minimum drag coefficient and growth rate) lacked information for 4–5 species (11.1–13.8% of the total taxa) and two traits (distance travelled downstream or upstream by fry or adults) lacked information for 10 species (27.8% of the total taxa).

Translating taxonomic changes into changes in traits in the community

Predicted (habitat models) and observed (field surveys) changes in taxa density (log-transformed) after restoration were translated into predicted and observed changes in trait categories. To that end, we multiplied the predicted and the observed changes in log-density of taxa by their trait category profiles. For the main channels, each bypassed reach was considered

separately. For the floodplain channels, sites were pooled (see Castella *et al.*, 2015). As indicated above, in all of the taxonomic articles predictions could be made only for a subset of modelled taxa for which enough information was available (see Table 1). Consequently, predictions of changes in trait categories were computed using the modelled taxa only. In contrast, observed changes in traits could be computed for both the modelled taxa and the whole community (Table 1).

Statistical analyses of changes in traits

For comparisons of observed and predicted changes that were not made with similar units of density in the three articles (number of individuals per dm^{-3} for CHAN FISH, number of individuals per dm^{-2} for CHAN INV and number of individuals per m^{-2} for FLOOPL INV), we standardised the predicted values obtained from each taxonomic article (mean equal to 0 and variance equal to 1). We also standardised the observed changes, using the mean and standard deviation of the predicted values of a given taxonomic article. This technical standardisation ensured the comparability between the predicted and the observed changes in traits among the three datasets.

As in the three taxonomic articles, we used linear regression to quantify the strength of relationships between observed and the predicted changes in traits (instead of taxa changes). In addition, to assess whether the predicted changes in traits of the subset of modelled taxa could be used to predict overall changes in the trait composition of the whole community, we regressed observed changes in traits obtained for the total list of taxa with predicted changes in traits for modelled taxa. Comparisons were made for each dataset (CHAN INV, CHAN FISH and FLOOPL INV), for all traits and by sets of traits. We compared the adjusted R^2 values between observations and predictions obtained at the trait and at the taxonomic levels. The 95% confidence intervals around the adjusted R^2 values were computed using Walker’s alias resampling method (Ripley, 1987). In addition, we designed permutation tests to assess whether R^2 values at the trait level significantly improved those obtained at the taxonomic level, that is, if the trait description reduced noise in taxonomic responses to flow restoration. Specifically, we compared adjusted R^2 values obtained for traits (observed value) with similar values obtained after a random permutation ($N = 999$) of the trait category profiles of taxa (simulated values) as a null model. At each permutation, we multiplied the predicted and the observed log-density

changes of taxa by the permuted trait category profiles, standardised the resulting predicted and observed changes in traits according to the above-mentioned procedure and then computed the adjusted R^2 value.

Statistics and graphical outputs were performed with R freeware (R Development Core Team, 2013) including the *ade4* library (Dray, Dufour & Chessel, 2007).

Results

Predicted versus observed changes in trait responses

Weighting trait categories by the observed and predicted changes in log-density of modelled taxa, the models developed in the three taxonomic articles of the Special Issue predicted 2–92% of the observed changes in trait log-density after restoration (Table 4a). Highest agreements were obtained for fish (86–92% if omitting Chautagne; Table 4a; Fig. 1b). In contrast, traits of restored floodplain channel invertebrate communities had the lowest explained variance (23%; Table 4a; Fig. 1c), whereas traits of main channel invertebrates had fairly higher explained variance (75–79%; Table 4a; Fig. 1a). Using the whole community for computing observed trait-level changes provided similar results for main channel fish and floodplain channel invertebrates, whereas a decrease in explained variance occurred at the Pierre-Bénite reach for main channel invertebrates (Table 4b).

Trait versus taxonomic predictions

Predictive trait models were statistically significant in five of six cases for modelled taxa and for the whole

community (Table 4a,b; Fig. 1a–c), whereas they were significant in all cases for taxon models, for which R^2 values ranged between 4 and 74% (Table 4c; Fig. 1d–f). With few exceptions (Pierre-Bénite in CHAN INV and Chautagne in CHAN FISH; Table 4a,c), the predictive power of trait models was higher than that of taxon models, for both modelled taxa and the whole community. However, the permutation procedure demonstrated that the observed R^2 values obtained for traits significantly improved those obtained from taxa in only one case for modelled taxa and three cases for the whole community (bold cases in Table 4a,b). Trait R^2 values were significantly lower in one case (Pierre-Bénite; Table 4b,c).

Predicting changes for sets of traits

We further investigated how these patterns varied for the four sets of traits. Using invertebrates in the main channels, the performance of the models was significant for the four sets of traits, for both modelled taxa and for the whole community (CHAN INV in Table 5; Fig. 2). Trait categories that were mainly favoured by restoration included locomotion features such as clinging (Fig. 3a), biological and physiological features such as passive filter feeding and scraping (Fig. 3b) and gill respiration, life-history features such as aquatic egg laying, small size (5–10 mm), and plurivoltine and univoltine cycles and morphological features such as high body flexibility and cylindrical form (see Figure S1).

When using fish species in the main channels, predicted and observed changes did not match significantly for morphological, biological or

Table 4 Regression parameters (with 95% confidence intervals for slope (\pm) and the R^2 estimates in brackets) between observed and predicted changes in the trait category-weighted log-densities for the three data sets considered (CHAN INV: invertebrates in the main channels; CHAN FISH: fish in the main channels; FLOODPL INV: invertebrates in the floodplain channels)

Data set	Reach	(a) Traits of modelled taxa			(b) Traits of all taxa			(c) Ln-densities of modelled taxa		
		R^2	Slope	P	R^2	Slope	P	R^2	Slope	P
CHAN INV	CHAU	0.75 [0.58–0.86]	1.12 \pm 0.17	<10 ⁻¹⁶	0.60 [0.39–0.75]	1.95 \pm 0.43	<10 ⁻¹¹	0.33 [0.01–0.66]	1.94 \pm 0.96	<10 ⁻³
	PBE	0.79 [0.67–0.88]	1.38 \pm 0.19	<10 ⁻¹⁶	0.22 [0.01–0.49]	1.29 \pm 0.64	<10 ⁻³	0.74 [0.43–0.89]	1.92 \pm 0.49	<10 ⁻⁶
CHAN FISH	CHAU	0.02 [0.00–0.14]	0.05 \pm 0.06	ns	0.03 [0.00–0.13]	0.05 \pm 0.06	ns	0.52 [0.01–0.83]	0.53 \pm 0.29	<0.004
	BELL	0.92 [0.87–0.95]	0.91 \pm 0.06	<10 ⁻¹⁶	0.93 [0.89–0.96]	1.21 \pm 0.08	<10 ⁻¹⁶	0.42 [0.00–0.94]	0.69 \pm 0.46	<0.013
FLOODPL INV	PBE	0.86 [0.78–0.93]	0.52 \pm 0.05	<10 ⁻¹⁶	0.84 [0.74–0.91]	0.64 \pm 0.06	<10 ⁻¹⁶	0.74 [0.51–0.92]	0.75 \pm 0.26	<10 ⁻³
		0.23 [0.06–0.41]	0.75 \pm 0.36	<10 ⁻⁴	0.22 [0.06, 0.44]	1.01 \pm 0.49	<10 ⁻⁴	0.04 [0.01–0.11]	0.18 \pm 0.10	<10 ⁻³

Results are shown by reach for the main channels (CHAU: Chautagne; BELL: Belley; PBE: Pierre-Bénite). Observed changes in traits are calculated using alternatively (a) modelled taxa used for predictions and (b) all taxa in the community. Similar results obtained at the taxonomic level (regressions between observed and predicted changes in the log-densities of modelled taxa) are shown for comparison (c). Bold values in (a) and (b) indicate when R^2 at the trait and taxonomic levels significantly differ according to permutation tests (ns: not significant at $P < 0.05$).

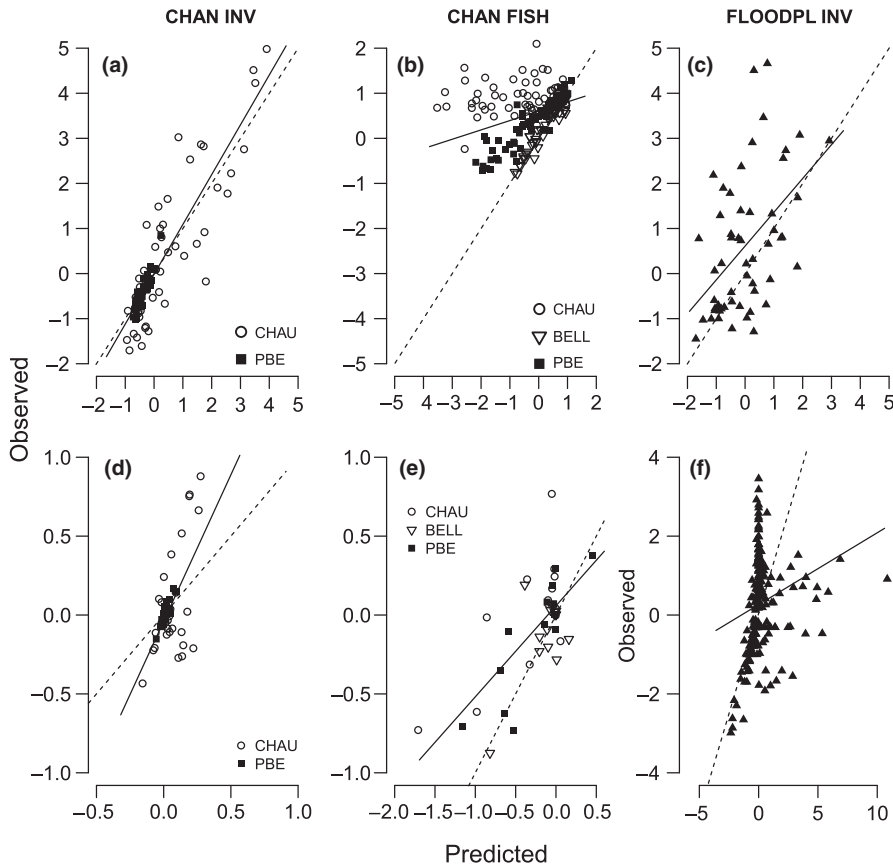


Fig. 1 Observed (standardized; see Methods) versus predicted (standardized; see Methods) changes in (a–c) trait category-weighted log-densities (each dot is a trait category) and (d–f) taxa log-densities (each dot is a taxon) in the restored reaches for invertebrate taxa in the main channels (CHAN INV), fish species in the main channels (CHAN FISH) and invertebrate taxa in the floodplain channels (FLOODPL INV). All trait categories are pooled, and legends show symbols for reaches (CHAU: Chautagne; BELL: Belley; PBE: Pierre-Bénite). The regression line (plain) and the line of perfect agreement (dashed) are shown. See Table 4 for statistics details by reach.

Table 5 Regression parameters (with 95% confidence intervals for slope (\pm) and the R^2 estimates in brackets) between observed and predicted changes in the trait category-weighted log-densities

Set of traits/data set	(a) Modelled taxa			(b) All taxa		
	R^2	Slope	P	R^2	Slope	P
Life history						
CHAN INV	0.76 [0.49, 0.91]	1.10 ± 0.17	$<10^{-16}$	0.63 [0.33, 0.83]	0.81 ± 0.17	$<10^{-11}$
CHAN FISH	0.23 [0.10, 0.40]	0.25 ± 0.08	$<10^{-8}$	0.19 [0.08, 0.35]	0.45 ± 0.15	$<10^{-7}$
FLOODPL INV	0.22 [0.03, 0.51]	0.84 ± 0.58	<0.009	0.17 [0.00, 0.48]	0.50 ± 0.39	<0.020
Locomotion and dispersal						
CHAN INV	0.87 [0.37, 0.98]	1.23 ± 0.22	$<10^{-8}$	0.62 [0.00, 0.90]	0.78 ± 0.27	$<10^{-4}$
CHAN FISH	0.17 [0.00, 0.56]	0.22 ± 0.16	<0.010	0.21 [0.02, 0.57]	0.48 ± 0.30	<0.004
FLOODPL INV	0.35 [0.00, 0.84]	0.88 ± 0.71	<0.043	0.42 [0.00, 0.86]	0.64 ± 0.46	<0.025
Morphology						
CHAN INV	0.74 [0.04, 0.97]	0.77 ± 0.24	$<10^{-4}$	0.67 [0.00, 0.91]	0.91 ± 0.35	$<10^{-3}$
CHAN FISH	0.00 [0.00, 0.33]	0.03 ± 0.18	ns	0.00 [0.00, 0.39]	0.14 ± 0.33	ns
FLOODPL INV	0.00 [0.00, 0.72]	0.19 ± 1.37	ns	0.00 [0.00, 0.93]	0.14 ± 0.74	ns
Biology and physiology						
CHAN INV	0.82 [0.49, 0.95]	1.21 ± 0.24	$<10^{-8}$	0.67 [0.31, 0.92]	0.75 ± 0.22	$<10^{-5}$
CHAN FISH	0.12 [0.00, 0.80]	0.19 ± 0.19	ns	0.17 [0.00, 0.89]	0.44 ± 0.38	<0.038
FLOODPL INV	0.23 [0.00, 0.78]	0.72 ± 0.71	ns	0.25 [0.00, 0.74]	0.51 ± 0.47	ns

Trait categories were grouped by sets of traits for each dataset (CHAN INV: invertebrates in the main channels; CHAN FISH: fish in the main channels; and FLOODPL INV: invertebrates in the floodplain channels). Observed changes were calculated using alternatively (a) modelled taxa used for predictions and (b) all taxa in the community (ns: not significant at $P < 0.05$).

physiological traits (CHAN FISH in Table 5; Fig. 2). When omitting the Chautagne reach data, predicted and observed changes in traits matched significantly

(modelled taxa, $R^2 = 0.53$ [0.25–0.84]; 0.56 ± 0.21 ; $P < 10^{-4}$; whole fish community, $R^2 = 0.68$ [0.49–0.80]; 1.16 ± 0.32 ; $P < 10^{-6}$). However, the direction of

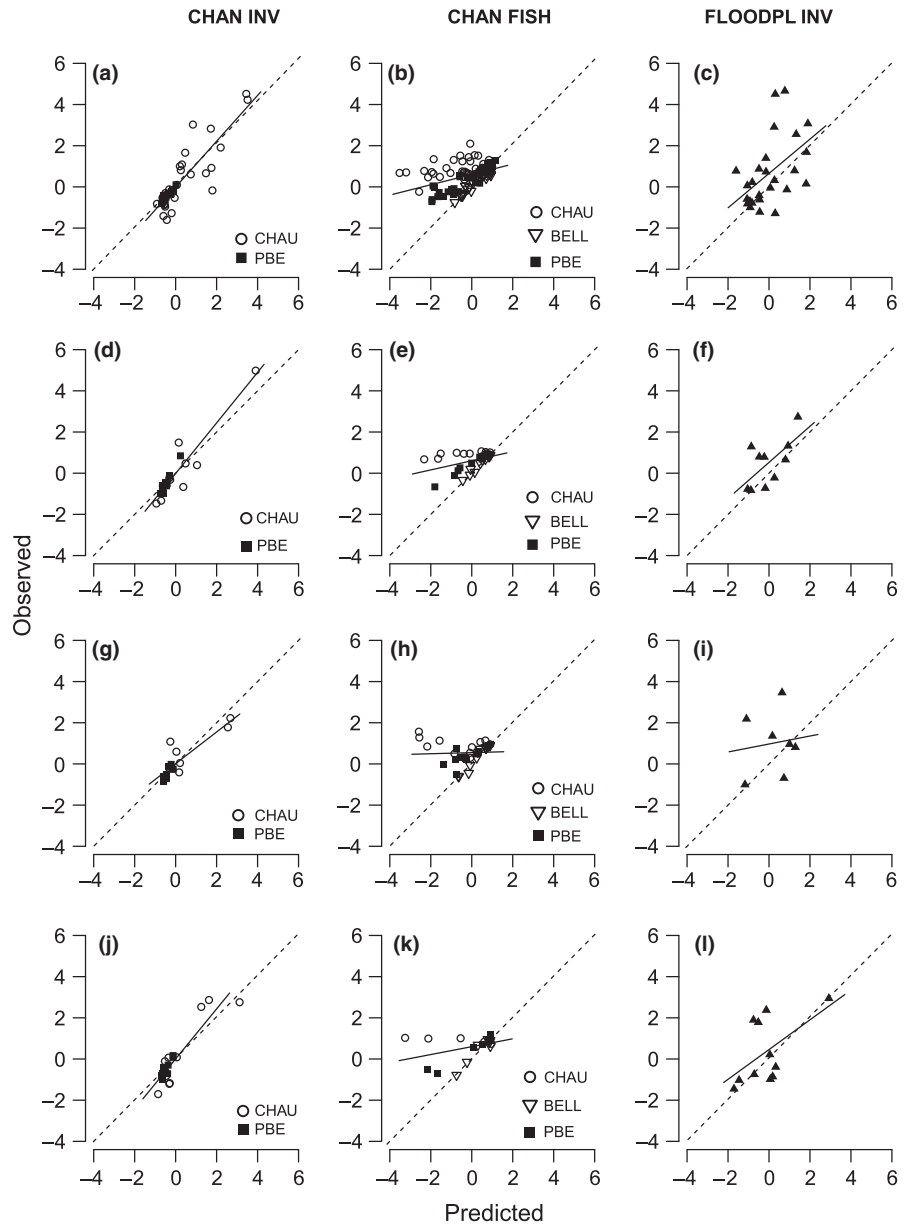


Fig. 2 Observed (standardized; see Methods) versus predicted (standardized; see Methods) changes in life history (a–c), locomotion and dispersal (d–f), morphology (g–i) and biology and physiology (j–l) trait category-weighted log-densities in the restored reaches, as in Fig. 1 but detailed by sets of traits. The regression line (plain) and the line of perfect agreement (dashed) are shown. See Table 5 for regression statistics.

changes of the minimum drag coefficient was opposite from expectations, with low minimum drag decreasing after restoration (cd1 in Fig. 3c). Similarly, low swimming coefficient and high shape coefficient unexpectedly dominated communities after restoration (sw1 and sh3 in Figure S2). In contrast, predicted changes in several locomotion and dispersal and life-history attributes significantly matched observed changes (CHAN FISH in Table 5; Fig. 2). Restoration generally favoured low relative fecundity (3–4; Fig. 3d), intermediate growth rates (0.2–0.4; Figure S2), late age at maturity (3–5 years), intermediate length at maturity (100–250 mm), large size (300–1000 mm) and high mobility (>10 km for adults; Figure S2).

Invertebrates in the floodplain channels also showed discrepancies between predicted and observed changes for morphological and biological and physiological features (FLOODPL INV in Table 5; Fig. 2). In contrast, predicted changes in several life-history features significantly matched observed changes (FLOODPL INV in Table 5; Fig. 2). Trait categories that were mainly favoured by reconnection in floodplain channels included locomotion features such as clinging (Fig. 3e), biological and physiological features such as gill respiration (Fig. 3f), and life-history features such as aquatic egg laying, small numbers of descendants per reproductive cycle, univoltine cycles and long life duration of adults (Figure S3).

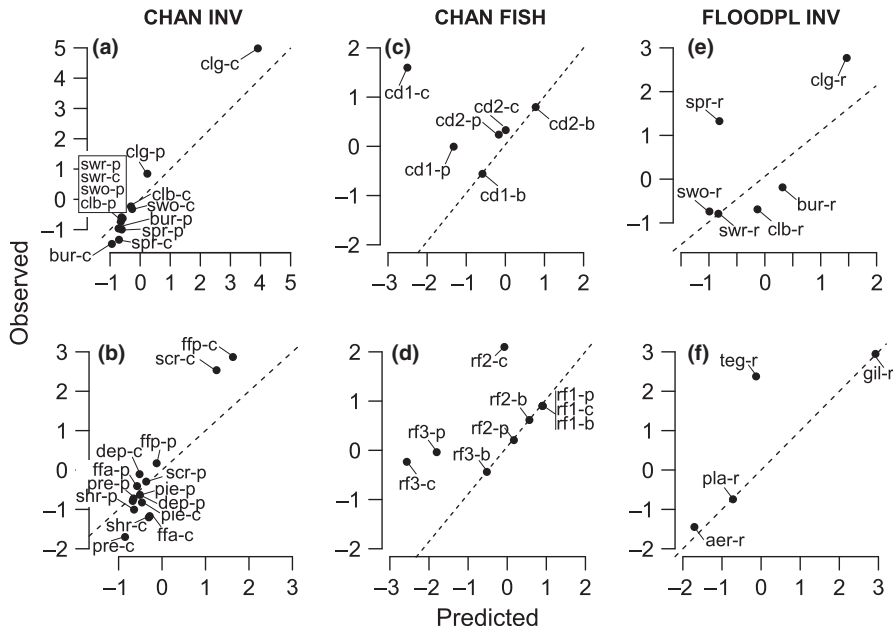


Fig. 3 Observed (standardized; see Methods) versus predicted (standardized; see Methods) changes in selected trait category-weighted log-densities in the restored reaches for invertebrates in the main channels (CHAN INV) with (a) locomotion and attachment and (b) feeding habits; fish in the main channels (CHAN FISH) with (c) minimum drag coefficient and (d) relative fecundity; and invertebrates in the floodplain channels (FLOODPL INV) with (e) locomotion and attachment and (f) respiration types. Codes for categories include three letters (see Tables 2 and 3 for acronyms) and ‘c’ for Chautagne reach, ‘b’ for Belley reach, ‘p’ for Pierre-Bénite reach or ‘r’ for reconnected channel. The line (dashed) of perfect agreement is shown.

Discussion

Increasing minimum flow in by-passed and floodplain channels of a large river changes the distribution of hydraulic characteristics that directly influence fish (flow velocities and depths) and benthic invertebrates (near-bottom hydraulic forces). As a result, worldwide, hydrological constraints have been shown to favour invertebrate species with more resistant and/or resilient traits (see Gallardo *et al.*, 2014) and affect size, fecundity and swimming capabilities of fish species (see Lamouroux, Poff & Angermeier, 2002). Therefore, restoration based on increased minimum flow and enhanced lateral connectivity within the Rhône floodplain was expected to shift the trait composition of communities accordingly.

We showed that the significant changes in species density after flow restoration and connectivity enhancement translated into changes in the trait composition of aquatic communities. This suggests that the trait approach can assist comparisons of the consistency of ecological responses among multiple datasets. In addition, our approach enabled us to test whether models based on a subset of taxa could predict community-level changes in traits, whether trait observations reduced the biological ‘noise’ resulting from the complex responses of individual taxa and whether changes in traits matched general expectations derived from the literature.

Predicted versus observed changes in trait responses

Using modelled taxa from the main channels, we observed significant agreement (75–92% of explained

variance) between predicted and observed changes in traits, with a noticeably higher explained variance for fish. Fish may respond more strongly to flow in the water column, whereas invertebrate responses may have a more complex response to the characteristics of near-bed hydraulics that vary at a finer spatial scale and are influenced, for example, by substrate roughness (Statzner, Gore & Resh, 1988). The similarity of results obtained for observed changes in traits based only on modelled taxa and those based on the whole community suggests that predictions for modelled taxa were appropriate for predicting community-level changes. In one case (Pierre-Bénite invertebrate communities), however, the explained variance in the observed trait log-density changes dropped from 79 to 22%. However, the selected modelled taxa at Pierre-Bénite represented only 30% of the log-density of the whole community. In particular, orthoclad and tanytarsine Diptera, which contributed greatly to the among-year variability (Mérigoux *et al.*, 2015), were not included in the habitat models, which may have caused this decrease in explained variance. In comparison, modelled taxa at Chautagne represented *c.* 50% of the log-density of the whole invertebrate community. In this latter case, the prediction of observed changes in traits dropped only from 75 to 60% when considering all taxa. Finally, for fish in the main channel, the 14 species considered in the habitat models represented 92–97% of the total density of individuals (Lamouroux & Olivier, 2015).

In contrast, using floodplain channel invertebrates, predicted changes in traits poorly matched observed ones. In this study, we selected reconnected sites in

floodplain channels because these sites underwent increased flow comparable to the main channels, allowing better predictions of taxonomic changes. Several reasons may explain why changes in floodplain channels were more difficult to predict than changes in the main channel (see Castella *et al.*, 2015). For example, initial communities of disconnected floodplain channels may depend on complex interactions between the main channel and the floodplain (effects of backwater at the downstream end, interaction with ground water). In addition, the connectivity models used to predict taxon and trait responses (see Castella *et al.*, 2015) were not based on the response of organisms to near-bottom flow, which is prominent in connected channel. These connectivity models were inherently more difficult to validate due to the complex and sometimes lagged response of organisms to changing processes associated with flow increase (e.g. organic matter content, sediment heterogeneity).

Trait versus taxonomic predictions

Whereas taxon responses suffer from the low generality inherent to the natural variation of populations, traits describing resistance and resilience patterns shared by all organisms may reduce this intrinsic noise. Therefore, several authors have reported a higher stability of trait responses than taxonomic responses across environmental gradients (Charvet *et al.*, 2000; Archaimbault, Usseglio-Polatera & Vanden Bossche, 2005; Bonada, Dolédec & Statzner, 2007). Comparing trait-explained variance to a null model led to a significant improvement for only one of six cases and three of six cases for the modelled taxa and the whole community, respectively. Reasons for this result may include the current state of knowledge on species traits in the data sources used in this study, although we considered traits that were demonstrated to be related to hydraulics (Lamouroux *et al.*, 2004; for invertebrates; Lamouroux *et al.*, 2002; for fish). In addition, species may use various combinations of traits to face the same flow changes (alternative suite of traits; Resh *et al.*, 1994; Verberk *et al.*, 2013), and the species response may depend on the degree of correlation between one of its traits that responds to flow changes and other traits (phylogenetic link; Verberk *et al.*, 2013). In one case (fish communities at Chautagne), predictions made from taxa outperformed those made from traits. A potential explanation for this pattern is that only a few species contributed to the observed changes after restoration at Chautagne (Lamouroux & Olivier, 2015). Because average current velocities were already high at Chautagne before restora-

tion (0.35 m s^{-1} before and 0.74 m s^{-1} after restoration; Lamouroux & Olivier, 2015), these species may share traits adapted to conditions of fast flow, which may have reduced some of the differences between the predicted and observed changes in traits.

Expectations from the literature and predictions of changes in sets of traits

For main channel invertebrates, the match between predicted and observed changes in traits was significant for all sets of traits studied (life history, locomotion and dispersal, morphology, biology and physiology). This result suggests that in the main channel, invertebrate communities shifted towards enhanced resistance to the increase in near-bottom flow forces (clinging ability), as expected from the literature (Horrigan & Baird, 2008; Statzner & Bêche, 2010). In contrast, body flexibility, which may confer some resistance in temporally variable habitats, shifted from low values to a combination of high values and no flexibility after restoration; this combination is associated with cylindrical forms that allow organisms to minimise drag force. The contrasts in body flexibility may reflect the different ways species can manage increases in minimum flow after restoration. The association between highly flexible bodies and cylindrical forms represents a potential trait combination that provides species with an adaptive solution to manage new flow conditions. Finally, the balance of feeding groups changed from shredders towards passive filter feeders, suggesting a shift from CPOM- towards FPOM-based ecosystems, which generally occurs in larger river communities (Vannote *et al.*, 1980). In addition, communities were dominated by gill and tegument respiration, suggesting a recovery of insect species generally vulnerable to the interactive effects of warming and hypoxia associated with low flow (Verberk & Bilton, 2013).

In contrast to main channel invertebrates, floodplain channel invertebrates showed no relationship between predicted and observed changes in traits for sets of morphological, biological and physiological features. However, as with the main channel invertebrates, the predicted decrease in floodplain channel invertebrates with aerial respiration and the predicted increase in invertebrates with aquatic (gill) respiration were observed, suggesting cooler and better oxygenated waters in reconnected sites (see Verberk & Bilton, 2013). This shift occurred together with an enhancement of resistance to the increased near-bottom flow forces (clinging ability), a pattern also observed in the main channel invertebrate communities. In contrast to the main channel invertebrate

communities, floodplain channel invertebrates did not show strong patterns in feeding habits, which explains the lack of agreement between predicted and observed changes in biological and physiological features. Nevertheless, a match between predicted and observed decreases in predators followed previous observations made by Paillex, Castella & Carron (2007) and Paillex *et al.* (2009) that reconnection may shift towards fewer predators because they are late settlers (Mackay, 1992) and towards invertebrates with better colonisation abilities. The later aspect was only partially confirmed because we observed fewer plurivoltine and more univoltine taxa after restoration than predicted.

For fish communities, contrary to expectations, observed and predicted effects of minimum discharge increases in the main channel on morphological traits (fish morphometrics and their drag resistance) did not match (Sagnes & Statzner, 2009). That is, the expected relationships between the global increase of water velocities at the reach scale and the hydrodynamic capabilities of fish communities were not confirmed. This mismatch may also be due to the limits of the category definitions used for these traits. Indeed, among the 14 modelled species of fish, all but one have a low (<0.3) minimum drag coefficient and all but three have a low (<0.4) swimming coefficient. In addition, because category positions result from density-weighted responses, unequal densities associated with the different categories may complicate the interpretation of the relative positions of categories. For morphological traits, real fish field measurements considering intraspecific variability would likely be more appropriate for assessing the effect of restoration on fish swimming abilities. Finally, it is also possible that fish shape is more closely related to hydraulic characteristics in reaches that are little affected by flow increase, such as the relative proportions of riffle-type and pool-type habitats (Lamouroux *et al.*, 2002).

In contrast, the increase in hydraulic constraints in the different restored river reaches favoured the trait proportions that characterise periodic species (long lifespan, large body length, intermediate fecundity, large eggs and late maturation), in accordance with previous studies (Lamouroux *et al.*, 1999; Blanck *et al.*, 2007). Minimum flow restoration in the Rhône also involved the limitation of traits characterising opportunistic species (small body length, early maturation, small eggs and high fecundity). Consistently, Mims & Olden (2012) showed that an increase in the base flow index (the ratio of 7-day minimum flows and the mean annual flow, which increases with the minimum flow discharge) provided a higher predictability of hydraulic conditions

and good spawning conditions for fish, and subsequently increased the presence of periodic species while limiting the presence of opportunistic species (Winemiller & Rose, 1992). In the Rhône, minimum flow increases seem to have enhanced the predictability of habitat conditions and, as expected, reduced opportunist species, which prefer frequently disturbed environments (Winemiller & Rose, 1992; see also Mims *et al.*, 2010).

Overall, our results confirm that at a relatively short time scale (c. 6–15 years), strategies of fish communities can change as expected in relation to new environmental conditions in large rivers. Traits associated with the substrate and with recolonisation abilities of invertebrates were modified by restoration as expected from the literature. Consistent with the more pelagic behaviour of many fish species than benthic macroinvertebrates, traits characterising fish species of downstream river reaches (long lifespan, large body, late sexual maturity) were favoured (see Schlosser, 1990).

Outlook

Given the high amount of variability in species distributions inherent to most natural communities (Palmer, Ambrose & Poff, 1997), focusing on biological traits may help develop generalisations useful for assessing restoration effects at the community level. Here, our observations of similarities in some trait responses (locomotion, attachment and respiration) across reaches (main channels), which were fairly consistent with expectations, support the use of traits to better understand and predict the effects of flow change on aquatic communities. In addition, because taxa sharing given traits provide specific ecosystem services (nutrient cycling, organic matter decomposition and food resources), the trait composition of communities can be meaningfully used as a proxy of ecosystem functions (see Verberk *et al.*, 2010). Although a few fish traits have been considered to be potential subindicators of river restoration success in some studies (Woolsey *et al.*, 2007), to our knowledge, traits of benthic invertebrates that are known to be involved in various important aquatic ecosystem processes (nutrient cycling, organic matter decomposition, sediment retention) have not. However, changes in traits were not always consistent with predictions and literature expectations. Improved development of multiple-trait-based approaches for assessing river restoration success in large rivers would require as follows: (i) solving taxonomic difficulties (e.g. those linked to difficult groups such as Chironomidae), (ii) filling gaps in biological trait information associated with these taxa

(especially focusing on energetically favourable traits) and (iii) increasing knowledge about the hydraulic preferences of taxa. In addition, although life-history strategies in response to flow changes are well established for fish communities (Winemiller & Rose, 1992; Mims & Olden, 2012), defining such strategies for invertebrate communities in response to flow disturbances, although remaining challenging and requiring a step-by-step approach (see Verberk *et al.*, 2013), is critically needed for a predictive water management.

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Supporting Information

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

Figure S1. Observed versus predicted changes in trait categories for invertebrates in the main channels.

Figure S2. Observed versus predicted changes in trait categories for fish in the main channels.

Figure S3. Observed versus predicted changes in trait categories for invertebrates in the floodplain channels.