

# Testing predictions of changes in benthic invertebrate abundance and community structure after flow restoration in a large river (French Rhône)

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## SUMMARY

1. Principal threats to running waters are linked to human-made discharge modifications, but tools to predict the quantitative consequences of flow restoration for benthic invertebrates in large rivers remain untested.
2. Quantitative benthos samples from two bypassed reaches (Pierre-Bénite – PBE – and Chautagne – CHAU) of the French Rhône River were collected during four years each before and after minimum flow increases (from 10 to 100 m<sup>3</sup> s<sup>-1</sup> at PBE and from 10 to 50 m<sup>3</sup> s<sup>-1</sup> at CHAU). These samples provided observed ln-density changes for the 50 and 62 (PBE and CHAU, respectively) most abundant taxa (typically species or genera). For about half of the 'model' taxa among them, distinct preference models for bottom shear stress categories were available from four reaches of the Upper Rhône River and from various German rivers. Linking these preference models with a statistical hydraulic model predicting frequencies of shear stress categories for any given discharge, we predicted ln-density changes of the model taxa after restoration.
3. Community structure of the abundant taxa changed clearly and rapidly after restoration at PBE but less clearly at CHAU. Our predictions explained a considerable amount of mean ln-density changes of our model taxa observed after restoration (75 and 30% at PBE and CHAU, respectively). They also explained (67 and 40% at PBE and CHAU, respectively) the model taxa scores along the principal components analysis axis that summarised the community variations of all abundant taxa before and after restoration. For taxa not identified to species (assessed as genus, tribe or family), the predicted ln-density changes were sometimes inaccurate at PBE (a Lower Rhône site), suggesting that the transferability of preference models for taxonomic levels above that of species can be problematic.
4. If further developed, statistical habitat models focussing on ecologically relevant physical variables (in our case shear stress) should enable reliable quantitative assessments of associations between flow restoration efforts and achievable ecological improvement.

*Keywords:* hydropower, minimum flow, observations vs. predictions, statistical habitat model, taxon-specific hydraulic preference

## Introduction

Globally, budgets for water resource management such as running water restoration are very high. Thus, environmental managers have long-requested effective tools

to restore these often highly altered systems (Lamouroux *et al.*, 2015). Scientific tools guiding restoration projects have to account for the nonlinear responses of running water systems, because environmental improvement achieved per budget unit significantly decreases as total

money spent for individual restoration measures (e.g. wastewater treatment, riparian buffer strips or discharge allocations to regulated rivers) increases (Lamouroux *et al.*, 2015). Therefore, such tools should quantitatively predict ecological changes as a function of restoration effort, and this criterion could be added to the six criteria for ecologically successful river restoration proposed by Palmer *et al.* (2005) and Jansson *et al.* (2005).

Discharge modifications and associated inundation regimes represent a principal threat to running water systems, so accurate predictions of hydrological patterns and ecological responses in rivers and floodplains are a prerequisite for successful river restoration (Arthington *et al.*, 2010). Early tools for guiding flow restoration in regulated rivers were developed in the late 1970s, providing quantitative predictions of habitat suitability for lotic fish and invertebrates across varying discharge allocations (for overviews of these early developments, see Hardy, 1998; Gore, Layzer & Mead, 2001; Jowett, 2003). Habitat models link a physical model for a given stream reach with biological models that reflect taxa preferences for the physical habitat. Over the last decade, these habitat models were (i) simplified and generalised to predict responses of species or flow-preference guilds; (ii) expanded to predict responses of animals and plants living in river floodplains; and (iii) modified to use new modelling techniques (Lamouroux *et al.*, 2015).

Beyond the efforts to predict the ecological consequences of restored discharge allocations, several projects assessed the accuracy of such predictions through after-restoration observations or other validation procedures. These assessments included (i) recruitment of trees or species composition of grass communities in floodplains (Rood *et al.*, 2003; Leyer, 2005); (ii) invertebrate species richness and trait patterns in secondary floodplain channels (Paillex *et al.*, 2009); (iii) species richness, Shannon–Wiener diversity or abundance of benthic invertebrates in the main, lotic river channel (Fuchs, 1994; Gore, Crawford & Addison, 1998; Zhang, Malmqvist & Englund, 1998); and (iv) abundance, population dynamics and community structure of fish in the main, lotic river channel (Lamouroux *et al.*, 1999, 2006; Gouraud *et al.*, 2001). Thus, in contrast to other river restoration projects (see Palmer *et al.*, 2005), flow restoration projects relatively often checked the reliability of model predictions through real-world observations.

This latter statement does not apply to lotic invertebrates of the main channel of large rivers. Our study provides such a reliability check for several reasons: (i) flow restoration tools for large rivers are urgently needed as many large rivers are among the most

impacted ecosystems worldwide (Huckstorf, Lewin & Wolter, 2008); (ii) for large rivers, restoration of a near-natural hydrology (e.g. c. 80–90% of natural discharge patterns; Arthington & Pusey, 2003) is not a realistic option (Gore & Shields, 1995; Strange, Fausch & Covich, 1999) and perhaps even not required to reach the restoration objectives (Jowett & Biggs, 2009); and (iii) discharge-related habitat suitability differs between smaller streams and larger rivers, with the latter being less ‘at risk’ under a given relative discharge reduction (Gore & Hamilton, 1996; Jowett, 1997). Here, we test predictions of changes in abundance of many benthic invertebrate taxa in two bypassed reaches of the French Rhône River (Pierre-Bénite and Chautagne; PBE and CHAU hereafter) for which we had substantial data before and after flow restoration. Observed changes in taxa abundance and community structure are both compared to predictions. In these reaches, the target minimum discharge was increased from 10 or 20 m<sup>3</sup> s<sup>-1</sup> (depending on the season) to 100 m<sup>3</sup> s<sup>-1</sup> at PBE and from 10 or 20 to 50 or 70 m<sup>3</sup> s<sup>-1</sup> at CHAU. We used these flow restoration in two large river reaches as large-scale experiments to test the transferability and predictive power of statistical habitat models that were almost entirely based on data from other sites than those studied here (see Lamouroux *et al.*, 1992, 2013; Dolédec *et al.*, 2007; Méricoux *et al.*, 2009).

## Methods

### *The Rhône River and its Pierre-Bénite and Chautagne reaches*

A recent monograph provides detailed information on biogeographic setting, physiography, climate, land use, geomorphology, hydrology, biogeochemistry, biodiversity, management and conservation of the main river and its major tributaries (Olivier *et al.*, 2009). Major modifications of the Rhône catchment by humans (through agriculture and livestock breeding) started c. 6000 years ago. Particularly in the 19th century, the morphology of the French Rhône was reshaped to enable navigation and to provide flood protection. From 1899 to 1986, 20 hydroelectric developments were implemented on the French Rhône. Most of these have a diversion dam directing the discharge through an artificial channel to a power plant, whereas the bypassed old river channel receives a minimum discharge and drains flows exceeding the maximum discharge rate processed by the power plant. Across the 16 bypassed river reaches, minimum flows range

between 1/300 and 1/5 of the unregulated mean flow (Lamouroux *et al.*, 2006).

Subsequent to local and national initiatives, a large restoration programme of the Rhône was implemented by the French government in 1998; it aims to restore the ecological attributes of a large river (Lamouroux *et al.*, 2006, Lamouroux *et al.*, 2015; Olivier *et al.*, 2009). This programme has involved cooperation among managers, scientists and stakeholders, which resulted in the developments of scientific surveys to assess restoration success/failure (Lamouroux *et al.*, 2015). The various planned restoration measures include increases of minimum flows in eight bypassed reaches, starting with PBE in August 2000 and followed by CHAU in July 2004. These minimum flow increases provide the first occasion to test tools that have been developed for fish (Lamouroux *et al.*, 1999, 2006) and later for invertebrates (Dolédéc *et al.*, 2007; Mériçoux *et al.*, 2009) to predict the ecological consequences of flow restoration.

Daily discharge and temperature were available in the two reaches during the invertebrate sampling, and hydraulic descriptions of reaches are detailed in Lamouroux & Olivier (2015). The diversion dam of the bypassed reach at PBE is 6 km downstream of Lyon (see Lamouroux *et al.*, 2015; for maps and general characteristics). The reach is 10 km long, includes two riffles, has partly armoured banks, no important tributaries, and is on average 160 m wide and 3.7 m deep at mean unregulated discharge ( $1030 \text{ m}^3 \text{ s}^{-1}$ ). Its last 4 km is under the influence of a downstream reservoir (Vaugris), which limited our study to the free-flowing upper 6 km of the reach. Water quality and temperature (typically  $6^\circ\text{C}$  in winter and  $21^\circ\text{C}$  in summer) did not change between the pre- and the post-restoration periods, and water quality indicators were rated as good or very good according to national criteria (Lamouroux *et al.*, 2015). Therefore, we ignored these environmental variables and focussed on flow-related changes here.

Before August 2000, the target minimum flow in the bypassed reach at PBE was  $20 \text{ m}^3 \text{ s}^{-1}$  (mean width/depth: 108/1.5 m) between April and August and  $10 \text{ m}^3 \text{ s}^{-1}$  (101/1.3 m) during the other months. Afterwards, the target minimum flow was  $100 \text{ m}^3 \text{ s}^{-1}$  (127/2.2 m), corresponding to a mean velocity increase from *c.* 8 to  $36 \text{ cm s}^{-1}$ . Flow is frequently close to the target minimum flow in the bypassed reach, but is higher when the total discharge of the Rhône is higher than the maximum discharge processed by the power plant ( $1380 \text{ m}^3 \text{ s}^{-1}$ ; Olivier *et al.*, 2009). In addition, maintenance works of the power plant may cause discharge increases. Consequently, before restoration, mean daily

discharge at PBE was never as low as  $10 \text{ m}^3 \text{ s}^{-1}$  and exceeded  $20 \text{ m}^3 \text{ s}^{-1}$  during *c.* 70% of the days (Fig. 1). Likewise, after restoration, target minimum flow was exceeded during *c.* 95% of the days. Over the period assessed in Fig. 1, daily discharge was 11 (minimum), 24 (median), 2651 (maximum) and  $160 \pm 8$  [mean  $\pm$  standard error (SE)]  $\text{m}^3 \text{ s}^{-1}$  before restoration and 95, 151, 3469 and  $352 \pm 11 \text{ m}^3 \text{ s}^{-1}$  after restoration (note that Fig. 1 is based on data covering the 12 months preceding each of the eight campaigns of invertebrate sampling). Consequently, the management mode at PBE partly conserved the unregulated discharge variability, which should have increased the difficulty of predicting the ecological consequences of the minimum flow increase.

The diversion dam of the bypassed reach at CHAU is located 148 km upstream of Lyon. The reach is 8.5 km long, includes several riffles, has partly armoured banks and no important tributaries. The 1.5-km-long subreach where invertebrates were sampled is on average 110 m wide and 1.6 m deep at mean unregulated discharge ( $412 \text{ m}^3 \text{ s}^{-1}$ ). Water quality and water temperature (typically  $5^\circ\text{C}$  in winter and  $19^\circ\text{C}$  in summer) were similar before and after restoration.

Before July 2004, the target minimum flow in the sampled reach at CHAU was  $20 \text{ m}^3 \text{ s}^{-1}$  (mean width/depth: 56/0.7 m) between June and November and  $10 \text{ m}^3 \text{ s}^{-1}$  (49/0.5 m) during the other months. Afterwards, the target minimum flow was  $50 \text{ m}^3 \text{ s}^{-1}$  (69/0.9 m) between November to April and  $70 \text{ m}^3 \text{ s}^{-1}$  (75/1.0 m) during the other months, corresponding to a mean velocity increase from *c.* 39 to  $84 \text{ cm s}^{-1}$ . At CHAU, the power plant processes at maximum  $700 \text{ m}^3 \text{ s}^{-1}$  (Olivier *et al.*, 2009). In addition, like at PBE, maintenance works of the power

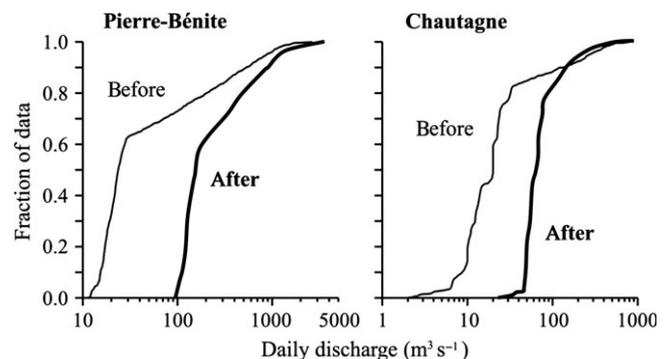


Fig. 1 Cumulative mean daily discharge frequency before and after flow restoration in August 2000 in the bypassed reach at Pierre-Bénite (PBE) and in July 2004 in the bypassed reach at Chautagne (CHAU), including only data covering the 12 months preceding each of the campaigns of benthic invertebrate sampling.

plant may cause discharge increases. Consequently, before restoration, mean daily discharge at CHAU exceeded  $10 \text{ m}^3 \text{ s}^{-1}$  during *c.* 80% of the days (Fig. 1). Likewise, after restoration, target minimum flow was exceeded during many days. Over the period assessed by Fig. 1, daily discharge was 2 (minimum), 20 (median), 797 (maximum) and  $49 \pm 2$  (mean  $\pm$  SE)  $\text{m}^3 \text{ s}^{-1}$  before restoration and 19, 65, 899 and  $86 \pm 2 \text{ m}^3 \text{ s}^{-1}$  after restoration. Consequently, as at PBE, the management mode at CHAU partly conserved the unregulated discharge variability, which again should have increased the difficulty of predicting the ecological consequences of the minimum flow increase.

#### *Invertebrate sampling and processing*

The PBE bypassed reach has *c.* 75% run and 25% riffle habitats (Lamouroux *et al.*, 2006). We assessed invertebrate densities for runs at a site situated 3.1 km downstream from the diversion dam and for riffles in one of the two riffles remaining in the reach, situated 4.5 km downstream from the dam. We sampled these sites when discharge was near the target minimum flow in summer (typically June) and autumn (typically October) before (1995, 1996, 1998, 1999) and after [2001, 2002, 2003, 2007/8 (combining autumn 2007 with summer 2008)] restoration. Due to financial and logistic constraints in this deeper reach, at each site and on each occasion, we took one dredge sample (mesh size: 0.5 mm) from *c.* 3  $\text{m}^2$  of the channel centre (representing *c.* 90% of the site surface) from a boat. In addition, we took four Surber samples (mesh size: 0.5 mm) from 0.05  $\text{m}^2$  each near the banks (representing *c.* 10% of the site surface), trying to include substratum types according to their relative cover.

At CHAU's bypassed reach, 20 invertebrate samples were taken on two occasions (spring and summer) before (in 2002) and after (in 2006, 2008, 2009 and 2010) restoration using a Hess-type sampler (area: 0.05  $\text{m}^2$ ; mesh size: 0.2 mm). Samples were taken at regular intervals over the 1.5-km subreach and across the width of the river in wadable areas. In the laboratory, samples were sieved through a 0.4-mm mesh. To these data, we added 3 years of data sampled in other contexts (unpublished reports from two of our co-authors: JD and J-FF) to increase the amount of data before restoration. These samples were collected with a Surber sampler (area: 0.05  $\text{m}^2$ ; mesh size: 0.5 mm) in spring 1997 (20 samples) and in summer and autumn 1999 and 2000 (8 samples on each occasion). Given that a low and/or unbalanced sampling effort before and after any restoration measure

would reduce statistical power to detect ecological changes (Vaudor *et al.*, 2015), we did not consider the available invertebrate data from two other Rhône reaches more recently restored (Belley and Brégnier-Cordon, see Lamouroux *et al.*, 2015).

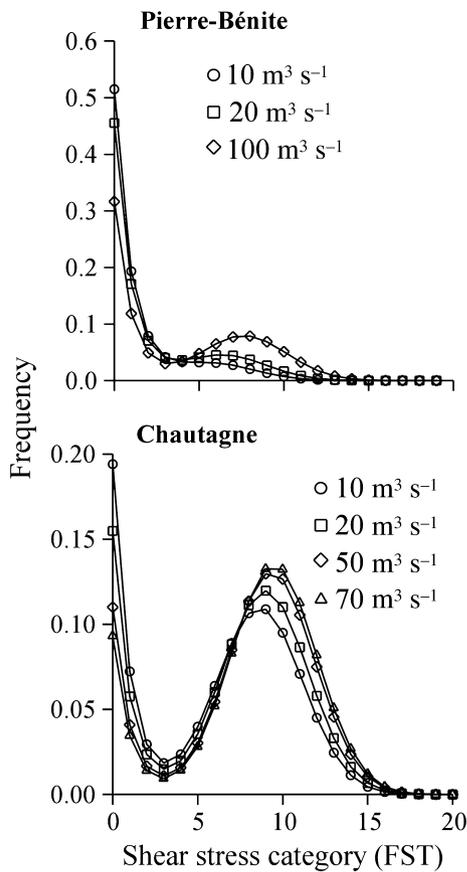
Independent of the method (dredge, Surber or Hess), invertebrates were sampled from the upper *c.* 5 cm of the sediments, brushed from larger stones and preserved in 4% formaldehyde or 70% alcohol. In the laboratory, invertebrates were sorted, identified and counted at the lowest possible taxonomic level [usually species or genus using keys such as Tachet *et al.* (2010), rarely to tribe/subfamily/family (dipterans) or order/class (e.g. oligochaetes)].

#### *Habitat modelling*

Our habitat models link the microhabitat and reach scales to predict changes caused by flow restoration. The models are based on hydraulic preference models for shear stress categories of individual taxa at the microhabitat scale. We do not use them to predict absolute density at the scale of microhabitats, but we aimed to predict density changes as a function of restoration at the larger scale of river reaches.

Bottom shear stress has important physical consequences for benthic invertebrates (e.g. Statzner & Borcardt, 1994; Mériçoux & Dolédec, 2004; Steuer, Newton & Zigler, 2008; Lamouroux *et al.*, 2015). Thus, we used the statistical habitat model FSTress (Lamouroux, 1998; principles described in Lamouroux *et al.*, 1992) to predict invertebrate density changes (for details, see Mériçoux *et al.*, 2009; note that samples from CHAU contributed to 20% of the data used in the preference models for most taxa, see Appendices S1 & S2). Physical input variables are average width-discharge and depth-discharge relationships for a reach that were available at our sites from repeated field measurements described in Lamouroux *et al.* (1999) and Lamouroux & Olivier (2015). From these relationships, FSTress predicts the frequency distribution of local shear stress categories (indicated by FST hemispheres, Statzner, Kohmann & Hildrew, 1991) in a reach at any discharge, for example for the three (PBE) or four (CHAU) target minimum flows before and after restoration (Fig. 2).

The biological components of FSTress used here are FST-preference models of Dolédec *et al.* (2007) and Mériçoux *et al.* (2009). In short, these models assume that  $\ln(\text{density}+1)$  of a given taxon (with density in individuals  $\text{dm}^{-2}$ ) varies proportionally to FST-habitat suitability indices across local quantitative samples of any



**Fig. 2** Predicted frequency distribution of bottom shear stress categories at three (PBE) or four (CHAU) target minimum flow values (before and after flow restoration) in the two studied bypassed reaches.

campaign (i.e. site  $\times$  sampling occasion). When used with the preference models (see Appendix S3 for details), FSTress predicts reach-averaged 'habitat values'  $HV$ s that are expected to be proportional to the reach-averaged  $\ln$ -densities ( $LD$ s) of the taxa within the reach. For any discharge,  $HV$  is calculated as the average (across FST-values) of habitat suitability indices corresponding to given FST-values weighted by the estimated FST-frequencies. As a result, using the subscripts B (before flow restoration) and A (after), we would obtain

$$LD_A = LD_B(HV_A HV_B^{-1}),$$

which provides the expected density change

$$LD_A - LD_B = LD_B(HV_A HV_B^{-1} - 1)$$

Thus, if  $HV_A$  is three times  $HV_B$ ,  $LD_A$  should also be three times  $LD_B$ . Note that this approach predicts changes only for taxa already occurring in a reach before restoration.

### Observed invertebrate changes

An initial list of 106 taxa at PBE and 111 at CHAU was used, after excluding gastropod and annelid taxa that were not identified at lower levels. Rare taxa (occurring with  $\leq 50$  individuals across all samples and/or in less than three samples) were excluded from the analyses because they could not contribute to the predictive tests (Vaudor *et al.*, 2015). Some additional taxa (nine at PBE and 14 at CHAU) were defined at coarser levels than the basic list (e.g. Sphaeriidae in addition to *Pisidium* spp. and *Sphaerium* spp.) to classify young instars that were difficult to assign to basic levels and had more than 50 individuals. In the end, our analyses of community changes involved 50 taxa at PBE and 62 at CHAU (listed in Appendices S1 & S2). For these, we transformed each taxon and each sample (32 dredges and 128 Surbers at PBE and 200 Hess samples and 52 Surbers at CHAU) into  $\ln$ -(density +1). For consistency with the habitat model that predicts shear stress conditions at the reach scale and ignores seasonal variations (see below), we calculated a reach-averaged  $\ln$ -density ( $LD$ ) of samples per taxon and per year [weighting the samples according to the relative abundance of habitats (run, riffle, channel centre, near banks)]. For each reach, we performed a principal components analysis (PCA) of mean annual  $\ln$ -densities to assess among-year changes of the invertebrate community structure.

### Testing predictions

When testing predictions of the habitat model, we ignored the taxa that had weak preferences for FST hemispheres (i.e. preference models with low  $R^2$ -values in Dolédec *et al.*, 2007; Mériçoux *et al.*, 2009; see Appendices S1 & S2). This choice was related to the fact that preference models were averaged from multiple rivers and seasons. Therefore, weak preferences could be due to low abundance and/or complex preference variations of these taxa across rivers and seasons. Consequently, we could not assume that taxa with weak preference models should not respond to hydraulic changes in the Rhône. We also did not consider three outlier taxa that did not respond as predicted due to reasons other than hydraulics (see our discussion). Our final test was based on a subgroup of 22 or 30 'model' taxa at PBE and CHAU, respectively (Appendices S1 & S2). We tested whether observed density changes corresponded to changes predicted by FSTress based on the lowest target minimum flow before restoration [i.e.  $10 \text{ m}^3 \text{ s}^{-1}$ , which should have produced maximum low-flow effects

during the period it prevailed (see Fig. 2 and our discussion) and after restoration (i.e. PBE:  $100 \text{ m}^3 \text{ s}^{-1}$ ; CHAU:  $50 \text{ m}^3 \text{ s}^{-1}$ ). Because observed low flows differed from the target minimum flows, we also tested predictions based on other discharge rates (Q80 and Q50, i.e. values above which the daily discharge mean is 80% and 50% of the days).

Through this approach, we produced one prediction per taxon and discharge increase so that we reduced the observations to one value of change per taxon (mean annual  $LD_A$  – mean annual  $LD_B$ ). To assess how the direction and magnitude of changes in model taxa density were predicted, we tested whether observed taxa changes had the same direction as predicted changes (chi-squared tests) and regressed observed ln-density changes vs. predicted ones. To assess how the main observed changes in community structure were related to our taxa predictions, we also regressed the scores of the model taxa on the first axes of the community PCA vs. their predicted density changes.

For the two regressions, we analysed the residuals of the observed–predicted relations to assess potential causes of unexplained changes. We tested the correlation between residuals, taxa hydraulic preference and preference strength (expressed as an average FST-value and a  $R^2$ -value, respectively; Dolédec *et al.*, 2007; Mérigoux *et al.*, 2009; Appendices S1 & S2). We also tested the effect of the source of the preference model (Appendix S1) at PBE only, because nearly all models used at CHAU came from one source (Appendix S2).

## Results

### Changes in raw (untransformed) abundances

Among the most abundant taxa at PBE, 32 of 50 had significantly ( $P < 0.05$ ) changing raw abundances in the near-bank samples after restoration, with 20 of them decreasing and 12 of them increasing (Appendix S1). In the channel centre of PBE, the raw abundance of only 12 taxa changed significantly, with five of them decreasing and seven of them increasing. Across habitat types, two taxa [Corixidae, *Theodoxus fluviatilis*] went locally extinct after restoration. In contrast, five new taxa appeared after restoration, among them invasive species that colonised the Rhône during the study period. These invasives were *Corophium curvispinum*, *Dikerogammarus villosus* (requiring the creation of the taxon ‘Gammaridae’ for juvenile *Dikerogammarus* and *Gammarus*) and *Hypania invalida*, for which FST preferences were not available. Among the most abundant taxa at CHAU, 47 of 62 had

significantly ( $P < 0.05$ ) changing raw abundances in the samples after restoration, with 29 of them decreasing and 18 of them increasing (Appendix S2). During the study period, three new invasive taxa appeared after restoration at CHAU. These invasives were *Corbicula fluminea*, *D. villosus* and Gammaridae (juveniles).

A subgroup of 23 taxa among the 50 abundant ones at PBE had known, distinct FST preferences (see Appendix S1). These preferences originated from Rhône sites >100 km upstream of PBE (17 taxa) or from German rivers (6 taxa) (Table 1). Fifteen of these taxa had significantly changing raw abundances in near-bank samples after restoration, with 10 of them decreasing and five of them increasing. In the channel centre, the raw abundance of only seven taxa changed, with three of them decreasing and four of them increasing (Table 1). Given that one taxon among the 23 (*T. fluviatilis*) went locally

**Table 1** Abundant taxa at PBE for which FST-preference models explaining  $\geq 15\%$  of the variability in ln-density of each taxon were available. For these, we indicate increase (+), decrease (–) or stability ( $\pm$ ) in raw abundance (plus significance levels) near the banks and in the channel centre after flow restoration as well as the data sources of FST-preference models. See Appendix S1 for details on abundance changes

Code	Taxon	Bank*	Centre*	Data†
AFLU	<i>Ancylus fluviatilis</i>	+ ***	+ ns	RR
ASEL	Asellidae	–**	–ns	RR
BASP	<i>Baetis</i> spp.	+***	+ns	RR
BFUS	<i>Baetis fuscatus</i>	+***	+*	GR
CASP	<i>Caenis</i> spp.	–ns	+ ns	RR
CHSP	Chironomini	–**	–*	RR
CLUC	<i>Caenis luctuosa</i>	–**	–ns	RR
DPOL	<i>Dreissena polymorpha</i>	+ns	+ns	RR
DTIG	<i>Dugesia tigrina</i>	–ns	+ns	RR
ESSP	<i>Esolus</i> spp.	+ns	–ns	RR
GASP	<i>Gammarus</i> spp.	–**	–ns	GR
GCOM	<i>Glossiphonia complanata</i>	–**	–ns	GR
GFOF	<i>Gammarus fossarum</i>	–ns	$\pm$ ns	GR
HCON	<i>Hydropsyche contubernalis</i>	–**	+ns	RR
HEXO	<i>Hydropsyche exocellata</i>	–ns	+ns	RR
HMOD	<i>Hydropsyche modesta</i>	+ns	+ns	RR
HSUL	<i>Heptagenia sulphurea</i>	+**	+**	RR
HYSF	<i>Hydropsyche</i> spp.	–**	+**	RR
MISP	<i>Micronecta</i> spp.	+**	+ns	RR
RABL	<i>Radix balthica</i> /labiata	–**	–*	GR
SIGN	<i>Serratella ignita</i>	–**	–ns	GR
SIMU	Simuliidae	+ns	+*	RR
TFLU‡	<i>Theodoxus fluviatilis</i>	–***	–***	RR

\*Significance levels of Mann–Whitney tests comparing before–after are ns:  $P \geq 0.05$ ; \*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; and \*\*\*:  $P < 0.001$ .

†RR: preference model with Rhône River data from upstream of PBE (Mérigoux *et al.*, 2009); GR: preference model with German River data (Dolédec *et al.*, 2007).

‡Ignored in all subsequent before–after statistical comparisons (see discussion for rationale).

extinct after restoration (see discussion for potential causes), we ignored it in all subsequent before–after statistical comparisons and illustrated it simply as outlier when possible. This explains that the final number of model taxa equalled 22 at PBE.

As at PBE, a subgroup of 32 taxa among the 62 abundant ones at CHAU had known, distinct FST preferences (see Appendix S2) and these preferences originated from Rhône sites (28 taxa) or from German rivers (4 taxa, Table 2). Of these taxa, 22 had significantly changing raw abundances in samples after restoration, with 16 of them decreasing and six of them increasing (Table 2). Given that two taxa among the 32 (*Gammarus* spp. and *Gammarus fossarum*) were very abundant before restoration but marginally abundant after restoration (see discussion for causes that are probably not flow-

related), we ignored them in all subsequent before–after statistical comparisons and illustrated them simply as outliers when possible. This explains that the final number of model taxa equalled 30 at CHAU.

These raw abundance data illustrate that among our abundant taxa (all or with known, distinct FST preferences), at PBE almost twice as many taxa decreased as increased near the banks after restoration, whereas similar numbers of taxa decreased and increased in the channel centre. At CHAU, more than 60% of the taxa decreased in abundance after restoration.

#### Observed changes in community structure

The PCA on the mean annual reach ln-densities of the 50 most abundant taxa at PBE separated the year with the lowest summer discharge (1996) from all other years (Fig. 3). The data scatter was similarly great before and after restoration, and the data did not order systematically along the years passed since restoration (Fig. 3). Years before restoration were all on the negative side and those after restoration were all on the positive side of axis F1, which explained three times more of the among-year inertia than axis F2 (Fig. 3). Therefore, we illustrate the position of the taxa only along axis F1 (Fig. 3).

At the negative side of axis F1 appeared all four chironomid taxa (Tanytarsini, Orthoclaadiinae, Chironomini, Tanypodinae) and two gastropod taxa [*Radix balthica/labiata*, *T. fluviatilis*], that is, lower minimum flow before restoration favoured relatively similar (i.e. Chironomidae and Gastropoda) taxa. At the positive side of this axis appeared *Psychomyia pusilla*, *Ancylus fluviatilis*, *Hydropsyche* spp., Simuliidae, *Dreissena polymorpha* and *Hydroptila* spp., that is, flow restoration favoured a more diverse fauna (different families and/or orders). The remaining taxa were positioned near the intersection with axis F2 (Fig. 3), illustrating that a few of our most abundant taxa contributed substantially to the temporal changes in community structure.

The PCA on the mean annual reach ln-densities of the 62 most abundant taxa at CHAU separated the year 2002 from all other years on the axis F2 (Fig. 3). The F1 axis weakly separated the other years before restoration from years after restoration (except 2006 that had a spring fauna similar to the fauna before restoration). The data scatter was great after restoration, and again the data did not order systematically along the years passed since restoration (Fig. 3).

The axis F1 explained more than twice of the among-year inertia explained by axis F2 so that we illustrate the position of the taxa again only along axis F1 (Fig. 3). At

**Table 2** Abundant taxa at CHAU for which FST-preference models explaining  $\geq 15\%$  of variability in ln-density of each taxon were available. See Table 1 for further details and Appendix S2 for details on abundance changes

Code	Taxon	Test	Data
AFLU	<i>Ancylus fluviatilis</i>	+++	RR
ASEL	Asellidae	–+++	RR
BASP	<i>Baetis</i> spp.	+*	RR
BFUS	<i>Baetis fuscatus</i>	–ns	GR
BRHO	<i>Baetis rhodani</i>	–*	RR
BVAR	<i>Baetis vardarensis</i>	–ns	RR
CLUC	<i>Caenis luctuosa</i>	–+++	RR
CASP	<i>Caenis</i> spp.	+ns	RR
CHSP	Chironomini	–+++	RR
DPOL	<i>Dreissena polymorpha</i>	–ns	RR
DTIG	<i>Dugesia tigrina</i>	–*	RR
ELSP	<i>Elmis</i> spp.	–ns	RR
ESSP	<i>Esolus</i> spp.	–ns	RR
GASP*	<i>Gammarus</i> spp.	–+++	GR
GFOS*	<i>Gammarus fossarum</i>	–+++	GR
HCON	<i>Hydropsyche contubernalis</i>	++	RR
HEXO	<i>Hydropsyche exocellata</i>	–ns	RR
HINC	<i>Hydropsyche incognita</i>	+*	RR
HMOD	<i>Hydropsyche modesta</i>	–+++	RR
HSIL	<i>Hydropsyche siltalai</i>	–+++	RR
HSUL	<i>Heptagenia sulphurea</i>	–ns	RR
HYSP	<i>Hydropsyche</i> spp.	–*	RR
LESP	<i>Leuctra</i> spp.	–ns	RR
LISP	<i>Limnius</i> spp.	–+++	RR
PFLA	<i>Polycentropus flavomaculatus</i>	–+++	RR
PISP	<i>Pisidium</i> spp.	–*	RR
POLY	Polycentropodidae	–+++	RR
RHPS	<i>Rhithrogena</i> spp.	–*	RR
RHSP	<i>Rhyacophila</i> s. stricto spp.	–+++	RR
SIGN	<i>Serratella ignita</i>	–ns	GR
SIMU	Simuliidae	+++	RR
TFLU	<i>Theodoxus fluviatilis</i>	+++	RR

\*Ignored in all subsequent before–after statistical comparisons (see discussion for rationale).

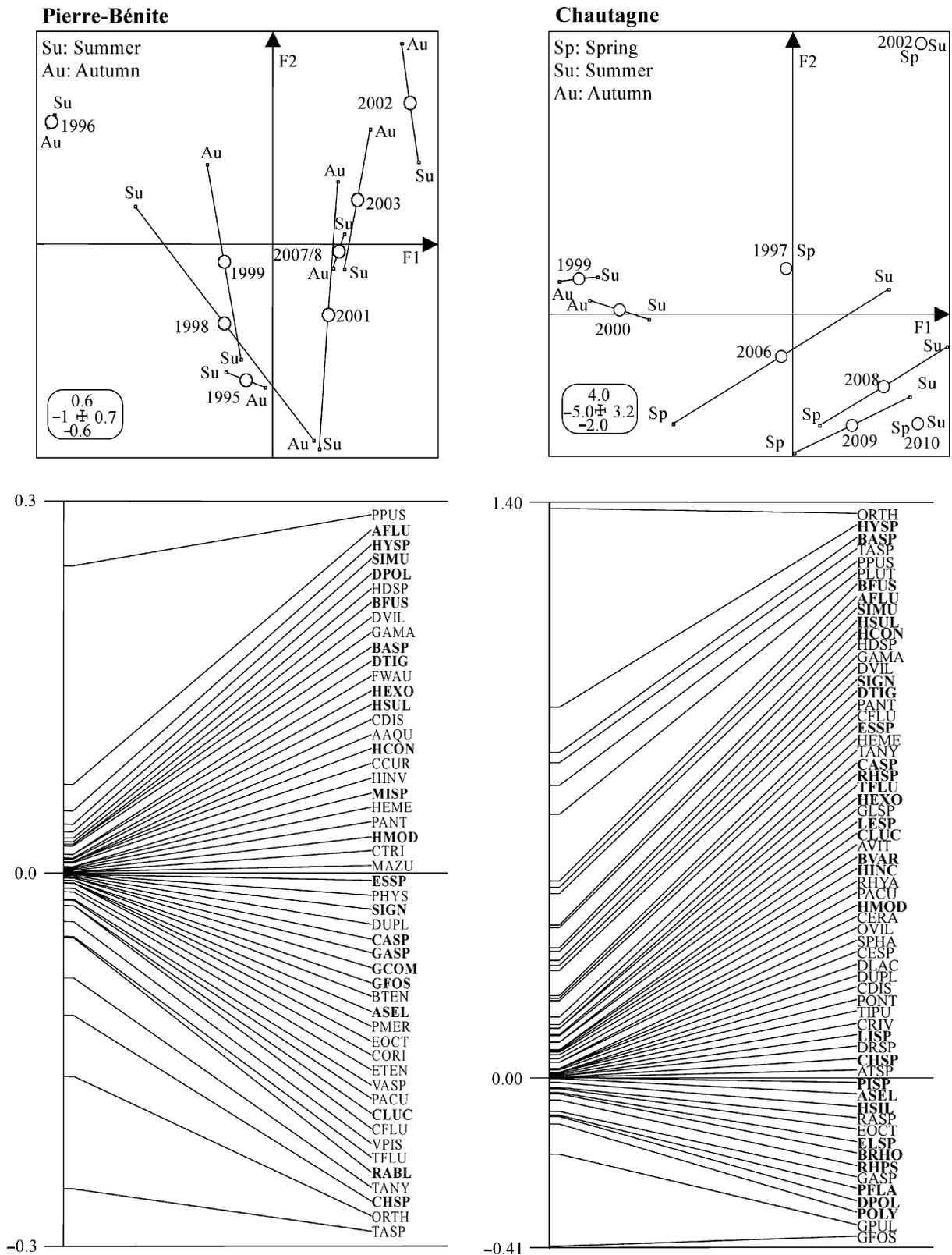


Fig. 3 Year scores (and seasons projected as supplementary data) obtained by principal components analysis (PCA) on the mean annual reach ln-densities of the most abundant taxa (top: 50 taxa at PBE and 62 taxa at CHAU) and taxon scores on axis F1 (bottom, indicating our model taxa in bold) (see Tables 1 and 2 and Appendices S1 & S2 for taxa labels). Axis F1 explained 60 and 54% and axis F2 20 and 23% of the among-year inertia at PBE and CHAU, respectively.

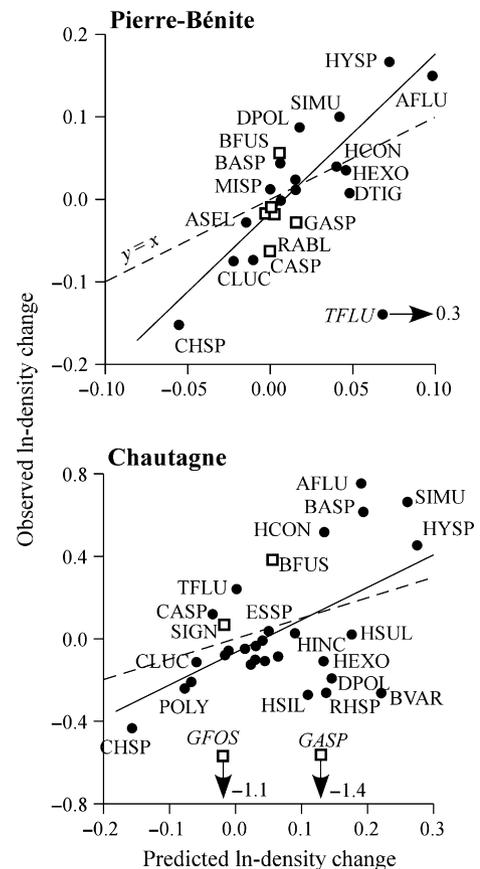
the negative side of axis F1 appeared the three gammarid taxa *G. fossarum*, *G. pulex* and *Gammarus* spp., the two trichopteran taxa Polycentropodidae and *Polycentropus flavomaculatus* and the mollusc *D. polymorpha*, that is, lower minimum flow or other factors (see discussion on invasive species below) before restoration favoured again relatively similar taxa. At the positive side of axis F1 appeared the two chironomid taxa Orthocladiinae and Tanytarsini, the two trichopteran taxa *Hydropsyche* spp. and *P. pusilla*, and the two ephemeropteran taxa *Baetis* spp. and *Potamanthus luteus*. Remaining taxa were again positioned near the intersection with axis F2 (Fig. 3).

### Testing predictions

The model taxa represented 65% (at PBE) and 67% (at CHAU) of the total sampled abundance considered for the community PCA (when chironomids not considered by our models were not taken into account; see discussion). In addition, F1-scores of the model taxa in the PCA of abundant taxa were well distributed within the range of F1-scores of abundant taxa (Fig. 3). Thus, the model taxa contributed strongly to the observed community changes at PBE and CHAU.

For the model taxa, observed directions of changes were related to predicted ones at PBE ( $P = 0.008$ ) but not at CHAU ( $P = 0.5$ ). However, observed ln-density changes of the model taxa were significantly related to predictions at PBE and CHAU, without obvious outliers other than those omitted from the analyses (Fig. 4). At PBE, the slope of the regression was  $c. 2$  and the 95% confidence limits (CL) did not include 1 (Table 3), whereas its intercept was near 0 (included in the 95% CL). Thus, at PBE, the observed changes far from 0 differed from the predictions. At CHAU, the data scatter of the regression between observed and predicted densities was greater than at PBE (Fig. 4) so that the 95% CL of the slope included 1 and that of the intercept included 0 (Table 3). The residuals of the regressions in Fig. 4 were not significantly related to any of the potential explanatory variables ( $P > 0.41$  for all tests).

When repeating our tests for observed Q80s and Q50s prevailing before and after restoration at PBE,  $R^2$ -values and significance of the regressions were similar for all three flow scenarios, whereas the slope of the regressions increased from target minimum flow to Q80s to Q50s (Table 3). Likewise, at CHAU,  $R^2$ -values and significance of the regression were similar for all three flow scenarios and the regression slope increased (Table 3), but the 95% CL of the slope included 1 also for the Q80 and Q50 predictions.



**Fig. 4** Regressions between observed and predicted (for the target minimum flows) mean ln-density changes after restoration of the 22 model taxa (ignoring the outlier TFLU) at PBE and of the 30 model taxa (ignoring the outliers GASP and GFOS) at CHAU, indicating taxa labels (see Tables 1 & 2) and data source of preferences model by full circles (Upper Rhône) or open squares (Germany). See Table 3 for regressions and statistics.

Regressing scores of the model taxa on PCA axes F1 from Fig. 3 (assessing the community structure of all abundant taxa) vs. predicted ln-density changes of the model taxa provided highly significant regressions (Fig. 5). Thus, our models accurately predicted important components of the community structure changes. In contrast, taxa scores on axis F2 (not illustrated) were not related to predictions ( $P = 0.104$  and  $0.200$  at PBE and CHAU, respectively). Residuals of the regressions in Fig. 5 were again not significantly related to any of the potential explanatory variables ( $P > 0.12$  for all tests).

## Discussion

### Changes in raw abundances

Changes in raw abundances of the most abundant taxa after restoration corresponded to expectations at PBE.

**Table 3** Results of the regressions  $y = a + bx$  between observed (benthic sample surveys:  $y$ ) and predicted (statistical habitat model:  $x$ ) changes in taxon average ln-density (PBE:  $N = 22$ ; CHAU:  $N = 30$ ) in two restored reaches for the target minimum flow (corresponding to Fig. 4) and at two alternative observed discharge percentiles. For the target minimum flow, we provide more details (including 95% confidence limits of parameter estimates) than for the similar models at the alternative flows

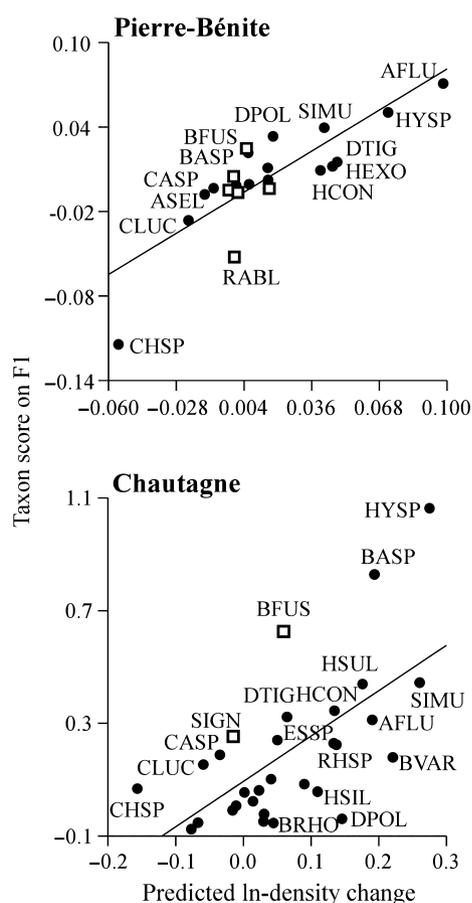
Reach	Target minimum flow				Observed Q80			Observed Q50		
	$R^2$	a	b	P	$R^2$	b	P	$R^2$	b	P
PBE	0.746	$-0.016 \pm 0.019$	$1.92 \pm 0.52$	$<10^{-6}$	0.752	2.54	$<10^{-6}$	0.754	2.75	$<10^{-6}$
CHAU	0.297	$0.065 \pm 0.115$	$1.58 \pm 0.94$	0.002	0.297	1.67	0.002	0.301	2.33	0.002

There, near the banks, more taxa significantly decreased (lentic forms) or increased (lotic forms) than in the channel centre because a discharge increase from *c.* 1% to 10% of the mean unregulated flow should produce greater physical habitat changes near the banks (from lentic to lotic) than in the channel centre (from less lotic to more lotic). However, differences in sample size could also have contributed to these differences between banks ( $N = 128$ ) and channel centre ( $N = 32$ ). In comparison, raw abundance changes at CHAU corresponded equivo-

cally to expectations. Corresponding to our expectations, taxa having a clear preference for lentic conditions such as *Caenis luctuosa*, Chironomini, *Dendrocoelum lacteum* and Polycentropodidae (see Mériçoux *et al.*, 2009) were significantly less abundant after restoration because lentic conditions were clearly rarer after restoration (Fig. 2). In contrast, taxa that prefer conditions near FST-value 10 such as the species of *Baetis* and *Hydropsyche* (see Mériçoux *et al.*, 2009) equivocally corresponded to our expectations because the habitat changes near FST-value 10 were less important than near FST-value 0 (Fig. 2).

Among the taxa disappearing after restoration at PBE were the Corixidae, that is, forms that are lentic swimmers (Tachet *et al.*, 2010), and therefore may have drifted out the bypassed reach at increased current velocities. In contrast, *T. fluviatilis*, which also disappeared, has a preference for high FST-conditions at an annual scale (Mériçoux *et al.*, 2009). At the seasonal scale, however, this species prefers low FST-conditions in spring and higher FST-conditions in autumn (Mériçoux & Dolédec, 2004), which could be one reason for its disappearance after restoration. Another potential reason relates to the function of its radula and digestive system, which limits its optimal food exploitation to a few algal taxa (Neumann, 1961). Given that the increased water depth after restoration reduced the amount of photosynthetic active radiation (PAR) at the river bottom by *c.* 50% (calculated with eqn SH11, Statzner & Sperling, 1993), this depth increase potentially reduced the algal food required by *Theodoxus* to an unsupportable level (see Kiffney, Richardson & Bull, 2003 for such linked effects from PAR to periphyton to benthic invertebrates, and Dewson, James & Death, 2007, for a review of algal responses to changing velocity and depth). The example of *Theodoxus* illustrates that biological details of taxa beyond their annual FST preferences may affect their abundance changes. In contrast to PBE, none of the 62 most abundant taxa disappeared after restoration at CHAU.

Among the species that appeared at PBE and at CHAU after restoration were four invaders that recently



**Fig. 5** Regressions between scores of the model taxa on axis F1 of the community PCA (see Fig. 3) and their predicted ln-density change at PBE ( $N = 22$ ,  $R^2 = 0.672$ ,  $P < 10^{-5}$ ) and CHAU ( $N = 30$ ,  $R^2 = 0.396$ ,  $P < 10^{-3}$ ). See Fig. 4 for further details.

colonised the Rhône and other European rivers (Bij de Vaate *et al.*, 2002; Devin *et al.*, 2005). Invasiveness of these taxa is favoured by biological attributes that are not simply flow dependent (Statzner, Bonada & Dolédec, 2008), that is, their appearance after restoration was a coincidence and not caused by restoration. Because biotic interactions between invasive (e.g. *D. villosus*) and native (e.g. *Gammarus* spp.) species such as predation by the former on the latter can increase with increasing FST-conditions (Felten, Dolédec & Statzner, 2008), these biological invasions are another potential source of inaccurate predictions by our models. Such biotic interactions may explain the strong reduction in the abundance of the native *Gammarus* species at CHAU, which were abundant before restoration but faced an elevated abundance of *D. villosus* since restoration. In comparison, at PBE, native *Gammarus* species were less abundant before and *D. villosus* was less abundant after restoration and the observed abundance changes of the native *Gammarus* species were less spectacular at PBE.

#### Observed changes in community structure

Axis F1 of the PCA of the mean annual reach ln-densities of the most abundant taxa explained the lion's share of the among-year inertia at both PBE and CHAU. Chironomid taxa not considered by our models (Orthocladiinae and Tanytarsini) had high abundance that changed after restoration, in different directions at PBE and CHAU. Discussing these changes is limited by the taxonomic resolution, because these taxa are defined at coarse levels. They contain many species that likely differ between the two reaches and whose hydraulic preferences are unknown.

At PBE, before–after restoration years were well separated along F1, with taxa on its before-side having no clear or low FST preferences (except *Theodoxus*, see above) and taxa on its after-side having no clear or high FST preferences (Dolédec *et al.*, 2007; Méricoux *et al.*, 2009). Thus, the structure of the invertebrate community clearly changed after restoration and often corresponded with the FST preferences of the taxa. At CHAU, these changes were not as clear as at PBE and this could have again been due to the above-discussed differences in the physical habitat changes at the two sites.

Particularly at PBE, taxon-specific tolerances for near-bed flow (i.e. FST) conditions caused these changes. If flow decreases below or increases above the tolerated lower or upper level, invertebrates start to drift, for example because of respiratory problems at low flow and unbearable forces at high flow (Dewson *et al.*, 2007;

Lamouroux *et al.*, 2010). As long as flow remains outside the tolerated range, invertebrates continue to drift and may travel long distances (Vinikour, 1981). As a consequence, river invertebrates may react rapidly to significant flow changes, which facilitates community adjustment (e.g. colonisation) after restoration (Decker, Bradford & Higgins, 2008; Muehlbauer *et al.*, 2009). Correspondingly, we observed no systematic changes in the community structure with years passed since restoration.

#### Testing predictions

Our model taxa contributed substantially to the total abundance and to community changes along PCA axis F1. At PBE, using models developed with data from river reaches other than PBE, we correctly predicted the directions of changes and 75% of the variability in the observed mean ln-density changes after restoration for our 22 model taxa. In addition, we predicted 67% of the scores of model taxa on the axis reflecting the main changes in community structure. Finally, in both cases, unpredicted observed variability was not related to model characteristics (preferences of taxa and their strengths; model data sources). Thus, the unpredicted observed variability in changes of the model invertebrates should have been due to other factors than the FST-conditions, factors that vary as well with discharge and typically have interacting effects on invertebrates (Dewson *et al.*, 2007; Matthaei, Pigott & Townsend, 2010). At CHAU, we predicted 30% of the variability in the observed mean ln-density changes after restoration for our 30 model taxa, but the direction of changes was not well predicted. We also predicted 40% of the scores of model taxa on the axis reflecting the main changes in community structure. This lower precision of our predictions at CHAU compared with PBE presumably relates to the heterogeneous data available for CHAU before restoration. As at PBE, unpredicted observed variability was not related to model characteristics at CHAU.

However, our model under-predicted the magnitude of changes as the observed slopes relating observations to predictions were >1. Under-prediction was significant at PBE where the data scatter was lower and the 95% CL of the slope was narrower. This inaccuracy of the predicted density changes at PBE potentially relates to three systematic error sources. First (i), the sampling efficiency might have changed due to the restoration so that the observed abundance estimates before and after restoration were not comparable. Second (ii), the physical habitat changes, that is, the changing frequency of local shear stress categories per reach, might not have

been accurately predicted. Finally (iii), the preference models of the taxa, entirely developed from data from multiple sites other than PBE, might be not transferable to PBE. This could have been particularly problematic for taxa described above the species level that could include different species at PBE than in model calibration sites and different species before and after restoration. Having no solid argument concerning (i), we focus on the potential error sources (ii) and (iii) here. Concerning (ii), the hydraulic FST-model was developed and cross-validated with data from smaller streams from two regions in Germany that had a discharge range of 0.003–11.9 m<sup>3</sup> s<sup>-1</sup> (Lamouroux *et al.*, 1992). Thus, the predictions of shear stress frequency distributions after restoration for PBE (and CHAU) were performed for discharges distinctly above the data range available for the model development, which would be one potential error source. Concerning (iii), the slope of the regression at PBE in Fig. 4 was largely affected by three taxa described above the species level, which were *Hydropsyche* spp., Simuliidae and Chironomini. Given that the hydraulic preferences within an invertebrate species can change with age or size (e.g. Statzner & Borcardt, 1994), it is not surprising that the transferability of preference curves to predict density changes at independent sites should decrease when considering genera, tribes or families that potentially were represented by other species at the sites used to develop the preference models. Thus, lacking skills or motivation to identify benthic invertebrates in quantitative samples to the species level is presumably a handicap for accurately predicting density changes after restoration.

### Management implications

Given the numerous environmental factors and technical difficulties (e.g. identification limits) potentially interfering with our predictions of the effects of flow restoration, our models provided convincing predictions of taxa abundance changes that partly explained community changes. Similarly, predictions of fish community changes after restoration at PBE and CHAU corresponded well to the observed changes (Lamouroux & Olivier, 2015). In both cases, predictions of physical habitat changes were made with simple statistical hydraulic models (predicting frequency distributions of physical conditions) considering variables relevant for invertebrates (shear stress in FST-categories) or fish (point velocity and water depth in categories). These hydraulic predictions were then linked to preference models of

invertebrate or fish taxa to the respective, relevant physical variables. This modelling approach is perhaps a solution of a frequently evoked problem (Lamouroux *et al.*, 2010, 2013; Lancaster & Downes, 2010; Poff & Zimmerman, 2010): it seemingly provides general, transferable quantitative relationships between flow alterations and ecological responses. If further developed by current and forthcoming studies on flow restoration in other bypassed reaches (Mérigoux *et al.*, 2009; Lamouroux *et al.*, 2015), this approach could provide managers with reliable tools for quantitative assessments of associations between restoration effort (i.e. costs for discharge increases) and achievable ecological improvement such as abundance of taxa, community structure, associated changes of bioindicator indices or functional biological traits.

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### Supporting Information

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

**Appendix S1.** Mean raw abundance data from the Surber and dredge samples of the 50 most abundant taxa before and after restoration at PBE, statistics of before–after comparisons and the state of preference model for each taxon.

**Appendix S2.** Mean raw abundance data from the Surber and Hess samples of the 62 most abundant taxa before and after restoration at CHAU, statistics of before–after comparisons and the state of preference model for each taxon.

**Appendix S3.** Computing predicted and observed ln-densities of model taxa.

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