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Pierre Marle, J er emie Riquier, Pablo Timoner, H el ene Mayor, Vera I. Slaveykova, et al.. The interplay of flow processes shapes aquatic invertebrate successions in floodplain channels - A modelling applied to restoration scenarios. *Science of the Total Environment*, 2021, 750, pp.142081. 10.1016/j.scitotenv.2020.142081 . hal-02931379

HAL Id: hal-02931379

<https://hal.science/hal-02931379>

Submitted on 27 Jul 2022

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The interplay of flow processes shapes aquatic invertebrate successions in floodplain channels - A modelling applied to restoration scenarios



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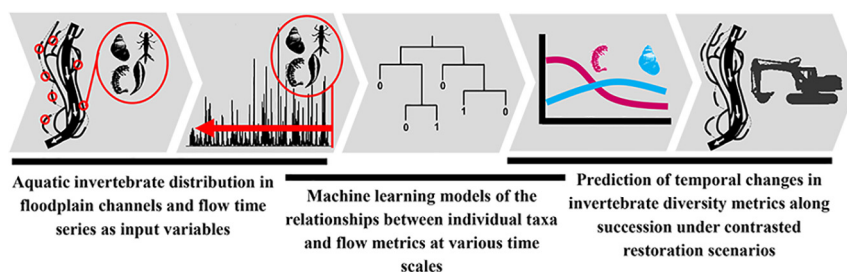
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HIGHLIGHTS

- Backflow and overflow connections are meaningful in floodplain diversity models.
- The occurrence of zoobenthic taxa is related to the duration of these flow processes.
- Stacked models can simulate diversity changes along floodplain channel succession.
- The models predict diversity changes under contrasted reconnection scenarios.
- This approach can improve decision-making in floodplain restoration.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 26 June 2020

Received in revised form 25 August 2020

Accepted 28 August 2020

Available online 6 September 2020

Editor: Sergi Sabater

Keywords:

Floodplain

Alpha-diversity

Machine learning

Lateral connectivity

Ecological succession

Invertebrates

ABSTRACT

The high biotic diversity supported by floodplains is ruled by the interplay of geomorphic and hydrological processes at various time scales, from daily fluctuations to decennial successions. Because understanding such processes is a key question in river restoration, we attempted to model changes in taxonomic richness in an assemblage of 58 macroinvertebrate taxa (21 gastropoda and 37 ephemeroptera, plecoptera and trichoptera, EPT) along two successional sequences typical for former braided channels. Individual models relating the occurrence of taxa to overflow and backflow durations were developed from field measurements in 19 floodplain channels of the Rhône floodplain (France) monitored over 10 years. The models were combined to simulate diversity changes along a progressive alluviation and disconnection sequence after the reconnection with the main river of a previously isolated channel. Two scenarios were considered: (i) an upstream + downstream reconnection creating a lotic channel, (ii) a downstream reconnection creating a semi-lotic channel. Reconnection led to a direct increase in invertebrate richness (on average $\times 2.5$). However, taxonomical richness showed a constant decrease as isolation progressed and reached an average of 2 for EPT and 7 for gastropods at the end of the scenarios. With more than 80% of the taxonomic models with an AUC equal or higher than 0.7 and slopes of linear relations between observed and predicted richness of 0.75 (gastropods) and 1 (EPT), the Boosted Regression Trees (BRT) provided a good basis for prediction of species assemblages. These models can be used to quantify a priori the sustainability and ecological efficiency of restoration actions and help floodplain restoration planning and management.

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1. Introduction

Large river floodplains are dynamic systems supporting a diversity of habitat conditions and associated communities dependent upon unique hydrological and geomorphological processes (Amoros and Petts, 1993; Rolls et al., 2018; Thorp et al., 2006). Variations in these processes act over multiple spatial and temporal scales and shape the spatial patterns of floodplain biodiversity (Amoros and Bornette, 2002; Ward et al., 1999). The lateral hydrological connectivity (LHC), i.e. the surface bidirectional water-mediated exchanges of water, matter (e.g. sediment, organic matter, nutrients) and organisms between the river channel and floodplain habitats (Arscott et al., 2005; Keruzoré et al., 2013; Paillex et al., 2015; Goździewska et al., 2016; Wohl, 2017; Liu and Wang, 2018), although essential for riverine ecosystem function and diversity, has been severely affected by man-induced river modifications worldwide. LHC is currently a primary target in floodplain habitat restorations, especially regarding floodplain channel restoration (e.g. Amoros, 2001; Amoros and Bornette, 2002; Tockner et al., 2008; Lamouroux et al., 2015; Lemke et al., 2017).

Because of its dynamic nature and temporal fluctuations, the measurement of LHC for floodplain water bodies and the assessment of its effects upon biotic diversity are not straightforward. Two approaches have been employed: (i) direct measurements based upon hydrological variables such as the duration, frequency or intensity of surface connections between the river and the floodplain channels (Bogan et al., 2013; Fournier et al., 2015; Rader et al., 2008; Richter and Richter, 2000; Riquier et al., 2015, 2017; Warfe et al., 2014), (ii) indirect assessments based upon environmental characteristics of the floodplain channels, such as the amount of hydrophytic vegetation or the organic matter content of the sediment, considered as proxy integrating effects of LHC, especially the shear stress developed during connection phases (Arscott et al., 2005; Besacier-Monbertrand et al., 2010; Gallardo et al., 2014; Paillex et al., 2007, 2013). The LHC metric developed under the latter approach was shown to be in good accordance with hydrological metrics in the case of the Rhône floodplain (Riquier, 2015; Riquier et al., 2015) and to provide a suitable explanatory variable for several invertebrate metrics. However, the indirect approach using surrogate environmental variables can be seen as relying on some variables of only local significance (e.g. water electrical conductivity or the diversity of sediment grain size might be highly catchment

dependent). From an applied point of view, the surrogate variables or their combination might also be difficult to use practically to guide restoration actions when decisions about discharges and water levels are needed.

Another aspect of LHC that renders its assessment complex is the fact that the surface connection between the river and floodplain water bodies encompasses at least two hydrological processes that occur during the rising limb of discharge and are best visualised in the case of floodplain channels that are disconnected upstream from the river, but preserve a permanent downstream connection (Fig. 1, stage B). The first one is the downstream connection that creates an entry of river water, suspended solids and biological propagules that are transported upstream in the floodplain channel (Riquier et al., 2015, 2017). This process has usually no scouring effect and is prone to enhance fine sediment deposition in the downstream parts of floodplain channels. We call this process “backflow” hereafter. Backflow does not take place in permanently flowing floodplain channels that are connected upstream with the river. The second process starts when the river stage in the main channel exceeds the altitude of the upstream alluvial plug of the floodplain channel. This upstream connection, called “upstream overflow” hereafter, is usually associated with increased shear stress, the enhancement of scouring and coarser sediment erosion and deposition. As in backflow, suspended solids and organisms can also be transported from the river into the floodplain channel, but also exported from it (Amoros and Petts, 1993). Consideration of these two processes (i.e. downstream backflow vs. upstream overflow) and of their relative importance in individual floodplain water bodies has, to our knowledge, never been taken into account in floodplain biodiversity assessments and models. However, one can hypothesize that at a floodplain scale, the range of backflow vs. upstream overflow relative importance might be a key driver of the spatial diversity of the biota. On a temporal scale, the sequence of disconnection and terrestrialization of a floodplain channel can also be seen as a transition from an upstream overflow dominated (stage A, Fig. 1) to a backflow dominated system (stage B, Fig. 1). Ultimately, floodplain channel restoration actions can be directed to modify the temporal and spatial distribution of the two processes through controls over the river discharge, the depth of dredged water bodies and the elevation of alluvial plugs (Riquier et al., 2017; Ward and Stanford, 1995).

The aim of this paper is to investigate how combinations of explanatory hydrological variables describing both overflow and

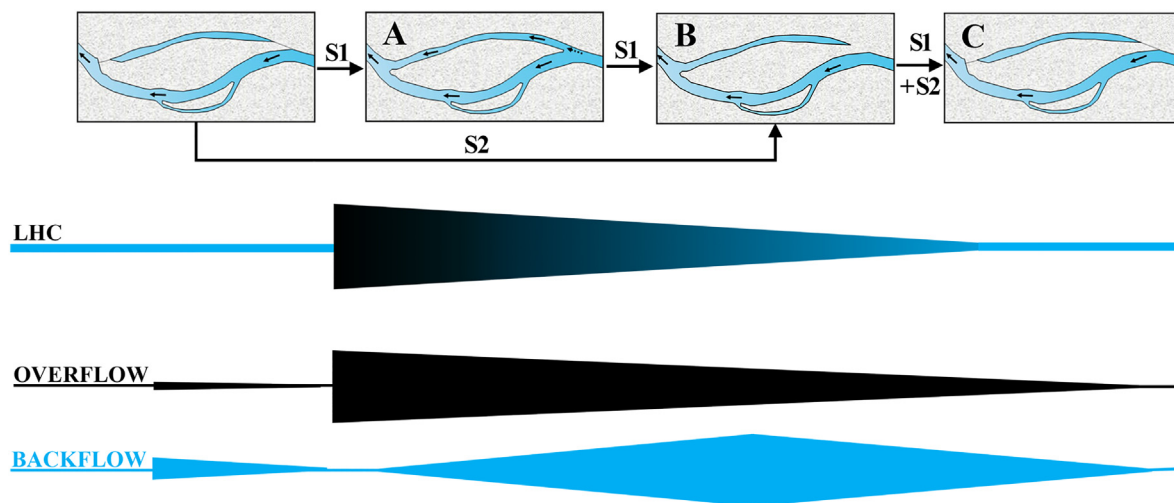


Fig. 1. Two scenarios S1 and S2 of floodplain channel succession: A – Upstream overflow dominated channel (fully connected, essentially lotic; eutotamon); B – Backflow dominated channel (semi-connected, semi-lotic; parapotamon); C – Progressive disconnection of the floodplain channel (isolated, predominantly lentic; plesiopotamon). The color gradient refers to the relative importance of the two flow processes: overflow (black) and backflow (blue) connections in the lateral hydrological connectivity (LHC). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

backflow processes can be used to predict changes in macroinvertebrate diversity along successional sequences in floodplain channels. This study is relevant to current questions regarding river-floodplain restorations where a dearth of precise guidelines relating hydrological controls and biodiversity changes exists (Booth and Loheide, 2012; Lamouroux et al., 2015; Olden et al., 2014; Palmer and Ruhli, 2019; Reckendorfer et al., 2006; Richter and Richter, 2000; Rolls et al., 2018). We combined (i) data generated by the monitoring of aquatic macroinvertebrates in the Rhône floodplain under restoration (Castella et al., 2015; Lamouroux and Olivier, 2015; Paillex et al., 2009); (ii) models quantifying backflow, upstream overflow and sedimentation metrics for floodplain channels in the same sites (Dépret et al., 2017; Riquier et al., 2015, 2017) and (iii) Boosted Regression Trees (hereafter, BRT), that are flexible modelling techniques accounting for dependencies among explanatory variables (Elith et al., 2008; James et al., 2013; Ridgeway, 2006).

We simulated two successional scenarios in three floodplain channels similar to those described for the French upper Rhône in Bravard et al. (1986) and Amoros et al. (1987a, 1987b). The changes in upstream overflow and backflow durations along the succession were used to predict changes in invertebrate diversity metrics through time. The two scenarios incorporated a reconnection with the main river channel that could be caused either naturally by flood scouring or by restoration, as actually carried for the Rhône (Lamouroux and Olivier, 2015).

Two metrics were used as dependent variables reflecting macroinvertebrate diversity: (i) the taxonomic richness of ephemeroptera, plecoptera and trichoptera (EPT) known to increase with lotic conditions, high hydrological connectivity and water quality, especially oxygenation (Dolédéc et al., 2007; Gallardo et al., 2014; Mérigoux et al., 2009) and (ii) the taxonomic richness of aquatic gastropoda known to increase with disconnection and late successional stages in floodplain waterbodies (Jurkiewicz-Karnkowska and Karnkowski, 2013; Reckendorfer et al., 2006). Time series for the two invertebrate

metrics were calculated from species occurrence data predicted by BRT that used upstream overflow and backflow time series as inputs. We expected EPT and gastropod richness to respond differentially to changes in LHC (Gallardo et al., 2014; Paillex et al., 2007). For the ecological reasons given above, EPT richness is expected to increase with upstream overflow connection (Paillex et al., 2009). On the contrary, gastropod richness is expected to increase with upstream disconnection and the dominance of backflow (Obolowski et al., 2015; Reckendorfer et al., 2006; Tockner et al., 1999). Field observations derived from monitoring channels of known cut-off age, hydrologic regime and sedimentation rate in the Rhône floodplain (Castella et al., 2015; Dépret et al., 2017; Džubáková et al., 2015; Riquier et al., 2015, 2017) were used to validate the richness metrics derived from BRT models in a synchronic approach (Amoros et al., 1987b).

Our study seeks to develop models of alpha diversity changes in single floodplain channels under natural or man-induced modifications. It is anticipated that such models could be ultimately combined to anticipate beta diversity changes at the scale of entire floodplains.

2. Material and methods

2.1. Sites

Data were collected between 2006 and 2016 in two adjacent reaches of the French upper Rhône River (sectors of Belley [BELL] and Brégnier-Cordon [BREG], Fig. 2) as part of the long-term monitoring of the river restoration (Lamouroux and Olivier, 2015). Nineteen floodplain channels were sampled, covering the full array of lateral hydrological connectivity, from channels completely and permanently connected at both ends to the main river, to channels fully disconnected at average water level. Some of these channels were restored through dredging and/or reconnection to the river in 2005 (BELL) and 2006 (BREG; Appendix A).

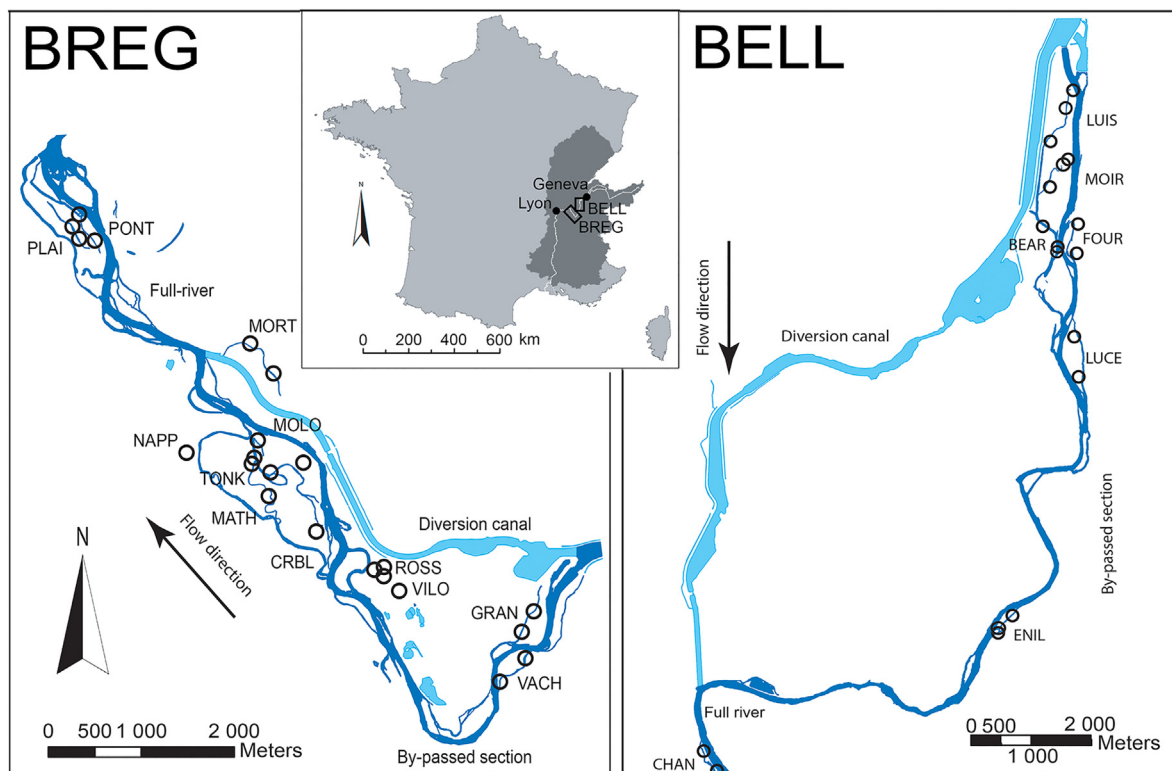


Fig. 2. The Rhône River and the study reaches: location in France and the two reaches Belley (BELL) and Brégnier-Cordon (BREG) showing the studied channels and sampling sites (circles). The light-blue stretch is the diversion canal and other artificial water bodies, and the dark-blue one the regulated bypassed section and the full river. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Macroinvertebrate data

In most floodplain channels, zoobenthic assemblages were sampled in two sites (upstream and downstream portions of the channel). In two channels, sampling was limited to one site, and extended to three in four others (Appendix A). In each site, three samples were randomly distributed along a 30 m stretch. In lentic conditions, macroinvertebrates were sampled within a 0.5 × 0.5 m metal frame with a hand net (mesh size 500 μ). Aquatic macrophytes and the sediment surface (i.e. litter) were covered. In lotic conditions, the same surface area was sampled with the same net in a kick-sampling approach to cover the mineral substrate, as well as debris and macrophytes when present. The material collected was fixed in ethanol and sorted in the laboratory. Benthic invertebrates were identified to species or genus when possible. Diptera were identified to family. Sampling was repeated in spring (March–April) and summer (June–July). Sampling was carried out every two years for both sectors (starting years: 2007 for BELL and 2008 for BREG). The BELL sector was additionally sampled in 2012 and 2016. A total of 1347 samples was used and all analyses used the sum of the three samples collected in a given site on the same date, as unit for modelling.

2.3. Hydrological data

For each floodplain channel, the river discharge threshold, for which overflow (Fig. 3; Q_{up}) and backflow (Fig. 3; Q_{down}) connections are initiated, were estimated combining field observations, topographic field measurements (DGPS), stage–discharge relationships for the more connected floodplain channels (as described in Riquier et al., 2015) and a raster-based method developed on an airborne LiDAR DEM covering the floodplain for the more isolated channels (as described in Džubáková et al., 2015). For each floodplain channel, we quantified overflow and backflow (O and B; Fig. 3) durations in days for a range of time periods prior to each invertebrate sampling event. Seven periods were calculated, ranging from 1 month to 1 year (Fig. 3). The shorter durations took rapid hydrological events into account (e.g. flood disturbance by upstream overflow connection). The longest (1 year) was set to cover the longest larval stage duration known in the taxa found. Longer time periods (> 1 year) were not considered in this study.

Backflow and overflow connection durations were separately calculated using the hydrostats package (Bond, 2015) within the R statistical environment (R Development Core Team, 2016) according to the hourly discharge time series recorded in the bypassed sections and the full-river from 2006 to 2016 and provided by the *Compagnie Nationale du*

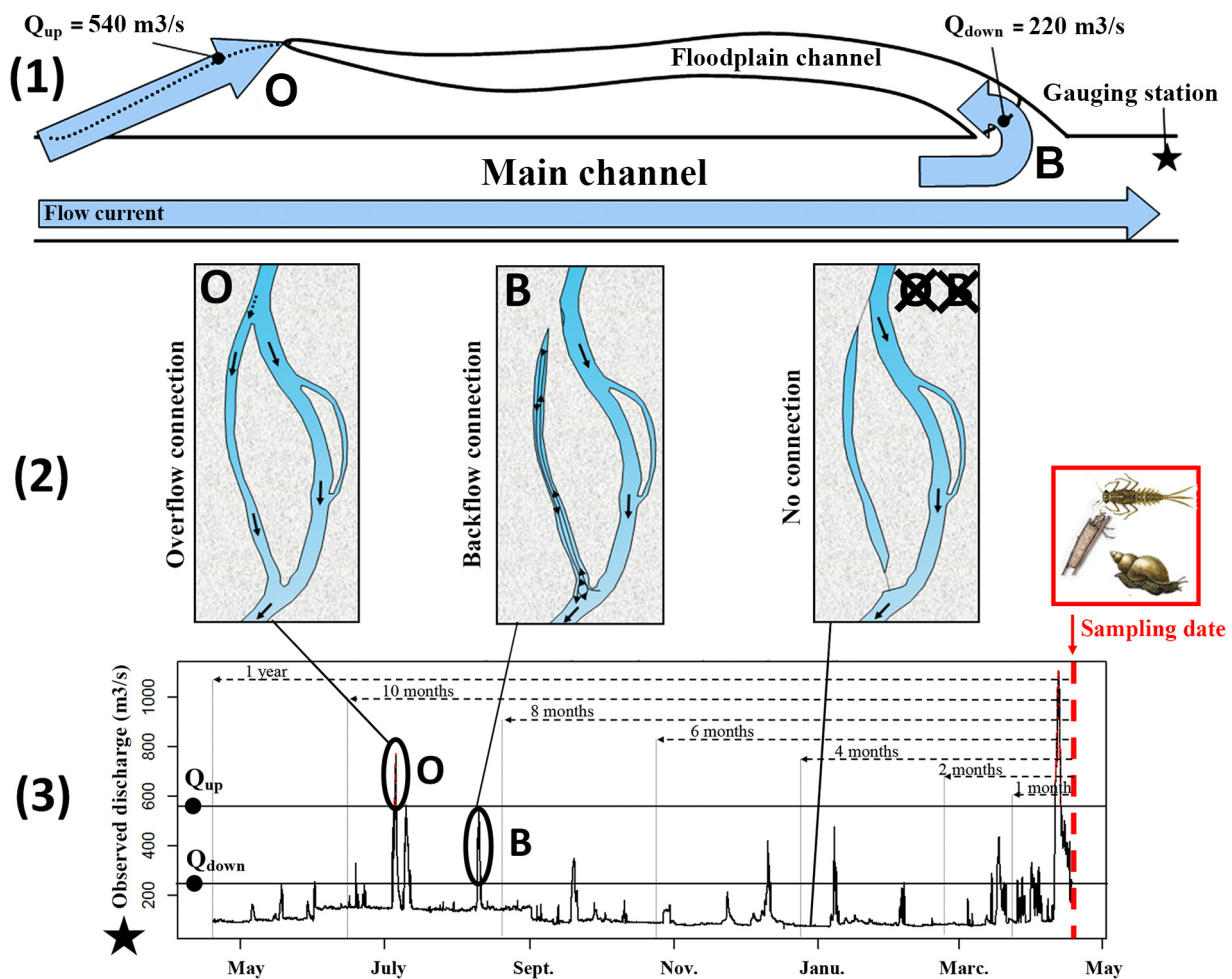


Fig. 3. Illustration of the approach used in the calculation of backflow (B) and upstream overflow (O) connection durations. (1) The two processes illustrated for a semi-connected channel (parapatamon), (2) the three flow conditions (O denotes the absence of connection) that occur in the floodplain–channel according to (3) the hourly discharge time series recorded in the main channel at a gauging station. Overflow (O) and backflow (B) connection durations were calculated for different time periods from one month to one year (dashed arrows) before the invertebrate sampling date (in red). Q_{up} : upstream overflow connection threshold, Q_{down} : backflow connection threshold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Rhône (CNR). The 14 hydrological variables (2 flow processes x 7 durations) were used as predictors in species distribution modelling.

2.4. Scenarios of lateral connectivity changes and channel succession according to floodplain channel development

In scenario 1, a disconnected floodplain channel is fully (i.e. upstream and downstream) reconnected to the river. As a consequence, an overflow-dominated period begins, during which the progressive build-up of an upstream alluvial plug starts. It leads to the upstream disconnection of the channel after 22 years. After 40 years, the backflow influence supersedes upstream overflow and the build-up of a downstream alluvial plug leads to the total disconnection of the channel 260 years after the initial reconnection (Fig. 1).

In scenario 2, a disconnected floodplain channel is reconnected to the river, but only downstream. The dominant backflow processes initiated by the reconnection lead to a progressive build-up of a downstream alluvial plug through fine sediment accumulation. The duration and frequency of flooding events overflowing into the channel are maintained and remain constant along the scenario. Two variants of this scenario were computed from real field examples used as starting points. The variants did not differ in the duration of the backflow-dominated period (≈ 20 years, duration of stage B; Fig. 1), but in the duration until full disconnection (160 vs. 105 years, duration of stage C; Fig. 1).

In both scenarios, variations in overflow and backflow durations along the succession were based upon literature data for the Rhône River concerning sedimentation rates i.e. build-up of alluvial plugs (Amoros et al., 1987a, 1987b; Bravard et al., 1986; Riquier et al., 2017). For scenario 1, we considered a “theoretical” channel for which the duration of each succession phases were set up following Amoros et al. (1987a). In scenario 2, we retained the MOLO and PONT channels covered in Riquier et al. (2017) and differing in sedimentation rates. The main geomorphological and hydrological features of the two channels are described in Table 1.

2.5. Upstream plug aggradation (Scenario 1)

The upstream part of lotic braided floodplain channels is usually gradually blocked by the formation of a plug bar made of coarse sediment (Constantine et al., 2010; Van Denderen et al., 2019a, 2019b). The upstream plug subsequently consolidates through vegetation encroachment that enhances finer sedimentation (Amoros and Bornette, 2002; Piégay et al., 2002). We did not find precise rates of upstream plug aggradation in fluvial systems like the Rhône. However, we estimated the process could be relatively fast (i.e. 10–100 years; Bravard et al., 1986) and considered it follows a logistic curve.

Table 1

Main geomorphological and hydrological features of the two channels used as starting points in the succession scenario 2 [adapted from Riquier et al., 2017]. For upstream connection duration, averages are associated with the min-max range in brackets.

Channel	MOLO	PONT
Length (km)	1.7	0.7
Connection type	Semi-connected (stage B ^a)	Semi-connected (stage B ^a)
Upstream overflow threshold Q_{up} ($m^3 \cdot s^{-1}$)	560	1266
Average upstream overflow duration (days yr^{-1})	3.2 (range 0–14)	1.7 (range 0–4)
Average number of upstream overflow events ($nb \cdot yr^{-1}$)	5.1 (range 0–10)	1.8 (range 0–4)
Average fine sedimentation rate ($cm \cdot yr^{-1}$) ten years after restoration	9.4 (range 7.2–12.2)	10.9 (range 6.5–15.7)
Location	BREG/Bypassed section	BREG/Full river section

^a The letters correspond to the floodplain stage described in Fig. 1.

The termination of stage A (Fig. 1) was estimated when the maximum annual duration of upstream overflow connection for 10 consecutive years fell below 365 days/year. This was obtained after 23 years in scenario 1. This estimate is in agreement with in situ observations. Indeed, the first upstream disconnection in restored channels of the Upper-Rhône was observed 15 years after full reconnection (ENIL channel, BELL sector; Fig. 2).

2.6. Fine sediment infilling, downstream plug accretion and lifespans (Scenario 1 & 2)

Once disconnected at their upstream entrance, floodplain channels are progressively filled with fine sediment. Then, inputs and accumulation rates of fine sediments and the occurrence of scouring phases gradually decrease as the channels close off following the elevation of bed level and the establishment of a downstream plug (Riquier et al., 2017; Van Denderen et al., 2019a, 2019b).

In our simulations, the progressive infilling of the channel (stage B and C; Fig. 1), i.e. the downstream closure of the channels followed by their transition to an isolated temporary pool until complete terrestrialization, was estimated using the trend models proposed by Riquier et al. (2017). These models link channel-averaged values of fine sediment thickness (derived from in-situ measures repeated every 10 m along the channel centerline, hereafter local measures) to time since restoration using two alternative parametric equations, either with a power or an exponential term (see Eqs. (1) and (2) in Appendix B). The two equations were estimated following two modelling approaches: (i) a channel-based one (conventional approach), with the two regression coefficients fitted independently for each channel or (ii) using NonLinear Mixed-Effect models, with a first general and fixed rate parameter (β) that reflects the constant decay rate shared by all modelled channels, and a shape parameter (α), considered as a random component exclusive for each channel. Based on in-situ measures of sediment thickness, we considered both models (i) and (ii) as representative trajectories of infilling and downstream plug accretion for the two floodplain channels considered by the present study (Table 1). For Scenario 2, channels were considered terrestrialized once the extrapolated average sedimentation thickness reached the initial average water depth of the channel. For the first scenario, downstream plug accretion was described by a logarithmic shape (until $Q_{up} = 1406 m^3/s$), as the most comparable to those of the Scenario 2.

MOLO and PONT channels (Scenario 2) showed high fine sedimentation rates and a very low scouring capacity in comparison to other restored floodplain channels of the Rhône River. For each of them, six field surveys were conducted in the ten years following restoration (on average every two years from 2006 to 2016). A survey consisted of local measures (25 and 19 points for MOLO and PONT, respectively) of water depth and fine sediment thickness [see Section 2.2 of Riquier et al., 2017 for further details]. The evolution of sediment thickness in PONT and MOLO was estimated following a power equation [the most realistic for this type of floodplain channel; see Section 4.3 of Riquier et al., 2017] of the two models (Eq. (1), Appendix B). We used local values of fine sediment thickness and initial water depths instead of channel-averaged ones to account for longitudinal variability of water depth within the two channels. For the first approach (i), regression coefficients were estimated individually for each local measure of fine sediment thickness (individual point-based models) using the `nlminb` function of the Stats package (R Development Core Team, 2016). Regarding (ii) the NLME model, which allows inclusion of fixed and random effects in the regression, we considered the β parameter as a fixed parameter shared by all local measures performed in MOLO and PONT channels (i.e. reflecting a constant decay rate shared by all modelled local station), whereas the α parameter was allowed to vary across local measures. This model was fitted by maximum likelihood with the `nlme`

function of the package nlme (R Development Core Team, 2016). The main parameters used to estimate the potential persistence of floodplain channels as aquatic habitats and their range of values are summarized in Table 2. This approach allowed us to refine their potential life span estimates. Specifically, using local values of sedimentation rate allowed us (i) to obtain more representative trends for the elevation of downstream alluvial plugs and (ii) to consider floodplain channels could persist as isolated pools for a longer time than using channel-averaged sedimentation values. It must be noted, such models did not consider potential changes in floodplain channel - main channel interactions that could substantially affect sedimentation rates and the potential life span of the channels [e.g. base level variations due to main channel incision/aggradation or contraction/expansion; Piégay et al., 2008; Piégay et al., 2000 and Riquier et al., 2017].

The termination of stage B (Fig. 1) was estimated when the maximum annual duration of backflow connection for 10 consecutive years did not exceed 350 days/year. These estimates are derived from model extrapolation in the case of scenario 2. The downstream disconnection was obtained after 69 and 20 years in scenario 1 and 2 respectively. Regarding scenario 2, these estimates were consistent with field observations. The first events of downstream disconnections were observed 12 years after downstream reconnection in both MOLO and PONT. To estimate the life span of channels as aquatic habitats (termination of stage C; scenario 2; Fig. 1), we considered the initial local channel depths using (i) the average discharge and (ii) the discharge exceeded three months a year (Table 2). The latter corresponds to the minimum hydroperiod necessary to consider the isolated channel as temporary, below this threshold the isolated channel was considered as terrestrial (Amoros et al., 1987b). These two channels were considered terrestrialized once all the extrapolated local sediment thickness, derived from the NLME models or the conventional ones, reached the initial local water depth of the channel (Table 2).

Finally, regardless estimated life span of the channels (scenario 1), we stopped our simulations when Q_{down} reached Q_{up} . In this way, we estimated the channel in scenario 1 could persist for several centuries and the simulation was stopped 259 years after reconnection. For MOLO and PONT (scenario 2), we estimated their life span could range between 72 (water level for the average discharge) and 88 years (water level for the discharge exceeded three months a year) and between 44 and 55 years, respectively, when considering the NLME model. These estimated ranges reached 141–187 years and 106–145 years, respectively, when using the channel-based models. For PONT and MOLO, the simulations were stopped 180 years and 125 years after reconnection, respectively. This approach allowed us to refine their potential life span estimates. For instance, the life span of MOLO and PONT in scenario 2 was estimated from two to three decades for MOLO and PONT by Riquier et al. (2017). Specifically, using local values of sedimentation rate allowed us (i) to obtain more representative trends for the elevation of downstream alluvial plugs and (ii) to consider floodplain channels could persist as isolated pools for a longer time than using channel-averaged sedimentation values.

2.7. Estimation of connection discharge thresholds (Scenario 1 & 2)

Upper values for upstream and downstream connection discharges were set to 1400 m³/s and 1100 m³/s, respectively in the

first scenario. These thresholds were the maximum values recorded by Džubáková et al. (2015) for the most disconnected, but still permanent, channel in the studied sectors (VILO, BREG sector; Fig. 2 and Appendix A). In scenario 1, upstream connection thresholds were estimated between the minimal flow and 1406 m³/s, downstream ones between the minimal flow and 1100 m³/s. In scenario 2, upstream connection thresholds were estimated at 560 m³/s (Q_{up}) for MOLO and 1266 m³/s (Q_{up}) for PONT (Fig. 1). The downstream connection thresholds, related to the downstream plug accretion, were estimated from the minimal flow to 560 m³/s (Q_{up}) for MOLO and 1266 m³/s (Q_{up} ; Table 1) for PONT.

2.8. Statistical analysis

Gradient boosted regression trees (GBRT) are an ensemble machine learning technique that estimates the relationships between explanatory (here duration of flow connections) and response variables (here the occurrence of a taxa), based on tree averaging (Elith et al., 2008; Friedman, 2001). It showed good predictive performances compared to other methods (Elith et al., 2008; James et al., 2013) and has been applied in the context of rivers and floodplains (Feld et al., 2016; Fernandes et al., 2016; McMillan and Noe, 2017). Moreover, interactions between predictors can be taken into account (gbm library version 2.1.4; Ridgeway (2006)), further enhancing its predictive capacities (Elith et al., 2008). In our case, this allowed to account for potential interactions between overflow and backflow in semi-connected channels.

A Bernoulli distribution was used to build occurrence models for 58 taxa. Fifteen explanatory variables were used for all models: 14 hydrological predictors (2 flow processes x 7 time durations prior to invertebrate samplings) and a dummy seasonal factor (spring, summer). Four parameters can be set when running GBRT: the bagging fraction bf , the tree complexity tc , the learning rate lr . The following settings were chosen, based upon recommendations available in the literature (Elith et al., 2008; James et al., 2013; Mohan et al., 2011): $bf = 0.7$, $tc = 5$ and $lr = 0.001$. Smaller learning rates tend to result in better accuracy but require more iterations. The 58 "full" models predicted taxa occurrences twice a year (i.e. spring and summer) for the duration of each scenario.

Predicted occurrence probabilities were converted to binary presence/absence using the Kappa maximization threshold (Monserud and Leemans, 1992) calculated with the `optim.thresh` function (SDMTools version 1.1 in the R package; VanDerWal et al., 2014). Predicted species occurrences were assembled into a single dataset for calculation of the two diversity metrics (gastropod and EPT richness). The quality of the prediction was assessed by the area under the curve (AUC) (Powers and Ailab, 2011) and the contribution of the variables using their relative influence (Friedman, 2001).

Statistical analyses were conducted in the R statistical environment (version 1.1.423, R Development Core Team, 2016). We fitted GBRT using the `gbm` package (version 2.1.4, Ridgeway, 2006). We used the `ggplot2` package (Wickham, 2009) for all graphics. A nonparametric loess regression was displayed using the `loess` function (`span = 0.1` for scenario trends and 0.5 for other curves) in the `ggplot2` package (Wickham, 2009).

Table 2

Summary of the parameters used to estimate the sedimentation trajectories and associated potential life span of floodplain channels (Scenario 2).

Channel	Number of surveys between 2006 (restoration) and 2016	Non Linear Mixed-Effects model	Conventional models (individual point-based models)	Initial local water depth (in cm)	
		Min.-max. values of α /fixed value of β	Min.-max. values of α /min.-max. values of β	Mean (min./max.), average discharge	Mean (min./max.), discharge exceeded three months a year
MOLO	6	20.9–32.6/0.45	14.1–63.9/0.19–0.83	184.9 (148.0/227.3)	206.5 (169.6/248.9)
PONT	6	22.8–34.9/0.45	10.8–49.2/0.00–0.64	205.3 (170.3/231.9)	224.3 (189.3/250.9)

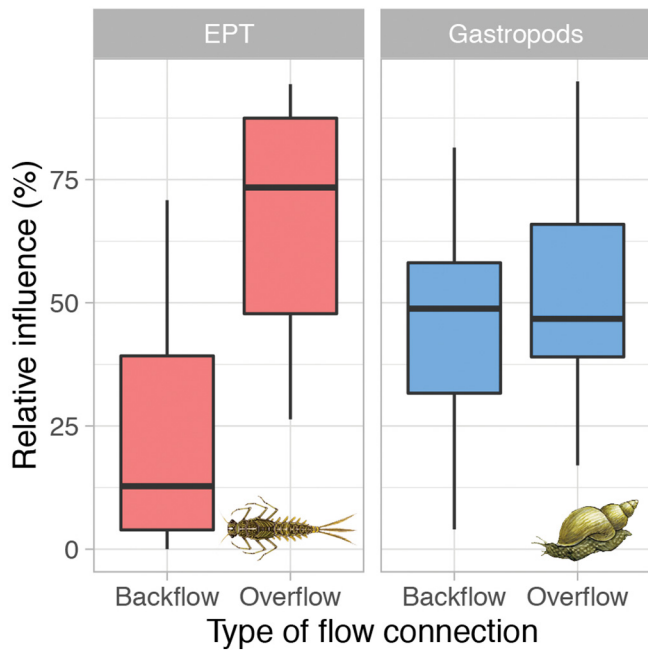


Fig. 4. Relative influences of backflow and upstream overflow predictors in the full GBRT models for EPT (37 models) and gastropods (21 models).

2.9. Calculation and validation of the predicted diversity metrics

To ensure the representativeness of predictions (Barnard et al., 2019; Zhang and Li, 2018), the full dataset was randomly split into calibration and testing sets (70% and 30% of the data, respectively) and each split was iterated 50 times (i.e. 50-folds cross validation) (Barnard et al., 2019; Scherrer et al., 2018; Zhang and Li, 2018).

For each iteration, we quantified the accuracy of the model predictions compared to the testing set at two levels: (i) for the taxa models with the calculation of the cross-validated area under-the-curve (Appendix C); and (ii) for the taxonomical richness by computing the slope, the intercept and the R-squared of the linear regression model of predicted versus observed values contained in the testing set. Following Jusup et al. (2009), the linear Hypothesis function from the car package (Fox and Weisberg, 2019) in R was used to compute Wald-test-based comparisons between a given model i.e. the linear relation of observed vs. predicted values, and the restricted equality model $y = x$.

In each scenario, because predictions were produced at each iteration, the random split procedure reported 50 different datasets that were subsequently averaged to provide a final occurrence prediction for each taxa. In order to reduce overestimation of species richness (Guisan and Rahbek, 2011; Jiménez-Valverde and Lobo, 2007), richness metrics were calculated for the predicted assemblages (i.e. the assemblage of predicted EPT and gastropod taxa) by summing the averaged predicted occurrences of taxa of the final dataset.

3. Results

3.1. Performance of the taxonomic models and contribution of the hydrological variables

The predictive performance of the taxonomic models was relatively high with an overall median cross-validated AUC of 0.81 and 81% of the species with AUC ≥ 0.7 . Only 4 EPT and 7 gastropod models had a lower performance (median AUC < 0.7 ; Appendix C). The EPT models showed upstream overflow having a higher relative contribution (median: 73.4%) than backflow (median 12.8%) (Fig. 4). In gastropods, the influences of backflow and overflow durations were more equilibrated with a slightly higher contribution of the former (median 48.8% for backflow versus 46.8% for overflow) (Fig. 4). The seasonal effect only had a marginal contribution of 7.8% and 1.4% (median values for EPT and gastropod, respectively).

However, in more than half of the gastropod models (11 out of 21), overflow durations had a higher contribution than backflow, while the overflow durations were the most influential in over three quarters of the EPT models (30 out of 37).

The comparison of the relative influence of different durations for calculation of antecedent connections revealed the dominance of the longest duration (Fig. 5). This was true both for backflow and overflow durations, where the connections calculated over the one-year period had approximately twice as much influence as all other time periods considered individually.

3.2. Changes in taxonomic richness under scenario 1

In the case of gastropods (Fig. 6), the full reconnection did increase richness in the short term (pre-reconnection richness average = 1.6 versus stage A-richness average = 3.3), but the stage A values remained within the pre-reconnection min-max range. The onset of upstream disconnection initiated a rapid richness increase that peaked at the middle

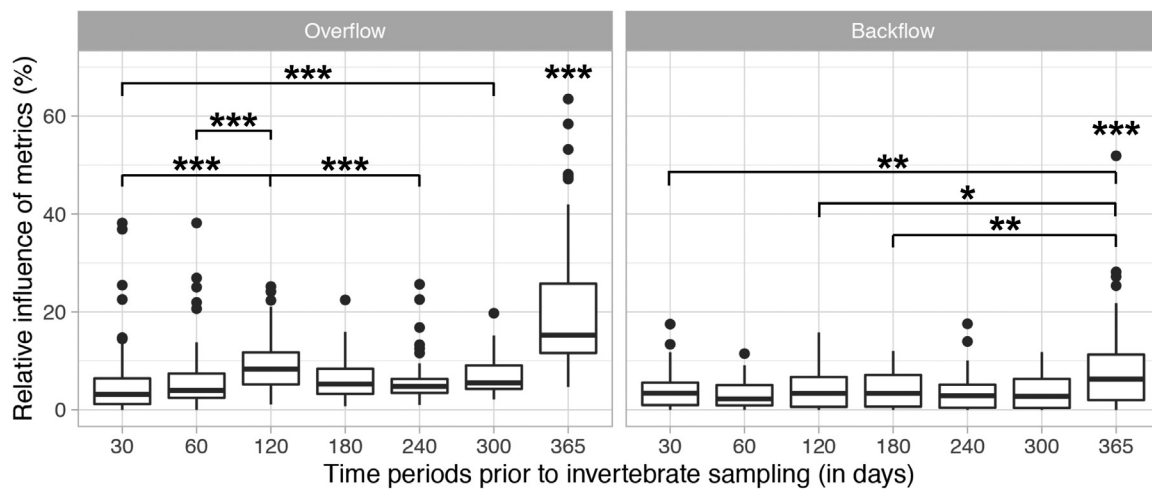


Fig. 5. Relative influence of the two predictors (durations of backflow and upstream overflow connections) in the 58 taxa models, for a range of durations (from one month to one year) prior to the invertebrate samplings. Significance of differences was tested using the Wilcoxon test (unpaired) ***, $P < 0.001$; **, $P < 0.05$ and *, $P < 0.1$. The time period “365” is statistically different from all other time periods with at least $P < 0.1$.

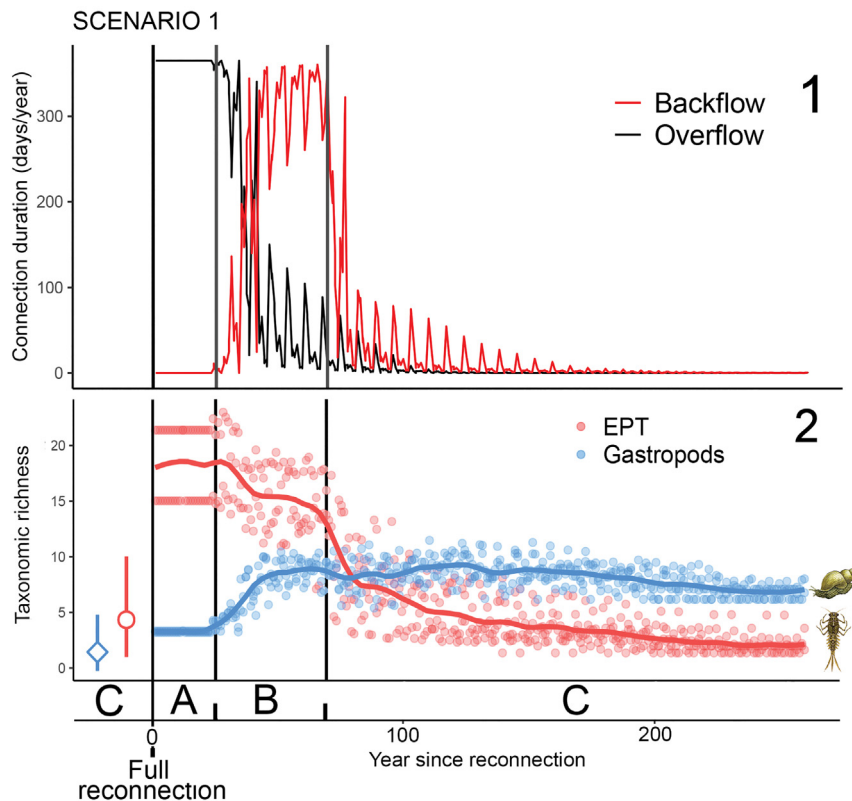


Fig. 6. Temporal succession in a floodplain channel following full reconnection with the river (Scenario 1). (1): backflow and upstream overflow duration used as predictors, (2): predicted EPT and gastropod richness. Trends are based on local regression fitting (LOESS, span = 0.1). In (2), pre-reconnection averages and min-max ranges are derived from observed values in ENIL AM, VACH AM and LUIS AM disconnected sites. Closed points on plot 2 are richness values predicted twice a year from the assembled 58 predicted taxa. A: upstream overflow dominated stage; B: backflow dominated stage and C: progressive disconnection of the channel. We stopped our simulations when Q_{down} reached Q_{up} .

of the disconnected stage (years 100–175, maximum richness 11.5 at year 110). It slowly decreased afterwards as isolation progressed.

In the case of EPT (Fig. 6), the full reconnection tripled the average richness in a short time (pre-reconnection richness average 4.3, stage A-richness average 18.5). EPT richness peaked during the semi-connected stage (years 25–40), especially at its very beginning (maximum richness 23 at year 28). The transition with the disconnected stage (after year 69) caused a decrease in EPT richness that dropped below the initial average richness after year 125.

The taxonomic succession heatmap (Appendix D) represents the occurrence probability of the 58 taxa averaged by decade. Along the succession, a clear switch at years 30–50 (stage B) was observed in the assemblage of taxa: a first group (before years 30–50; one third of the total assemblage) was dominated by EPT and a second group (after years 30–50; two thirds of the total assemblage) reflected a more balanced assemblage with gastropod and EPT taxa. Most of the earlier group prevailed during stage A and until the onset of stage B. Within the second group, a more gradual succession of species occurred through time. In addition, taxa were more persistent in time as shown by e.g. *Planorbis carinatus*, *Cloeon dipterum* and *Bi-thynia tentaculata* that had among the longer persistence times (≈ 200 years). The last species appearing along the succession were the gastropods *Anisus vorticulus* and *Acroloxus lacustris* that reached their highest occurrence probability during the 15th decade after reconnection (Appendix D).

3.3. Changes in taxonomic richness under scenario 2

In scenario 2, upstream overflow connection was kept constant to emphasize the effects of decreasing backflow duration along the progressive downstream isolation of the floodplain channels.

3.3.1. MOLO channel

In the case of gastropods, the downstream reconnection initiated a rapid increase in taxonomic richness (from 1 before reconnection to an average of 10 during stage A) that peaked during the semi-connected phase (years 0–20, maximum 10.9 at year 20, stage C). It slowly decreased afterwards as isolation progressed, until an average of 5.9 at year 180 (Fig. 7).

As in the first scenario, EPT richness peaked during the semi-connected phase (stage B at years 0–19, maximum 16 at year 4, 9 and 17) after a rapid post-reconnection increase from 0 to 1 to an average of 10.2. The transition with the disconnected stage C caused a constant decrease and a drop from an average of 9.9 at year 20 to 3.95 at year 180 (Fig. 7).

3.3.2. PONT channel

In the case of gastropods, the onset of downstream reconnection initiated an increase in taxonomic richness (from 6 before reconnection to an average of 10.6 during stage B) that peaked at the beginning of the semi-connected phase (years 20–40 of stage C, maximum 11.9 at year 32). It slowly decreased afterward as isolation progressed until an average of 6.8 at year 125 (Fig. 8).

In the case of EPT, after a rapid increase following the downstream reconnection (from an average of 1.5 before reconnection to 8.4 at the beginning of stage B), the richness peaked at the beginning of the disconnected phase (years 20–30 of stage C, maximum 11.6 at year 22). After year 30, the richness showed a constant decrease and reached 2.5 in average at year 125 (Fig. 8).

The scenario of progressive isolation following downstream reconnection applied to the cases of both PONT and MOLO channels, allowed an examination of the effects of the duration of backflow connection on the richness metrics, in the absence of variations in upstream overflow connection (Fig. 9). In both taxonomic groups and sites, the lowest

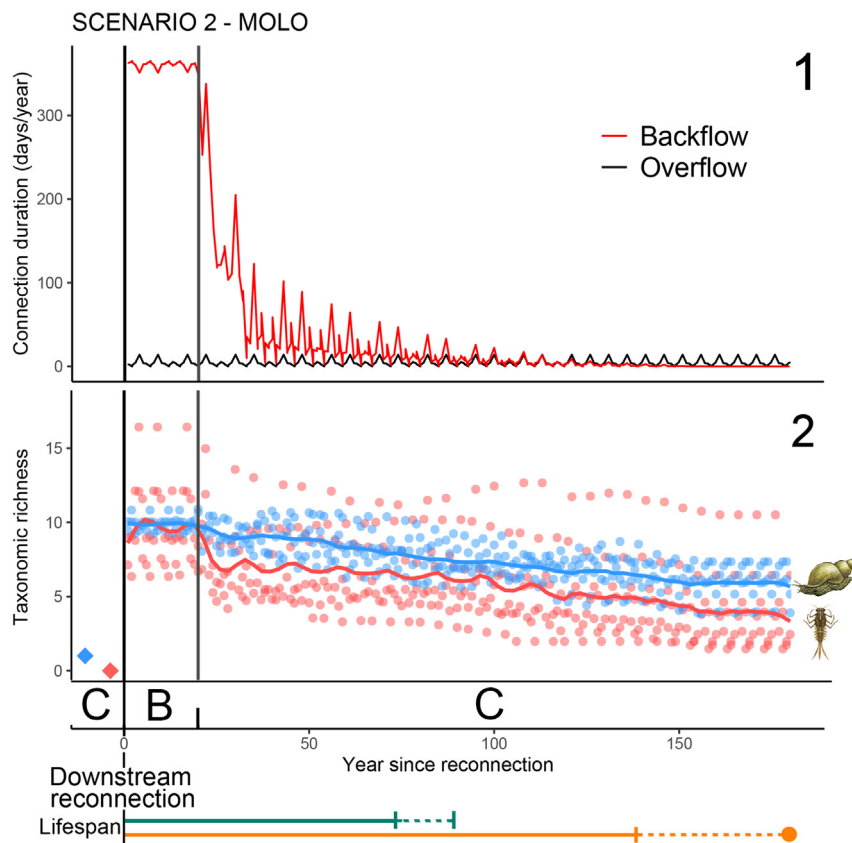


Fig. 7. Temporal succession in the MOLO floodplain channel following downstream reconnection with the river (Scenario 2): (1): backflow and upstream overflow duration used as predictors, (2): EPT and gastropod richness. Trends are based on local regression fitting (LOESS). Diamonds on the left part of plot 2 refer to the observed values before reconnection, used for comparison with the predicted values after reconnection. The circles on plot 2 are taxonomic richness predicted twice a year from the assembled dataset of the 58 predicted taxa. B: backflow dominated phase, C: progressive downstream disconnection of the channel. Estimated lifespan ranges of the aquatic phase (bottom lines) are indicated as dashed lines and calculated using average discharge in the main channel (first tick) and the discharge exceeded three months a year (second tick). The green line depicts estimates derived from the NLME models and the orange line those from channel-based ones (second tick out of simulation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

range of backflow duration (i.e. below 25 days/year) entailed a reduction of richness to its minimum level. Increasing backflow duration to its maximum lead to a constant increase in EPT richness in both channels. In the gastropods, the richness reached a maximum between 25 and 75 days/year of backflow duration, followed by a quasi-plateau (PONT) or a slight increase (MOLO) (Fig. 9).

3.4. Testing richness predictions

Richness predictions calculated from the assembled 58 taxa predicted with the GBRT models were compared with the observed data. Fig. 10 shows the scatter plots of the predicted vs. observed values for Gastropods (A) and EPT (B). The adjusted R^2 for the two metrics were 0.39 and 0.49 for gastropod and EPT richness, respectively (Table 3). The predictive power of the models was good for gastropods and EPT richness with a close agreement between predicted and observed values (Fig. 10 and Table 3). The identity between the predicted vs. observed linear relation and the identity line cannot be rejected in the case of EPT richness ($P > 0.05$; Table 3). However, the model showed a constant overestimation of around 2.6 taxa when compared with the observed EPT richness (Fig. 10 and Table 3). For gastropod richness, the overestimation decreased between 2.2 close to 0 as the observed richness increased (Fig. 10 and Table 3).

4. Discussion

The need for models of alternative scenarios applied to river restoration and for coupled restoration mechanisms acting both upon

floodplain habitats and water/sediment flows in the river itself was advocated by e.g. Richards et al. (2002); Amoros et al. (1987b) or Whipple and Viers (2019). The scenarios presented here couple changes in river fluxes and floodplain dynamics to demonstrate the possibility of modeling changes in lateral hydrological connectivity in a floodplain channel and their effects upon significant components of its macrobenthic biota i.e. EPT insects and gastropods. Such connectivity changes could be “natural”, as in the case of progressive upstream disconnection and subsequent terrestrialization, or man-induced through upstream reconnection, a common practice in floodplain channel restoration (Amoros, 2001; Lamouroux et al., 2015; Palmer et al., 2005; Roni et al., 2019; Wohl et al., 2015).

4.1. Upstream overflow and backflow as distinct components of lateral hydrological connectivity

Predictive models associating hydraulic, biotic and sometimes sedimentation components were already developed for terrestrial vegetation or habitat successions in floodplains (Baptist et al., 2004; Benjankar et al., 2011; De Jager et al., 2019; García-Arias et al., 2013; Loheide and Booth, 2011), most of the time with the aim of informing restoration and management decisions. However, similar models remain rare in the case of floodplain aquatic/semi-aquatic biota, where they are often conceptual (Bornette et al., 2008; Cabezas et al., 2008) or based upon surrogates for lateral hydrological connectivity (Castella et al., 2015; Paillex et al., 2007). Reckendorfer et al. (2006) modelled the distribution of aquatic molluscs in a Danubian floodplain as a function of the average number of days of upstream connection of the

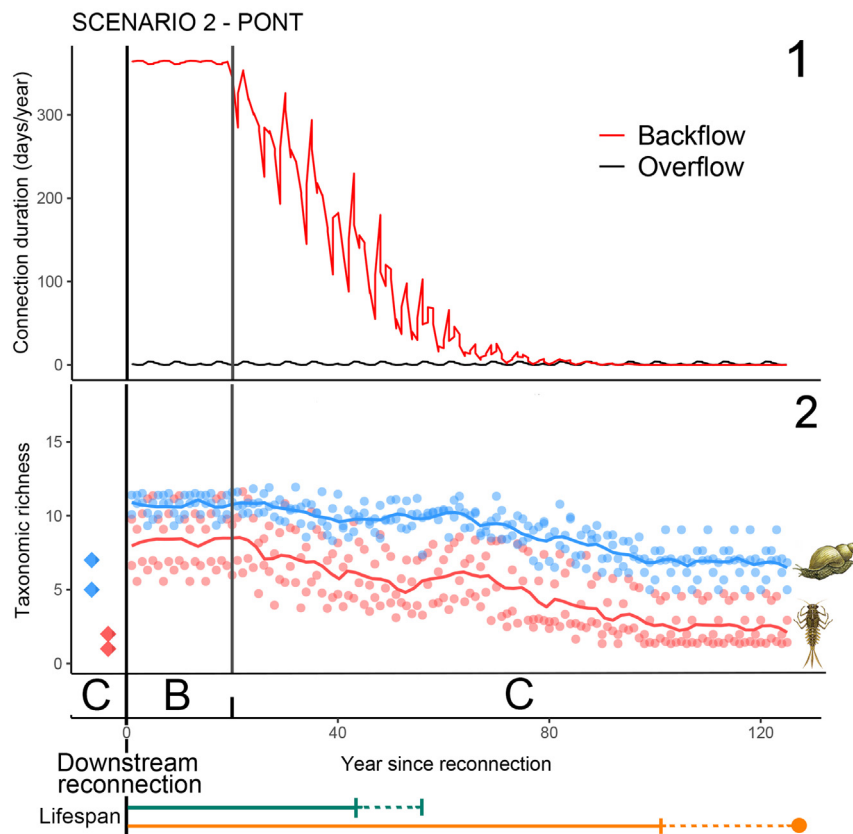


Fig. 8. Temporal succession in the PONT floodplain channel following downstream reconnection with the river (Scenario 2): (1): backflow and upstream overflow duration used as predictors, (2): EPT and gastropod richness. Trends are based on local regression fitting (LOESS). Diamonds on the left part of plot 2 refer to the observed values before reconnection, used for comparison with the predicted values after reconnection. The circles on plot 2 are taxonomic richness predicted twice a year from the assembled dataset of the 58 predicted taxa. B: backflow dominated phase, C: progressive downstream disconnection of the channel. Estimated lifespan ranges of the aquatic phase (bottom lines) are indicated as dashed lines and calculated using average discharge in the main channel (first tick) and the discharge exceeded three months a year (second tick). The green line depicts estimates derived from the NLME models and the orange line those from channel-based ones (second tick out of simulation). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

waterbodies with the main river, calculated over 30 years. In comparison, the models we propose offer potential improvements. They are based upon actual hydrological metrics (discharge connection thresholds and durations) instead of surrogates and allow therefore a more direct transfer to engineers in the planning, design and decision-making processes, e.g. in the case of floodplain restoration. Furthermore, beside the duration of upstream connection, our models incorporate downstream backflow as a predictor in invertebrate occurrence models. Amoros (2001) did highlight the importance of downstream backflow in river floodplain channel succession and restoration. To our knowledge, these two components of lateral hydrological connectivity have never been combined to model invertebrate occurrences in floodplain channels. Yet, downstream backflow is regarded as a key process in sedimentation dynamics and floodplain channel evolution, albeit complex to model (Citterio and Piégay, 2009; Constantine et al., 2010; Costigan and Gerken, 2016; Le Coz et al., 2010). We showed the duration of backflow was more influential in gastropod models than in EPT. It superseded overflow influence in almost the half of the species for this group. Indeed, backflow processes, that do not entail the same level of hydraulic constraints as upstream overflow, control the transport and deposition of fine suspended sediment in the downstream part of floodplain channels (e.g. Citterio and Piégay, 2009; Riquier et al., 2017). They are therefore likely to influence both the turbidity and nutrient content of the water, as well as the grain size and organic content of the sediment (Amoros, 2001). These are critical in the quantitative and qualitative development of submerged macrophytes that provide shelter from flow disturbances, egg-laying sites and a substrate for periphyton growing, which in turn, are highly influential for gastropod species

distribution (Brönmark, 1989; Costil and Clement, 1996; Wilson and Ricciardi, 2009).

4.2. Model validation and relevance for floodplain restoration and conservation

The total number of species modelled from the two zoobenthic groups combined was 58 out of the 67 species of EPT and gastropods known from the French upper Rhône River (unpublished data from the Rhône River restoration programme). With more than 80% of the taxonomic models with an AUC equal or higher than 0.7 and slopes of linear relations between observed and predicted richness of 0.75 (gastropods) and 1 (EPT), the GBRT provided a good basis for prediction of species assemblages. Expressed as a proportion of the total richness per group, the residuals were very similar between the two taxa (maximum residual/group richness = 0.63 in the EPT and 0.6 in the gastropods). The stacking of individual taxonomic models also enabled reconstruction of the succession of assemblages along the progressive isolation of the floodplain channel. The modelled assemblages proved equally coherent with existing synchronic descriptions of species assemblages in former channels of different age and lateral connectivity (Amoros and Petts, 1993; Castella et al., 1984; Foeckler, 1991; Jurkiewicz-Karnkowska and Karnkowski, 2013; Reckendorfer et al., 2006). However, the overprediction in species richness, approximately 2 units in the EPT case, is a known drawback of stacked species distribution models (Mateo et al., 2012) and should be accounted for. Stacked models are known to overestimate total richness in the case of taxa with low richness and to tend underestimate in the opposite case

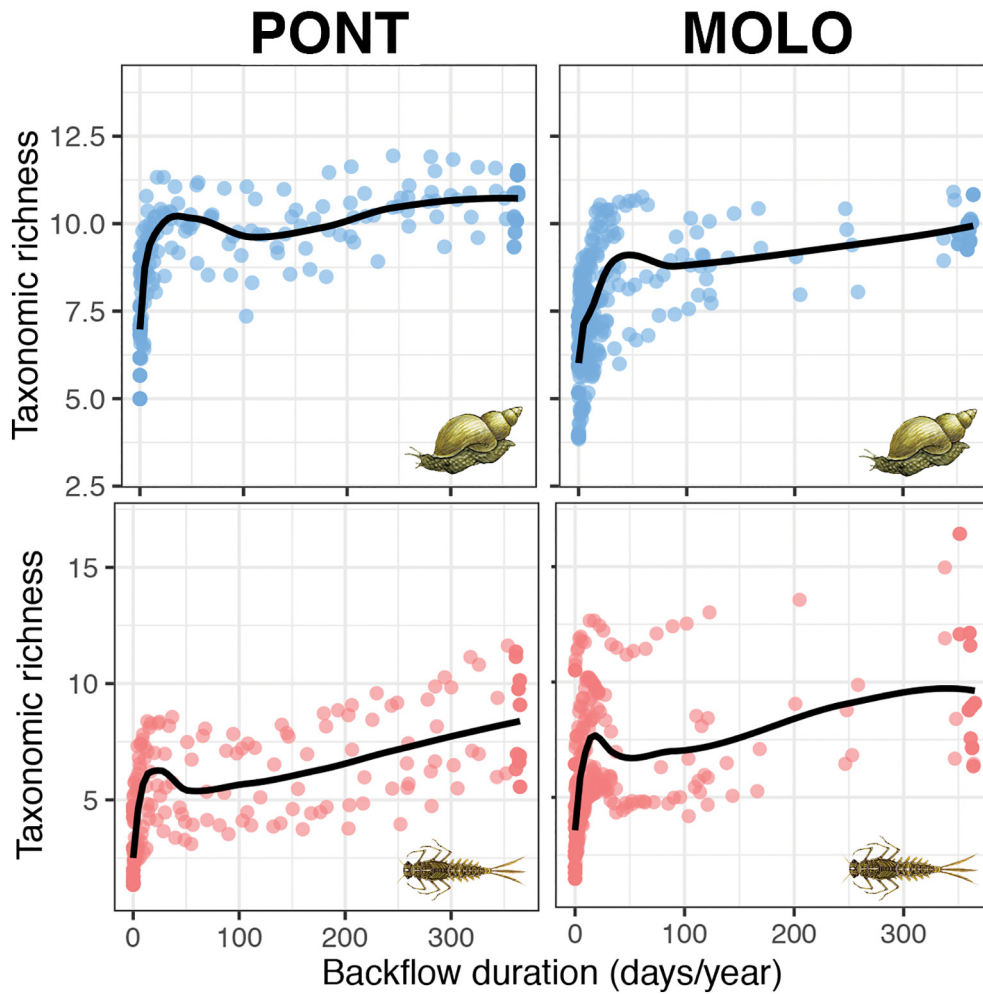


Fig. 9. Relations between the duration of backflow connection and the predicted Gastropod (top) and EPT richness (bottom) in the PONT and MOLO sites subjected to downstream reconnection followed by a progressive siltation and disconnection (Scenario 2). Trends are based on local regression fitting (LOESS).

(Calabrese et al., 2014). Such overprediction of taxonomic richness likely occurred because all sites are used at least once at some stage across the 50 iterations of the split-sampling procedure, and thus no observation remains fully independent for the final evaluation at the

assemblage level (Scherrer et al., 2018). The underestimation of the higher species richness in gastropods occurred likely because, overall, the AUC were less good in this taxa than for EPT, for which richness was constantly overestimated (Appendix C).

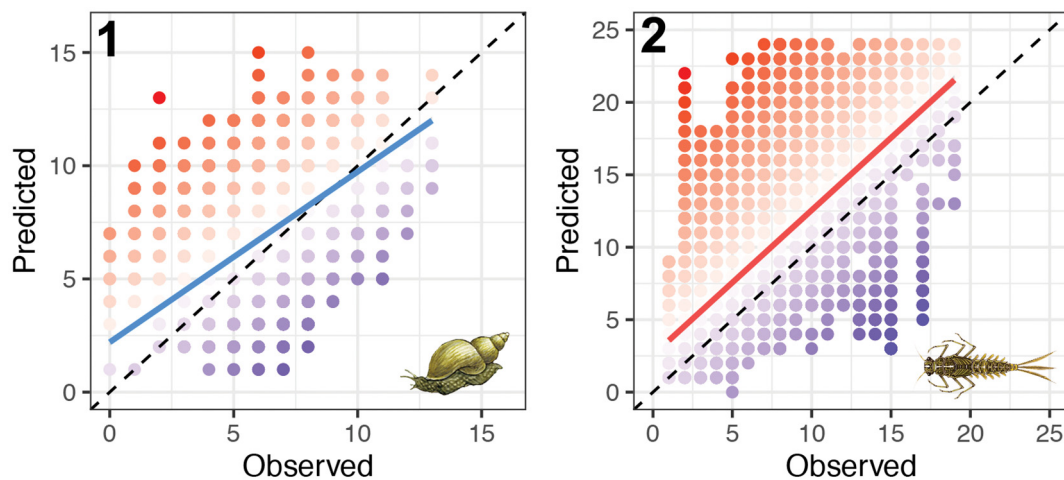


Fig. 10. Linear relationships (± 0.95 CI) between predicted (GBM models) and observed taxonomic richness (1: gastropods, 2: EPT insects). The dashed line is the identity line $y = x$. Colors identify negative (blue) and positive (red) residuals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Parameters of the linear regressions between observed and predicted taxonomical richness, with their respective standard errors in brackets. *P*-values are given for the test of the difference (Wald test) with the $y = x$ relation.

	R ²	Intercept	Slope	P-value
Gastropod richness	0.39	2.2 (±0.07)	0.75 (±0.01)	<0.001
EPT richness	0.49	2.57 (±0.1)	1. (±0.01)	0.93

From an ecological point of view, the trends predicted for both EPT and gastropod richness were coherent with previous knowledge about the distribution of these taxa along floodplain channel succession and lateral connectivity gradients (Gallardo et al., 2014; Paillex et al., 2007; Reckendorfer et al., 2006). In this respect, EPT richness increased with hydrological connectivity and gastropod richness peaked at periods of moderate to low hydrological connectivity. In scenario 1 (full reconnection), the predicted peak of gastropod richness obtained during a phase of decreasing overflow frequency is compatible with the estimate of maximal richness for this taxon at a connection frequency of one month/year produced by Reckendorfer et al. (2006).

We showed clear differences between the full reconnection and the downstream reconnection scenarios. The former induced a higher increase in EPT richness than the latter and a phase of maximum diversity (considering EPT and gastropods combined) during an intermediate phase of simultaneous high backflow influence (above 200 days/year) and decreasing, but still frequent overflow connections (between 25 and 100 days/year approximately). The downstream reconnection scenarios induced a lower EPT richness. In this case, the total richness (EPT plus gastropods) was maintained until the initiation of episodes of downstream disconnection that entailed a slow and constant decrease in both EPT and gastropod richness. Regarding gastropod richness, it should be underlined that aquatic species characteristics for late semi-aquatic successional stages (e.g. *Aplexa hypnorum*, *Anisus spirorbis*, *Planorbis planorbis*) were missing from the models because of their very low occurrence or absence from the Rhône floodplain dataset. When accounted for, such species could reduce the decrease rate of gastropod richness at late successional stages (Bogan et al., 2013; Jurkiewicz-Karnkowska and Karnkowski, 2013; Nicolet et al., 2004).

For these reasons, the proposed models can be of interest to inform decisions related to the type of reconnection to select for a floodplain channel (e.g. full vs. downstream-only), given local geomorphological, hydrological or technical constraints in a restoration project. The sedimentation rate in restored channels is a crucial issue bearing consequences upon the life duration of these habitats (Riquier et al., 2017) and the potential need to plan for recurring restoration operation. Variations in this controlling factor could be implemented in the models to test consequences in terms of invertebrate diversity. Equally, because the importance of disconnected water bodies for the maintenance of floodplain biodiversity and, more generally, the need to preserve abandonment processes was highlighted (Dufour et al., 2015; Schomaker and Wolter, 2011), the proposed models could be used to simulate progressive channel abandonment and the associated diversity trends; quantify a priori the sustainability and ecological efficiency of restoration actions and finally provide benchmarks to monitor restoration progress.

4.3. Development perspectives

Even though restoration of a single floodplain channel considered in isolation could be a practical objective (Henry et al., 2002), more often, as in the case of large river restoration projects (Lamouroux et al., 2015; Olden et al., 2014; Palmer et al., 2005; Pander et al., 2018; Schiemer et al., 1999), entire floodplain sectors encompassing an array of water bodies are tackled through multiple restoration actions such as discharge modifications, channel reconnections and deepening. It is

therefore anticipated to expand the principles used here to develop scenarios of alpha and beta diversity changes at the scale of floodplain sectors including a diversity of channel types and restoration procedures.

To this aim, several ways of improvement for the models presented here can be investigated. Concerning the hydromorphological part of the models, the results suggest that the investigation of longer temporal scales (>1 year) for flow connection durations might be worthy of investigation. Indeed, beyond the sole consideration of the life-cycle duration of invertebrates, high energy overflow events might have long-lasting consequences, e.g. upon the distribution of sediment and habitat patches within a given channel. In addition, there is a need to better account for the variability of processes occurring during upstream overflow connections, notably regarding magnitude of the flood flows. If associated with high shear stress, they impact the biota via physical scouring (Junk and Wantzen, 2004) that may dislodge individuals and bed material including macrophytes and sediments. But such upstream connection can occur with low shear stress, especially in the case of isolated sites away from the main channel and have the same effect as backflows. Therefore, the computation of critical shear stress for sediment motion is crucial to account for direct effects upon the biota and for the physical succession of floodplain channels (e.g. self-rejuvenation capacity). Integrating the potential effects of base level changes in relation to adjustments of the main channel geometry in the vicinity of floodplain channels also remains an important challenge. Finally, for a better applicability, there is also a need to improve the models of upstream and downstream plug accretions that proved to be critical as break points in the temporal changes of diversity metrics.

Regarding the taxonomic models, a primary objective could be the incorporation of further taxonomic groups (e.g. Crustaceans, Odonata, Heteroptera, Coleoptera) to account for potentially missing components of the benthic taxonomic and functional diversity. This raises the question of the modelling strategy [species vs. community modelling; Zurell et al., 2020] that currently does not incorporate potential interactions between taxa, an overlooked factor in benthic ecology (Holomuzki et al., 2010). This question is particularly relevant in large rivers and their floodplains, where current rates of introduction of exogenous species are high (Beisel et al., 2017; Besacier-Monbertrand et al., 2010) and the effects of such species in the local assemblages far from being unequivocal (Marescaux et al., 2016; Strayer, 2010). To the same extent, considerations related to the time taken by various taxa for recolonization of restored running waters (Lorenz et al., 2009) and the dispersal propensity of various taxa (Li et al., 2016) need to be incorporated in future developments of the successional models proposed here.

5. Conclusion

The aim of this paper was to investigate how combinations of hydrological variables can be used to predict changes in macroinvertebrate diversity along successional sequences in floodplain channels. Our study showed that the two components of hydrological connectivity i.e. the overflow and the backflow clearly influenced the changes in species assemblages during succession in floodplain channels. We evaluated the effects of two types of restoration on invertebrate assemblages: a full and a partial (i.e. downstream only) reconnections of an isolated floodplain channel. Even if both entailed a significant increase in invertebrate richness, the full reconnection was the most beneficial for the total richness (EPT plus gastropods). In temperate large river floodplains, such models can help restoration planning through a better prediction of the consequences of changes in hydraulic connectivity and sedimentation rates upon aquatic biodiversity at a decadal to centennial time scale. The distinction made here between two ecologically relevant connectivity processes, also increases the flexibility of the predictive models and opens avenues for further developments.

CRediT authorship contribution statement

Pierre Marle: Conceptualization, Methodology, Validation, Formal analysis, Writing - original draft, Writing - review & editing. **Jérémié Riquier:** Conceptualization, Methodology, Validation, Writing - original draft, Writing - review & editing, Visualization. **Pablo Timoner:** Methodology, Validation. **Hélène Mayor:** Data curation. **Vera I. Slaveykova:** Writing - review & editing, Visualization, Validation, Funding acquisition, Project administration. **Emmanuel Castella:** Conceptualization, Methodology, Validation, Writing - review & editing, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was funded by the Agence de l'Eau Rhône-Méditerranée-Corse, the Compagnie Nationale du Rhône, the Région Auvergne-Rhône-Alpes, the Région Provence-Alpes-Côte d'Azur and Electricité de France. The work was performed in the context of the OHM Vallée du Rhône, the LabEx DRIIHM and in the EUR H2O'Lyon (ANR-17-EURE-0018) of Université de Lyon. We thank all the research teams involved in the monitoring of the Rhône River ecological restoration (RhônEco programme) for making data available and for discussions. We thank the Syndicat du Haut-Rhône for their technical support. We are grateful for the helpful suggestions and comments by two anonymous reviewers.

Appendix. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.142081>.

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