To link to this article : DOI:10.1016/j.watres.2017.01.061
URL : http://dx.doi.org/10.1016/j.watres.2017.01.061

To cite this version : Colas, Fanny and Baudoin, Jean-Marc and Gob, Frédéric and Tamisier, Vincent and Valette, Laurent and Kreutzenberger, Karl and Lambrigot, Didier and Chauvet, Eric *Scale dependency in the hydromorphological control of a stream ecosystem functioning*. (2017) Water Research, vol. 115. pp. 60-73. ISSN 0043-1354

Scale dependency in the hydromorphological control of a stream ecosystem functioning

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Keywords:
Hydromorphology
Leaf breakdown
Scaling effect
Ecosystem functioning
Multiple stressors

A B S T R A C T

Physical habitat degradation is prevalent in river ecosystems. Although still little is known about the ecological consequences of altered hydromorphology, understanding the factors at play can contribute to sustainable environmental management.

In this study we aimed to identify the hydromorphological features controlling a key ecosystem function and the spatial scales where such linkages operate. As hydromorphological and chemical pressures often occur in parallel, we examined the relative importance of hydromorphological and chemical factors as determinants of leaf breakdown.

Leaf breakdown assays were investigated at 82 sites of rivers throughout the French territory. Leaf breakdown data were then crossed with data on water quality and with a multi-scale hydromorphological assessment (i.e. upstream catchment, river segment, reach and habitat) when quantitative data were available.

Microbial and total leaf breakdown rates exhibited differential responses to both hydromorphological and chemical alterations. Relationships between the chemical quality of the water and leaf breakdown were weak, while hydromorphological integrity explained independently up to 84.2% of leaf breakdown. Hydrological and morphological parameters were the main predictors of microbial leaf breakdown, whereas hydrological parameters had a major effect on total leaf breakdown, particularly at large scales, while morphological parameters were important at smaller scales. Microbial leaf breakdown were best predicted by hydromorphological features defined at the upstream catchment level whereas total leaf breakdown were best predicted by reach and habitat level geomorphic variables.

This study demonstrates the use of leaf breakdown in a biomonitoring context and the importance of hydromorphological integrity for the functioning of running water. It provides new insights for environmental decision-makers to identify the management and restoration actions that have to be undertaken including the hydromorphogical features that should be kept in minimal maintenance to support leaf breakdown.

1. Introduction

The ecological integrity of river ecosystems throughout the world is impacted by numerous anthropogenic stressors that threaten the sustainability of key services provided by those ecosystems. The ecosystem services are directly linked to ecosystem processes which basically involve the transfer of energy and

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http://dx.doi.org/10.1016/j.watres.2017.01.061

materials from the combined activity of organisms, such as primary production, decomposition of organic matter, or nutrient retention. Direct measurement of ecosystem processes remains largely neglected in river health assessment programs, even though the incorporation of such functional indictors has been repeatedly proposed (Gessner and Chauvet, 2002; Young and Collier, 2009; Palmer and Febria, 2012; Colas et al., 2016). To date, most bioassessment tools of the ecological state of rivers developed under the European Water Framework Directive (WFD) are based on community attributes (Birk et al., 2012) that only partially highlight specific changes in ecosystem functioning and processes (e.g. Reyjol et al., 2014). Yet, in addition to providing a direct measure of valuable ecosystem services, functional indicators provide an integrated measure of ecosystem integrity over time and space and across organisms at different organizational levels (e.g. Bunn et al., 1999; Bunn and Davies, 2000; Gessner and Chauvet, 2002). As such, they are likely to exhibit a strong sensitivity to a wide range of stressors and may have utility for discriminating low levels of impairment (Palmer et al., 2005; Baudoin et al., 2008; Young et al., 2008; Young and Collier, 2009; Friberg, 2014). There are a variety of indicators based on ecosystem process measurement that might be used in biomonitoring programs (Gessner and Chauvet, 2002; Young and Collier, 2009; Elosegi and Sabater, 2012). Among them, leaf breakdown is a prime candidate because of its central role in river ecosystem functioning, the considerable scientific background on both the abiotic and biotic mechanisms involved and on the effect of various physical and chemical stressors, and the relative ease and low cost of the measurement method (e.g. Gessner and Chauvet, 2002; Young and Collier, 2009). Despite its potential value to assess river health, the application of standardized leaf breakdown bioassays in a context of biomonitoring remains rare (Friberg, 2014).

Almost 50% of European river water bodies are reported to be below good ecological status due to degraded habitat conditions (http://www.eea.europa.eu) and hydromorphological alterations such as damming, embankment, channelization and non-natural water level fluctuations are the most common type of pressure identified in these rivers (Malmqvist and Rundle, 2002; Nilsson et al., 2005). Considering this, the impacts of habitat degradation on river health are receiving increasing attention. While there is considerable evidence suggesting the importance of habitats to support both the structural and the functional components of river ecosystems (e.g. Beisel et al., 1998; Friberg et al., 2009; Elosegi et al., 2010; Elosegi and Sabater, 2012; Arroita et al., 2015), current understanding of the links between river ecology and hydromorphology is still incomplete (e.g. Vaughan et al., 2009). Surprisingly, few studies reported clear impacts of habitat degradation, which can be explained from inappropriate assessment strategies and the co-occurrence of other types of pressures such as chemical ones (Friberg, 2014). Some studies reported synergistic impacts of chemical and physical stressors on biological communities and ecosystem functioning (e.g Rasmussen et al., 2012; Colas et al., 2013) suggesting that disentangling the effects of degraded habitats necessitates separating the roles of hydromorphic modifications from reduced water quality. Most studies are based on comparisons between unaltered and altered sites and do not provide quantitative information on such linkages, while such quantitative analysis is required for effective prediction and river management (Vaughan et al., 2009). Within Europe, numerous methodologies have been developed (e.g. Raven et al., 1998; Chandesris et al., 2008; Gob et al., 2014; Gurnell et al., 2016) to evaluate the hydromorphological characteristics and quality of rivers following the requirements of the WFD that include key elements such as the hydrological regime, sediment and aquatic organisms continuity and river channel morphology. While such methods may provide quantitative data to demonstrate hydromorphological and ecological linkages, they remain scarcely used in studies on biological responses to hydromorphological pressures. Legislators and water agencies have historically paid much closer attention to water quality than other aspects of river condition. As a result, the biotic indices traditionally used in the biomonitoring of rivers have been developed to target chemical pollution (Friberg et al., 2006) potentially making them less sensitive to other impacts such as habitat degradation. While rivers are spatially nested, most studies have focused on the reach scale, notably on the wetted channel, without considering the different relationships linking the key components of hydromorphological features to ecological integrity over different spatial scales. Yet the ability to detect impacts of stressors is scale-dependent; hence a multi-scale approach is necessary to identify which hydromorphological features are key to maintaining ecological integrity of aquatic ecosystems and understanding the spatial scales at which are they relevant (Gove et al., 2001; Elosegi et al., 2010).

The main objective of this study was to provide quantitative information on hydromorphological and ecology linkages using leaf breakdown as an indicator of ecosystem integrity. As such an understanding is essential in order to adapt scale-appropriate strategies to manage and restore river ecosystems, we firstly investigated which features of river hydromorphology at each spatial scale exert the strongest influences on leaf breakdown. Then, we aimed to determine at which spatial scale hydromorphological features of rivers are likely to best predict patterns of leaf litter breakdown. Finally, we compared this scaling effect with the impacts of chemical quality of the water in order to discriminate the importance of each type of pressure (i.e. chemical and hydromorphological) in the impairment of ecosystem functioning. To this end, leaf breakdown assays were investigated on 82 sites distributed throughout the French territory along a gradient of physical and chemical alterations in collaboration with practitioners of water agencies. Leaf breakdown data were then crossed with data on water chemistry and hydromorphological features at four spatial scales (i.e. upstream catchment, river segment, reach and habitat) using the standard protocols developed to fulfill WFD requirements when quantitative data were available.

2. Materials & methods

2.1. Leaf breakdown

In the present paper, 82 sites of first- to fourth-order streams distributed throughout the French territory were investigated (Fig. 1). For each water agency, several pairs of sites (undisturbed/impaired sites) were selected covering the main hydromorphological pressures (e.g. damming, embankment, and channelization) and for which restoration projects were planned for 2015. Senescent alder (*Alnus glutinosa* Gaertn.) leaves were collected from trees before abscission at a latitude of 43°17′44.2″ N and a longitude of 1°39′52.9″ E using large nets suspended above the ground directly under trees in the autumn 2013 and air-dried in the laboratory. Litter bags were made by placing 4 g (±0.029) of air-dried leaves into fine mesh (15 × 20 cm, 500 μm mesh size) and coarse mesh (15 × 20 cm, 10 mm mesh size) bags to restrict or allow invertebrates access, respectively. Thus, leaf breakdown rates in fine-mesh bags provide an indication of microbial leaf breakdown (i.e. bacteria and fungi, named hereafter “microbial LB”) whereas decomposition rates in coarse-mesh bags are indicative of total leaf breakdown (i.e. microbial and invertebrates, named hereafter “total LB”). Leaf bags were deployed during the winter of 2014 (from December 2013 to March 2014) depending on low flow conditions. At each site, four iron bars were anchored in littoral areas. Littoral

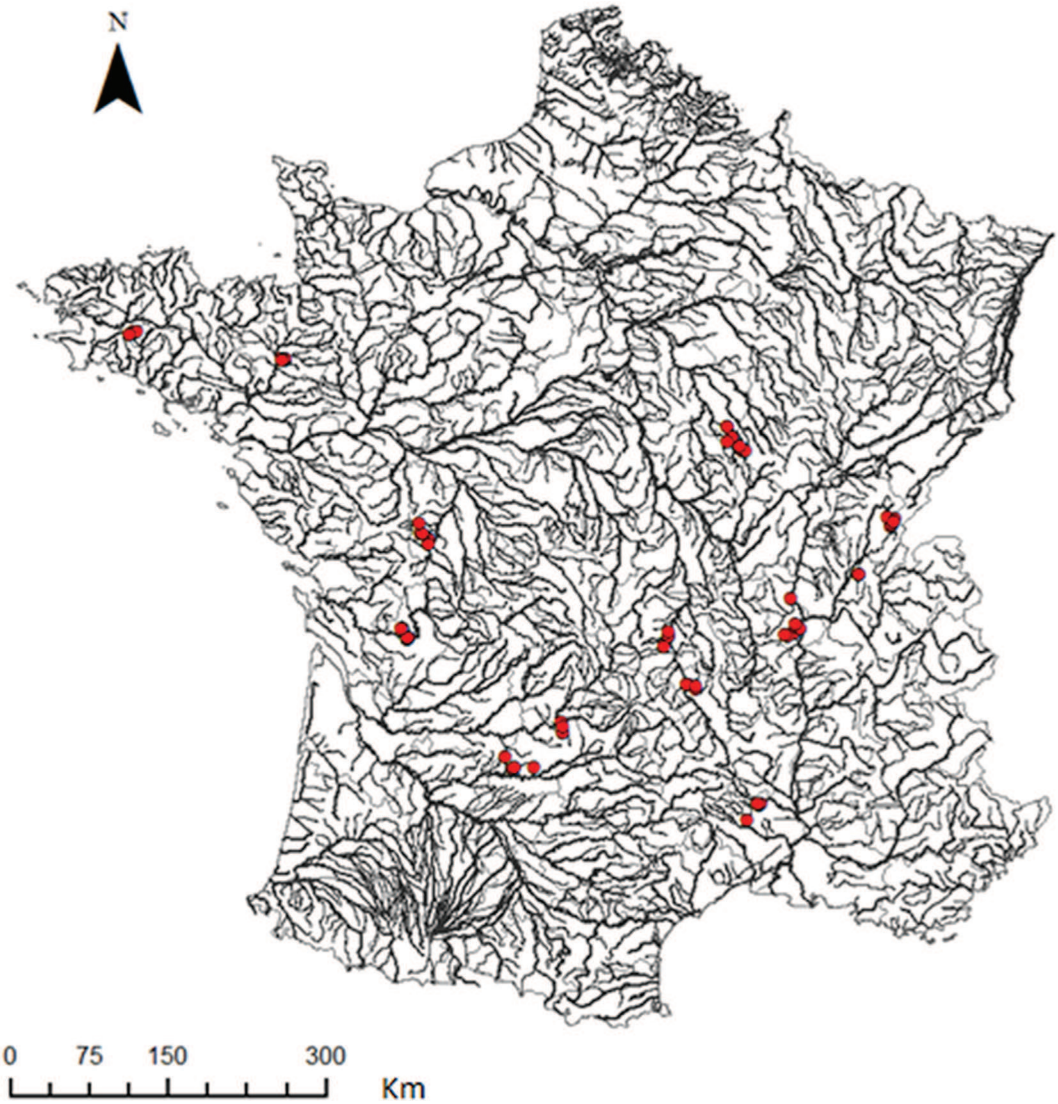

Fig. 1. Location of the study sites over France.

habitats were preferentially selected because they are natural areas of detritus accumulation in streams, and in order to limit the variability associated with hydraulic conditions and allow comparison between streams. One data logger was placed at the last iron bar on each site to record water temperature every thirty minutes during the experiment. At each iron bar named hereafter block, two fine and coarse mesh bags were fastened, immersed and retrieved as follows: one coarse mesh bag at 7 days; one fine and coarse mesh bag at 21 days and one fine mesh bag at 42 days. Leaf bags were immediately placed in individual sealed plastic bags with river water, and then transported in a cool box and immediately frozen (−20 °C). A total of 1312 leaf bags were employed and were immersed simultaneously during the 2014 winter field campaign with the collaboration of the managers being trained about the protocol. Then, after thawing of the leaf bags, the leaves were individually rinsed with water to remove fine particulate matter and invertebrates. The remaining leaf material was oven-dried to constant mass (105 °C, 48 h) and weighed to the nearest 0.05 mg. Subsamples (500 mg) were ignited in a muffle furnace (550 °C, 4 h) to relate dry mass to ash-free dry mass (AFDM). Four additional leaf bags were kept in the laboratory by each manager before starting the experiment to estimate the initial oven-dried mass and AFDM of all leaf bags. Leaf breakdown data were then crossed with data on hydromorphological and chemical pressures at various spatial scales when it was possible.

2.2. Environmental settings

We evaluated the pressures to which the sites are subjected using methodologies developed under the WFD for assessing the impact of hydromorphological and chemical pressures on stream "health". To do this, we chose four main spatial scales: upstream catchment, river segment, reach and habitat. The hydromorphological and physico-chemical parameters considered in this study at each spatial scale are listed and described in Table 1.

2.2.1. Hydromorphological pressures at large scales

The scale-hierarchic river audit system (SYRAH-CE) for France (Chandesris et al., 2008; Van Looy et al., 2015) is a method for determining the risk of hydromorphological alteration of homogeneous river segments (i.e. measuring about 2.5 km on average). This segmenting into hydro-morphologically homogeneous river segments is based on a semi-automatic GIS process that distinguishes confluences, geomorphological boundaries, and changes in

Table 1
Hydromorphological parameters at each spatial scale and physic-chemical parameters at reach-scale used in statistical analyses. *p* refers to probabilities of impairment according to SYRAH-CE methodology. † indicates $\log_{10}$-transformed variables.

Scale	Full names	Short names	Min	Mean	Max
Upstream catchment	*River continuity*				
	Biological continuity (*p*)	BC	0.14	0.68	0.90
	Biological continuity for migratory species (*p*)	BCMS	0.00	0.40	0.90
	Lateral continuity (*p*)	LC	0.04	0.43	0.72
	Continuity of sediment transport (*p*)	SR	0.10	0.68	1.00
	Hydrological regime				
	Connection to groundwater bodies (*p*)	CGB	0.69	0.79	1.00
	Dynamics of water flow (*p*)	DYNA	0.67	0.89	0.95
	Quantity of water flow (*p*)	QUANT	0.02	0.32	0.77
	River morphology				
	River bed structure and substrate (*p*)	RBSS	0.01	0.22	0.43
	Structure of the riparian zone (*p*)	SRZ	0.00	0.42	0.76
	Variation in channel depth and width (*p*)	DEWI	0.00	0.21	0.63
River segment	*River continuity*				
	Biological continuity (*p*)	BC	0.00	0.45	0.90
	Biological continuity for migratory species (*p*)	BCMS	0.00	0.25	0.90
	Lateral continuity (*p*)	LC	0.00	0.46	0.76
	Continuity of sediment transport (*p*)	SR	0.00	0.42	1.00
	Hydrological regime				
	Connection to groundwater bodies (*p*)	CGB	0.00	0.65	1.00
	Dynamics of water flow (*p*)	DYNA	0.14	0.63	0.90
	Quantity of water flow (*p*)	QUANT	0.00	0.27	0.77
	River morphology				
	River bed structure and substrate (*p*)	RBSS	0.00	0.20	0.54
	Structure of the riparian zone (*p*)	SRZ	0.00	0.40	0.81
	Variation in channel depth and width (*p*)	DEWI	0.00	0.17	0.72
Reach	Average bankfull width (m)	BFWi	1.5	5.3	14.7
	Average flow velocity (m s^{-1})	VELO	0.03	0.33	0.90
	Average pool depth (m)	PODE	0.03	0.11	0.30
	Average water depth (m)	DEPT	0.06	0.22	0.66
	Bankfull discharge ($m^3 s^{-1}$)	Qb	0.01	0.65	4.52
	Channel slope (%)	SLOP	0.13	6.2	28.9
	Coefficient variation of bankfull width	CV_Wi†	0.06	0.16	0.43
	Froude number at bankfull	FROU†	0.02	0.15	0.37
	Median particle size of the bed surface (mm)	D50	2.00	34.6	82.5
	Width of riparian vegetation (m)	RIPA†	0.00	10.8	25.0
	River roughness coefficients	K†	0.96	13.2	82.4
	Specific stream power at 'bankfull' (W m^{-2})	$\omega_0^{\dagger}$	0.07	13.3	68.9
	Shear stress (N m^2)	SHS†	0.20	18.1	55.2
	Average width to depth ratio	W/D	3.41	11.5	33.5
Habitat	Bankfull width (m)	BFWi†	2.30	13.1	25.0
	Bed wet width (m)	WBWi†	1.70	7.90	23.7
	Depth (m)	DEPT†	0.09	0.29	0.97
	Granulometry (mm)	GRANU†	0.00	141.2	1024.0
	Substrate richness	SUBS	1.00	1.40	4.00
	Velocity (m. s^{-1})	VELO†	0.01	0.21	0.75
Chemical variables at reach scale	Ammonium (μg.L^{-1})	$NH^{4+\dagger}$	44.9	86.3	270.3
	Anions (mg.L^{-1})	Cl^- and $F^{-\dagger}$	1.20	13.1	30.7
	Cations (mg.L^{-1})	K^+ and $Na^{+\dagger}$	9.10	44.2	97.0
	Dissolved organic carbon (mg.L^{-1})	DOC†	0.47	3.21	15.9
	Dissolved oxygen (mg.L^{-1})	DO†	5.90	10.0	12.6
	Nitrate (mg.L^{-1})	$NO_3^{-\dagger}$	0.20	2.50	10.8
	Nitrite (mg.L^{-1})	$NO_2^{-\dagger}$	0.00	0.01	0.04
	pH	pH	5.90	7.50	8.40
	Phosphate (mg.L^{-1})	$PO_4^{2-\dagger}$	0.01	0.03	0.11
	Soluble reactive phosphorus (μg.L^{-1})	SRP†	0.00	13.8	71.7
	Specific conductance (μs.cm^{-1})	COND	38.0	313.4	660.0
	Sulphate (mg.L^{-1})	$SO_4^{2-\dagger}$	0.32	4.23	14.4

valley floor width and form. The assessment was conducted at the scale of the entire French river network for each of these river segments. Its main aim is to detect non-natural hydromorphological damage that can induce the degradation of the ecological status of rivers, especially through the degradation of the aquatic and riparian habitats. Alteration risk was determined on the basis of natural features and anthropogenic pressures exerted in the upstream watershed and in watercourse corridors (see Appendix A). Information was collected from all the pertinent national geographical information systems available in France [i.e. BD TOPO® and BD CARTHAGE® of the IGN, national geographic institute, the French database HYDRO (http://www.hydro.eaufrance.fr/), the French agricultural census (http://www.agreste.agriculture.gouv.fr/)], and in particular from the French topographic database (BD TOPO®) that corresponds to an enriched 1:25 000 scale map. With 11 themes (e.g. water network and features, vegetation, land relief, road and rail networks, energy infrastructures, buildings) and 1 m precision, it is the most complete and precise database available in France. To assess the potential impact of these multi-scale pressures on hydromorphological functioning, GIS information was converted into a hydromorphological alteration risk using Bayesian Belief Networks

(BBNs). These BBNs were constructed for ten hydromorphological parameters according key elements included in the WFD (see Appendix A). The level of impairment of each of these ten parameters is described through the probability of belonging to each of the five following alteration classes (i.e. very low, low, medium, good, and very good) and reported at upstream catchment and river segment scales. In our study, the probability of belonging to the "very low" alteration class has been considered. A total of 62 upstream catchment and river segment have been successfully identified on the French topography map used to trace river network (i.e. BD Cartage®) and for which data on land use and hydromorphological assessment are available. Conversely, 21% of sites, mainly small headwater streams (called zero- and first-order streams with catchment area under 15 km^2) do not appear on any map and consequently have been removed from the analyses.

2.2.2. Hydromorphological data at reach and habitat scales

Hydromorphological data at reach level was collected using CARHYCE protocol (Gob et al., 2014) at the end of the leaf breakdown experiment. Relevant and complete data were available for only 42 sites because of the difficulties of application of the protocol, notably for low-order rivers. This standardized field survey is based on the hydraulics geometry theory. The bankfull width and depth averaged from measurements on 15 cross-sections spaced of one bankfull width were used to characterize the channel morphology. On every cross-section a minimum of 7 measurements of depth were made and for each measurement the sediment size is noted. The nature of the bank (artificial material, vegetal bank protection or natural bank) and the structure and composition of the riparian vegetation were also detailed at every cross-section. At the station scale, additional grain size (Wolman pebble count) and substrate clogging measurements were made on a riffle. Finally the water slope and discharge were measured using a spirit level and electromagnetic flowmeter respectively. At the habitat scale, measurements related to micro-habitats where leaf bag was anchored were made at each field campaign of leaf retrieval including water depth, velocity, sediment grain size, nature of the substrate, bankfull and bed wet width. For input variables in the statistical analyses, we chose to perform the mean value of each parameter measured at each date of leaf bag retrieval.

2.2.3. Physico-chemical data

For each site, water was sampled at the beginning and at the end of the leaf breakdown experiment and immediately frozen (−20 °C). Fourteen major physic-chemical variables were measured according to national standards (NF EN ISO 10304-1, 1339; AFNOR NF EN ISO 14911) including anions and cations (Fluoride, Chloride, Bromide, Sodium and Potassium), variables related to eutrophication (NH_4^+, NO_3^-, NO_2^-, PO_4^{2-} and Soluble reactive phosphorus − SRP), dissolved organic carbon (DOC) and sulphate (SO_4^{2-}). In addition, pH, conductivity and dissolved oxygen were measured at each date of leaf bag retrieval. We chose as input data for statistical analyses the mean value of concentrations measured at each field campaign.

2.3. Data analyses

All analyses were performed using R version 3.1.0 (R Core Team, 2008). Microbial and total leaf breakdown rates (k) were estimated by fitting the AFDM data from each block to the degree day exponential model (Petersen and Cummins, 1974)

$$Y_t = Y_0 e^{-kt} \tag{1}$$

where Y_t is the AFDM remaining at time t, Y_0 is the initial AFDM at the beginning of the experiment and t is the sum of the mean daily temperature (in degrees) corresponding at each sampling date. We chose as input data for statistical analyses the mean value of microbial and total leaf breakdown rate calculated at each block. Leaf breakdown rates were arcsine squareroot − transformed before performing the analyses in order to fit normal distribution. Transformations used for environmental variables are listed in Table 1. Mean values for selected hydromorphological parameters at habitat scale and chemical variables at reach scale have been used. Generalized Linear Models (GLM) with Gaussian family and identity link were built to model leaf breakdown using hydromorphological features and chemical parameters of water as predictors. Models were performed for each spatial scale separately. Before modelling, the predictors were initially checked for collinearity using Spearman's rank correlation test. Collinearity was assumed for $|\rho| \geq 0.7$ (see Dormann et al., 2013). In this situation, one variable of the two correlated variables was selected as an input variable for GLM but both were considered for the interpretation. The leave-one-out cross-validation (LOOCV) method was used for model selection in order to avoid overfitting. LOOCV is a special case of K-fold cross validation where the number of folds is the same number of observations (i.e. K = n). Models with the lowest prediction error, Mallow's Cp Statistic and Bayesian Information Criterion, and conversely the highest adjusted r-square were considered as the best-fit models. When models were quite similar, models with lowest complexity were selected. The best-fit models were checked for overall model and predictor-specific significances through the χ^2-test. The amount of deviance accounted for (D^2) of models was calculated according to the formula proposed by Guisan and Zimmermann (2000) (Eq. (2)):

$$D^2 = \frac{model\$null.deviance - model\$deviance}{model\$null.deviance} \tag{2}$$

Model assumptions were checked for the homogeneity of variance using the Breuch Pagan test, normal distribution of model residuals using Shapiro Wilk's W test, independence (lack of correlation) of error terms using the Durbin-Watson test and identification of influential observation using residual-leverage plots and Cook's distances. Variance inflation factors (VIF) were calculated for each predictor of best-fit models to detect collinearity, assumed for values superior to 5. Hierarchical partitioning was used to identify the best predictors according to their joint and independent effects in each best-fit model (Chevan and Sutherland, 1991; Walsh and MacNally, 2004). The significance of independent effects of each predictor was calculated using a randomization test with 500 interactions (Mac Nally, 2002). Synthetic indices of hydromorphological integrity at each spatial scale and water quality for leaf breakdown were used to compare (i) the importance of hydromorphological integrity at each spatial scale and (ii) the importance of chemical quality *vs.* hydromorphological integrity. Each index was compiled using the best predictors of the corresponding model as an indicator. Because variables were measured in different units and on different scales, indicators were first standardized and then, combined together using an additive aggregation (Dobbie and Dail, 2013).

3. Results

3.1. Relationships between hydromorphology and leaf breakdown at four spatial scales

High collinearity ($\rho \geq 0.7$) occurred between hydromorphological parameters at each spatial scale (detailed spearman rank correlation coefficients and levels of significance are available in the Supporting information, Appendix B), justifying the strategy to include not more than one of these predictors into each GLM (Table 2). For the LOOCV procedures, full models comprised 8 predictors for upstream catchment and river segment models, 11 and 5 predictors for reach and habitat models, respectively.

3.1.1. Models results for microbial leaf breakdown

At upstream catchment scale, the reduced-model selected using the LOOCV procedure included six predictors (Table 3) which explained 62.9% of the microbial LB variation. The best predictors were the damage risk on the river bed structure and substrate (RBSS), on the quantity (QUANT) and the dynamics (DYNA) of water flow, which independently contributed to 35%, 31.6% and 13.2% of microbial LB variation, respectively. Microbial LB decreased with increased damage risk on these three parameters. At river segment scale, the reduced model explained 52.9% of the microbial LB variation (Table 3), which was independently explained by the damage risk on the river bed structure and substrate (RBSS), on the quantity (QUANT) and the dynamics (DYNA) of water flow at 46.5%, 19.2% and 14.6%, respectively. Microbial LB decreased with increased damage risk on these three parameters. 42.2% of the microbial LB variation was explained by the reduced model coming from reach spatial scale (Table 3). The best predictors were the average width to depth ratio and the average water depth, which independently contributed to 58.2% and 41.8% of microbial LB variation, respectively. Microbial LB decreased when the average water depth increases and the width to depth ratio decreases. At habitat spatial scale, the reduced model explained 30.7% of the microbial LB variation (Table 3). Water velocity was the only predictor selected by the LOOCV procedure. Microbial LB increased with higher water velocity. Nonetheless, because model residuals did not follow the normal distribution, the reduced model at habitat scale was excluded from next analyses. Statistical qualities of reduced models coming from each spatial scale were compared based on three information criterion: the explained deviance (D^2), the Nash-Sutcliffe efficiency (NSE) and the Root Mean Square Error (RMSE) of each model (Table 5). The percentages of deviance explained strongly varied between spatial scales. The best model results considering the deviance explained were achieved for hydromorphological features coming from the upstream catchment spatial scale (deviance explained: 62.9%). The weakest model was for reach scale (deviance explained: 42.2%). Concerning the models' performance, the best model was achieved for the upstream catchment for which NSE is higher and RMSE lower than for other models, indicating that model better fits observed data. The model with highest difference from the observed data was the reach model.

The same pressures exert significant effects on microbial LB at the upstream catchment and river segments levels. The resulted increase in impairment risks on river bed structure and substrate (i.e. decrease in sediment thickness and in flow facies variety, deficit of the coarsest sediment, increase in sediment clogging) and on quantity and dynamics of water flow (i.e. alteration of seasonality of flow regime, decrease in low flow and flood peak, increase in frequency and intensity of flood) was negatively correlated with microbial LB. Bankfull width and depth were the main predictors of microbial LB at reach scale with a lowest microbial LB in narrower and deeper river channels. The variables describing hydromorphological pressures at upstream catchment level provided better explanation of variation in microbial LB.

3.1.2. Models results for total leaf breakdown

At upstream catchment scale, the reduced-model selected using

Table 2
Variables exhibiting high collinearity ($\rho \geq 0.7$) justifying to discard all but one of them in statistical analyses. Detailed spearman rank correlation coefficients and levels of significance are available in the Supporting information (Appendix B).

Datasets	Correlated variables	ρ	Selected variable
Upstream catchment	RBSS and LC	0.82	SSLIT
	DEWI and LC	0.84	PRLA
	SR and BC	0.90	QS
River segment	RBSS and LC	0.75	SSLIT
	SR and BC	0.71	QS
Reach	SLOP and SHS	0.83	SHS
	SHS and ω_0	0.86	SHS
	FROU and VELO	0.95	FROU
Habitat	BFWi and WBWi	0.91	BFWi
Water chemistry	PO_4^{2-} and SRP	0.70	SRP
	Na^+ and Cl^-	0.90	Cl^-

Table 3
Results derived from GLM and the hierarchical partitioning of variance on microbial leaf breakdown to hydromorphological parameters at each spatial scale and for full model.[a]

Models		D^2 (%)	Predictors	Coefficients	*P*-value	IE (%)	JE (%)	MC
Individual model	Upstream catchment *(n = 62)*	62.9	RBSS	−0.042	$P < 0.001$	35.0*	−1.2	
			RS	0.012	n.s.	7.6	0.05	
			BCMS	−0.005	n.s.	3.6	−2.8	
			SRZ	0.015	$P < 0.01$	9.1	−7.4	
			QUANT	−0.023	$P < 0.001$	31.6*	2.7	
			DYNA	−0.016	$P < 0.001$	13.2*	4.1	
	River segment *(n = 62)*	52.9	RBSS	−0.024	$P < 0.001$	46.5*	−1.5	
			DEWI	0.006	n.s.	4.5	−4.4	
			SR	0.005	n.s.	7.8	−7.8	
			SRZ	0.002	n.s.	7.6	7.3	
			QUANT	−0.011	$P < 0.001$	19.2*	3.0	
			DYNA	−0.010	$P < 0.001$	14.6*	6.3	
	Reach *(n = 42)*	42.2	W/D	0.019	$P < 0.001$	58.2*	10.5	
			DEPT	−0.014	$P < 0.05$	41.8*	10.5	
	Habitat *(n = 82)*	30.7	VELO	0.028	$P < 0.001$			×
Full model *(n = 41)*		82.9	QI_WS	0.033	$P < 0.001$	54.3*	38.9	
			QI_RS	0.012	$P < 0.01$	30.9*	36.1	
			QI_RE	0.004	n.s.	14.8	21.6	

* represents significant effects ($P < 0.05$) as determined by randomization tests. MC column reports results of model checking including normality of residuals, homoscedasticity and independence. A cross signifies that the model assumptions were not checked. QI_WS, QI_RS and QI_RE refer to synthetic indices of hydromorphological integrity computed at upstream catchment, river segment and reach scales, respectively.

[a] Variables shown for each model were conserved using a cross-validation procedure. The independent (IE) and joint (JE) effects value are presented as percentages of the total explained variance accounted for (D^2) for each explanatory variable as calculated using hierarchical partitioning and may be positive (i.e. additive) or negative (i.e. suppressive).

Table 4
Results derived from generalized linear models and the hierarchical partitioning of variance on total leaf breakdown to hydromorphological parameters at each spatial scale and for full model.[a]

Models		D^2 (%)	Predictors	Coefficients	*P*-value	IE (%)	JE (%)	MC
Individual model	Upstream catchment *(n = 62)*	33.1	CGB	−0.356	$P < 0.001$	41.9*	−6.3	
			SR	−0.003	n.s.	6.4	4.5	
			RBSS	−0.042	n.s.	18.1	−5.9	
			DYNA	−0.161	$P < 0.001$	33.5*	2.7	
	River segment *(n = 62)*	54.4	CGB	−0.031	$P < 0.001$	38.9*	11.8	
			RBSS	−0.006	n.s.	7.6	8.8	
			DEWI	0.023	n.s.	8.5	−7.7	
			SR	−0.017	$P < 0.01$	22.6*	4.4	
			QUANT	0.008	n.s.	2.9	1.9	
			SRZ	−0.009	n.s.	2.7	1.8	
			DYNA	−0.014	$P < 0.05$	16.9*	15.7	
	Reach *(n = 42)*	57.6	W/D	0.026	$P < 0.05$	26.0*	−10.7	
			SHS	−0.009	$P < 0.001$	62.9*	−10.7	
	Habitat *(n = 82)*	24.9	BFWi	−0.014	$P < 0.001$	60.8*	−29.8	
			DEPT	0.137	$P < 0.001$	39.2*	−29.8	
Full model *(n = 41)*		59.5	QI_WS	0.003	n.s.	8.9	−5.0	
			QI_RS	0.08	$P < 0.01$	10.5	18.5	
			QI_RE	0.09	$P < 0.001$	55.4*	20.5	
			QI_PA	0.05	$P < 0.001$	25.1*	16.4	

* represents significant effects ($P < 0.05$) as determined by randomization tests. MC column reports results of model checking including normality of residuals, homoscedasticity and independence. A cross signifies that the model assumptions were not checked. QI_WS, QI_RS, QI_RE and QI_PA refer to synthetic indices of hydromorphological integrity computed at upstream watershed, river segment, reach and habitat scales, respectively.

[a] Variables shown for each model were conserved using a cross-validation procedure. The independent (IE) and joint (JE) effects value are presented as percentages of the total explained variance accounted for (D^2) for each explanatory variable as calculated using hierarchical partitioning and may be positive (i.e. additive) or negative (i.e. suppressive).

the LOOCV procedure included four predictors (Table 4) which explained 33.1% of the total LB variation. The best predictors were the damage risk on the connection to groundwater bodies (CGB) and on the dynamics of water flow (DYNA), which independently contributed to 41.9% and 33.5% of total LB variation, respectively. Total LB decreased with increased damage risk on these two parameters at upstream catchment spatial scale. At river segment scale, the reduced model explained 54.4% of the total LB variation, which was independently explained by the damage risk on the connection to groundwater bodies, on the continuity of sediment transport (SR) and the dynamics of water flow (DYNA) at 38.9%, 22.6% and 16.9%, respectively. Total LB decreased with increased damage risk on these three parameters at river segment spatial scale. The reduced model at reach spatial scale explained 57.6% of the total LB variation. The main predictors were the shear stress (SHS) and the average width to depth ratio (W/D) which independently contributed to 62.9% and 26.0% of total LB variation, respectively. Total LB increased in reaches with lower shear stress and higher width to depth ratio. At habitat spatial scale, the reduced model explained 24.9% of the total LB variation. The best predictors were the bankfull width and the water depth, which independently contributed to 60.8% and 39.2% of total LB variation, respectively. Total LB was higher in habitats with the lowest bankfull width and highest water depth. The best model results considering the deviance explained was achieved for hydromorphological features at reach spatial scale (deviance explained: 57.6%; Table 5). The weakest model was for habitat scale (deviance explained: 24.9%). Regarding the models' performance, the best model was achieved for reach scale for which NSE is higher and RMSE lower than for other models, indicating that this model better fits observed data. The model with the greatest differences when compared to observed data was the habitat model.

The lowest total LBs were reported in rivers sites belonging to upstream catchments where pressures occurred leading to the decrease in low flow replenishment capacity (e.g. damming, river incision, straightness) and the alteration of seasonality of flow regime (e.g. abstraction of water, irrigation, damming). Similarly, lowest total LBs were reported in sites belonging to river segments

Table 5
Comparison of best-fit models coming from GLM performed at each spatial scale for microbial and total leaf breakdown according to the goodness of fit using the total deviance (D^2), the Nash-Sutcliffe efficiency (NSE) and the Root Mean Square Error (RMSE)[a].

Leaf breakdown	Scale	D^2	NSE	RMSE
Microbial LB	Upstream catchment	62.9	0.63	0.004
	River segment	52.9	0.53	0.005
	Reach	42.2	0.36	0.006
Total LB	Upstream catchment	33.1	0.33	0.013
	River segment	54.4	0.58	0.009
	Reach	57.6	0.54	0.008
	Habitat	24.9	0.29	0.017

[a] The model with the highest deviance and NSE but the lowest RMSE was considered the best-fit model i.e. the most parsimonious model.

with increased impairment risks in low flow replenishment capacity, in seasonality of flow regime and in sediment regime (i.e. decrease in sediment transport, increased storage of sediment load). At reach scale, lowest total LBs were reported in narrowest and deepest channels with resulting high shear stress. Leaf packs anchored to deepest habitats exhibited highest total LB. The variables coming from measurement of channel cross-sections provided better explanation of variation in total LB.

3.2. Scaling effect of hydromorphological integrity on leaf breakdown

For microbial LB, the full model explained 82.9% of the total variation (Table 3). Integrity indices coming from the upstream catchment and river segment consistently explained most of variance in microbial leaf breakdown change, both independently (54.3 and 30.9%, respectively) and as joint effects (38.9 and 36.1%, respectively) with other predictor variables. Microbial LB increased significantly when hydromorphological integrity in the upstream catchment and river segment increased (Fig. 2). The weakest predictor was the hydromorphological integrity index at reach scale, despite a positive relationship with microbial LB (Fig. 2). For total

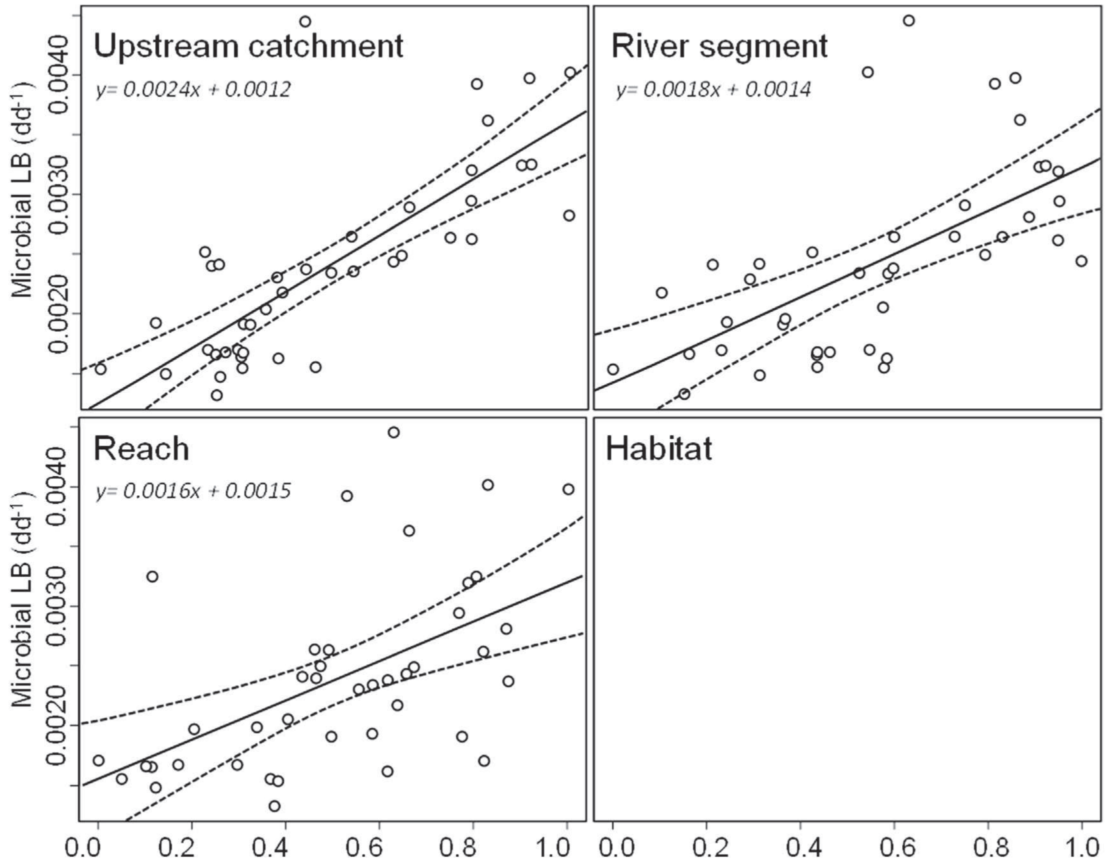

Fig. 2. Relationship between microbial leaf breakdown rate and hydromorphological integrity index at each spatial scale. All figures show the microbial leaf breakdown predicted along the range of each index (solid black lines) and associated 95% confidence intervals (dotted lines). The relationship is not displayed for the habitat scale where Pearson's model residuals did not follow a normal distribution.

LB, the full model explained 59.5% of the total variation (Table 4). Integrity indices from the reach and habitat scale consistently explained most of variance in total leaf breakdown change, both independently (55.4 and 25.1%, respectively) and as joint effects (20.5 and 16.4%, respectively) with other predictor variables. Total LB increased significantly when hydromorphological integrity at reach and habitat spatial scale increased (Fig. 3). The weakest predictor was the hydromorphological integrity index at the upstream catchment scale (Fig. 3).

3.3. *Relative contribution of hydromorphological and water quality attributes*

3.3.1. *Models results for water quality*

High collinearity occurred between soluble reactive phosphorus and phosphate concentrations parameters ($\rho = 0.7$) and between chloride and sodium concentrations ($\rho = 0.9$), justifying the strategy to include not more than one of these predictors in the GLM (Table 2). The reduced-models selected after the LOOCV procedure included eight predictors for microbial leaf breakdown and five predictors for total leaf breakdown (Table 6). For microbial LB, the reduced-model explained 49.3% of the variation. The concentrations in dissolved oxygen (DO), in soluble reactive phosphorus (SRP), in potassium (K^+) and in dissolved organic carbon (DOC) explained most of variance in microbial leaf breakdown change, both independently (29.5, 20.3, 10.5 and 8.4%, respectively) and as joint effects (21.9, 23.6, 8.7 and 14.5%, respectively) with other predictor variables. The streams with the highest concentrations in phosphorus, potassium and dissolved oxygen and organic carbon, exhibit the highest microbial LB. For total LB, the reduced-model explained 33.2% of the variation. The concentrations in dissolved oxygen (DO) and in soluble reactive phosphorus (SRP) were the best predictors of total leaf breakdown change, which independently contributed to 44.0% and 32.5%, respectively. Total LB increased with higher concentrations of dissolved oxygen but decreased in streams with higher concentrations of soluble reactive phosphorus.

3.3.2. *Comparison between hydromorphological and water quality*

For both, the hydromorphological integrity index exhibited the main independent effect on the variation of the microbial and the total LB at 78.9% and 84.2%, respectively (Fig. 4). Microbial and total LB increased when hydromorphological integrity increased (Fig. 5). The chemical quality index contributed independently to 21.1% and 15.8% of microbial and total LB, respectively. Microbial LB increased when chemical quality increased, while no clear pattern was observed for total LB (Fig. 5).

4. Discussion

4.1. *Key hydromorphogical characteristics supporting leaf breakdown*

This study provides evidence on the importance of the hydromorphological integrity of streams in supporting key ecological processes and disentangles the mechanisms involved in the impairment of leaf breakdown. Microbial and total leaf breakdown exhibited differential responses and sensitivity to hydrological and morphological parameters at different spatial scales. In general, the

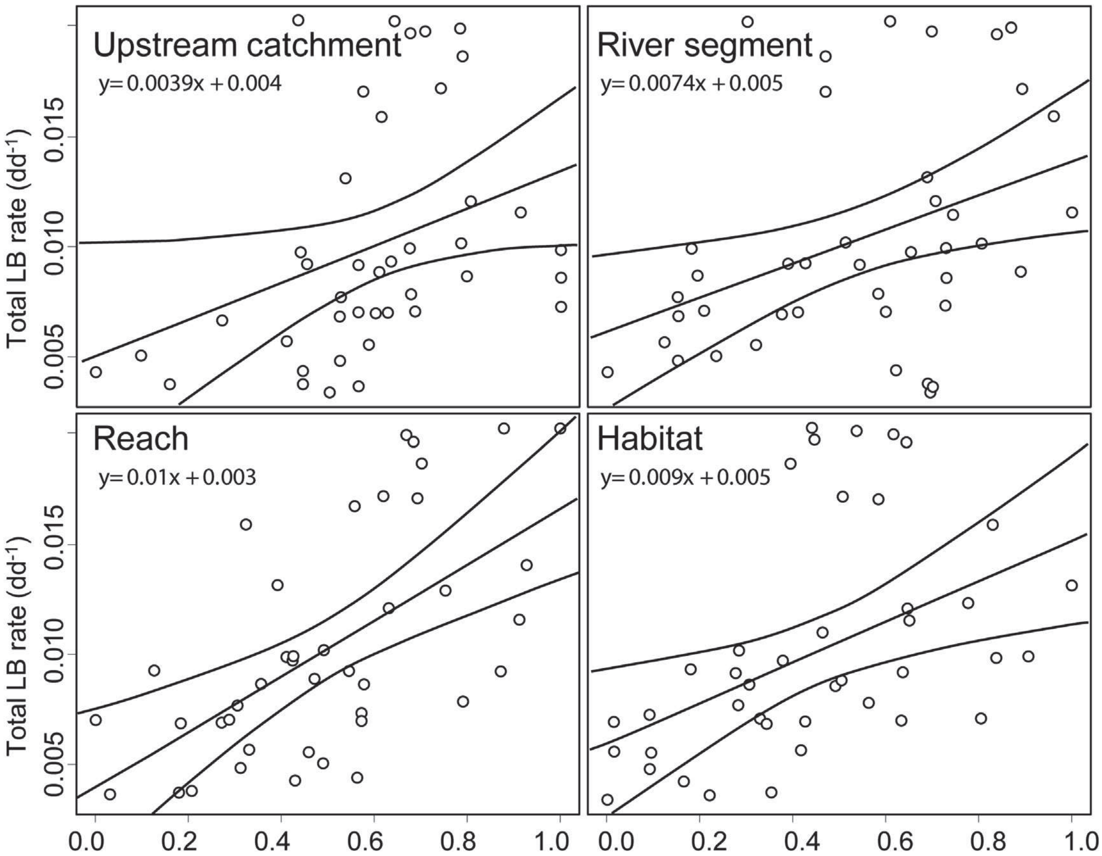

Fig. 3. Relationship between total leaf breakdown rate and hydromorphological integrity index at each spatial scale. All figures show the total leaf breakdown predicted along the range of each index (solid black lines) and associated 95% confidence intervals (dotted lines).

Table 6
Results derived from GLM and the hierarchical partitioning of variance on microbial and total leaf breakdown to physico-chemical parameters at reach spatial scale[a].

Models	D^2 (%)	Predictors	Coefficients	*P*-value	IE (%)	JE (%)	MC
Microbial LB *(n = 82)*	49.3	SRP	0.001	$P < 0.001$	20.3*	23.6	
		DOC	0.003	n.s.	8.4*	14.5	
		NO_3^-	−0.009	n.s.	14.2	−12.8	
		SO_4^{2-}	−0.004	n.s.	3.0	−0.3	
		K^+	0.008	$P < 0.01$	10.5*	8.7	
		COND	0.0002	$P < 0.01$	6.4	−5.2	
		DO	0.020	$P < 0.001$	29.5*	21.9	
		pH	−0.002	n.s.	7.5	13.4	
Total LB *(n = 82)*	33.2	DO	0.089	$P < 0.01$	44.0*	−23.1	
		SRP	−0.008	$P < 0.001$	32.5*	−18.7	
		SO_4^{2-}	−0.003	n.s.	7.3	−0.8	
		K^+	0.015	n.s.	7.8	−7.2	
		pH	0.005	n.s.	8.4	−6.3	

* represents significant effects ($P < 0.05$) as determined by randomization tests. MC column reports results of model checking including normality of residuals, homoscedasticity and independence. A cross signifies that the model assumptions were not checked.
[a] Variables shown for each model were conserved using a cross-validation procedure. The independent (IE) and joint (JE) effects value are presented as percentages of the total explained variance accounted for (D^2) for each explanatory variable as calculated using hierarchical partitioning and may be positive (i.e. additive) or negative (i.e. suppressive).

performance of the models was higher for microbial than for total leaf breakdown, suggesting a greater sensitivity of microbial leaf breakdown to hydromorphological pressures and/or a higher variability of total leaf breakdown. Physical abrasion and fragmentation due to the combined effects of current velocity and suspended fine sediment must have played a major role in this variability (Ferreira et al., 2006). In contrast, water circulation patterns may be altered within fine mesh bags possibly reducing physical leaf fragmentation and abrasion (Hieber and Gessner, 2002). Anthropogenic perturbations (e.g. the presence of dams, irrigation, artificialization of catchments and straightness) leading to reduced low flow, decreases in flow facies variety and an altered hydrological regime were negatively correlated with microbial leaf breakdown. Water current is an essential driver for the production, the release and the dispersal of aquatic hyphomycete conidia, which are the dominant propagules responsible for the rapid expansion of fungal populations (Bärlocher, 2009). Therefore, human activities leading to reduced flow may profoundly reduce conidial dispersal and consequently the colonization of organic matter by aquatic hyphomycetes (Colas et al., 2016). In addition to

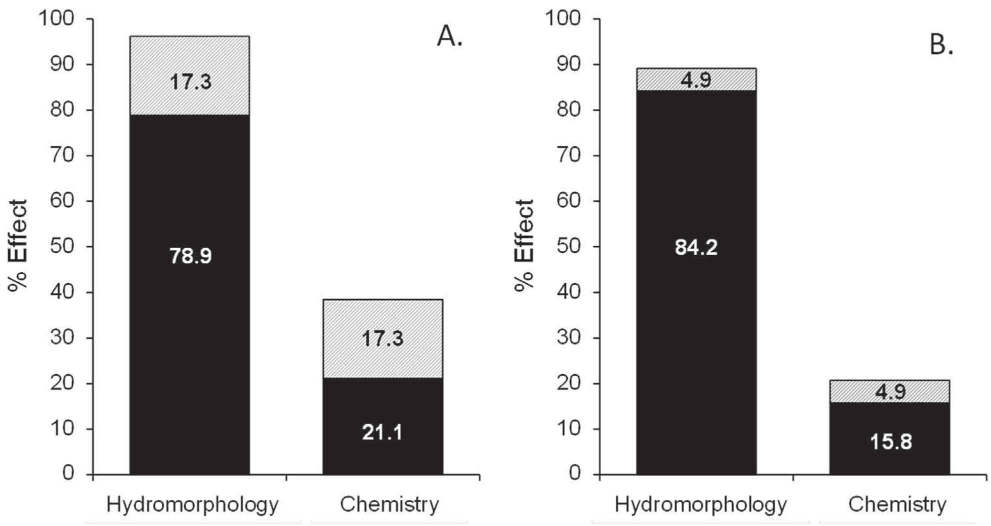

Fig. 4. Results derived from the hierarchical partitioning of variance for microbial (A) and total (B) leaf breakdown. The relative independent (black bars) and joint (striped bar) effects of chemical quality and hydromorphological integrity are given as a percentage of the total explained variance accounted for.

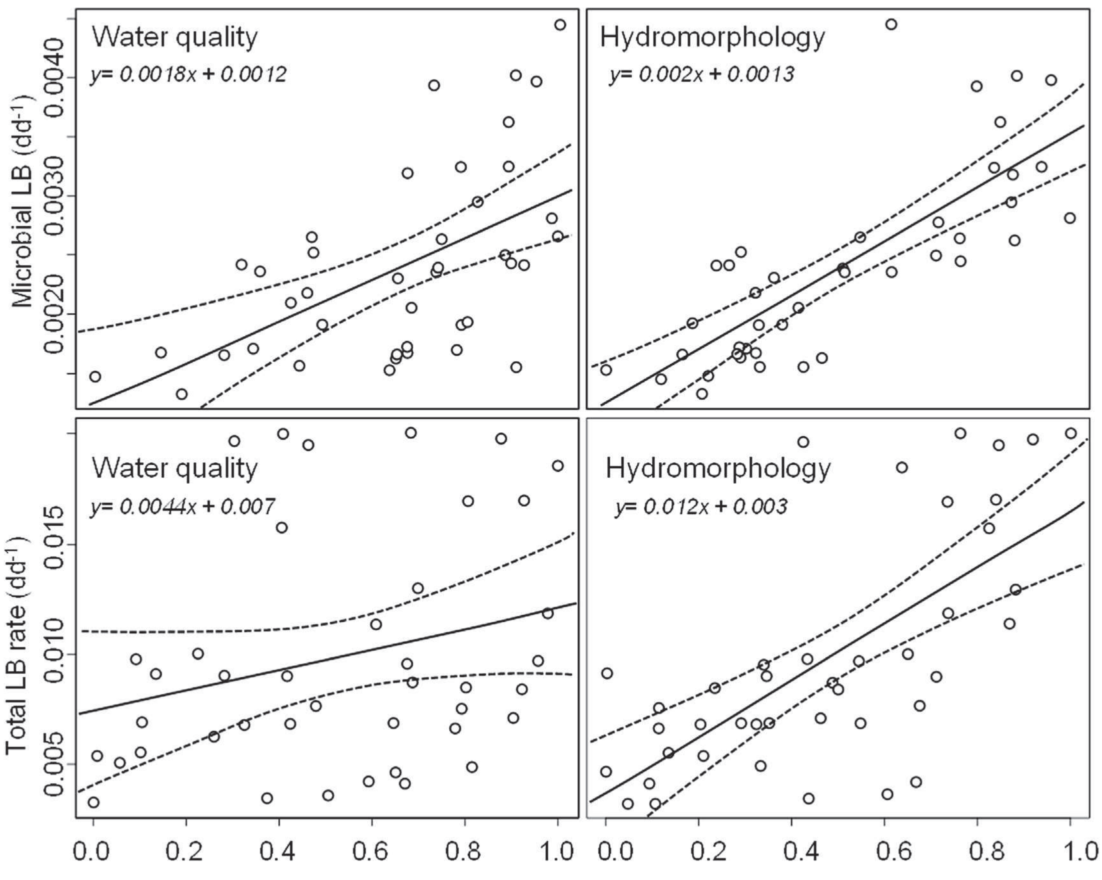

Fig. 5. Relationship between leaf breakdown rate and hydromorphological or chemical index. All figures show the leaf breakdown predicted along the range of each index (solid black lines) and associated 95% confidence intervals (dotted lines).

hydrological characteristics, hydromorphological pressures leading to a deficit of coarse sediment, decrease in sediment thickness and increase in sediment clogging were negatively correlated with microbial leaf breakdown. Streambed sediments constitute a long-term reservoir of fungal inoculum (Bärlocher et al., 2008). The structure and porosity of sediment matrix and the presence of organic carbon are important controlling factors for the dispersal and diversity of fungal communities (e.g. Bärlocher et al., 2006; Marmonier et al., 2010; Navel et al., 2012; Cornut et al., 2014; Ghate and Sridhar, 2015). Channelization typically modifies the sediment transport capacity of rivers, triggering morphological adjustments and leading to increased sediment clogging notably in agricultural areas due to increased input of fine sediment. Such alterations of river bed structure and substrate may profoundly impair fungal communities and associated leaf breakdown. This study elucidates that hydrological parameters have a major influence on total leaf breakdown particularly when defined at a large scale whereas morphological characteristics have a greater influence when defined at smaller scales. More specifically, total leaf breakdown was negatively correlated with the decrease in low flow replenishment capacity, the altered hydrological regime (i.e. alteration of the daily flow regime), the decrease in sediment transport capacity and the storage of sediment load that mainly occurs because of damming, diking and straightness. Such alterations lead to changes in channel sinuosity, the succession of facies, bank erosion and sediment discharge that may lead to significant modification of in-stream habitats for invertebrate communities as suggested by models performed at smaller scales. Indeed, total leaf breakdown were the lowest in uniform, narrow and deep channel with high velocity gradient. In such a constrained channel notably with a width/depth ratio <10, the suspended load may dominate total load leading to higher levels of clogging with fine sediments (Stewardson et al., 2016) and changes in riverbed composition and hyporheic chemical environment (Jones et al., 2012). In this channel, the retention potential of organic matter tends to decrease due to the lack of an effective retention structure (e.g. boulders, large woody debris) and high velocity gradient leading to decreased abundance and diversity of leaf-shredding invertebrates (e.g. Abelho, 2001; Lamouroux et al., 2004; Lepori et al., 2005; Muotka and Syrjänen, 2007). Therefore, the reduced leaf breakdown reported in this study is likely to be due to the impairment of macroinvertebrate diversity and abundance in response to reduced habitat heterogeneity as flow and substrate characteristics govern the distribution of invertebrates in streams and rivers (e.g. Beisel et al., 1998, 2000; Lancaster, 2000; Negishi et al., 2002).

4.2. *Importance of scales in ecology-hydromorphology linkages*

As expected, the relationship between hydromorphology and ecosystem functioning depends on the spatial scale of observation and the biological compartment considered. Indeed, microbial leaf breakdown was best predicted by hydromorphological features defined at the upstream catchment level probably due to the importance for fungal communities of hydrological characteristics that depend on processes operating at a large scale. In contrast, total leaf breakdown was best predicted by reach and habitat-level geomorphic variables probably due to the importance of instream habitats for invertebrate communities. In their study on 8 first- and second-order headwater streams, Sponseller and Benfield (2001) already reported a positive correlation between invertebrate-mediated leaf breakdown and mean particle size but they did not identify a significant correlation with land cover at the watershed level. Studies focusing on macroinvertebrate communities reported similarly weaker relationships between the watershed variables and lotic macroinvertebrate community composition in comparison with reach and local scales variables (e.g. Chaves et al., 2005; Feld and Hering, 2007; Johnson et al., 2007; Sandin, 2009). In contrast, some studies reported a stronger association between macroinvertebrate communities and watershed variables than between habitat and reach variables (Townsend et al., 2003; Urban et al., 2006; Dahm et al., 2013; Villeneuve et al., 2015). On one hand, these contrasted results may be related to the nature of variables used to describe the various spatial scales. Indeed, the latter studies focused on chemical parameters at local scale instead of hydromorphological variables or did not include quantitative data on hydromorphological features. On the other hand, in our study, some missing information as well as the heterogeneity of data used may have also influenced the scaling effect that we observed. The stream catchment size may also explain these conflicting results. Indeed, some authors emphasize that the catchment-wide land use variables may be more relevant for large catchment (superior to 100 km^2) whereas local scale variables (e.g. local instream habitat) may be more important in smaller streams (Johnson et al., 2001; Roy et al., 2003; Buck et al., 2004; Heino et al., 2004).

4.3. *Ranking hydromorphological and chemical alterations*

Dissolved oxygen was the main predictor of microbial and total leaf breakdown probably because high dissolved oxygen concentrations favor aerobic microbial respiration and fungal activities (e.g. Chergui and Pattee, 1988; Medeiros et al., 2008). Concentrations in phosphorus reactive soluble (SRP) were significantly correlated with higher microbial leaf breakdown. Numerous studies have reported that elevated concentrations of phosphorus in water stimulate fungal activity and conidial production leading to increased leaf breakdown (e.g. Suberkropp, 1998; Robinson and Gessner, 2000; Gulis and Suberkropp, 2004). In contrast, SRP concentrations were negatively correlated with total leaf breakdown suggesting that the positive effect of increased fungal activity in nutrient-enriched sites might be offset by other factors such as pollution from agricultural land use as suggested by the negative correlation between sulphate concentration and total leaf breakdown. Interestingly, potassium concentrations were positively correlated with microbial leaf breakdown. Potassium is an essential element for living cells performing important functions including osmoregulation, activation of enzyme synthesis and it is also involved in the stabilization of intracellular structures (Hughes and Poole, 1989; Gharieb, 2001). To maintain the proper intracellular potassium concentration, fungi must take up potassium from an external medium such as water or plant detritus (Benito et al., 2011). For both microbial and total leaf breakdown, relationships with the chemical quality of the water were weaker than with hydromorphological integrity, which independently explained up to 84.2% of the leaf breakdown. Some studies have already reported that macroinvertebrate assemblages and related biotic indices respond more to the channel morphological characteristics than water quality (Walters et al., 2009; Wyżga et al., 2013). Yet, chemical changes among sites were probably not sufficient to induce significant effects on leaf breakdown compared to hydromorphological changes. Furthermore, extrapolation of these results should deserve special attention because SYRAH parameters that we used to characterize hydromorphology were built using land cover data including human activities (e.g. surface of urbanization, agriculture, engineering works), inducing some overlap with water quality. As an illustration, the assessment of impairment risk of river bed structure and substrate by the SYRAH-CE approach is performed using four contributing latent variables including clogging by fine sediments. This latent variable is estimated by combining information on soil erosion, channel straightness and the surface in intensive agriculture. Consequently, the impairment risk of river bed structure and substrate may also indicate potential water quality impairment such as the decrease in oxygenation due to low flow conditions or sediments clogging, the increased nutrient concentrations or the presence of pollutants related to agricultural land use (e.g. pesticides). Complementary field experiments should thus include a more accurate characterization of water quality in space and time. Subsequent studies could select sites with a wide range of chemical pressures crossed with hydromorphological alterations to confirm the relative importance of hydromorphological integrity compared to chemical quality.

4.4. *Prospects for future eco-hydromorphological studies*

This study exemplifies the use of leaf breakdown in the biomonitoring of hydromorphological alterations. More specifically, leaf breakdown successfully responds to hydromorphological alterations and as such may provide a promising tool for indicating restoration success. Hydromorphological methodologies used in this study were chosen in order to fulfill the WFD requirements related to the assessment of quality parameters defined as "support" for the wellbeing of biological elements (Annex V, 1.1.1 WFD). Though these methodologies successfully identified the impacts of hydromorphological pressures on leaf breakdown, it appeared that the quantitative description of river characteristics collected with the CARHYCE protocol does probably not allow a complete integration of habitat complexity and heterogeneity. This lack of integration may have underestimate the importance of reach and habitat scales in explanation of leaf breakdown patterns, notably for invertebrate-mediated leaf processing. The data coming from the CARHYCE protocol however allowed identifying hydrological and morphological parameters that are key for leaf breakdown. If they do not unravel direct causalities and notably which pressures are exerted, they allow approaching them indirectly as the bed geometry described by the CARHYCE protocol may be considered a response parameter to anthropogenic pressures exerted at catchment scale. It is why it will have to be coupled to a larger extent in future studies to the SYRAH-CE assessment, which provides a complete picture of environmental impairment. Furthermore, even if water authority experts confirmed the SYRAH-CE assessment in 80% of the cases (Van Looy et al., 2015), the set of pressures and driving forces used is nonetheless not exhaustive. Besides, the bayesian belief networks (BBN) are constructed with causal relationships that were primarily quantified with elicited prior conditional probability tables by an expert panel and are consequently strongly dependent on current knowledge of geomorphological and hydrological processes. BBNs provide the most probable impairment level and the diagnostic confidence in the causal relationships for the impairment, given in the probability distribution. Here, we used probability for very high alteration as an indicator of the pressure level. Such an approach should be treated with caution as low probability does not necessarily suggest that the reach is not impaired to a lesser extent. Subsequent studies will provide more insight in the comparison of model results along the entire probability distribution. The multi-scale approach used in this study has distinctly increased the models' performance and as such the understanding of hydromorphology-ecology linkages highlighting the importance of such a hierarchical framework to design and deliver sustainable river management strategies. Yet, even if we have taken into account the hierarchically spatial organization of hydromorphological features and pressures operating on river ecosystems, we did not include links between spatial scales. To improve our understanding of the functioning of river ecosystems, subsequent studies should disentangle inter-scale relationships, for instance between pressures operating in the upstream catchment and resulting alterations of cross-section channels or prevailing chemical conditions at reach scale, by using raw data on the hydromorphological processes and structures for the different spatial scales.

5. Conclusion

This study allowed us to demonstrate the importance of hydromorphological integrity in the functioning of running waters. More specifically, this study identifies the hydromorphological pressures and factors controlling leaf breakdown and the spatial scales where such linkages operate. By combining an assessment of hydromorphological integrity based on protocols applied to biomonitoring networks and leaf breakdown assays, this framework should provide environmental decision-makers with the means to identify priority areas for restoration based on the damage risk of leaf litter processing and the management and restoration actions that have to be undertaken to maintain this key ecosystem function. For instance, small-scale restoration at a given point (e.g. diversification of flow facies or substrate within the wetted riverbed) in a context of a strongly altered upstream catchment is expected to lead to little improvement in ecological integrity compared to restoration that aims to considerably improve hydrological and morphological stream components by considering the processes that operate at the floodplain and upstream catchment levels. To be complete, further researches are needed, including on the causal links between the different spatial scales. Finally, this study has involved the direct transfer of a biomonitoring tool based on leaf breakdown to river managers providing interesting prospects for including the assessment of ecosystem functioning in current biomonitoring schemes.

Acknowledgements

This study was supported by the French national agency for water and aquatic ecosystems (ONEMA - Project 221-39). The authors thank the teams of the territorial services of Onema and their partners (i.e. Haut Jura and Morvan Natural Park) for their assistance during field and laboratory work. Finally, the authors would like to thank Julien Cornut, Sophie Chambord, Sylvain Lamothe and Frédéric Julien for their assistance in field and laboratory work. The authors are grateful to the anonymous reviewers for their suggestions that have significantly improved the quality of the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.watres.2017.01.061.

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