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Direct and indirect effects of multiple stressors on stream invertebrates across watershed, reach and site scales: a structural equation modelling better informing on hydromorphological impacts.

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Abstract

The purpose of our approach was to take into account the nested spatial scales driving stream functioning in the description of pressures/ecological status links by analysing the results of a hierarchical model. The development of this model has allowed us to answer the following questions: Does the consideration of the indirect links between anthropogenic pressures and stream ecological status modify the hierarchy of pressure types impacting benthic invertebrates? Do the different nested scales play different roles in the anthropogenic pressures/ecological status relationship? Does this model lead to better understanding of the specific role of hydromorphology in the evaluation of stream ecological status?

To achieve that goal, we used the Partial Least Square (PLS) path modelling method to develop a structural model linking variables describing (i) land use and hydromorphological alterations at the watershed scale, (ii) hydromorphological alterations at the reach scale, (iii) nutrients-organic matter contamination levels at the site scale, and (iv) substrate characteristics at the sampling site scale, to explain variation in values of a macroinvertebrate-based multimetric index: the French I₂M₂.

We have highlighted the importance of land use effects exerted on both hydromorphological and chemical characteristics of streams observed at finer scales and their subsequent indirect impact on stream ecological status. Hydromorphological alterations have an effect on the substrate mosaic structure and on the concentrations of nutrients and organic matter at site scale. This result implies that stream hydromorphology can have a major indirect effect on macroinvertebrate assemblages and that the hierarchy of impacts of anthropogenic pressures on stream ecological status generally described in the literature - often determining strategic restoration priorities - has to be re-examined. Finally, the effects of nutrients and organic matter on macroinvertebrate assemblages are lower than expected when all the indirect effects of land use and hydromorphological alterations are taken into account.

1. Introduction

Streams are open systems, and the structure, composition and functioning of the biocenoses they host are closely linked to peri-riverine human activities. In any ecosystems, functional processes interact at multiple spatial and temporal scales (Hynes, 1975; Lévêque, 2001). Streams more or less directly collect the rainfall water within the watershed. Any alteration of the neighbouring terrestrial ecosystems has potential impacts on stream water flow and fluxes of elements - and thus on the downstream aquatic ecosystems - over long distance and at long-term. The linear structure of streams makes autochthonous biotic communities particularly vulnerable to both (i) transversal structures that disrupt water, sediment and biological flows; and (ii) engineered in-stream or riverine structures brought to protect neighbouring areas from extreme meteorological events (Wasson et al., 1993). It has long been recognized that (i) stream functioning is organized according to a hierarchy of spatial scales (Allan, 2004; Frissell et al., 1986; Poff et al., 1997; Roth et al., 1996; Thorp, 2014; Thorp et al., 2006) from the regional scale to the microhabitat scale via the watershed and reach scales, and that (ii) the processes and structures observed at the largest scales (regional, watershed) influence the processes and structures observed at the smallest ones (reach, site). Streams are therefore complex dynamic systems, resulting from continuous adaptations of the liquid and solid compartments in permanent interaction. The geological and geographic contexts coupled with the climatic and hydrological regimes govern stream hydromorphological characteristics (Omernik, 1987). The hydromorphological, hydraulic and thermal characteristics of streams drive the available within-stream physical habitats. Local physical habitats, chemical conditions and the composition and attributes of the potential pool of colonists will determine the local species assemblage, in terms of both composition and structure. In addition to this schematic view, account must be taken of the natural variability of habitats (e.g. inter-annual variations in thermal and hydrological regimes) to which biological communities should be adapted (Piffady et al., 2013).

Moreover, according to the DPSIR concept (Driving forces, Pressures, State, Impact and Response; Kristensen, 2004), human activities (agriculture, urbanization) create driving forces for changes in the abiotic components (physico-chemistry, hydromorphology) of streams via the effects of combined pressures (chemical discharges, physical alterations). These anthropogenic pressures can be ranked hierarchically according to the relative importance of their impact at the different nested spatial scales described by Frissell et al. (1986; from watershed to habitat). Large sectors of intense human activity (e.g. agriculture, urbanization, industries) can have severe impact on the physico-chemical, hydromorphological and hydrological characteristics of streams, via sediment transport alteration, nutrient enrichment, toxic pollution, hydrological modifications, riparian clearing or habitat loss (Allan, 2004; Novotny et al., 2009; Paul and Meyer, 2001). Moreover, flow management for flood prevention, hydroelectricity production and irrigation modify hydraulic regimes, with possible hydromorphological (e.g. disruption in sediment transport continuity, stream bed incision) and thermal (water warming) drawbacks that modify local habitat conditions for biotic communities (Poff et al., 1997; Verdonschot et al., 2016; Villeneuve et al., 2015). The local degradation of stream channel geometry can modify habitats and biogeochemical processes (e.g. disruption of lateral connectivity, loss of connection with neighbouring terrestrial habitats and loss of effective cleaning action; Baker et al., 2012; Weigelhofer et al., 2013). Point and diffuse discharges of toxic substances

can also impair stream water quality and biotic communities (Archaimbault et al., 2010; Novotny, 2004; Usseglio-Polatera et al., 2001).

The European Water Framework Directive (WFD; European Council, 2000) does not only involve the assessment of the ecological status of water bodies but also the diagnostic of human activity impacts on water bodies. Consequently, it is necessary to provide practical guidelines to aquatic ecosystem managers for facilitating the design of efficient restoration strategies at the scale of coherent management units (e.g. the watershed and reach scales for streams). Although streams are subject to a large variety of significant driving forces and pressures, land use, eutrophication and habitat destruction have been clearly identified as the pressures exhibiting the greatest impacts (Stendera et al. 2012). Changes in land use, hydromorphology and physico-chemistry have already been linked individually to variations in biotic indices based on the taxonomic and/or functional characteristics of assemblages of macrophytes, diatoms, fish and macroinvertebrates (Dahm et al., 2013; Feld, 2013; Marzin et al., 2012; Sponseller et al., 2001; Sundermann et al., 2013; Villeneuve et al., 2015; Wasson et al., 2010). These studies have demonstrated that the links between pressures and biological indices are influenced by the spatial scale at which each pressure is taken into account (Allan, 2004; Allan et al., 1997; King et al., 2005; Lammert and Allan, 1999; Roth et al., 1996). Thus, watershed, hydromorphological reach and riparian corridor are spatial scales that considerably structure the effects of anthropogenic pressures on the ecological status of rivers observed at site scale (see also Marzin et al., 2012; Wasson et al., 2010). Shortly, the previous works have evidenced (i) the significant response of biotic indices to environmental variables characterizing gradients of nutrients, organic matter, hydromorphological pressures and land use at the watershed scale, (ii) the similarity of the core response pattern of all these biotic indices, but (iii) some between-indices differences in responses to specific pressure types, mainly regarding hydromorphology. Nevertheless, most of the time, the factors related to hydromorphological alteration have been ranked only at the third place (in order of decreasing importance of stream ecological status drivers) after physico-chemical and land-use factors. Both Dahm et al. (2013) and Villeneuve et al. (2015) have shown that the effects of hydromorphological pressures on biotic assemblages could be measured, but their impact on the set of tested biological metrics was relatively low. In summary, it seems possible to predict and clearly explain the ecological status of streams on the basis of pressure descriptors. However, the pressure descriptors selected in previous works didn't specifically take into account the multiple nested spatial scales that structure both the anthropogenic pressures and the longitudinal functioning of streams.

The main objective of our study was to explicitly examine the importance of the nested spatial organisation of streams on the links between anthropogenic pressures and stream ecological status, by building - and analysing the results of - a model based on the Partial Least Squares (PLS hereafter) path modelling method (Jakobowicz, 2007; Tenenhaus et al., 2005; Wold, 1982). This method was applied for simultaneously analysing the effects of latent variables (i.e. variables which are not directly observed but supposed to enter into the functioning of the streams under study: e.g. land-use, hydromorphological and physico-chemical pressures) on the ecological status of rivers synthetically measured in this study by the macroinvertebrate-based French biotic index for wadeable rivers [I_2M_2 ; (Mondy et al., 2012)], as an example of one of the multimetric indices already in use [see Birk et al. (2012) for a review]. The development of this model should allow us to answer the following questions:

- How does the consideration of the indirect links between anthropogenic pressures and stream ecological status modify the hierarchy of pressure types impacting benthic invertebrates?
- Do the different nested spatial scales play different roles in the anthropogenic pressures/ecological status relationships?
- Does the new PLS model tested lead to a better understanding of the specific role of hydromorphology in the evaluation of stream ecological status?

2. Material and methods

2.1 Typological classification of sites

The concept of “ecoregion” was adapted to aquatic ecosystems by Omernik (1987) to define water quality and regionalised management objectives and has been widely used in the USA (Omernik, 2004). The concept of “hydro-ecoregion” (HER), developed in France by Wasson et al. (2002), has been based on a top-down approach whose basic principle for stream classification relies much more on the global control factors (i.e. geology, relief and climate at the watershed scale) rather than their consequences at local level. This concept relies on the hypothesis of a hierarchical organization and control of stream habitat and functioning, in particular at the different nested spatial scales from the watershed to the micro-habitat (Frissell et al., 1986). Wasson et al. (2010) have demonstrated that hydro-ecoregions have the capacity to provide robust typological support for better analysing the causal links between land use and benthic macroinvertebrate assemblages.

For this study, we have chosen to avoid hydro-ecoregions with a too specific hydrological and morphological functioning. Consequently we have discarded the hydro-ecoregions of the mountain and Mediterranean regions, selecting only hydro-ecoregions of lowlands and hills (altitude lower than 450 m). More precisely, we have focused the analysis on two groups of hydro-ecoregions distinguished by their geology: ‘limestone’ vs. ‘non-limestone’. Streams of both groups were allocated to two size-based sub-groups to analyse independently small-sized wadeable streams (Strahler ranks from 1 to 3) and medium-sized wadeable streams (Strahler ranks from 4 to 6).

2.2 Biological data

We used information on benthic macroinvertebrate assemblages from a database of 1200 sites of the French monitoring network (RCS) achieved during the 2007-2012 period (Fig. 1).

From this database, it was possible to achieve a sufficient number of sampling events performed in the four groups of sites previously defined (§ 2.1). The first group, representing small non-limestone streams, consisted of 638 sampling events from 160 sites. The second group, representing medium-sized non-limestone streams, included 492 sampling events from 127 sites. The third group,

representing small limestone streams, was composed of 817 sampling events from 228 sites. The last group, representing medium-sized limestone streams, had 460 sampling events from 128 sites.

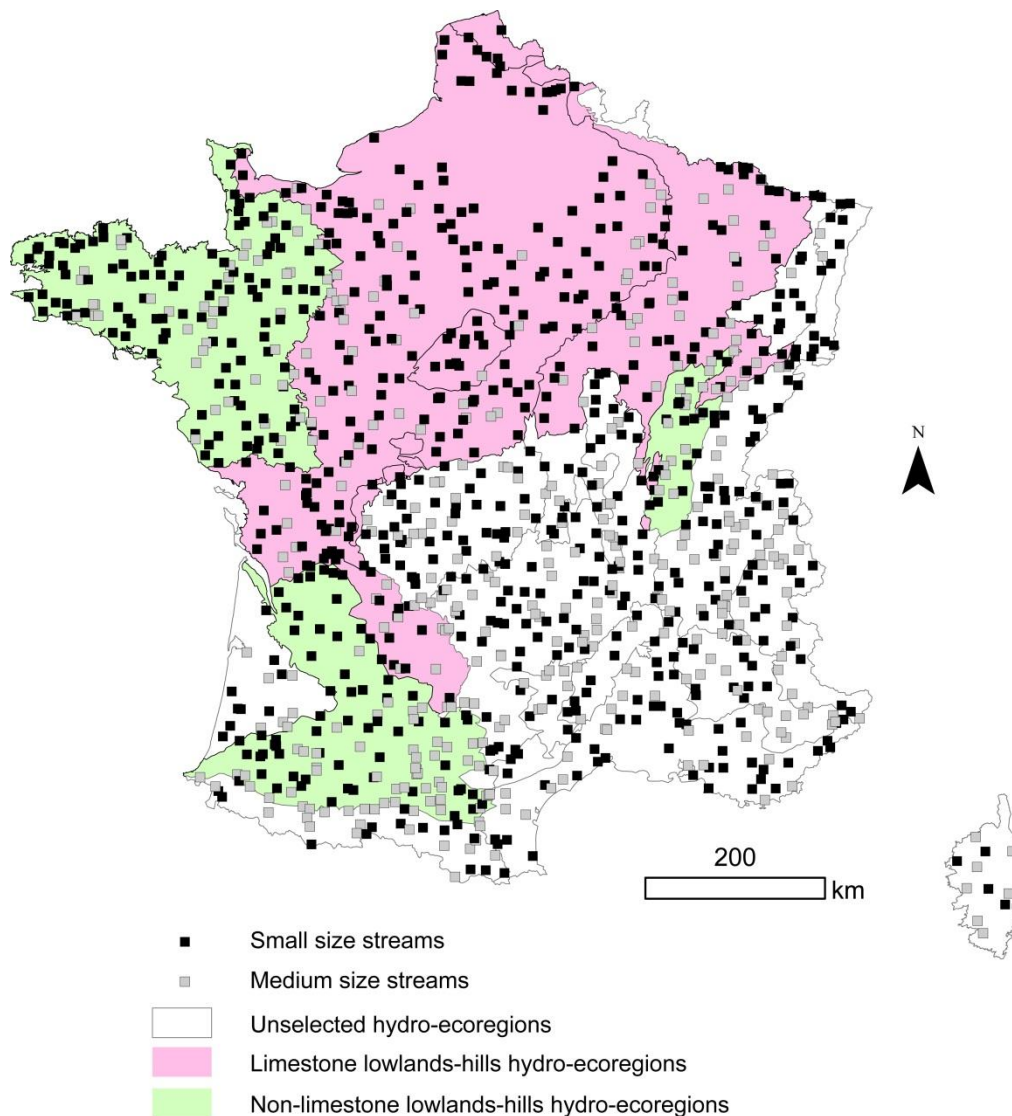


Figure 1. Spatial distribution of the 1200 sites of the French control and monitoring network (RCS) involved in this study.

The benthic macroinvertebrate assemblages were sampled using a common standardized protocol (AFNOR, 2009). The ecological quality of the sites was evaluated with the WFD-compliant biotic index proposed by Mondy et al. (2012) for French wadeable rivers (I_2M_2). This index takes into account the expected reference conditions for the corresponding river type and integrates several types of pressures through the combination and weighting (by pressure-type specific metric discrimination efficiency) of five taxonomy-based and trait-based metrics: (i) Shannon diversity index, (ii) original Average Score Per Taxon (ASPT), (iii) taxonomic richness, (iv) the relative frequency of polyvoltine organisms, and (v) the relative frequency of ovoviviparous organisms (see Mondy et al., 2012 for further details). These metrics were selected according to their ability to discriminate "impaired" sites from "least impaired" sites (based on 17 physico-chemical and hydromorphological pressure categories), their non-redundancy and their stability under reference conditions. Based on the applied sampling and sorting/identification strategies (AFNOR, 2009 and 2010, respectively), the I_2M_2

calculation process takes into account the deviation between the observed scores of individual metrics for a tested site and the corresponding river type-specific reference scores. Therefore, the I_2M_2 scores are expressed as Ecological Quality Ratios (EQR) with values close to “1” being indicative of near reference status and the values close to “0” indicating severe deviation from reference conditions.

2.3 Land use data

The layer of geographic data used was CORINE Land Cover (CLC) 2006 (Büttner and Kosztra, 2007). It covers the entire territory and is based on a standardized nomenclature ranked according to 44 items distributed in five main types of territorial cover: (i) urban, (ii) agricultural land, (iii) forests and semi-natural habitats, (iv) wetlands and (v) bodies of water.

On the basis of the stream catchment delimited beforehand by a digital field model, we calculated for each stream site the relative surface (%) of four groups of land use categories (Table 1) according to CORINE Land Cover nomenclature: (i) urbanization of the watershed (gathering urban areas, industrial and commercial areas, roads and highways, mines, dumps and construction sites, non-agricultural artificial green spaces), (ii) intensive agriculture (i.e. arable lands, permanent crops, orchards, vineyards, annual crops associated with permanent crops, cropping and field systems), (iii) non-intensive agriculture (i.e. meadows, territories mainly occupied by agriculture with considerable natural vegetation, agro-forestry territories) and non-anthropized spaces (i.e. forests and semi-natural habitats, wetlands, ponds).

2.4 Hydromorphological data

Two main types of descriptors of the pressures exerted on stream hydromorphological functioning were used: (i) descriptors at the watershed scale and (ii) descriptors at the hydromorphological reach scale (Table 1). At the watershed scale, we used information gathered during the 2000 national agricultural census on drainage, irrigation, erosion and ponds to characterize possible disturbance of both natural sediment and water flows. At the hydromorphological reach scale, we selected several descriptors of the hydromorphological alteration risk including the rate of upstream dams, the rate of stream crossings, the rate of roads in the stream vicinity, the rate of roads in the flood plain, the rate of dikes in the stream vicinity, the rate of dikes in the flood plain, the rate of “wind-break” afforestation on the banks, the rate of riparian forest on the banks, the rate of afforestation in the stream vicinity, the rate of “artificial” land use close to the stream vicinity, the rate of straight channel, the rate of surplus width and the depth/width ratio. These descriptors are generated using information from BD TOPO® database (3D vector description of the elements of the territory and of its infrastructures, of metric precision, exploitable on scales ranging from 1: 5000 to 1: 50000). These variables were assessed for each of the selected sites from the database, at the relevant spatial scales (watershed or reach).

Table 1. Description of pressure variables.

Scale	Variable	Average values (min-max range)
Watershed	urbanization of catchment: urbanized zones, industrial and commercial zones, transport networks, mines, dumps and construction sites, artificial green spaces, non agricultural spaces	3.3 (0.0-58.7)
Watershed	intensive agriculture: arable land, permanent crops, orchards, vineyards, olive orchards, annual crops linked to permanent crops, crop and field systems	35.5 (0.0-100.0)
Watershed	non-intensive agriculture: meadows, land mainly devoted to agriculture with considerable presence of natural vegetation, agro-forestry land	20.3 (0.0-89.9)
Watershed	non anthropized space: forests and semi-natural environments, wetlands, ponds	40.8 (0.0-100.0)
Watershed	Erosion	0.6 (0.0-3.4)
Watershed	Drainage ratio	0.03 (0.0-1.0)
Watershed	Irrigation ratio	0.03 (0.00-0.47)
Watershed	Ponds storage	0.03 (0.00-2.24)
Reach	Rate of roads/railways near the riverbed	7.8 (0.0-262.0)
Reach	Rate of roads/railways in the flood plain	111 (0-3087)
Reach	Rate of dykes in the riverbed	5 (0-393)
Reach	Rate of dikes in the flood plain	17 (0-764)
Reach	Rate of stream crossings	0.8 (0.0-8.5)
Reach	Rate of trees on banks "screen of trees"	77 (0-100)
Reach	Rate of vegetation on banks "riparian vegetation"	59 (0-100)
Reach	Rate of vegetation in riverbed	48 (0-100)
Reach	Rate of "artificial" type land use near riverbed	9.8 (0.0-100.0)
Reach	Rate of straightness	27.8 (0.0-100.0)
Reach	Rate of ponds in riverbed	0.7 (0.0-33.0)
Reach	Overwidth	41.4 (0.0-15742.0)
Reach	Anomaly index of Width/Depth ratio	3 (1-5)
Site	Suspended matter (mg/L)	20.5 (1.5-1347.0)
Site	Dissolved oxygen (mg/L)	10.1 (6.1-13.0)
Site	BOD5 at 20°C (mg/L)	1.6 (0.5-4.7)
Site	Ammonium (mg/L)	0.08 (0.00-0.47)
Site	Nitrites (mg/L)	0.01 (0.01-0.98)
Site	Nitrates (mg/L)	13.8 (0.3-70.4)
Site	Total Phosphorous (mg/L)	0.08 (0.01-0.48)
Site	Substrates mosaic : bryophytes, hydrophytes, litter, branches and root mats, pebbles and stones, rocks, gravel, helophytes, mud, sand and silt, algae and uniform or artificial area	-

2.5 Physico-chemical data

Informations on the physico-chemical characteristics of sites were obtained from the monthly physico-chemical survey of these sites belonging to the French national monitoring network (RCS). We selected the following parameters: ammonium, nitrites, nitrates, total phosphorous concentrations in water and BOD5 (Table 1). The mean values of these parameters during a one-year period covering the 11 months prior to the date of macroinvertebrate assemblage sampling and the month following this date, were chosen as descriptors of the nutrient and organic matter pressures on site assemblages.

2.6 Substrate mosaic

The relative surface (%) of pre-defined substrate-types within the benthic mosaic of each sampling site was used to describe the local habitat conditions of selected sites. Following the French norm NF T90-333 (AFNOR, 2009), twelve substrate types were considered: (i) bryophytes, (ii) hydrophytes, (iii) litter, (iv) branches and root mats, (v) pebbles and stones, (vi) rocks, (vii) gravel, (viii) helophytes, (ix) mud, (x) sand and silt, (xi) algae and (xii) uniform or artificial areas (Table 1).

2.7 Modelling method: the PLS approach

The PLS path modelling method (Wold, 1982) is a statistical method allowing to model complex relationships between observed (= manifest) and latent variables. This method was recently used by Riseng et al. (2011) to develop large scale causal models linking agricultural land use to measured in-stream conditions. This type of model belongs to the structural equation models (SEM) (Bizzi et al., 2013; Grace et al., 2010) which encompass a large number of statistical methods used to estimate complex causal relationships between latent and manifest variables. In recent years, this approach has become increasingly popular in various scientific communities including econometrics and social sciences (Vinzi et al., 2010).

A structural PLS model is described by two sub-models: (1) the measurement model (or external model) linking the manifest variables to the corresponding latent variables, and (2) the structural model (or internal model) taking into account the relationships among the latent variables (Vinzi et al., 2010).

We first estimated the latent variables with the external model (Tenenhaus et al., 2005). The external estimation Y_j of the latent variable ξ_j was built as a linear combination of the manifest variables x_{jh} :

$$Y_j = \sum_h w_{jh} x_{jh}$$

where w_j was the column vector of the coefficients w_{jh} . Variable Y_j was forced by standardization.

Then the internal estimation Z_j of the latent variables was performed using external estimations Y_i of latent variables ξ_i linked to ξ_j :

$$Z_j \propto \sum_i e_{ji} Y_i$$

where the \propto sign means that the variable positioned on the left of this sign is obtained by reducing the variable positioned on the right.

These two steps were repeated until reaching convergence. Then we estimated the coefficients e_{ji} of the model, called path coefficients, by PLS regressions. The hypothesis of nullity of these coefficients (H_0) was then tested using the bootstrap method for resampling. All the coefficients presented in this work were significant.

The main advantage of this method lays in its capacity to evaluate the direct and indirect effects of a latent variable “A” on another latent variable “B” (Sanchez, 2013). The direct effect is given by the path coefficient between the two variables A and B. The indirect effect, which corresponds to the potential influence of A on B via a third variable “C”, is calculated as the product of the path coefficients between A and C and between C and B, respectively. Finally, the total effect of a latent variable A on a latent variable B corresponds to the sum of these direct and indirect effects. For an easier interpretation of the structural model, the direct and total effects were calculated and converted into percentages to better represent the contribution of the latent variables to the variance explained by the model and rounded to avoid decimals. The details of the algorithm developed by Wold (1982) are available in Tenenhaus et al. (2005) or Jakobowicz (2007).

The structural model was evaluated on the basis of the predictive pertinence of the latent variables. For this purpose, it is advisable to analyse the multiple R^2 . According to Croutsche (2002), three thresholds of multiple R^2 can be taken into account. The model can be considered as significant if R^2 is higher than 10%; tangent if R^2 is between 5% and 10%, and not significant if R^2 is lower than 5%. Multiple R^2 have been rounded to avoid decimals.

Lastly, each structural equation was evaluated by the Stone-Geisser’s coefficient Q^2 , also called cross-validated redundancy index by Tenenhaus et al. (2005). It includes a cross-validated R^2 test between the manifest variables of an endogenous latent variable and all the manifest variables associated with the latent variables explaining the endogenous latent variable, using the structural model estimated. If the Q^2 value is positive, the model exhibits predictive validity. If the Q^2 value is negative, the model has no predictive validity (Tenenhaus et al., 2005).

Applying this methodology, we have developed a structural model (Fig. 2) linking the latent variables of: (i) land use, hydromorphological alterations at watershed scale, (ii) hydromorphological alterations at reach scale, (iii) concentrations of nutrients and organic matter, and substrate mosaic composition at site scale, with the objective to explain variations in the I_2M_2 macroinvertebrate-based index, for the four selected stream types.

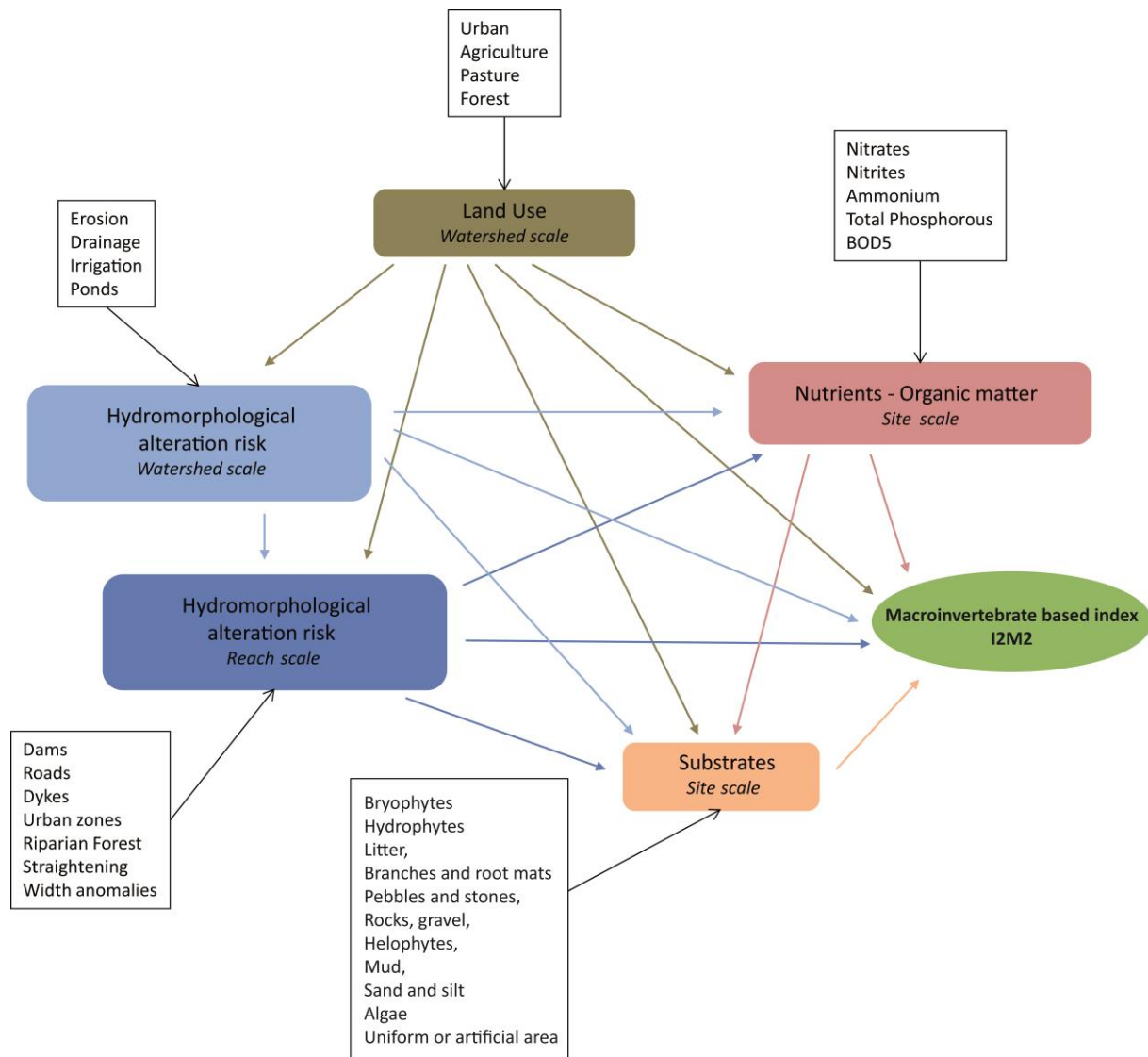


Figure 2: Design of the multiscale and multi-stressors structural model. Each latent variable is represented by a coloured box and each direct effect from this latent variable to another is represented by an arrow of the same colour. Each latent variable is a linear combination of the manifest variables listed in the black frame associated using a black arrow.

3. Results

3.1 Analysis and validation of the structural models

Analysing the validation index values for the structural model showed that this model is able to satisfactorily explain and predict the I_2M_2 values for the four selected stream types (Table 2) with a R^2 of 33% for the non-limestone small streams, 50% for the non-limestone medium streams, 44% for the limestone small streams and 40% for the limestone medium streams. All the Q^2 values being positive for the I_2M_2 (Table 2), the four models have shown good capacity of I_2M_2 prediction.

The hydromorphological alterations at the watershed scale were very poorly explained by land use at the same scale (R^2 varying from 1% to 4%; Fig. 3). The hydromorphological alterations at the reach scale were also rather poorly explained by land use and hydromorphological alterations at the watershed scale (R^2 from 10 to 19%; Fig. 3). At reach scale, most of the information was provided by land use (48 – 93% of the R^2 values; Fig. 3), underlining that the hydromorphological alteration risks at watershed and reach scales do not indicate the same processes.

The concentrations in nutrients and organic matter at the site scale were fairly explained by land use at the watershed scale and the risk of hydromorphological alterations both at the watershed and reach scales (R^2 varying from 27 to 57%, with always positive Q^2 values; Fig. 3).

The substrate mosaic of sampled sites was more or less successfully explained according to river types (R^2 varying from 10 to 51%; Fig. 3). It was better explained for medium-sized streams (51% and 28% for ‘non limestone’ and ‘limestone’ streams, respectively) than for small-sized streams (10% and 15%, respectively). The Q^2 values were positive only for medium-sized streams.

Table 2. Validation indices of the structural model : multiple R squared (R^2) and Stone-Geisser’s coefficient (Q^2). R^2 is the contribution to the variation in I_2M_2 values explained by the model. The model can be considered as significant if R^2 is higher than 10%; tangent if R^2 is between 5% and 10%, and not significant if R^2 is lower than 5%. Q^2 assess the model validity (If the Q^2 value is positive, the model exhibits predictive validity, if the Q^2 value is negative, the model has no predictive validity).

	Non limestone small streams		Non limestone medium streams		Limestone small streams		Limestone medium streams	
	R^2	Q^2	R^2	Q^2	R^2	Q^2	R^2	Q^2
Watershed hydromorphological alteration risk	2%	-0.14	4%	-0.11	1%	-0.16	1%	-0.09
Reach hydromorphological alteration risk	10%	-0.07	13%	-0.05	19%	-0.01	11%	-0.05
Nutrients and organic matter	27%	0.08	57%	0.36	42%	0.13	40%	0.15
Substrate mosaic	10%	-0.04	51%	0.07	15%	-0.03	28%	0.02
I_2M_2 biotic index	33%	0.24	50%	0.50	44%	0.32	40%	0.34

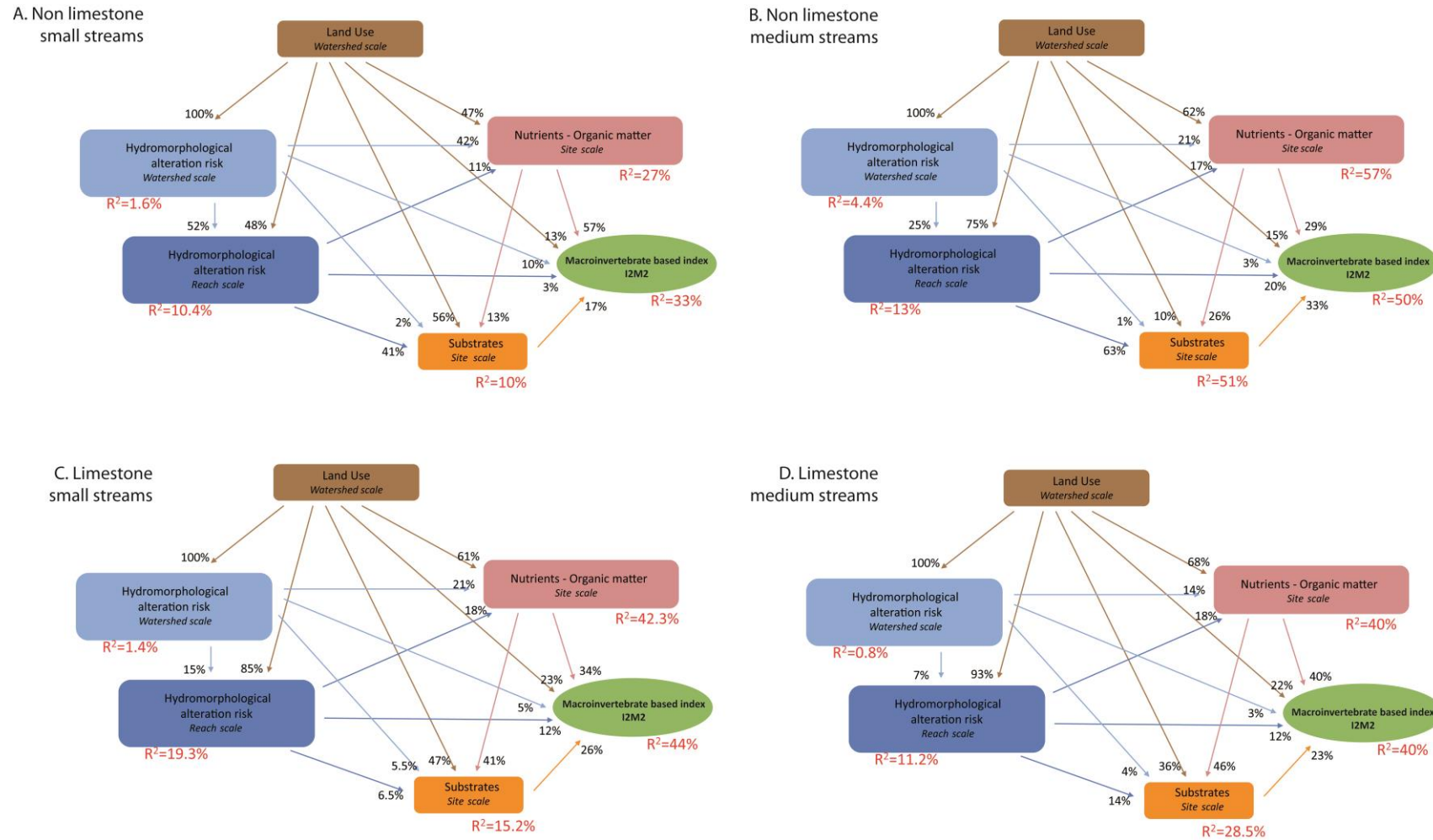


Figure 3. Models derived from PLS path modelling for non limestone small streams (A), non limestone medium streams (B), limestone small streams (C) and limestone medium streams (C). Each latent variable is represented by a coloured box and each direct effect from this latent variable to another is represented by an arrow of the same colour. R2 of each internal model are represented in red. Contributions of latent variables to the variation in I₂M₂ values explained by a model (in percentages of the model R2) are represented in black.

3.2 Direct effects

The latent variables with the greatest effects on the I_2M_2 values were most often the concentrations of nutrients and organic matter. However the response pattern differed according to stream type (Fig. 3). For non-limestone small streams, the order of decreasing contribution to the variation in I_2M_2 values explained by the model was: nutrients and organic matter (57%), substrate mosaic (17%), watershed land use (13%), hydromorphological alterations at the watershed (10%) and reach (3%) scales. For non-limestone medium-sized streams, this order was different: substrate mosaic (33%), nutrients and organic matter (29%), hydromorphological alterations at the reach scale (20%), watershed land use (15%) and hydromorphological alterations at the watershed scale (3%). For limestone small- and medium-sized streams, the order of decreasing contribution to I_2M_2 value variation was similar: nutrients and organic matter (34% and 40%, respectively), substrate mosaic (26% and 23%), watershed land use (23% and 22%), hydromorphological alterations at the reach (12% and 12%) and watershed (5% and 3%) scales.

3.3 Total effects (direct + indirect)

When focusing on the total effects (direct + indirect) of latent variables on the I_2M_2 values, although the variables with the major impact remained the concentrations in nutrients and organic matter for non-limestone small streams, the relative contributions of indirect effects considerably modified the hierarchical order of impacts of the other latent variables for the other stream types (Fig. 4). Indeed, for non-limestone small streams, the order of decreasing contribution to the variation in I_2M_2 values explained by the model was: nutrients and organic matter (42%), watershed land use (21%), hydromorphological alterations at the watershed scale (16%), substrate mosaic (15%) and hydromorphological alterations at the reach scale (6%). In contrast, in non-limestone medium-sized streams, the decreasing impact importance order was modified in: watershed land use (29%), hydromorphological alterations at the reach scale (29%), nutrients and organic matter (18%), substrate mosaic (17%) and hydromorphological alterations at the watershed scale (7%). For limestone small streams, this order was: watershed land use (33%), substrate mosaic (25.0%), nutrients and organic matter (19%), hydromorphological alterations at the reach (15%), and watershed (8%) scales. For limestone medium-sized streams, it was: watershed land use (35%), nutrients and organic matter (24%), substrate mosaic (18%), hydromorphological alterations at the reach (18%) and watershed (5%) scales.

3.4 Synthesis of the effects by spatial scale

Another potential way to consider the contributions of latent variables was to sum them by homogeneous level of spatial scale (Fig. 5). Land use and hydromorphological alterations at the watershed scale represented the watershed level. Hydromorphological alterations at the reach scale represented an intermediate spatial level covering pressures at the scale of the sub-watershed or the

hydromorphological reach. Substrate mosaic composition and concentrations in nutrients and organic matter represented explicative parameters observed directly at the site level.

When adding the direct contributions of the latent variables to the R^2 by level of scale, the site level exhibited the highest contribution to the variation in I_2M_2 values explained by the model (from 60% to 74% of the direct effect contribution to I_2M_2 variation). The remaining contribution was shared between the reach scale (from 3% to 20% of the R^2) and the watershed scale (from 18% to 28% of the R^2), thus exhibiting a greater contribution of the watershed scale to I_2M_2 variation.

When grouping the direct and indirect effects (= total effects), the watershed and reach scale effects on the biotic index values increased considerably, representing up to 65% of the total explained variance (42-65% according to stream types).

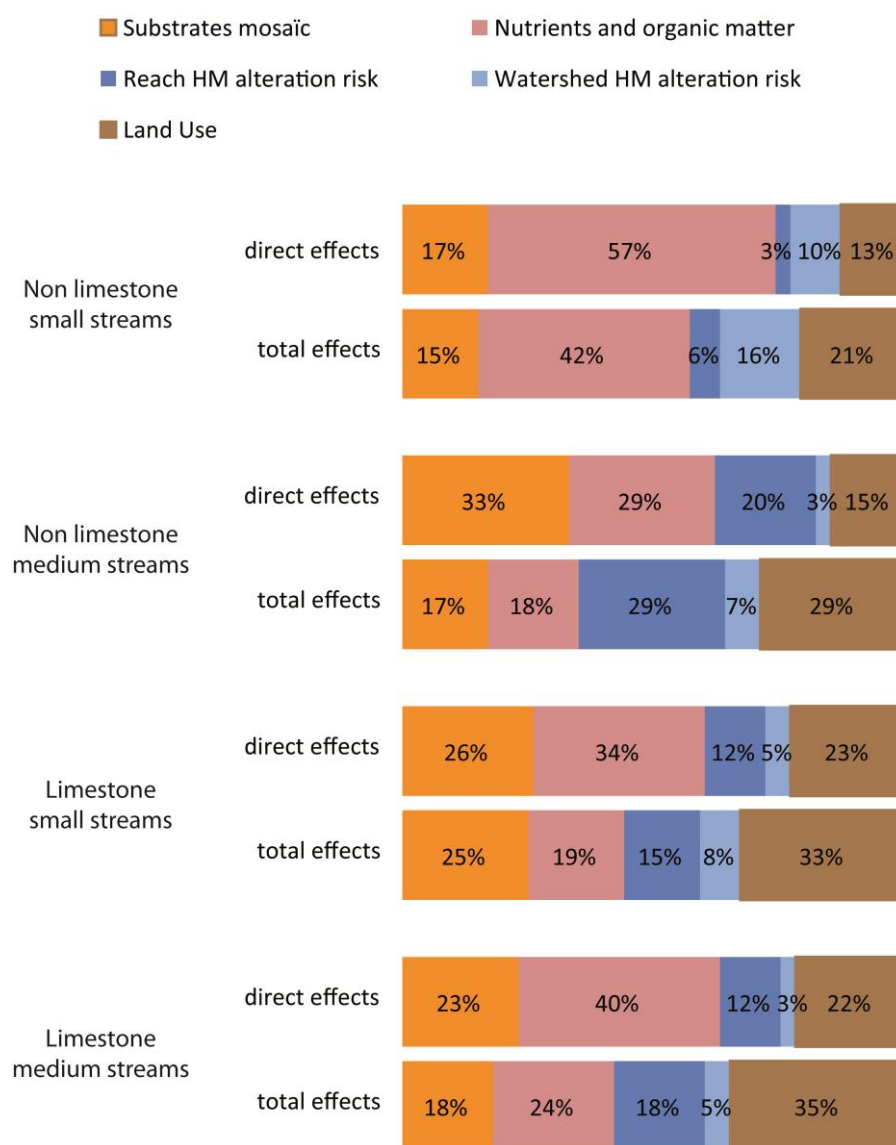


Figure 4. Relative contribution of latent variables to the variation in I_2M_2 values explained by the model taking into account direct effects only or total effects (directs + indirects) for the four stream types.

3.5 Focusing on the effects of hydromorphology

Lastly, the total of the direct contributions of the hydromorphological variables, both at the watershed and reach scales, represented from 13% to 23% of the total variance in the I_2M_2 values explained by the models (Fig. 4). These contributions increased from 6% (small-sized streams) to 13% (non-limestone medium-sized streams) when taking into account also the indirect effects of watershed and reach hydromorphology on the physico-chemical and habitat mosaic characteristics of sites, providing total contributions from 22% to 36% (depending on stream types) of the explained variance in I_2M_2 values.

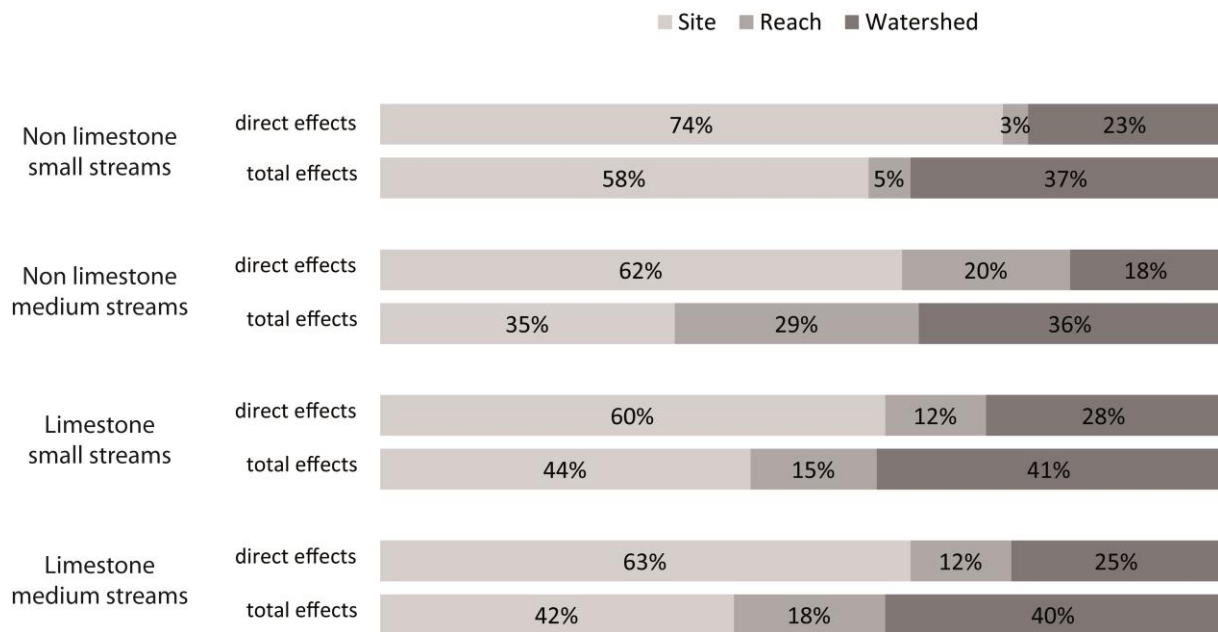


Figure 5. Relative contribution of scales levels to the variation in I_2M_2 values explained by the model taking into account direct effects only or total effects (directs + indirects) for the four stream types.

4. Discussion

The hierarchy of pressure categories can differ according to the type of stream studied. In hard water streams (i.e. limestone streams), hydromorphology and land use had a considerable impact on macroinvertebrate assemblages, sometimes greater than that of water physico-chemistry. In contrast, in soft-water small streams (i.e. non-limestone streams), physico-chemical parameters were the major drivers of the structure and composition of invertebrate assemblages, and then of the invertebrate-based biotic index variations. Hard-water habitats are naturally more productive than soft-water ones (Hill and Webster, 1982; Hill, 1992; Jin and Ward, 2007). Under natural conditions, low primary production limits the secondary production (Cross et al., 2006). The benthic invertebrate habitat conditions will be less buffered and more vulnerable to imbalance during physico-chemical stress in soft habitats. However, in hard-water habitats, since primary production is naturally higher, the secondary production would therefore be more stable and more effectively buffered when a physico-chemical stress occurs. Finally, stream ecological and geomorphic responses to anthropogenic pressures should be calibrated to the regional hydroclimatic, geological, and historical contexts in which the stream occurs, to determine the degree to which the responses of stream invertebrate assemblages to anthropogenic pressures are region-specific or region-independent and broadly transferable (Poff et al., 2006).

When considering only the direct effects of pressures, the variables acting at site scale were the major drivers of variation in stream ecological status. But when considering both the direct and indirect effects of anthropogenic pressures, the contributions of the variables acting at the watershed and reach scales greatly increased and became dominant, as predicted by most of the papers dealing with the hierarchical ordination of factors determining the ecological functioning of streams (e.g. Allan, 2004; Frissell et al., 1986; Poff et al., 1997; Roth et al., 1996; Thorp, 2014; Thorp et al., 2006; Wasson et al., 2002). At the watershed scale, the factors determining stream ecological functioning are depending on the “primary determinants” of geology (e.g. the nature of rocks), relief (geomorphology) and climate (temperatures and precipitations)(Frissell et al., 1986). Soils and vegetation within the watershed are components of the flow of water and sediment dynamics, although they are determined by geophysical and climatic characteristics. These factors influence processes at the reach scale, where abiotic factors of control drive the fluvial morpho-dynamics (e.g. bed shape and stability), the structure of the riverine vegetation (which significantly influences aquatic habitat conditions) and the stream connectivity (e.g. stream interactions with the floodable zone)(Montgomery & MacDonald 2002). Finally, at local scale, the biodiversity and productivity of benthic communities respond to key factors related to the physical habitat (hydraulics, substrate), the aquatic climate (light, temperature, dissolved gases, hydrochemistry) and the trophic resources (autochthonous primary production and exogenous organic matter)(Robinson et al. 2002). Moreover, the influence of habitat characteristics on major parameters like oxygenation and trophic resources led to assigning a preponderant role to the physical factors supporting in-stream biotic conditions.

Many studies examining the responses of biotic assemblages to various stressors acting at different spatial scales, have often shown a preponderant impact of physico-chemical parameters measured at the site scale (e.g. nutrients and organic matter). This major effect was followed, in order of decreasing importance of biotic impact, by land use at the watershed scale, and then by hydromorphological alteration factors, whose effects are much more difficult to evidence (Dahm et

al., 2013; Villeneuve et al., 2015). For example, Hering et al. (2006) have shown that assemblages of macroinvertebrates, diatoms, macrophytes and fish responded less strongly to land use gradient than to nutrient enrichment. However, their study did not take into account the indirect effects of land use. In addition, they have highlighted the potential alteration of biotic communities through numerous cause-effect relationships acting individually or in concert, including the effects of sedimentation and hydromorphological alteration, diffuse contaminations as well as direct inputs of toxic substances (metals, pesticides). Our results were consistent with these previous works that had shown the preponderant effect of water physico-chemistry – but also bottom substrate composition - on biotic assemblages at the site scale.

However, considering the indirect effects of land use has shown clearly that, except for non-limestone small streams, the global effect of land use on invertebrate assemblages could be more important than the global effect of nutrients and organic matter (cf. Fig. 4). Different human activities (urbanization, agriculture, industry, transport, etc.) generate strong pressures on the aquatic environments. These pressures can be expressed at the local and reach scales by metrics measuring physico-chemical and hydromorphological alterations, respectively. At the watershed scale, land use descriptors have also the potential to highlight the presence of stressor sources potentially altering the ecological status of rivers at the site scale (Allan, 2004). Indeed, several works have already demonstrated that land use has an effect on macroinvertebrate assemblages at multiple scales (Wang and Kanehl, 2003; Wang et al., 2007; Weigel et al., 2003). Consequently, whatever the scale of measurement applied to abiotic variables (watershed, reach or site), we can consider that the direct effects best measure the impact of individual variables at the site scale whereas the indirect effects best measure the impact of individual variables at larger scales.

Both urban and agricultural areas have a major direct impact on biotic assemblages, as highlighted by many authors (Allan, 2004; Clapcott et al., 2012; Dahm et al., 2013; Marzin et al., 2012; Marzin et al., 2013). Such link appears quite more clearly in the analysis of our model results due to the clear separation of direct from indirect effects, something that had not been done before. The presence of a heavily anthropized upstream catchment can have three types of impact on streams (Allan, 2004; Effenberger et al., 2006; Paul and Meyer, 2001; Stepenuck et al., 2002): it increases (i) runoff and thus erosion and diffuse pollution; (ii) chemical contamination; and (iii) the alteration of stream hydromorphological functioning (e.g. via riparian vegetation eradication, water course straightening and re-gauging, and stream bottom incision). As a result, land use can be an efficient indirect descriptor of the pressures exerted on a stream, at the different functional scales structuring this aquatic ecosystem (Allan, 2004). We have found similar results with our models with significant contributions of land use on the characteristics of the hydromorphological reach, the water physico-chemistry and the composition of the site substrates mosaic. Furthermore, when measuring the direct effects of land use at the site scale, we omitted all the indirect processes (e.g. the potential increase in N and P concentrations or in the clogging risk) that govern these effects.

The main objective of selecting hydromorphological alteration descriptors was to take into account explicitly alterations of non-natural origin that could be clearly correlated with the degradation of stream ecological status. This strategy has allowed us to consider different stream watershed (agriculture, urbanization, transport) and stream channel (transport, energy, tourism) uses, resulting in potential alterations of in-stream structures and hydromorphological processes. The observed responses of benthic macroinvertebrates to changes in hydromorphology (reach scale) support the results of a lot of previous studies (Buffagni et al., 2004; Hering et al., 2004; Lorenz et al., 2004).

However, in most of the previous studies (e.g. Dahm et al., 2013; Hering et al., 2006; Villeneuve et al., 2015), the biotic impact of hydromorphological alterations was considered as less important than that of physico-chemical parameters and land use with the conclusion that if the effects of hydromorphological pressures could be measured, their impact was relatively weak on biological metrics. Two aspects of our modelling design have advocated for re-evaluating the impact of hydromorphological pressures on stream macroinvertebrate assemblages: (i) the explicit taking into account of two levels of spatial scale (watershed and reach) and (ii) the analysis of indirect effects of hydromorphological alteration on physico-chemical characteristics and habitat mosaic attributes of sites. Indeed, the total contribution of hydromorphological descriptors - at both watershed and reach scales - to invertebrate-based biotic index variation corresponded to about the same amount of impact as land use, when considering either direct or indirect effects (Fig. 4). Enhancing the description of hydromorphological pressures has provided a better appraisal of the link between hydromorphology and stream biological status. Obviously, the alteration of hydromorphological processes at the reach scale directly acts on macroinvertebrate assemblages by degrading their benthic habitats. The presence of weirs or dikes, the alteration of banks, the degradation of the riparian vegetation and of the bed geometry can lead, in particular, to the modification of the in-stream facies which become more lentic, thereby directly modifying the available benthic substrate mosaic. Previous studies have already addressed the role of spatial scales in hydromorphological alterations–community relationships (Dahm et al., 2013; Feld and Hering, 2007; Hering et al., 2006; Lamouroux et al., 2004). In consistency with our results, they have highlighted the important role of processes acting at the reach scale in these relationships. Our analysis has reinforced the robustness of such results because based on a larger data set of 643 sites and more than 2,400 sampling events. Taking into account the alterations linked to erosion of agricultural surfaces, irrigation, drainage and water storage at large spatial scale allows the inclusion of processes acting at the watershed scale even if such processes can also act directly on biotic assemblages at the reach and site scales. The direct effects of these variables could be evidenced by an increase in suspended (and deposited) fine sediments and clogging risk, and more severe droughts. Moreover, we have demonstrated that stream hydromorphology has a direct effect on nutrient and organic matter flows. A modification of the morphological facies can potentially modify the residence time of molecules, the infiltration rate in the downwelling areas, the self-purification capacity of streams and other internal physico-chemical processes depending on hydromorphological conditions (Baker et al., 2012). Consequently, taking into account these indirect effects via the concentrations of nutrients and organic matter can enhance the explained proportion of the total effect of hydromorphology (at watershed and reach scales) on macroinvertebrate assemblage structure and functions.

Riseng et al. (2011) highlighted the ability of structural equations modelling to build conceptual causal models (i.e. models that represent the hypothesized causal linkages among variables in the system to analyze). The PLS Path modelling method, which belongs to the structural equation modelling (SEM) family, has allowed us (i) to develop a model taking into account the hierarchical spatial organization of streams by considering three scales (watershed, reach and site) and (ii) to evaluate both the direct and indirect effects of several categories of pressures on stream macroinvertebrate assemblages. Understanding the effects of multiple stressors - acting as multiple spatial scales - is not straightforward, in particular if strong stressor interactions are supposed to influence the responses of biological or ecological characteristics of biotic assemblages (Feld et al., 2016). Today, managers urgently need tools that can support them in the decision making process for protecting and restoring river ecosystems, either for biodiversity conservation or restoration

issues. The major interests of the holistic approach developed in this work are, in particular, to identify (i) the large upstream landscape structures generating the pressures significantly acting on stream ecological status at the site scale and (ii) the most suitable management scale for preserving or restoring a given site (Forbes et al 2008, Thoms et al., Van Looy et al., 2015, Vorosmarty et al., 2010). However, our approach does not describe the whole chain of causality ranging from large scale structures and human activities to natural local process alterations, potentially acting at the different scales of functioning of river ecosystems. Clearly understanding this chain of causality is an extremely ambitious challenge. However, current knowledge does not allow to quantify precisely all the mechanisms involved in such processes (Downes 2010, Norris et al., 2012). Many mechanisms are still unknown, or difficult to characterize due to the lack of data (e.g. disruption in sediment transport continuity or stream bed incision). But we are now able to provide two major pieces of information to managers based on solid evidence. First, the restoration or conservation actions conducted at the watershed or reach scales can have significant effects on stream ecological status at the site scale. Second, hydromorphological alterations play an important role in the relationship between nutrient/organic matter flows and stream ecological status.

5. Conclusions

The aim of this study was to address three specific points: the indirect effects of anthropogenic pressures on stream ecological status, the individual importance of processes at three nested spatial scales (watershed, reach and site) on stream ecological status, and the specific role of hydromorphology in pressures-impacts relationships.

First, taking into account the indirect structuring effects of anthropogenic pressures for explaining variations in the French invertebrate-based biotic index has made possible to revise the hierarchy of pressure-type impacts. Indeed, when focusing on the total (direct + indirect) effects of latent variables on the I_2M_2 values, the contribution of indirect effects can deeply modify the hierarchy of impacts of the different latent variables (except for small non-limestone streams). More precisely, the total contribution of land use and hydromorphological alteration risk to the biotic index value variations increases while the contribution of physico-chemical parameters (nutrient and organic matter concentrations) decreases.

Second, we have highlighted the importance of the site scale (physico-chemical variables and benthic substrate mosaic descriptors) in explaining stream biological condition. We have demonstrated also the important role of variables measured at the reach scale, both directly via their effects on local habitat features, and indirectly via their confounding effects on the relationship between water physico-chemistry and macroinvertebrate assemblage structure and composition (integrated by the biotic index). Lastly, we have shown that the variables measured at the watershed scale (i.e. land use and large scale hydromorphological characteristics) integrate all the types of upstream pressures acting at finer scales and play a strong structural role on the stream invertebrate assemblages through their indirect effects on all the pressure types.

Third, we have shown the indirect role of hydromorphology on the relationships between other pressures and stream ecological status. These relationships require further study to more precisely

identify the involved underlying processes, which are of particular interest for optimizing decision making on future physical restorations of streams.

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