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Method Article

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A process-based framework for diagnosing floodplain ecological functioning to guide riverine wetland restoration

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Abstract:

Riverine wetlands are key components of fluvial systems, but their restoration remains challenging. In most cases, restoration projects are designed at the local scale, often with the primary objective of increasing water depth soon after intervention. Such approaches often fail to deliver durable ecological benefits because they do not account for the processes that control wetland functioning.

This study proposes a hierarchical process-based framework that integrates climatic, geological, hydrogeological, geomorphological, physicochemical and ecological information to diagnose floodplain ecological functioning and identify the dominant controls operating from the catchment to the wetland scale. The framework first delineates functional river sectors and then identifies wetlands with the greatest potential for durable ecological restoration within the favourable sectors.

Restoration planning begin by identifying river sectors where geomorphological and hydrogeological conditions may be favourable (higher-gradient river sectors characterised by sufficient flow velocity during floods and significant inputs of good-quality groundwater). Within these favourable sectors, wetlands are subsequently prioritised according to their geomorphological, hydrogeological and trophic characteristics.

Applied to the Ognon River (France) as a case study, the framework identifies five functional sectors with contrasting restoration potential and demonstrates the practical implementation of the proposed hierarchical approach.

Because it is based on the hierarchical diagnosis of the dominant processes governing floodplain ecological functioning, the proposed framework provides a practical decision-support tool for restoration planning and may be transferable to temperate river systems.

Keywords: hydrogeology, hydrological connectivity, river incision, geomorphology, aquatic vegetation, flood

Statements and Declarations:

1.1. Statements and Declarations

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The authors declare that they have no competing interests.
Ethics Approval
Not applicable.
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Data Availability
Environmental data used in this study were obtained from publicly available databases or collected by the authors. The datasets generated or analysed during the study are available from the corresponding author upon reasonable request.
Author Contributions
G. Bornette: funding acquisition, conceptualization, project administration, methodology, supervision, validation, writing - original draft, writing - review and editing
C Henriot: conceptualization, methodology, writing - review and editing
J Coris: formal analysis, investigation, validation, visualization
A Chiarello: data curation, investigation, visualization, validation

2. Introduction

Freshwater ecosystems are key components of global biodiversity, acting as major biodiversity reservoirs, and providing a wide range of ecosystem services to billions of people worldwide (Millennium-Ecosystem-Assessment, 2005). However, they face cumulative threats and extensive losses due to human activities, posing significant risks to aquatic resources, biodiversity, and human and animal health.

Floodplains are among the most threatened freshwater ecosystems, facing multiple disruptions to their functioning, including embankments, weirs, dams, gravel extraction, eutrophication, river incision, discharge of toxic substances, artificialisation of riverbanks, and groundwater withdrawal. All these alterations lead to the loss of spatial and temporal heterogeneity, ecological productivity, and biodiversity in floodplains (Tockner and Stanford, 2002; Museth et al., 2011; Jähnig et al., 2022; Wenskus et al., 2025).

Riverine wetlands are key ecological components of floodplains and make an essential contribution to floodplain biodiversity and productivity (Tockner and Stanford, 2002; Bornette et al., 2008; Petsch et al., 2023). These ecosystems are functionally highly diverse, as their functioning and dynamics are governed by numerous interacting natural and anthropogenic factors. Furthermore, riverine wetlands are the main sites of aquatic primary production in floodplains and provide food, shelter, breeding sites, and temporary habitats for aquatic organisms (Junk et al., 1989; Amoros and Bornette, 2002; Steffensen et al., 2014; Feng et al., 2025; Teng et al., 2025).

Many studies have addressed the ecological functioning of riverine wetlands, mostly focusing on their physical description through parameters such as size, depth, water permanency, and chemical characteristics (Finlayson and van der Valk, 1995; Semeniuk and Semeniuk, 1995; Nummi et al., 2024). Most of these studies attempted to correlate physical and biological descriptors and therefore included partial assessments of biological communities.

Belletti et al. (2018) compared the restoration of river sections over a period of up to 15 years following restoration, incorporating interventions on the main channel (e.g. removal of dykes) and on the alluvial side channels (reconnection, dredging). This large-scale study reported an improvment in the hydromorphological quality of the sectors. However, restoration measures that increase lateral connectivity may simultaneously reduce habitat differentiation between the main channel and floodplain wetlands, potentially reducing biodiversity and the availability of refuges (Bravard et al., 1997; Paillex et al., 2012).

At the same time, studies have analysed the processes at work in the functioning and dynamics of alluvial plains, demonstrating 1) the key role of the nature of floods (whether erosive or depositional), that lead either to depositional processes, and a rapid filling of riverine wetlands (Rostan et al., 1997), or exportation of fine sediment during floods, that may slow down, and even stop long-term filling of channels (Bornette et al., 1994a; Bornette et al., 1994b), and 2) the role of connections between groundwater tables and wetlands, that may slow down, and even stop successional processes (Bornette and Amoros, 1991; Bornette et al., 1994a; Bornette et al., 1994c), depending on the wetland slope, hydraulic capacity, and groundwater discharge.

These studies have placed these various functional patterns within a geomorphological framework (Bornette et al., 1998; Bornette et al., 2008). Some research has even demonstrated the decisive role of these processes in the response of alluvial wetlands to ecological restoration through dredging (Combroux et al., 2002; Henry et al., 2002; Amoros et al., 2003). These studies showed that restoration may lead to depositional processes and sometimes limited ecological benefits or limited persistence of the restored aquatic stage. Furthermore, restoration efforts are often designed without adequately anticipating their ecological benefits and long-term persistence, due to a limited integration of robust scientific knowledge on ecosystem functioning (Schirmer et al., 2014; Riquier et al., 2017). These shortcomings often result in a short-lived aquatic phase, little or no short-term biodiversity gains, and may even promote the proliferation of invasive species (Combroux et al., 2002; DeMeester and deB. Richter, 2009; Moreno-Mateos et al., 2012; Paillex et al., 2012; Wang and Pei, 2012; Dieras et al., 2013; Verdonschot and Verdonschot, 2022).

Together, these findings highlight the need for a framework that connects floodplain-scale processes to expected wetland restoration outcomes while fully considering the complex hydraulic, hydrogeological, geomorphological, and trophic processes along floodplains and within wetlands, for planning management and restoration strategies that maximize both ecological benefits and long-term sustainability of restorations (Palmer et al., 2005).

The aim of this study is consequently to develop an operational framework built on floodplain-scale drivers to

support process-based diagnosis of riverine wetland functioning and subsequently guide restoration strategies, using the Ognon River (Eastern France) as a case study.
This objective requires a hydrosystem-scale analysis of floodplain functioning integrating multiple sources of ecological information into a coherent and operational framework to identify ecological drivers operating across broad spatial and temporal scales, enabling the functional delineation of the floodplain into river reaches, and the subsequent identification of wetlands where management actions can be strategically targeted, thereby maximizing the benefit of potential restorations (Belletti et al., 2018; Verdonschot and Verdonschot, 2022).
For this purpose, we combined climatic, geological, hydrogeological, geomorphological, and trophic status information. Aquatic vegetation was used as a complementary biological indicator providing information at the wetland scale on groundwater connectivity, influence of flood disturbances, and nutrient content of the riverine wetlands (Amoros et al., 2000; Bornette et al., 2008; Bornette and Puijalon, 2011; Corenblit et al., 2024). This approach allowed us to divide the floodplain into functional sectors. Subsequently, the ecological potential of each functional sector for wetland restoration was evaluated. Based on this sectorization, rules are provided to guide the selection of riverine wetlands within each functional sector according to their expected restoration benefits and the persistence of the restored aquatic stage.

3. Operational framework for floodplain sectorisation

The proposed framework for the functional sectorization of the floodplain is based on the hierarchical use of environmental drivers of floodplain functioning. At the largest (*i.e.,* floodplain) scale, climatic, geological, and hydrogeological factors act as primary controls. At the intermediate scale (*i.e* river reaches), geomorphological and trophic conditions modulate hydrological connectivity and disturbance regimes. At the local scale (*i.e.,* riverine wetlands), wetland geomorphology and connectivity with the river rule surface and groundwater connectivity, and nutrient content of the wetland, and thus ecosystem functioning and successional trajectory, thereby the potential needs for restoration.

3.1. Drivers acting at the floodplain scale

3.1.1. Climate

At the floodplain scale, climatic conditions rule temperature regimes and variability in river flow. Indeed, climate, by regulating rainfall, partly controls the river power and transport capacity (Ficke et al., 2007). Temperature governs the oxygen concentration in water and sediments (Jane et al., 2023), its concentration decreasing at high temperatures due to physical degassing and consumption by microbes . Temperature also governs vegetation dormancy (Bornette and Puijalon, 2011) and summer phytoplankton growth (Lürling et al., 2017; Dory et al., 2024). Consequently, increasing water temperatures strongly amplify the ecological impacts of nutrient enrichment (Jeppesen et al., 2009; Nazari-Sharabian et al., 2018). Climate rules also throught river flow the frequency and scale of floodplain inundation. At the floodplain scale, climate thus modulates flood frequency and intensity, eutrophication intensity and seasonal oxygen stress (Junk et al., 1989; Tockner and Stanford, 2002; Jeppesen et al., 2009).

3.1.2. Geology of the catchment area

Geological structures determine physico-chemical characteristics of surface water and groundwater feeding riverine wetlands, thereby influencing their primary production, succession rates, and biodiversity.
In a crystalline context, water pH and conductivity are low, and dissolved inorganic carbon is present at low concentrations. This has a major impact on aquatic primary producers, which require carbon to synthesise carbon chains (sugars, starch, lignin) through photosynthesis. In this context, angiosperm biodiversity is low, as few species can tolerate chronic carbon deficiency. Primary productivity also remains low, even though nitrogen and phosphorus concentrations are not limiting factors (Carbiener et al., 1995). Few aquatic plant species are adapted to this chronic limitation in carbon availability (*e.g.,* Isoetids such as *Lobelia dortmanna, Isoetes lacustris,* or *Littorella uniflora* (Keeley, 1998; Madsen et al., 2002). Conversely, in alkaline environments, many angiosperm species are able to use bicarbonate as a carbon source, thus avoiding carbon deficiency (Maberly and Madsen, 1998; Maberly and Madsen, 2002). This results in much higher biodiversity and plant biomass, with productivity becoming then limited by nitrogen and phosphorus.

3.1.3. Hydrogeology

Hydrogeology regulates groundwater inputs and physico-chemical characteristics of riverine wetlands. In siliceous massifs, aquifers are often absent or poorly developed, leading to limited groundwater inflows to the alluvial plain. In alkaline, and especially karstic contexts, aquifers are often well developed and can supply alluvial valleys with abundant carbonate-rich groundwater (Meybeck, 1987; Meybeck, 2003). Karstic groundwater inputs to riverine wetlands help to maintain cool, oxygenated conditions (Bornette and Large, 1995; Winter et al., 1998; Hayashi and Rosenberry, 2002). Phytoplankton development is limited, bacterial activity is reduced, and anoxic conditions are less frequent, thereby reducing the accumulation of ammonium and other reduced chemical compounds in sediments (Brunke and Gonser, 1997; Bornette and Puijalon, 2011). Despite the lower temperatures associated with karstic groundwater, submerged macrophytes are favoured because the positive effects of increased water transparency and sediment oxidation outweigh the negative effects of temperature on plant growth (Bornette and Puijalon, 2009; Bornette and Puijalon, 2011).

River incision alters the connectivity between groundwater and riverine wetlands. Incised river channels tend to drain lateral aquatic environments and adjacent aquifers, reducing surface and subsurface water exchanges between the river and its floodplain, and increasing hydraulic gradients between the river and the hillslope aquifer (Bravard et al., 1997; Amoros and Bornette, 2002). This shift in connectivity profoundly alters riverine wetland functioning and successional trajectories (Bornette and Heiler, 1994; Marston et al., 1995; Bornette et al., 1996).

3.1.4. Drivers acting at the river reach scale

3.1.4.1. Geomorphology

Geomorphology acts at river reach and wetland scales.

At the river reach scale, it controls hydrological connectivity, disturbance regimes and habitat characteristics. These factors, in turn, influence ecological processes and biodiversity patterns (Ward et al., 1999; Thoms, 2003). River dynamics are controlled by channel slope and sediment supply from watershed erosion. Anthropogenic pressures strongly influence these dynamics. River embankments, aggregate extraction, and hydroelectric dam construction, combined with upstream sediment deficits, have caused severe channel incision and reduced river mobility in most European watercourses (Galay, 1983; Arnaud-Fassetta, 2003). The incision of the riverbed reduces the frequency and intensity of river overflows into wetlands (Bravard, 1994; Bravard et al., 1997). Disconnected riverine wetlands are gradually filled with organic matter, and sediment mobilization during floods decreases markedly, and may even stop. As a consequence, the biodiversity of the river declines in response to the disappearance of riverine wetlands (Bayley, 1991, 1995; Tockner et al., 1999).

3.1.4.2. Nutrient dynamics

At the river reach scale, land use and hydrological connectivity control spatial patterns of nutrient enrichment (Hayashi and Rosenberry, 2002; Allan, 2004). Indeed, the nutrient content of surface waters is determined both by land use within the river reach (e.g. fertilized crops) and by urban effluents. In an unincised river, wastewater discharges into the main channel tend to cause river eutrophication, which leads to the nutrient enrichment of seepage water. In an incised river, river seepage is restricted to a narrow zone along the river channel, and has a limited influence on floodplain ecosystems. In this situation, agricultural practices, by fertilising the land, still contribute to increase nutrient concentrations in surface water and groundwater inputs from hillslopes.

3.1.5. Drivers acting at the riverine wetland scale

3.1.5.1. Geomorphology

Wetland morphologies are inherited from the river dynamics prevailing at the time of their formation and strongly govern their present-day functioning (Amoros and Bornette, 2002). More particularly, geomorphology controls wetland sinuosity, cross section, and relative slope, and consequently water velocity during floods, sediment dynamics, and successional trajectories. Riverine wetlands can display a wide range of morphologies, even within the same river reach. This leads to the coexistence within the same alluvial sector of riverine wetlands of different styles, created at different periods in the history of the river and therefore functioning differently (Bravard, 1987; Amoros and Bornette, 2002; Thoms, 2003).

Disturbances by floods are events that promote the establishment of high biodiversity in riverine wetlands. The intensity of this control depends on the frequency of overflows, but also on the morphology of the wetland and its slope (Bornette et al., 1998; Bornette et al., 2001).

Meandering riverine wetlands are comparable to the active river channel in terms of wetted channel cross-section. These are generated by the abandonment of river meanders under conditions of low channel slope and fine bed material (silt, clay, sand). During floods, water first enters the downstream part of the wetland and, as discharge increases, may subsequently overflow upstream. In this configuration, water masses originating from upstream and downstream collide within the meander wetland, promoting intense sedimentation. As a result, these wetlands have usually high sedimentation rates when they are connected to floods. When disconnected from floods, their dynamics depend primarily on nutrient availability. In nutrient-rich environments, plant productivity is high and wetlands fill relatively rapidly (Rostan et al., 1997; Citterio and Piégay, 2009) although generally much more slowly than during flood-driven sedimentation, from 1 to several cm.year^{-1} (Rostan et al., 1997). In nutrient-poor environments, productivity remains low and infilling rates are considerably reduced, allowing former meanders (oxbow lakes) to function as peat-forming systems (Bornette et al., 1998). In all cases, even if groundwater inflows are present, water renewal within such wetlands remains slow due to low channel slope and high hydraulic capacity. At advanced successional stages, particularly in highly eutrophic channels, sediment clogging progressively prevents groundwater inflows, further enhancing eutrophication processes (Bornette et al., 1994b; Bornette et al., 1998).

Braided-style riverine wetlands result from braided river pattern with multiple, shallow, parallel channels. These wetlands are weakly sinuous and have a cross-section that is low compared to that of the river channel. Their slope is usually steep, similar to that of the alluvial valley in which they formed. These channels are abandoned following the formation of alluvial plugs at their upstream and then downstream connections during floods. When groundwater inflows are significant and/or channel slope is steep, infilling dynamics may be slowed or even halted (Bornette et al., 1994a; Bornette et al., 1994b).

Anastomosing riverine wetlands originate from river systems with multiple channels, gentler slopes, and finer bed material than braided systems (Makaske, 2001). These wetlands can be highly sinuous, especially in their downstream sections, but share morphological similarities with braided channels, including relatively parallel banks and alternating riffles and pools (Liu and Wang, 2017). Their low gradient and sinuosity favour sediment deposition in their deepest and more sinuous parts during floods, leading to progressive disconnection from hyporheic exchanges as the channel bed becomes clogged. As a result, these channels tend to accumulate nutrient-rich fine sediments and are often colonised by species tolerant of eutrophic conditions (Liu and Wang, 2017).

3.1.5.2. Nutrient and contaminant inputs

The hydromorphological context outlined above partly determines the pace and intensity of eutrophication. Wetland eutrophication is driven by nutrient enrichment, particularly nitrogen and phosphorus, and can occur gradually and naturally during autogenic succession through the accumulation of detrital organic matter (Bornette et al., 1998). It can be accelerated and accentuated by global warming and human activities through increased inputs of organic matter, nitrogen, and phosphorus (Jarrige, 2012; Bornette et al., 2017). Eutrophication promotes the growth of floating plants and phytoplankton, among them toxic cyanobacteria in the more eutrophic situations, leading to a more rapid accumulation of organic matter (Carpenter, 2005). As a result, biological oxygen demand increases due to enhanced bacterial activity, promoting more frequent and intense anoxic conditions (Diaz and Rosenberg, 2008; Reddy and DeLaune, 2008), leading to a decline in aquatic fauna (*i.e.,* invertebrates and fishes). In addition to anoxia, the increased turbidity and the accumulation of unconsolidated organic sediments reduce light availability and root anchorage, further contributing to the decline of rooted macrophytes (Scheffer and van Nes, 2007). These conditions ultimately lead to the disappearance of rooted plants, and a strong decline in biodiversity (Jeppesen et al., 2000). Low-temperature groundwater inflows or flash floods that flush out part of the organic and nutrient-rich sediments can limit eutrophication (Henry et al., 2002).

Finally, a particularly severe impact arises from the release of pesticides and herbicides into watercourses through leaching from large-scale agriculture, which, as in terrestrial environments, can cause widespread mortality of aquatic species and, indirectly, the collapse of invertebrate populations, thereby reducing the food source for fish and birds (Beketov et al., 2013; Sharma et al., 2024). Although these contaminants can strongly impact aquatic organisms and food webs (Beketov et al., 2013; Sharma et al., 2024), their effects are not explicitly addressed here, as the present study focuses on nutrient-driven processes and hydromorphological controls of wetland functioning.

The functioning of riverine wetlands is consequently controlled by the interaction between hydrological connectivity, geomorphological dynamics, and groundwater inputs, which operate across spatial (*i.e.,* from the floodplain to each riverine wetland) and temporal scales. The integration of these hierarchical controls provides a transferable framework for identifying functional floodplain sectors and predicting wetland functioning across diverse hydrosystems.
This study addresses this gap by proposing a structured methodology that explicitly links data acquisition, functional interpretation, and restoration planning across spatial scales.

4. Materials and methods

The methodological approach formalises the processes to be documented at each spatial scale (*i.e.,* floodplain, river reaches, and riverine wetlands) to achieve a functional zoning of the floodplain that identifies the main controls on wetland functioning within each sector.

The top-down approach is organised as follows:

1) Compilation of knowledge concerning the climatic, geological, hydrogeological, geomorphological, agricultural pressures and physico-chemical characteristics of the floodplain,
2) Identification of large-scale controls (climate, geology, hydrogeology, nutrient content of surface and groundwater, anthropogenic land use: agriculture, grasslands, or forests), and of the spatial boundaries associated with changes in these controls,
3) Hierarchical integration of these limits for partitioning the floodplain into sectors with similar environmental conditions. Geology and hydrogeology define the major units; geomorphological and trophic characteristics then enable these to be subdivided, in particular according to the effects of river regulation and agricultural uses. Alkalinity helps to characterise these units, rather than necessarily constituting an independent basis for sector delineation,
4) For each identified sector, identification of the implications of the associated environmental constraints (mainly related to hydrogeology, geomorphology and trophic characteristics), for wetland dynamics,
5) For each wetland, knowing the functional context (main controls on wetland functioning within the sector), characterization of its specific functioning using biological (vegetation) and geomorphological (slope, sinuosity, connectivity) descriptors in order to determine the appropriate management approach (and, where necessary, to consider restoration strategies).

The method has been applied to the Ognon River, France, as a case study. The Ognon Valley is located in eastern France. The Ognon River is a tributary of the Saône River and drains a catchment area of 2,308 km² (Fig. 1). The Ognon River rises at an elevation of 904 m and flows into the Saône River at an elevation of 185 m, after a course of 214 km, with an average gradient of 3.3 ‰. Its average annual discharge at the Saône confluence is 34 $m^3.s^{-1}$.

The geology, hydrogeology, and land use of the floodplain were documented from BRGM (geology, https://infoterre.brgm.fr/page/cartes-geologiques), ADES (hydrogeology, https://ades.eaufrance.fr/), NAIADES (chemical characteristics of surface water, https://naiades.eaufrance.fr/), and Carte.Gouv (location and sinuosity of riverine wetlands, land use) national bases. These datasets were used to characterise environmental gradients and to identify spatial patterns in floodplain functioning. Topographic data were obtained from the French national 1:25,000 topographic map series (https://cartes.gouv.fr/explorer-les-cartes/).

Physico-chemical characteristics of surface water and groundwater were integrated in the functional zonation. For this purpose, the average values for each sampling point and each physico-chemical parameter were calculated (we selected sampling points in surface water and groundwater that were documented monthly over the last three years, *i.e*., from 2023 to 2025; ADES and NAÏADES national databases). The location of each sampled point is indicated in figures presented in supplementary material. Using R (R-4.5.0, v2025.04.0+450), a script was written to extract these data from an API (application programming interface) on the Hub'eau public data platform. The following APIs were used: ‘watercourse quality’ and ‘groundwater quality’. Ammonium, nitrates, and orthophosphates were used as indicators of water eutrophication, and we used P and N eutrophication classes indicated by carbiener and collaborators in the figures (Carbiener et al., 1990). The limits

of the classes for conductivity were chosen for distinguishing acidic, basic and neutral environments. Conductivity from our own measurements during the field visit of wetlands were also included in the map.

Geomorphological information (location of weirs, river slope, information about river alteration by human practices) has been previously documented (Malavoi, 2003).

Aquatic vegetation, which is mostly perennial, was used here as an integrative proxy of hydrological and biogeochemical conditions in the riverine wetlands. From May to July 2025, we visited each of the 105 wetlands across the alluvial plain once (n = 105 wetlands visited, 35 still having an aquatic zone and integrated in the final maps). We identified all the aquatic plant species present in each aquatic zone of the wetland. The relative slope of all the wetlands (dry or not) was calculated and integrated in a figure. the relative slope, interpreted in conjunction with sinuosity and connectivity, is an indicator of the relative propensity for sediment deposition during floods.

Most of them were related to the meandering pattern. Aquatic plants were used as biological indicators of water quality, hydraulic disturbance patterns, and connectivity with groundwater (Amoros et al., 2000). The trophic level, indication of groundwater inputs, potential influence of floods, was inferred from the presence of indicator species using the method published by Amoros et al., 2000.

We documented several functional qualitative indicators for each visited wetland: wetland cross-section (low, high), sinuosity (low, high), and grain size (organic sedimentary deposits, minerals, coarse grain size, and if possible thickness of deposits). Even if a single measure needs to be considered with caution, we also measured electrical conductivity of the water that was further plotted on the maps (see supplementary data). We also recorded qualitatively field indicators of hydraulic connectivity between the watercourse and the wetland (classified as : permanent: wetland connected permanently to the river, temporary: wetland connected temporary to the river, and occurrence of field evidence of connexions, or no field evidence of connection), based on evidence such as silt deposits on trees, flood marks, and mobile sediment banks.

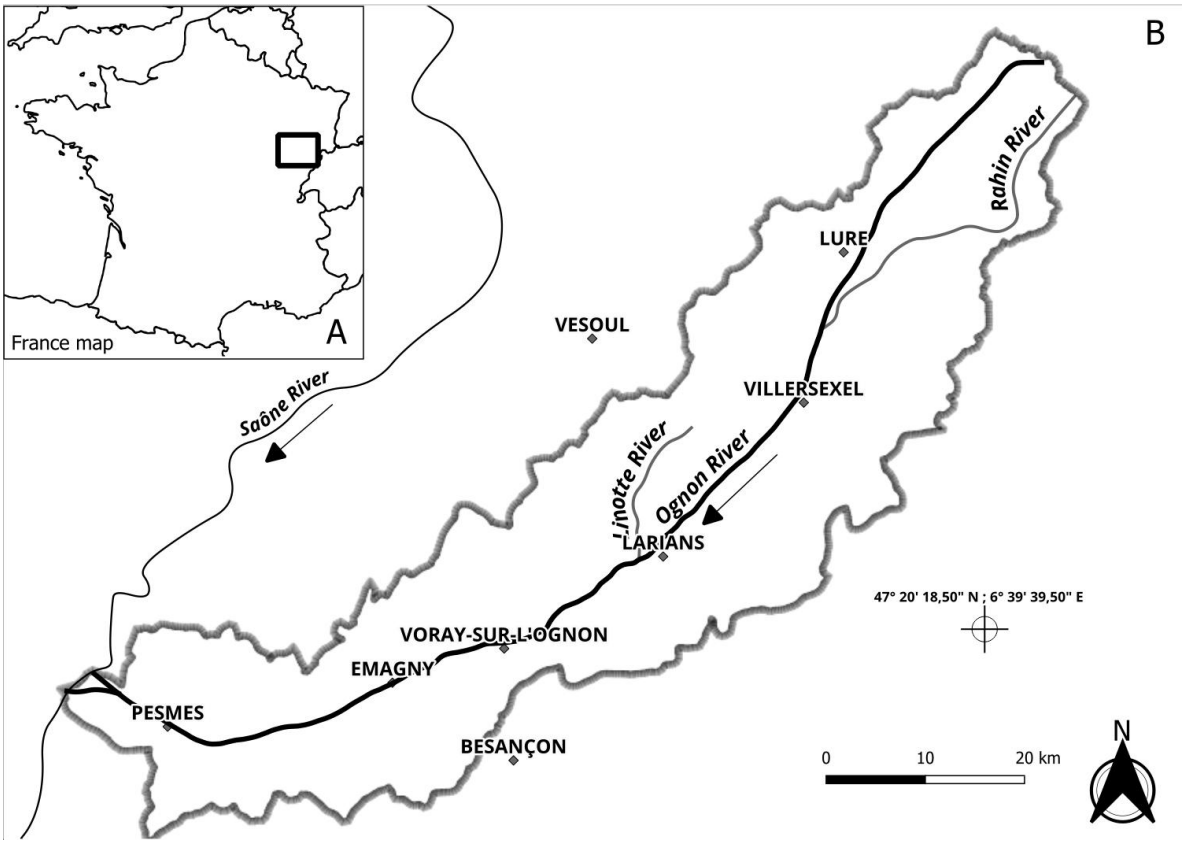


Figure 1. The Ognon River watershed, France. The gray line around the river indicates the limits of the watershed. Major cities and the main tributaries are shown on the map. The coordinate reference system is WGS84.

5. Results

5.1. Climate and hydrological context

The Ognon hydrological regime is pluvio-nival, with floods occurring mainly during the winter-spring period as a result of snowmelt and prolonged rainfall. The upstream mountainous section has a mountainous to semi-continental climate, characterised by abundant rainfall and sustained spring discharges promoting active channel dynamics. In the middle and lower valley, the climate becomes temperate to semi-continental, with moderate rainfall throughout the year, warmer summers, less pronounced winters, marked seasonal variability in river flows, and lower flood intensity.

5.2. Geological context

The geological characterisation of the river's watershed made it possible to identify the more alkaline and more crystalline areas, which directly regulate groundwater inputs to surface water, and consequently the water renewal and physico-chemical characteristics of riverine wetlands (Supplementary material 1 and 2).

Upstream, the river flows on the ancient crystalline basement of the Vosges Mountains, characterised by fissure-permeable terrain, poor water drainage, and a scarcity of springs. These siliceous alluvial deposits are low in carbonate. Around Lure, Holocene calcareous deposits cover Triassic carbonate-rich marls as far as Villersexel (right bank). Downstream of Villersexel on the right bank and Rougemont on the left bank, the limestones of the Middle and Upper Jurassic border the Middle and Lower Ognon Valley.

From the Vosges Mountains to the Saône River, the Ognon River and its main tributaries have deposited sificant layers of alluvial deposits, both recent and ancient, which originate from the destruction of crystalline rocks under the action of glacial erosion.

In addition to these longitudinal contrasts, the Ognon valley features four terraced slopes in its karstic section, which are still occurring almost exclusively on the left bank of the watercourse, on a gentle slope 4 to 5 km wide, while the right bank is mostly steep and largely encased in the limestone and marly limestone of the edge of the Vesoul plateaus (Campy, 1978). Along the right bank, the impermeable Lias formations (marl layers) form a barrier at the base of the limestone, so that the top of these marl layers is often marked by springs that flow into the river and therefore have little impact on the wetlands.

These geological features identify delineate two geologically and hydrogeologically distinct reaches. The upper acidic reach is characterized by a crystalline basement and associated siliceous alluvial deposits, which probably poorly contribute to the floodplain groundwater supplies. On the other hand, downstream of the city of Villersexel (along the right river bank) and Rougemont (along the left one), a lower alkaline reach is characterized by karstic formations (Lias and Middle to Upper Jurassic limestones), with potentially strong alkaline groundwater inputs to the floodplain, particularly along the left banks where preserved terraces border the river floodplain.

5.3. Hydrogeological context

The geological structure described above exerts a strong control on groundwater bodies and on the quality and quantity of groundwater inflows to the river and its associated wetlands.

Public databases (https://www.sandre.eaufrance.fr/v2/) identify 11 outcropping groundwater bodies, including two main ones that cover more than 60 % of the catchment area (Supplementary material 3). Upstream of the river, and as far as Villersexel on the right bank, the rock formations are slightly permeable and can be grouped into a low-flow acidic aquifer unit, which borders the permeable alluvial deposits of the river (existence of an accompanying water table). Downstream, the Jurassic limestone aquifer borders the river on the right bank,

from Villersexel to the confluence of the River and the Saône River (brownish polygons, Supplementary material 3). On the left bank, the terraced limestone aquifer rests on Lias marl and feeds the alluvial valley with alkaline water via resurgences in the riverine wetlands (orange polygones, Supplementary material 3). Information about the surface and groundwater conductivity, were superimposed on the map of groundwater bodies (triangular and diamond-shaped dots, Supplementary material 3).

Diagnoses of groundwater inflows based on vegetation were conducted for each aquatic riverine wetland and documented following established approaches (Bonetto et al., 1994; Amoros et al., 2000; Paran et al., 2015). As wetland–groundwater connectivity was not documented at individual wetland sites, the presence of groundwater inflows was inferred from the occurrence of species associated with cool well-oxygenated waters, which are unsually intolerant to root anoxia (Amoros et al.,2000; Fig. 2), allowing sites to be classified into two categories: those with vegetation-based evidence of groundwater inflows and those without evidence of such inflows (i.e., lacking indicator species). The spatial distribution of vegetation-based evidence of groundwater inflows was interpreted alongside geological and hydrogeological information to help delineate floodplain sectors potentially influenced by hillslope groundwater inputs.

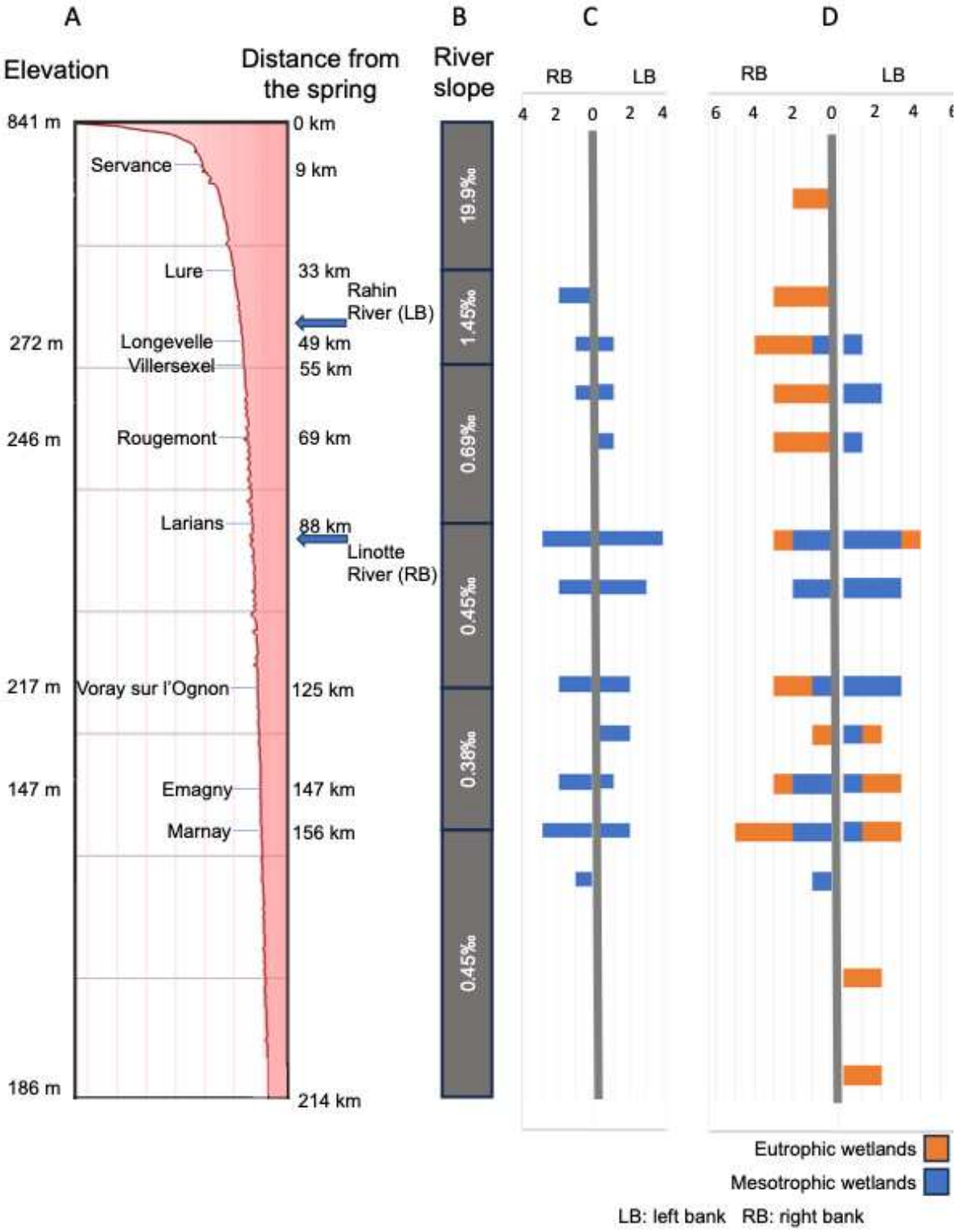


Figure 2. Geographical, geomorphological, and ecological features of the Ognon River, France. (A) River elevation along the watercourse. Key cities are presented. (B) River slope per river reach. (C) Number of groundwater-supplied wetlands per 10 km of watercourse based on the ecological requirements of observed

aquatic plants. (D) Number of wetlands per trophic level per 10 km of watercourse based on the ecological requirements of observed aquatic plants.

Riverine wetlands benefiting from groundwater inflows (*i.e.,* identified by indicator species, Fig. 2 and Supplementary material 3 were mostly located in the middle section of the river, between Villersexel and Marnay, a reach reported to be influenced by alkaline waters, particularly along the left bank (Fig. 2), indicating a strong convergence between biological and hydrogeological indicators.

Due to river incision (Bravard et al., 1997), riverine wetlands are poorly supplied by river water during low water levels. The physico-chemical quality of the riverine wetlands therefore results mainly from the phreatic context in which they are located, as indicated by the higher conductivity of wetland waters than in the river in the considered reaches (Supplementary material 3). It should be noted, however, that the wetlands located along sections of the river regulated by a weir are likely fed by backflows and seepage from the river, as they exhibit similar conductivity levels to the river itself.

5.4. Geomorphological patterns and flood disturbances

Historically, the Ognon River had a significant lateral mobility, with active meandering sections and locally anastomosed areas, indicating a natural ability to reshape its bed in response to floods and sediment transport dynamics (Malavoi, 2003). The lateral mobility of the riverbed is nowadays very limited: bank protection works carried out in the 1990s locked in the natural contours of the riverbed, reducing sediment inputs from bank erosion, and more than 45 weirs and dams along the watercourse (Malavoi, 2003) that trap alluvium and stabilise the longitudinal profile of the riverbed. Furthermore, extensive aggregate extraction in the 1950s-70s largely depleted the coarse reserves of the floodplain.

From its source to downstream to Villersexel, the river watercourse has a steep gradient (approximately 19.9 ‰ over the first four kilometres, then 1.45 ‰; Fig. 2). The river then takes on the characteristics of a lowland watercourse with a gradient reduced to around 0.45-0.69 ‰ until it joins the Saône River (Malavoi, 2003). The river functions there as a low-energy, sediment-starved system, dominated by incision and floodplain disconnection. This development has direct consequences on the river's ability to maintain a mosaic of diverse habitats.

These geomorphological alterations directly control groundwater levels and their connectivity to riverine wetlands. The incision of the minor riverbed leads to a concomitant sinking of the alluvial aquifer and increased drainage of the lateral aquifers by the river. The decline in the alluvial aquifer level results in the hydrological isolation of riverine wetlands located furthest from the river and can ultimately lead to the drying and collapse of aquatic communities, as they become disconnected and effectively perched above the main watercourse (Winter et al., 1998; Dehedin et al., 2013; De Wilde et al., 2015). In the same way, this leads to the disappearance of riparian forests that depend on a shallow water table, and thus the colonisation of the floodplain by colline species (Bravard et al., 1997; Solins and Cadenasso, 2020).

These longitudinal changes in slope, sediment supply, and channel adjustment define two sections (Fig. 2): (i) the section up to Villersexel with a steep profile, produces significant amounts of sand and gravel from the degradation of granite and sandstone, and benefits from the bedload inputs of the Rahin River with coarse bedload, while (ii) the downstream section (with a gentler slope) has an intermediate to low slope (Malavoi, 2003; Solins and Cadenasso, 2020). Despite these contrasts, both sectors have currently very low river mobility, probably because channel incision is too pronounced to be compensated, even in the upstream reach.

5.5. River eutrophication

Land use (crop, pasture, and woodlands; Supplementary material 4) and water quality data relating to nutrients (ammonium and phosphates; Supplementary material 5), and the functional assessment carried out for each wetland (regarding trophic status, Fig. 2) made it possible to characterize the trophic level of the Ognon river and riverine wetlands and to identify any longitudinal or lateral contrast.

The river showed high ammonium concentrations (Supplementary material 5), associated with eutrophic conditions according to the trophic scale established by Carbiener and collaborators (Carbiener et al., 1990) along its entire course, except for two more mesotrophic areas: the area between Larians and Voray-sur-l'Ognon (from kp 88 to kp 125, mainly on the left bank; Supplementary material 5) and the area between Lure and

Villersexel (from kp 33 to kp 55, on both banks; Supplementary material 5). Downstream from Emagny, the river floodplain is an area of high agricultural pressure (high proportion of crops; Supplementary material 4), and the water quality assessments indicate high nutrient levels (>1 $mg.L^{-1}$) for both ammonium and orthophosphates (Supplementary material 5). Few data were available on phosphorus contamination of groundwater, but the levels were always < 1 $mg.L^{-1}$ (Supplementary material 5). The trophic diagnosis done on wetlands based on aquatic plant species outlined also the intermediate to high trophic level (Fig. 2). Most wetlands identified as mesotrophic were also classified as groundwater-influenced, reflecting the overlap in the ecological requirements of the indicator species used for both diagnoses (Fig. 3).

5.6. Functional sectorisation of the floodplain

The integration of geological, hydrogeological, geomorphological, and trophic information, based on the identification and spatial comparison of their major discontinuities, allowed the delineation of functional floodplain sectors. Sector boundaries were identified where major changes in geological formations, hydrogeological conditions, or trophic status indicated a change in the dominant controls on floodplain functioning.

Two major structuring features emerge:

- The geological and hydrogeological contrasts between the upper crystalline part of the floodplain, with absent or shallow aquifers, and the lower part, which are alkaline, with significant inflows from the karstic massif into wetlands, particularly in the central sector; and
- The trophic contrast between the upper two-thirds of the floodplain being mesotrophic or eutrophic, depending on groundwater inflows in surface water, and the lower third being always eutrophic.

These geological, hydrogeological and trophic contrasts allow to identify a first sector. As the transition between crystalline and carbonate formations occurs at different locations on the two riverbanks, the downstream boundary of sector 1 is asymmetrical, extending from the river source to upstream of Longevelle on the right bank and Rougemont on the left bank (Fig. 3 ; sector 1). The river and its tributaries have low conductivity and are located in a Paleozoic geological context (Vosges bedrock, crystalline) that is low in carbonates. The conductivity of the aquifers and alluvial tributaries is low (0-200 µS.cm-1, often less than 100 µS.cm-1). The nutrient levels of surface and groundwater are intermediate to high (Supplementary material 5).

The middle part of the river differs slightly according to the bank:

- Along the right bank, from Longevelle to Emagny (sector 2, Fig. 3), the alluvial terraces have disappeared due to the lateral mobility of the river. The groundwater supply reaching the alluvial valley is alkaline. Conductivity is intermediate (around 400 µS.cm-1), and groundwater inflows are rather modest (fewer groundwater inflows in the riverine wetlands). This is potentially due to the impermeable Lias formations (marly layers) that form a barrier at the base of the limestone, so that the top of these marly levels is dotted with springs, but with low groundwater influxes in the wetlands located in the floodplain. The trophic levels of surface and groundwater are intermediate to high.
- Along the left bank, from Rougemont to Voray-sur-l'Ognon (sector 3, Fig. 3), the context is Holocene rocks (potentially resulting from the erosion of the south-western tip of the Vosges crystalline plateau in the upper dashed area of the zone Rougemont-Larians), and Jurassic carbonate rocks. The aquifers have very contrasting conductivities, resulting from the complex geological context of this sector. The riverine wetlands are influenced by these different sources and have intermediate conductivities (200-400 µS.cm-1, supplementary material 2). The trophic levels of surface and groundwater are intermediate to high, but several wetlands are characterized by mesotrophic waters resulting from probable good-quality groundwater supplies (directly visible through springs in some wetlands). The sector of Rougemont (dashed lines in Fig. 3), is chemically heterogeneous, reflecting the complex geological transition between the upper crystalline and lower alkaline geological context. This transition zone therefore represents a spatially heterogeneous area rather than a sharp functional boundary between the two major geological and hydrogeological contexts.

The lower part of the river extends from Voray-sur-l'Ognon (left bank) and Emagny (right bank) to the confluence with the Saône River (sectors 4 and 5, Fig. 3). The geological context is Pliocene along the alluvial valley on the left bank, and Jurassic (karstic) on the heights. Conductivities are high (around 600 µS.cm-1, Fig. 2). The trophic levels of surface and groundwater are high, both for ammonium nitrogen and phosphates, and mask any possible groundwater inputs. The two riverbanks were considered as distinct functional sectors because they are associated with different groundwater bodies.

Concerning geomorphology, although river slope exhibits a marked longitudinal discontinuity, the steepest upstream reach lacks riverine wetlands, while downstream wetlands occur along an already meandering river. Consequently, geomorphological characteristics did not justify further subdivision of the floodplain into functional sectors.

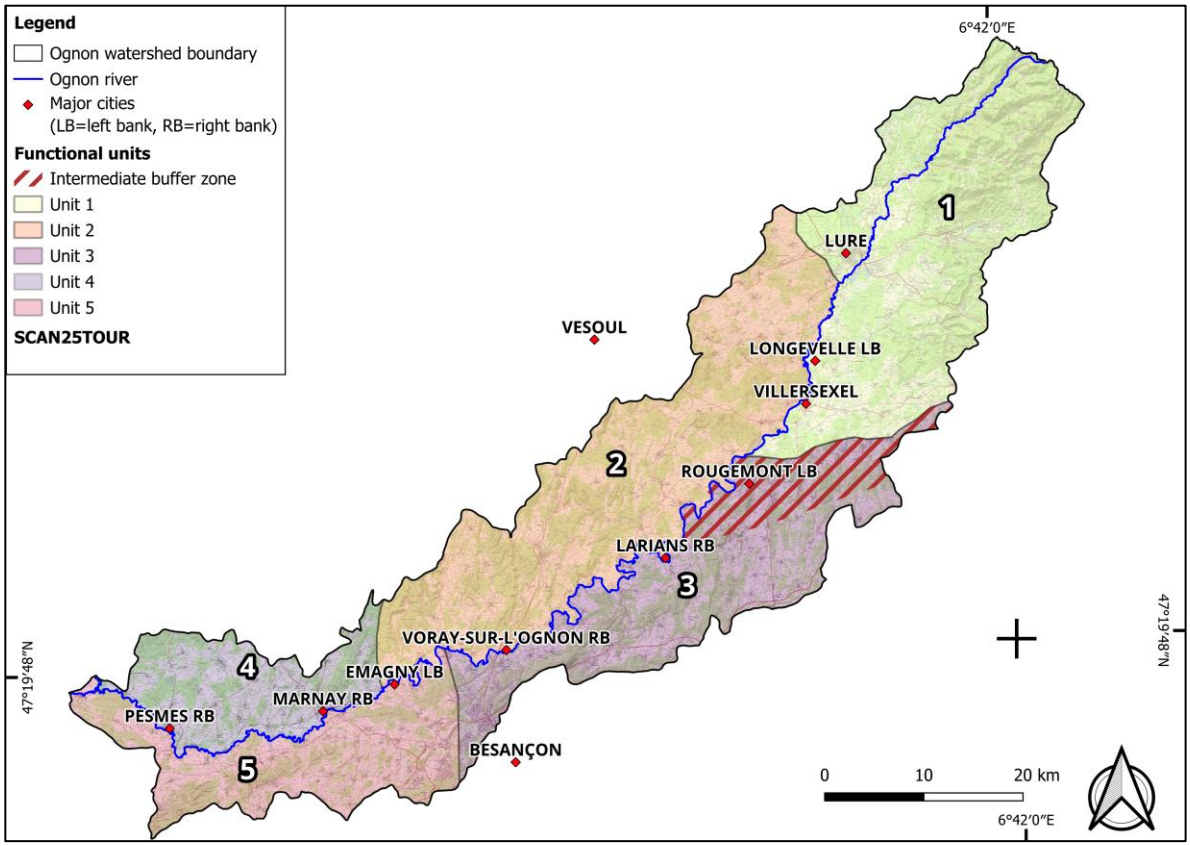


Figure 3. Functional sectorisation of the Ognon River watershed, France, resulting from the combination of geology, hydrogeology, river slope, agricultural pressure, ammonium nitrogen and phosphate content of surface and groundwater, and eutrophication (as indicated by plant communities in wetlands). RB: right bank, LB: left bank. The coordinate reference system is WGS84.

5.7. Functioning of riverine wetlands

Following the identification of functional sectors, wetlands potentially hydraulically active were delineated based on geomorphological criteria (mainly slope and indices of river overflows in the surrounding of the wetlands). Indeed, the pronounced incision of the riverbed (due to massive gravel extraction and flow-controlling structures such as weirs and dams), impedes any lateral divagation of the riverbed (Malavoi 2003). From an ecological point of view, the diagnosis for each riverine wetland was based on the identification of species indicative of hydraulic constraints.

We did not notice any symptom of river erosion in the wetlands during the inventory (neither physical, as coarse grain-size substrate, nor through the occurrence of species associated to flood disturbances, Amoros et al. 2000).

However, fine sediment deposits (silt and clay) were frequently observed in the wetlands. Based on wetland slopes estimated from river slope and wetland sinuosity, we inferred their potential susceptibility to erosive floods (Fig. 4).

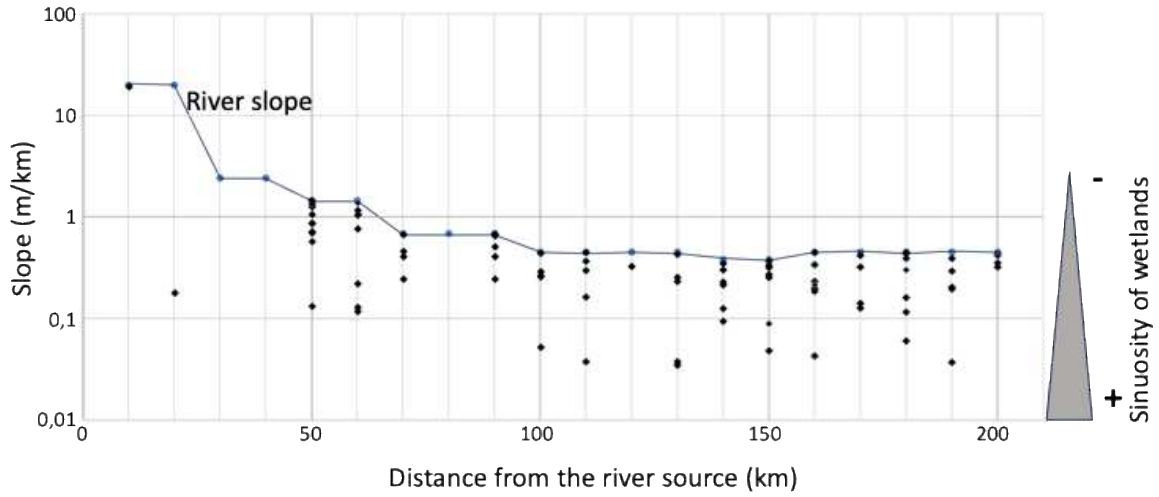


Figure 4. Longitudinal gradient of the Ognon river slope from its source to its confluence with the Saone River, and associated wetland slopes. Blue line indicates river slope. Black dots represent the slope value of each individual wetland. The longitudinal decline in river slope is associated with increasing attenuation of flood erosive power through sinuosity development in riverine wetlands.

The wetland slopes are the highest in the upper 60 km of the studied river, up to kilometric-point (kp) 40. The wetlands still have a high slope between kp 40 and kp 90 (dashed zone in the functional sector 3 along the left bank of the river, Fig. 3). However, even in this upstream area, the wetlands tend to be rather sinuous (meandering pattern). Downstream of kp 90, the river slope varies between 0.38 and 0.45 ‰, and the wetland slopes never exceed 0.45 ‰ (and were frequently below, Fig. 4). This pattern is consistent with the high proportion of meanders in this sector that are heavily silted.

Some linear secondary channels were observed along the left bank, whereas meandering patterns predominated on the right bank. A possible geomorphological interpretation of these patterns is that the meanders developed during a period of river equilibrium or aggradation (apparently before the 19th Century, as suggested by 18th Century Cassini maps and 19th Century military maps that showed already fixed meandering channels). When aggregate extraction began in the minor bed (Malavoi, 2003), the river incised, and in the first phase of the incision, the steeper slope of the bed may have favoured the formation of linear secondary channels by increasing the differential of altitude between the downstream connection of the meanders with the river and their upstream connection. This temporary increase in slope, which only prevailed during the phase when the incision front was located between the two confluences of the meandering wetlands with the river, allowed the formation of new linear branches. These linear secondary channels are therefore probably more recent than the meanders, and are currently no longer subjected to upstream flooding of the river (personal observations during floods).

These patterns highlight strong spatial variations in wetland functioning along the river, primarily controlled by slope, connectivity, and groundwater inputs. The implications of these controls for floodplain management are discussed below.

6. Discussion

The spatial partitioning of the floodplain provides a basis for analysing floodplain-scale management options and highlight functional contrasts along the river. The originality of this study lies in explicitly characterising how key controlling factors govern river functioning across spatial scales, and in integrating them into a hierarchical framework that supports practical management and restoration decisions.

6.1. Consequences for floodplain management

The upstream functional sector 1 (Fig. 3) is characterised by a steeply sloping river, low to medium mineralised waters, particularly in the upper reach that flows through the Vosges Mountains. The riverine wetlands have meso-eutrophic conditions. This sector has potential for the restoration of riverine wetlands, bearing in mind the low conductivity of the water in the Vosges area, which reflects low carbonate content and is typically associated with species-poor plant and animal communities characteristic of acidic waters. The impact of floods, and the potential for successful restoration, varies depending on wetland slope and the position of their upstream and downstream ends in relation to the river and any weirs it may contain. One may also consider that even in this upstream sector, we did not observe any river mobility, nor signs of erosion in the wetlands. This suggests limited overflows, likely due to a marked channel incision even in this upper reach.

The middle course functional sectors extend to Voray-sur-l'Ognon on the left bank and to Emagny on the right bank (sectors 2 and 3, Fig. 3). These sectors have a generally moderate to low slope and are influenced by karstic groundwater inputs. They are characterized by numerous meso-eutrophic riverine wetlands. Several have low sinuosity and may therefore offer favourable conditions for restoration, particularly along the less eutrophic left bank where groundwater supplies are observed in most wetlands. Intermediate persistence of restored aquatic stages are expected in comparable floodplain wetlands (from 30 to 60 years; Amoros et al., 2000).

The last functional zone covers the lower Ognon floodplain (sectors 4 and 5, Fig. 3). The slope is moderate to low, and the trophic level is high. The riverine wetlands are almost always very sinuous, which is unfavourable for effective and sustainable restoration and may adversely affect the river's sediment recharge. As the watercourse has been severely incised due to large-scale gravel extraction between the 1950s and 1980s, such restoration measures may hinder the river's ability to recover from severe incision. Indeed, if restored, these channels could act as sediment traps, potentially limiting the infilling of extraction pits located in the minor river bed. The absence of hydraulic disturbances and high trophic levels may favour 1) the colonisation by ubiquitous, even invasive plant species (*e.g., Ludwigia grandiflora*), and 2) phases of water anoxia, making the environment unfavourable to invertebrates and fish that require clear, oxygenated water.

As a synthesis, the functional sectors between Larians and Voray-sur-l'Ognon (particularly along the left bank; *i.e.,* sector 3 Fig. 3) and the area between Lure and Villersexel on both banks; Fig. 3) are those with the best trophic quality, the higher slopes, signs of groundwater supplies to the wetlands, and therefore the highest restoration potential for aquatic vegetation (with probable associated benefits for fauna). However, it should be noted that nutrient levels remain relatively high, even in these two functional sectors. This is a point to bear in mind during any restoration operations, in order to limit the risk of unwanted algal blooms, turbidity, and/or anoxia, which are harmful to both macrophytes and fauna.

6.2. Implications for restoration planning

Within each sector that is potentially suitable for restoration planning, the identification of wetlands suitable for restoration depends on their geomorphological, hydrological, hydrogeological, and trophic conditions. In a given functional sector, riverine wetlands can be classified into contrasted wetland types reflecting the dominant hydrogeomorphological and hydrogeological controls (Table 1). Given the relatively high nutrient levels and low channel gradient prevailing in much of the Ognon floodplain, the persistence of restored aquatic stages may be shorter than the indicative durations reported by Amoros et al. (2000) and quoted in Table 1, particularly in wetlands with limited groundwater inputs.

In the upstream functional sector 1 (Fig. 3), wetlands may remain connected to river dynamics and, locally, to the alluvial aquifer. Such context makes possible increases of groundwater influxes with meso-eutrophic waters, and floods may be restored under favourable hydraulic conditions. In intermediate functional sectors (i.e., sectors 2 and 3, Fig. 3), wetlands benefit frequently from groundwater inflows, which partly buffer eutrophication and maintain mesotrophic conditions despite sometimes strongly reduced hydraulic disturbances (in the sinuous channels). In such situation, restoration may only improve the connectivity between surface waer and groundwater in the wetlands, but the wetland slope may be insufficient to ensure long-term duration of the restored aquatic stage. In downstream functional sectors (*i.e.,* sectors 4 and 5, Fig. 3), weak hydraulic connectivity, high wetland sinuosity, and high nutrient loads lead to largely stagnant, eutrophic wetlands with limited expected ecological resilience in case of restoration. This classification highlights that the ecological

functioning of riverine wetlands is not independent, but directly emerges from large-scale geological, hydrogeological, and geomorphological controls.

Table 1. Range of potential functional trajectories in riverine wetlands as a function of physical controls operating at the floodplain scale (geomorphology and hydrological connectivity), and their implications for restoration strategies. The framework is related to alkaline geological context, where groundwater inflows influence sediment dynamics, physico-chemical characteristics of surface and groundwater, and ecological responses. In acidic systems, similar physical controls by the river are expected to occur, but groundwater inputs are generally absent or limited to weak seepage. Species richness and productivity are lower, and successional rates are slower, while the structure of functional trajectories remains comparable. Ranges are ordered from the most probable to less probable states depending on local conditions. Durability classes are indicative and based on ecological trajectories reported by Amoros et al. (2000), rather than on site-specific predictions validated for the Ognon floodplain.

Physical controls				**Ecological responses**				**Outcomes**	
Geomorphology			**Groundwater fluxes**	**Sediment dynamics**	**Physico-chemical conditions**	**Species richness**	**Productivity**	**Resulting duration of the aquatic stage**	**Need for restoration**
River slope	**River overflows**	**Wetland sinuosity**							
high to intermediate	no	low	groundwater inflows (hillslope aquifer dominant)	No siltation (groundwater flushing)	low water temperature, high oxygen content, usually oligotrophic	intermediate to low	intermediate to low	Potentially high (i.e. more than 60 years) due to groundwater drainage that stop terrestrialization: the wetland may function as a phreatic stream	No need for restoration, restoration is suitable if sudden river incision
		intermediate to high	groundwater inflows (hillslope aquifer dominant)	low siltation (slowed down by groundwater flushing, terrestrialization through organic matter accumulation	intermediate water temperature and oxygen content, usually oligo-mesotrophic	intermediate to low	intermediate	low rate terrestrialization, intermediate to high durability of the quatic stage (i.e. more than 30 years)	restoration suitable at the end of the aquatic stage
	yes	low	groundwater inflows (seepage water dominant)	no siltation (flood scouring and groudwater flushing)	water temperature and oxygen content related to water origin (surface, seepage), meso to eutrophic	high (intermediate disturbance hypothesis)	intermediate	Potentially high due to flood scouring	No need for restoration
		intermediate to high	groundwater inflows (seepage water dominant) that decreases with sediment	moderate to high siltation (flood sediment deposition)	high water temperature and low oxygen content in summer,	decrease through time	increase through time	intermediate to low, depending on the wetland depth and width, i.e. less than 30 years	restoration is not suitable, particularly in incised channels tu to

			accumulation		usually meso to eutrophic				gravel mining: the restoration then contributes to increase the sediment deficit through wetland siltation.
low	no	low	no groundwater inflows	terrestrialization through organic matter accumulation	usually eutrophic	low	intermediate to high	intermediate to low, depending on the wetland depth and width, i.e. less than 30 years	restoration is not suitable
		intermediate to high	no groundwater inflows	terrestrialization through organic matter accumulation	usually eutrophic	low	intermediate to high	intermediate to low, depending on the wetland depth and width, i.e. less than 30 years	restoration is not suitable
	yes	low	few groundwater inflows (seepage water dominant)	slowed down siltation (flood scouring, but clogging appears through time)	meso- to eutrophic	low to intermediate	intermediate to high	intermediate rate of terrestrialization, i.e. from 30 to 60 years	restoration is suitable in case of mesotrophic waters
		intermediate to high	no groundwater inflows	high siltation (sediment clogging)	usually highly eutrophic	low	high	high rate of terrestrialization very low duration of the quatic stage, i.e. less than 30 years	restoration is not suitable

The position of riverine wetlands relative to river weirs may also controls their hydrological functioning (Fig. 5). When the downstream outlet of a wetland is located upstream of a weir, it may benefit from artificially maintained water levels, partly compensating for channel incision. However, this may reduce the gradient of the wetland and the flow velocity during floods, thereby promoting sediment deposition. Conversely, wetlands with outlets located downstream of weirs may be subjected to enhanced drainage due to local lowering of the water surface profile, and higher flow velocities during floods.

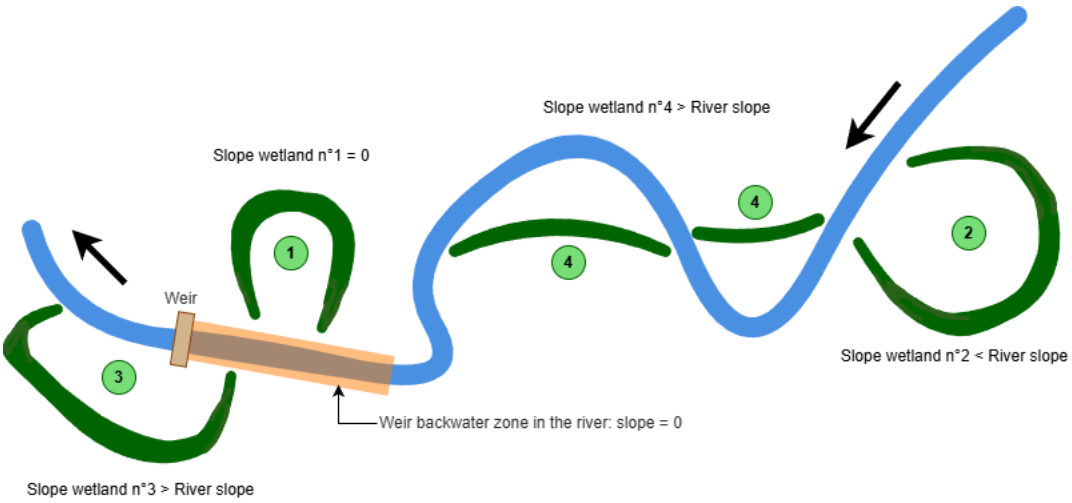


Figure 5. Conceptual hypothesis of how weirs affect water velocity during river flooding in wetlands, depending on the configuration of the wetlands. Within a river reach with a homogeneous slope, and for the same wetland sinuosity, the position of the wetland plugs relative to the weir affects the potential flow velocity in case of river overflow. The meander wetland 1 is located upstream the weir's backwater zone, in a section where the river has no gradient. Floods may induce intense siltation processes in this wetland. The meander wetlands 2 and 3 may benefit for increased flow velocity during floods, but, due to wetland sinuosity, that may be insufficient for sediment erosion and sustainability of the wetland aquatic phase. A linear channel that cuts off a river meander (4) is more favourable to sediment erosion during floods, and may be more perennial (duration of the aquatic stage).

5.3. Limits of the method

The method relies on the use of public databases, the content of which can vary significantly from one watercourse to another. In particular, there is an almost systematic lack of water quality data for alluvial wetlands. This means that such data must be documented before any decision is taken on potential restoration. Similarly, historical data concerning watercourses are compiled in public databases of old maps and photographs, which must be analysed before any restoration work is undertaken.

Finally, this study benefited from an in-depth analysis of the river's geomorphological functioning, the findings of which were essential for developing the functional mapping. This type of work, which is indispensable for producing functional mapping, is not always available, and is an prerequisite for elaboration the present diagnosis.

Finally, at the wetland level, the assessment relies heavily on the presence of plant species that act as indicators (of floodwater or groundwater). This tool is informative, but depends on the presence of a water film in which the species can thrive. Repeated drying out, like excess nutrients, can cause these indicator species to disappear and limit the tool's effectiveness. Furthermore, the absence of indicative species does not allow to conclude to absence of groundwater inputs. In this case, additional chemical measures must be carried out. However, for the Ognon floodplain, indicator species for groundwater have been observed in areas otherwise severely affected by eutrophication, near groundwater resurgences, which reinforces confidence in the reliability of this biological assessment method.

7. Conclusion

This work has enabled an functional mapping of the Ognon Valley, based on the hierarchical organisation of environmental controlling factors. This operational framework links large-scale environmental constraints to expected local wetland functioning and associated ecological trajectories, and may be accurate for defining management strategies for the alluvial plain, prioritising areas and wetlands to be preserved or restored, and more generally enhancing the ecological value of the valley.

This study highlights the critical role of publicly available datasets (geological, hydrogeological, geomorphological, water quality, and meteorological data) in supporting floodplain-scale functional analyses.

However, we have demonstrated that systematic visits to the riverine wetlands made it possible to significantly improve the existing sectorisation, leading to finer divisions and accounting for functional sub-sectors that are often not identified in large-scale studies, but which can behave very differently due to contrasts between the banks, and allowing the role of geology in river dynamics to be analysed in detail.

Unlike traditional ecoregional frameworks, which primarily reflect broad-scale environmental patterns, the proposed approach explicitly accounts for the spatial heterogeneity of the geological, hydrogeological, geomorphological, and trophic controls governing floodplain functioning. It therefore provides a complementary, process-based basis for identifying restoration priorities within large alluvial valleys.

This functional diagnosis of the Ognon Valley has highlighted a diversity of ecological and geomorphological situations along the entire length of the Ognon River, responding to relatively varied geological, hydrogeological, and trophic constraints. The proposed sectorisation is a tool for understanding the processes taking place within the riverine wetlands and provides a solid basis for defining appropriate restoration actions. The planned interventions will need to be adapted to the contexts of the different sectors: in upstream sector, river dynamics may be sufficient to consider restorations that do not require a lot of resources and to hope for self-maintenance of the floodplains through river dynamics and groundwater inputs. In intermediate areas, the risks of sedimentation during flooding must be taken into account and groundwater inflows should be leveraged, mainly on the left bank. In downstream sectors, the gentle slope, incision and marked eutrophication mean that action must be limited due to the degraded context.
This functional sectorization may facilitate the implementation of optimal long-term monitoring (sensors, flow measurements, monitoring of the accompanying water table and lateral flows), which afford the necessary validation, and quantification of key processes identified in the sectorization work.

This type of diagnosis may consequently be considered systematically in integrated river management projects in order to improve the long-term effectiveness of ecological measures. By translating widely recognized multi-scale controls into a concrete and transferable diagnostic framework, this study provides a practical basis for improving the effectiveness and long-term sustainability of floodplain restoration strategies. While the specific expression of functional sectors depends on local conditions, the hierarchical organisation of controlling factors is expected to be generalizable across temperate floodplain systems.

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Declaration of generative AI and AI-assisted technologies in the manuscript preparation process
During the preparation of this work, the first author used CHATGPT to improve the English and identify any missing information and inconsistencies in the line of reasoning. The author reviewed and edited the output as needed and take full responsibility for the content of the published article.

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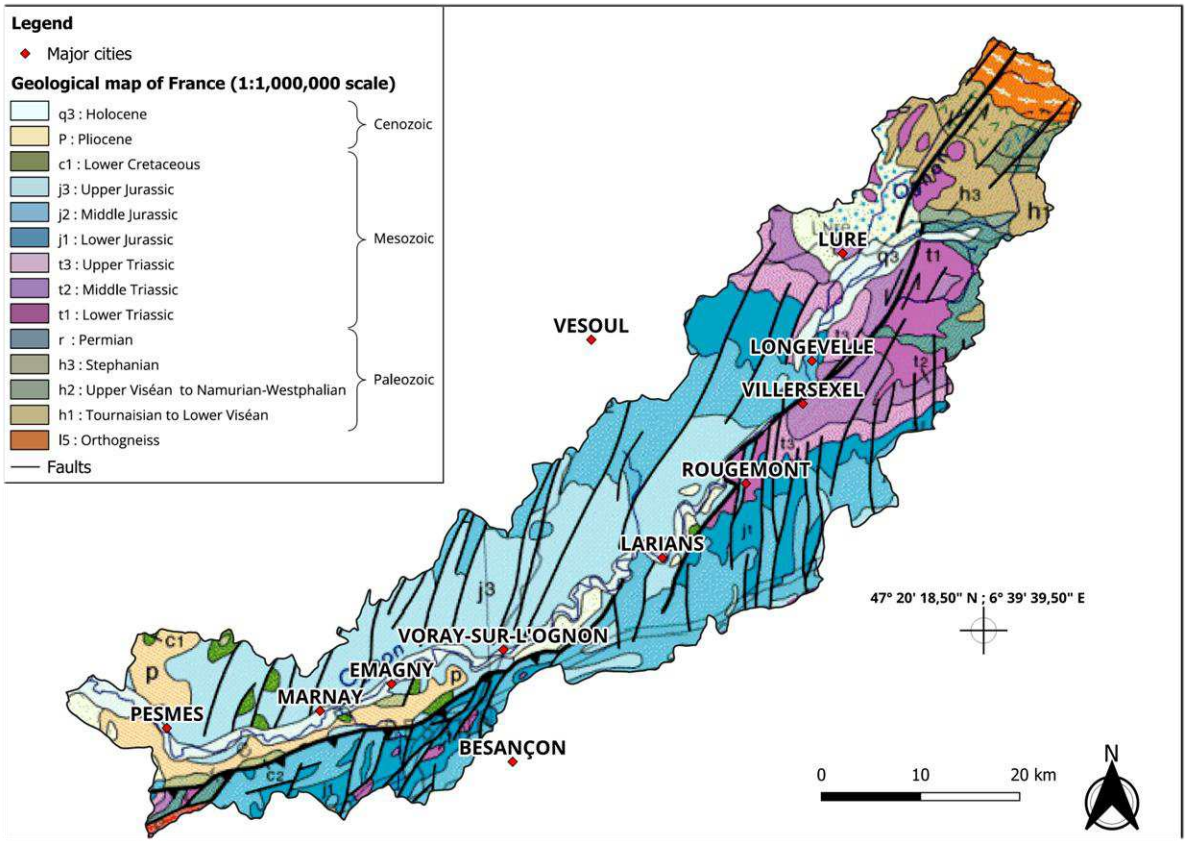
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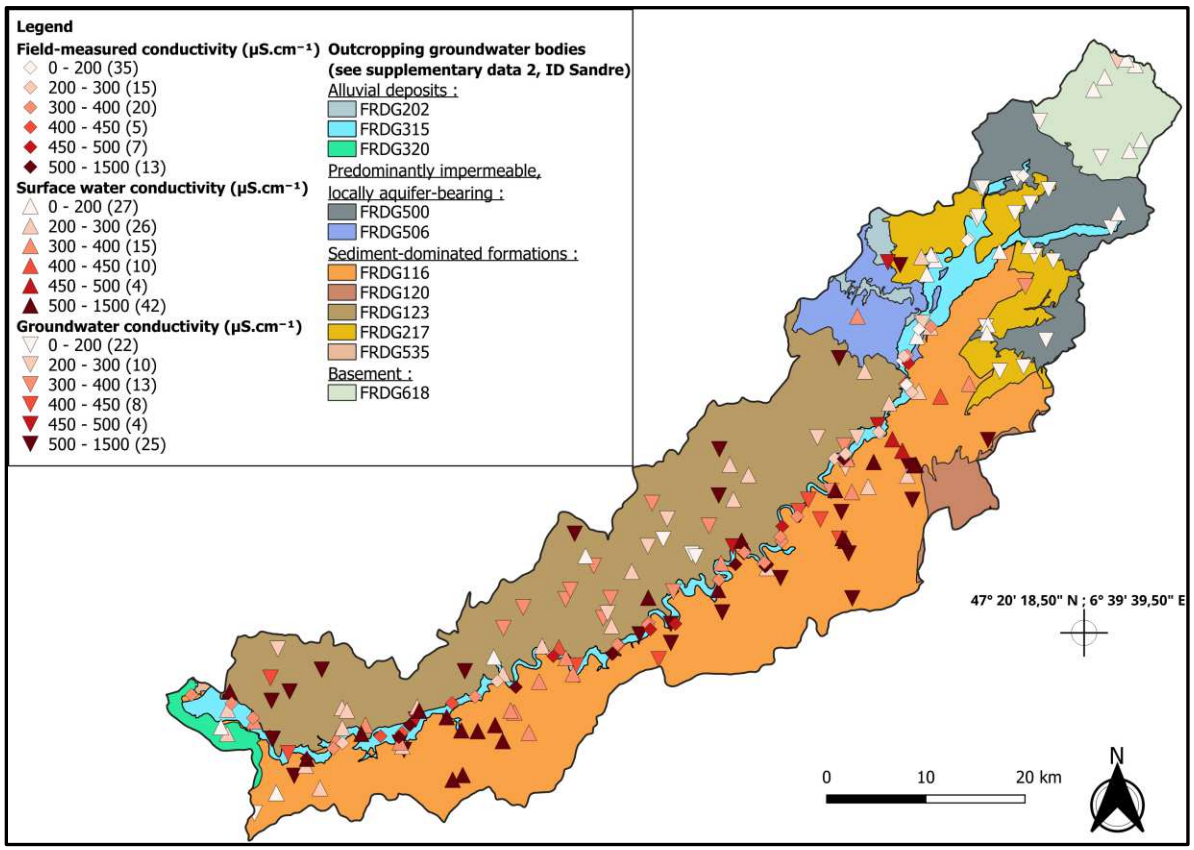
Supplementary material



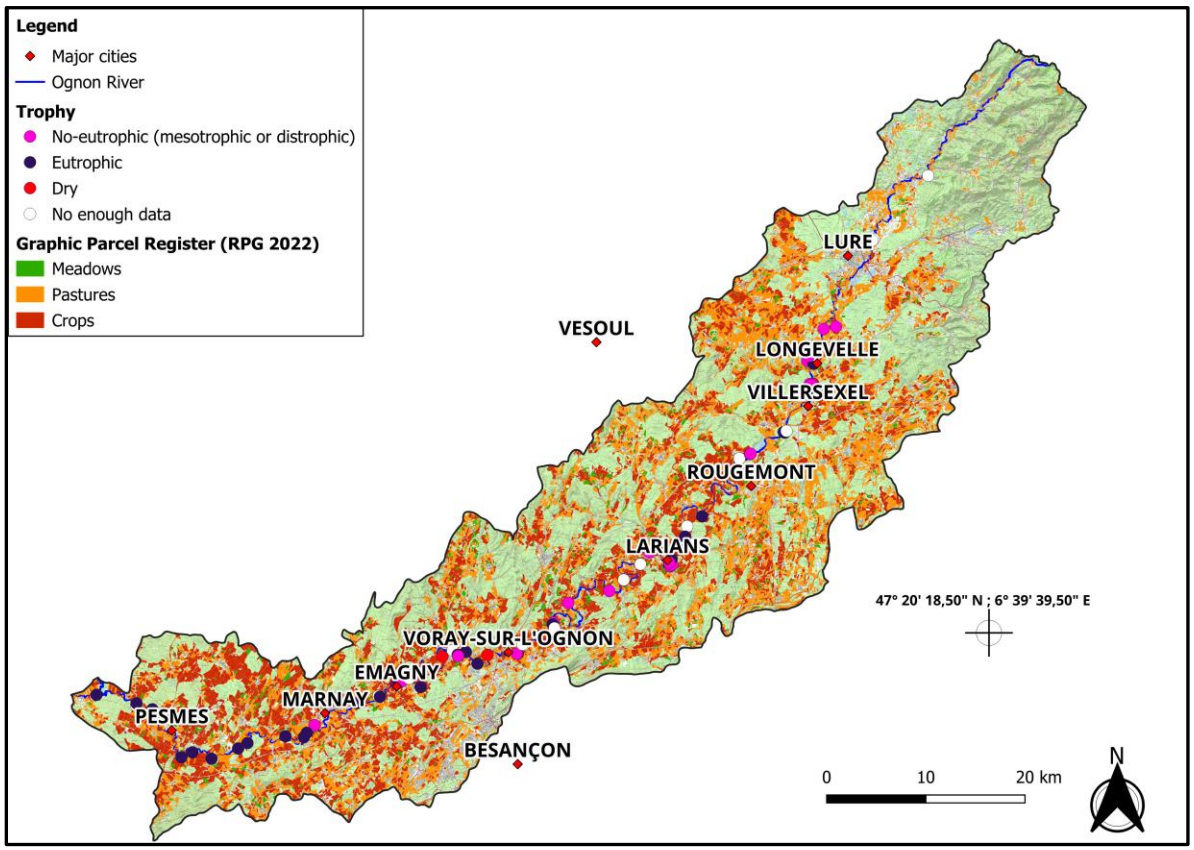
Supplementary material 1: Geological map of the watershed of the Ognon River, France. For a detailed code significance, see Supplementary material 2. The coordinate reference system is WGS84.

Code	Surface (m2)	Surface (% Ognon watershed)	Geological formation	Specificity
FRDG315	151928473,2	7,0	Fine clayey and silty alluvium	Permeable, with variable thickness ranging from a few tens of centimetres to 5 m
FRDG535	2515465,561	0,6	Marly domain of the Bresse	Low permeability of marls
FRDG320	24852285,7	1,5	Alluvium of the Saône–Doubs plain and the lower Loue valley	Major recharge zone for alluvial aquifers
FRDG123	742240874,4	32,6	Jurassic limestones	Localized karst networks
FRDG116	804250811,7	35,3	Limestone formations overlying Liassic marls	-
FRDG120	41545598,16	2,3	Jurassic limestones	Well-developed karst networks
FRDG506	80425208,22	3,9	Triassic and Liassic formations	Predominantly impermeable
FRDG202	20284331,93	1,3	Upper Muschelkalk limestones and Rhaetian sandstones and clays	Presence of aquifer units
FRDG217	25632609,25	1,6	Lower Triassic sandstones	Major aquifer due to sandstone porosity
FRDG500	176022591,1	8,1	Red sandstone and clay assemblage	Localized impermeable conditions
FRDG618	123607030,1	5,8	Vosgian basement	Low porosity

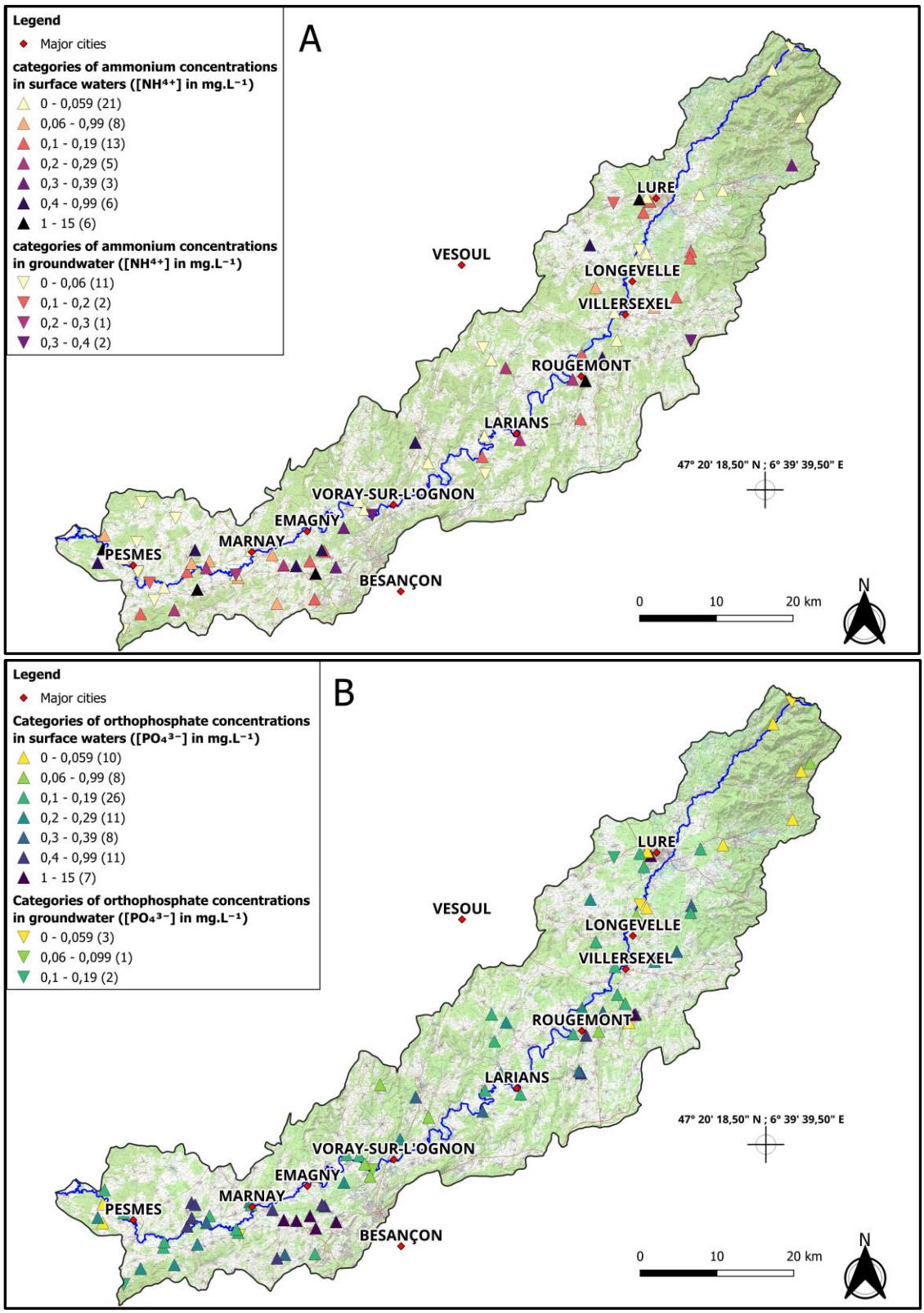
Supplementary material 2: Significance of geological codes used in supplementary material 1.



Supplementary material 3: Surface and groundawter conductivity of water in the Ognon River watershed, France. Diamond water-dots represent our own field-measured water conductivity, while triangle-dots represent surface and groundwater conductivity from public national databases. The coordinate reference system is WGS84.



Supplementary material 4: Land use of agricultural parcels (meadows, pasture, and farming) in the Ognon River watershed, France. The light green indicates forested areas. The dots plot surveyed wetlands and indicate their trophic level based on the requirements of aquatic vegetation. Wetlands that were dry at the date of the survey, or that were devoted of indicator species, are indicated. The coordinate reference system is WGS84.



Supplementary material 5: Nutrient contents of surface and groundwater in the Ognon River watershed, France. (A) Ammonium nitrogen content and (B) phosphate content. The coordinate reference system is WGS84.