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Tracking the effects of dam construction and restoration on side channel biodiversity using macrofossils in river sediment records

André-Marie Dendievel^{a,*}, Jérémie Riquier^b, Brice Mourier^a, Thierry Winiarski^a

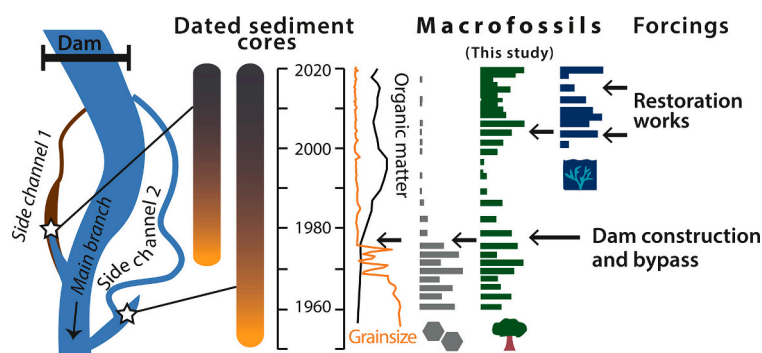
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HIGHLIGHTS

- Macrofossil records provide a history of habitats and biodiversity since 1950
- Riparian woodland & undergrowth remains are crucial to interpret restoration effect
- Combining macrofossils and sedimentology show multiple impacts from damming
- Macrofossil data reveal new wetland and aquatic plants after channel restoration
- Macrofossil study helps to define reference conditions to track restoration success

GRAPHICAL ABSTRACT



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ABSTRACT

During the last decades, fluvial sediment cores have been used to reconstruct and model pollution trends, especially for the post-1945 period. Ecological changes have been rarely studied in such recent sediment archives due to low organic levels and high hydro-sedimentary dynamics. Here, we address the challenge of reconstructing ecosystem changes along highly anthropized rivers by analysing plant macrofossils (e.g. seeds, wood fragments, mosses), animal and abiotic remains (mainly iron slags) accumulated in side channels. The main objective is to determine whether this approach – inspired from palaeoecology – is reliable. Interestingly, macrofossil records offer a coherent history of the species habitats and biodiversity on different sites on either side of a bypassed section of the Rhône River (France). Three main hydro-ecological phases are identified, linked to river developments. (1) A lotic phase, before damming, is marked by various local riparian forest taxa: black alder and willow macrofossils were regularly found in the cores, while black poplar is not recorded, despite its historical presence. (2) A synchronous terrestrialization phase (transition from an aquatic to a terrestrial ecosystem) is highlighted on both side channels in the late 1970s, due to the bypassing of the river and the subsequent lowering of the water level. During this phase, nitrophilous plants (nettles) expanded on both sites. (3) Finally, the effects of restoration also appeared in fluvial sediment cores, marked by new aquatic flora and fauna macrofossil taxa since 2000. Overall, this research demonstrated the potential of studying macrofossils in side channel deposits to understand the post-1945 history of riparian habitats and biodiversity, and their evolution after developments and/or restoration actions. This macrofossil approach could be considered as a tool to

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supplement monitoring data and to better interpret wetland changes with regard to hydromorphological adjustments along a river system over decades or centuries.

1. Introduction

During the Anthropocene, river ecosystem functioning has been altered by multiple human impacts (Kelly et al., 2018). Impacts are generally distinguished at the reach scale (Belletti et al., 2020; Bravard, 2018; Meybeck, 2013): (1) hydro-sedimentary changes resulting from the implementation of facilities for water control, navigation, agriculture, industrial activities or hydroelectric production (dykes, weirs, dams), (2) vegetation changes due to anthropogenic disconnection from the river network, and to the expansion of exotic plants, (3) degradation of ecosystem quality due to discharges and releases of contaminants (e.g. trace metal elements, persistent organic pollutants, microplastics, etc.).

River side channels are non-perennial habitats, more or less connected to the main stream, generally resulting from cut-off meanders or from avulsion processes (Bouska et al., 2023; Coles and Klingeman, 2014). Their persistence over time in river landscapes can vary greatly (from a few years to centuries). Since their creation to the paleochannel stage (terrestrial habitat), side channels undergo different phases of hydromorphological evolution, gradually decreasing their lateral connectivity with the main channel and causing ecological adjustments (e.g. Amoros et al., 1987; Hohensinner et al., 2014; Riquier et al., 2017; Marle et al., 2021). This biophysical evolution can be summarized in 3 main stages: (A) active secondary channels predominantly lotic (=“eupotamon” functioning unit described in Amoros et al., 1987), (B) semi-permanent side channels, blocked at their upstream end through the establishment of an alluvial plug, predominantly lentic with passive inundation from their downstream end, and occasionally lotic during major floods (=“parapotamon”), and (C) fully isolated channels, blocked at both ends, made of small and stagnant water bodies, marshes or riparian forests (=“plesiototamon”).

Along engineered rivers, the hydrogeomorphic and ecological evolution of side channels could be highly modified (Dépret et al., 2017; van Denderen et al., 2019). Indeed, numerous side channels have been bypassed and confined with dykes or groynes, sometimes equipped with sluices in order to improve navigation, to regulate floods, to gain arable land and/or to produce hydroelectricity, along rivers worldwide (Hohensinner et al., 2014). Side channels often become terrestrialized (stages B and C above described), i.e. only connected to the main river by upstream overflow during high waters or by passive inundation from their downstream end (backflow). Yet over the last 20 years, numerous side channels have been restored in Europe (Water Framework Directive: WFD 2000/60/EC) with the objective to return natural expansion zones to the river, to recover critical habitats for wildlife, and/or to improve sediment transport and ecological continuity (Boutet-Barry et al., 2014; Eschbach et al., 2021; Helfield et al., 2012; Piégay and Radakovitch, 2022).

Due to their gradual filling with fine sediments (i.e. < 2 mm) and to very frequent slow flow conditions through the year (i.e. stagnant water bodies), stages B and C side channels may accumulate and provide “fluvial archives” which are typically used to reconstruct pollution trends caused by industrial, urban or agricultural emissions over time (Ayrault et al., 2019; Dhivert et al., 2015; Matys Grygar et al., 2017; Vauclin et al., 2021b). Nevertheless, dealing with side channel deposits is a challenge because of their temporary nature (Piégay et al., 2008; Riquier et al., 2019). Another challenge is the study of biodiversity in side channels, especially to determine the impact of engineering works and the effectiveness of restoration for plant communities over time (> 50 years). Indeed, the ecological monitoring of side channels is relatively recent (< 20 years) and achieved at limited places, while long-term data assessed by combining satellite or aerial historical photographs with geomorphology, generally remain at the ecosystem level

(habitat structure or physiology), and rarely reach community or species levels (Demarquet et al., 2023; Piégay et al., 2023).

We propose to address the challenge of reconstructing biodiversity changes in side channels by analysing macrofossils in well dated (^{210}Pb and ^{137}Cs) post-1945 sediment cores. Macrofossils, comprised between 200 μm and 5 mm, include plant macroremains (e.g. seeds, buds, roots, leaf fragments) and animal fragments (e.g. micro-crustaceans such as *Daphnia* and Ostracoda, Mollusca, fish bones, and various insect fragments, mainly from Coleoptera). The quantification of abiotic particles is also included in our approach (e.g., quartz grains, basalt beads, and micro-waste such as iron slags or microplastics), in relationship with magnetic susceptibility measurements in order to trace sediment origin and accumulation. Such study, inspired from palaeoecology, has traditionally been performed over long timescales (> 500 years) in lake or bog sediment archives (e.g. Birks, 2017; Blaauw and Mauquoy, 2012; Carcaillet et al., 2018; Dendievel et al., 2023; Dendievel et al., 2022). Several works have confirmed the feasibility of such an approach to reconstruct the evolution of lake ecosystems during the last century and its relevance in helping public policy to find environmental benchmarks for ecological restoration (Bennion et al., 2011, 2018; Cheng et al., 2022; Davidson et al., 2005; Foster and Greenwood, 2016; Jeppesen et al., 2001; Zhang et al., 2022). However, in fluvial environments, macrofossil accumulations, especially plant macro-remains, have been rarely studied due to the risk of organic remains being poorly preserved, eroded or redeposited (Schaal and Naton, 2021). Among the main studies, the work supervised or initiated by G. Petts, in the UK and other places, has been fundamental (Gurnell et al., 2019). Diatom and Cladocera assemblages have also been the object of considerable study in sediments accumulated along Australian rivers, in relation to the impact of European colonisation and the increase in river turbidity (Reid et al., 2002). Severe changes in sedimentation rates, eutrophication and macrofossil assemblages have also been detected in sediment cores after river regulation which caused the permanent flooding of several alluvial wetlands (Kattel et al., 2017). On the Rhône and Rhine Rivers, pioneering research on subfossil Cladocera was conducted in the 1980s – 1990s to study the effects of civil engineering projects on dead arms' ecology (Amoros and Van Urk, 1989; Jurasz and Amoros, 1991). However, these works encountered several problems of dating caused by sediment remobilization (high lateral connectivity of the studied sites), and lacked sedimentological or historical data to improve interpretation. Today, the methods for studying fluvial sediment archives, by combining geohistorical approaches, grain-size analyses, geophysics with chronological models, offer the possibility of selecting more suitable sites (Vauclin et al., 2021b). This makes palaeoecological studies in river channel sediments more robust and relevant to reconstructing local species changes even in lotic ecosystems as demonstrated by the recent studies of Gastropoda, Trichoptera and Coleoptera assemblages in the Hull River sediments, UK (Seddon et al., 2019). Similarly, a study of a sediment core extracted from a palaeochannel of the Doubs River, France, used the macrofossil analysis as an accurate biodiversity indicator for aquatic environments and riverbanks, compared to pollen and eDNA (Schaal et al., 2019).

Based on these developments, our work will focus on plant, animal and abiotic macrofossil assemblages preserved in sediment cores of two side channels from either side of a bypassed section of the Rhône River (France). The overall aim of this study is to assess the potential of macrofossils preserved in river side channel cores to understand the history of riparian habitats and biodiversity over the recent decades. In particular, we will address the following questions: (i) Is the macrofossil signal reproducible on several sites across a river section?? (ii) What management history can be reconstructed based on macrofossil indicators, especially regarding engineering or restoration works effects?

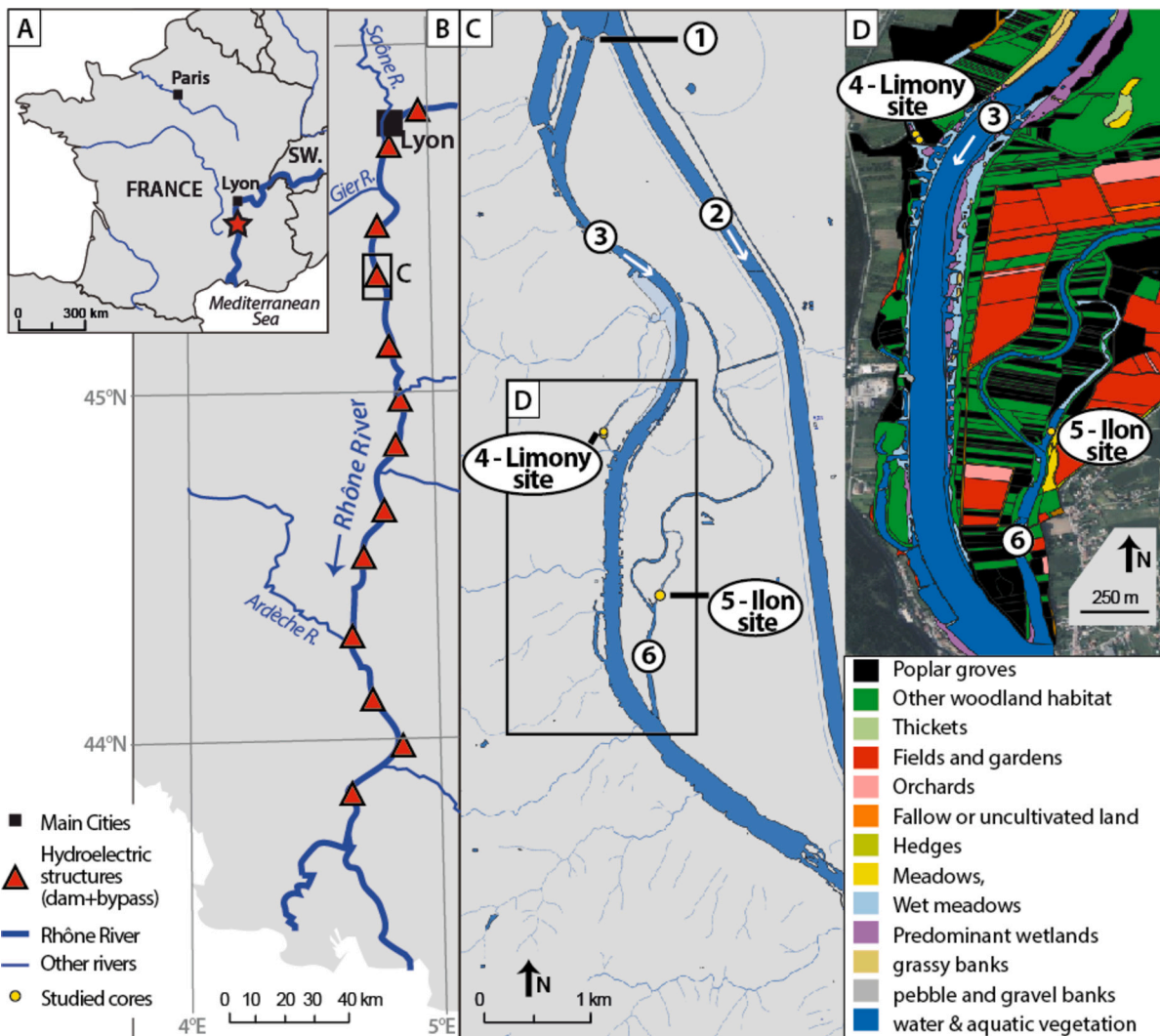


Fig. 1. A) Location of the Rhône River (from Switzerland [SW.] to France [FR]) and the study area of PDR (“Péage-de-Roussillon” sector, red star); B) Map of the equipped sections of the Rhône River, downstream of Lyon (FR); C) Focus on the studied PDR river section; D) Vegetation habitats around the coring sites: 1) Saint-Pierre-de-Boeuf Dam, 2) Artificial canal, 3) Old Rhône River (bypassed), 4) Limony side channel, 5) Ilon side channel, 6) La Platière side channel (sources: maps A and B adapted after [Vauclin et al., 2021b](#), map C: hydrographic network by IGN, 2022; map D: CEN Isère – Réserve Naturelle de la Platière 2008).

2. Material and methods

2.1. Regional background: Engineering and restoration works

The study area is a 12 km-long reach of the middle Rhône River valley (France), 50 km downstream of the city of Lyon (Fig. 1A). This river section, known as PDR (“Péage-de-Roussillon” sector), was straightened by dyke-fields in the 1880’s – 1890’s (Engineering Phase 1; cf. [Seignemartin et al., 2023](#)). Subsequently, the PDR sector was bypassed in 1977 by the “Saint-Pierre-de-Boeuf” dam (Engineering Phase 2), which directs the river discharge into an artificial canal to produce hydroelectricity (Fig. 1B and C). These modifications decreased the water discharge in the bypassed PDR sector from about $1080 \text{ m}^3 \cdot \text{s}^{-1}$ to a minimum flow of 10 to $20 \text{ m}^3 \cdot \text{s}^{-1}$ ([Seignemartin et al., 2023](#)). The bypassed historical course of the river (called “Old-Rhône”) is still used to accommodate floods that exceed the maximum discharge processed by the hydropower plant (i.e. $1600 \text{ m}^3 \cdot \text{s}^{-1}$). These engineering phases promoted dewatering and sediment accumulation on the old river margins and on side channels, as well as their colonisation by pioneering species ([Dépret et al., 2017](#); [Seignemartin et al., 2023](#)). Similar hydro-sedimentary changes are observed all along the whole Rhône river, as well as on over managed rivers worldwide ([Bravard, 2018](#); [Meade and Moody, 2010](#)).

The PDR sector has been protected since 1986 within the “Ile de Platière” Nature Reserve, which became a Site of Community Importance of the Natura 2000 Network in 2002, before evolving into a Special Area of Conservation (SAC) more recently ([MEDDE, 2014](#)). At the scale of the PDR sector, two main types of actions were achieved to restore the ecological functioning of bypassed side channels: (i) the minimum instream flow increase (MIFI), in 2014, to reach at least $50 \text{ m}^3 \cdot \text{s}^{-1}$ from September to February, and up to $125 \text{ m}^3 \cdot \text{s}^{-1}$ from April to June, in order to better consider the local species’ needs and promote higher water level in floodplain channels, (ii) excavation and terracing work, sometimes combined with alluvial plug(s) removal, was carried out to revive several side channels from 1992 to 2015 ([Borrette and Amoros, 1993](#); [Olivier et al., 2022](#)). These restorations were monitored by two research programs (RhônEco [since 1998] and OSR – Rhône Sediment Observatory [since 2009]), including quantification of the effects of restoration works on physical habitats and biological components ([Janssen et al., 2021](#)).

2.2. Coring sites and vegetation

The PDR sector is well known and documented, with several studies on the temporal trends of sediment accumulation and on pollutants in

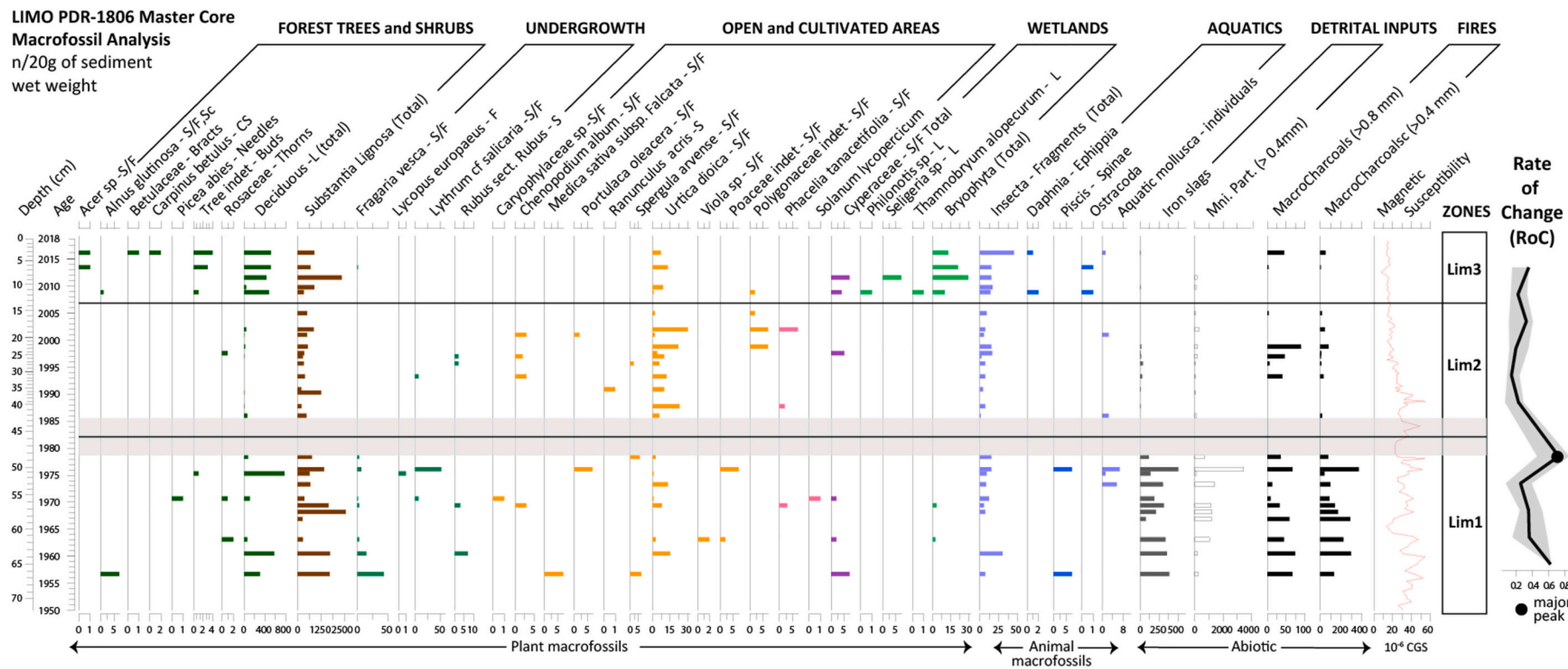


Fig. 2. Selected macrofossil taxa from the PDR-1806 master core (LIMO), magnetic susceptibility, and RoC. Abbreviations: CS = catkin scales, F = fruits, L = leaves, S = seeds, Min. Part. = Minerogenic particles >0.4 mm (i.e. medium and coarse sands). For the complete list of identified Mollusca species, see [Appendix 3](#). The Lim1–Lim2 limit is represented by a grey bar, in order to consider the macrofossil sampling resolution.

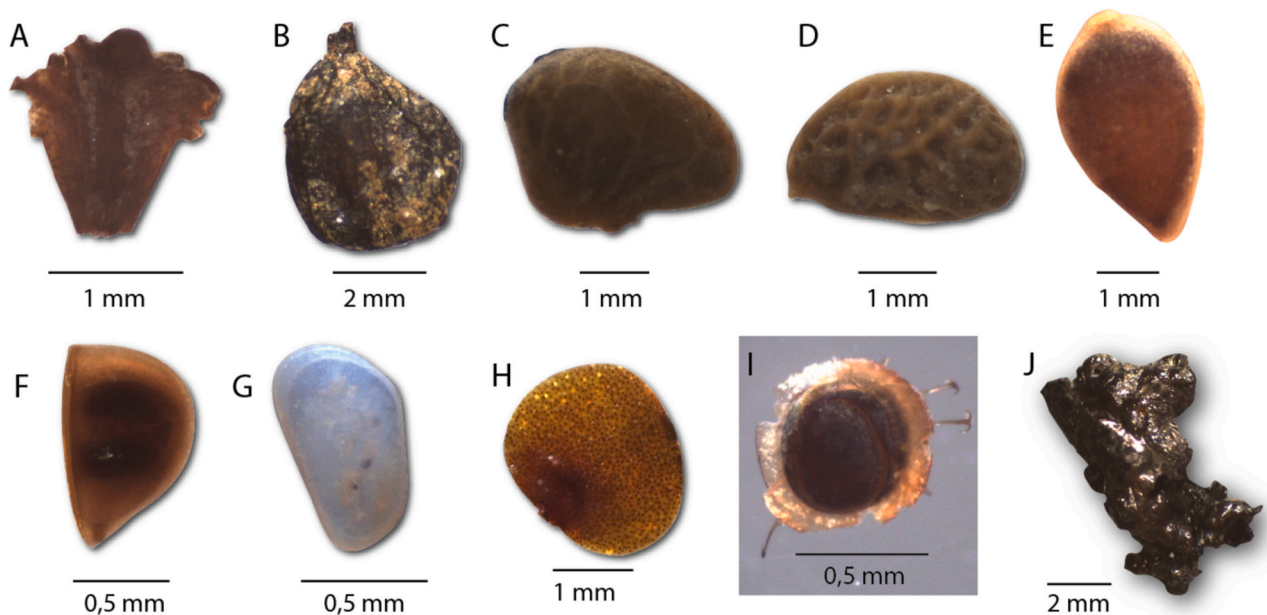


Fig. 3. Main macrofossils extracted from the studied cores. A-B) *Alnus glutinosa* (scale and seed), C) *Fragaria moschata* (seed), D) *Rubus sect. Rubus* (seed), E) *Urtica dioica* (seed), F) *Daphnia* sp. (ephippia), G) Ostracoda (shell), H) *Lemna minor* (seeds), I) *Cristatella mucedo* (statoblast), J) example of an iron slag.

bank structures and in the floodplain channels (Seignemartin et al., 2023; Tena et al., 2020; Vauclin et al., 2020). Based on these works, two sites were selected: one on each side of the bypassed reaches in order to analyse macrofossils from well-dated sediment cores (see Fig. 1C and D). The two side channels (ILON on the left bank, and Limony, called LIMO hereafter, on the right bank) presented similar features that can be found on various other rivers: they were active secondary channels, with a lotic functioning, during the 19th century CE, before being closed by submersible dykes during the 1880's engineering works (Seignemartin et al., 2023). The arrangement may vary because IILON is part of a large complex of arms on the left bank (for details, see Appendix 1.2). However, following the damming of the river in 1977, the two side channels terrestrialized, are now only flooded between 1.9 and 5.7 d.y^{-1} , mainly by backflow from their downstream ends (lentic conditions), and occasionally by upstream overflow events (Noclin, 2024). Both LIMO and IILON water levels increased following the 2014 MIFI, but only IILON was concerned by the mechanical removal of an alluvial plug at its downstream end in 2004. Thus, IILON is an aquatic side channel, in which we collected a 94 cm-long core (called "PDR-1802") by using an UWITEC gravity corer in 2018. The bottom of this sequence is dated back to the 1970's and continuously accumulated until 2018 (Vauclin et al., 2021b). In LIMO, two sediment cores were extracted from this terrestrial site by using a COBRA-TT device. These cores were extracted 1 m apart, and combined based on grain-size in order to form a 108 cm-long core, called "PDR-1806 master core". Its bottom is estimated to date back to the beginning of the 20th century, while the chronology of the top 60 cm is well secured from 1965 to 2018 (Vauclin et al., 2021b; see also Appendices 1.1 and 1.2). Geophysical (ground penetrating radar – GPR) analyses were also carried out at both sites to understand the geometry of the deposits and their significance on a local scale (Vauclin et al., 2021b).

Both side channels are surrounded by a riparian shrubby vegetation, while black and silver poplar (*Populus nigra* and *P. alba*), as well as box elder (*Acer negundo*), are planted next to the sites (Fig. 1D). A major clearing occurred next to the LIMO site in 2009–2010 (see Appendix 2.1). The floodplain margins are covered with fields and orchards. The flora of the PDR sector was listed at the end of the 2000s by the "Conservatoire d'Espaces Naturels" (CEN) and the RhônEco program, which provides basic data for discussing the presence/absence of taxa at the plot level.

2.3. Macrofossil analysis

The sediment cores were conserved in a cold room at 7°C at the ENTPE (UMR CNRS 5023 LEHNA-IAPHY, Vaulx-en-Velin). The macroremains analysis was achieved in the most organic part of the sediment cores (see Appendix 1 for details). For the PDR-1806 master core (LIMO), the sampling was carried out between 66 and 3 cm in depth (28 samples, mean resolution = 2.5 cm, 9.6 g and 8.7 mL by sample on average), i.e. from 1956 to 2017 according to the age model published by Vauclin et al. (2021b). For the PDR-1802 core (ILON), sampled were extracted from 93 cm to the top of the core, i.e. from 1972 to 2018 (24 samples, mean resolution = 4 cm, 9.2 g and 5.1 mL by sample on average).

After extraction, each sample was sieved under a gentle jet of water at several meshes (from $80 \mu\text{m}$ to $>1 \text{ mm}$). Compact and clayey samples were primarily immersed in 200 mL KOH (5 g/L) for 20 min to deflocculate the sediment. Macroremains $>400 \mu\text{m}$ were placed in a Petri dish with Ultra-Pure water, sorted and quantified using a Nikon SMZ 1270 stereomicroscope (magnification $\times 0.75$ to $\times 80$). Plant macrofossils were identified based on the regional data and on photographic atlases (e.g. Birks, 2017; Boulet, 2013; Cappers et al., 2006; Schoch et al., 1988). These reference works also contain photographs of several other biological groups, useful to identify of micro-crustaceans and insects to genus or family level (i.e. *Daphnia* resting eggs, ostracods, and Bryozoan statoblasts). Shell fragments were identified based on literature (Glöer and Meier-Brook, 2003). For particle analyses, three main types were identified according to their texture and aspect: (i) translucent elongated particles were defined minerogenic particles such as quartz, (ii) opaque black particles with sharp edges, sometimes with visible vessels (such as resin canals), were classified as macrocharcoals, (iii) black to grey shiny particles with conchoidal breaks, vacuoles or particular shapes, were identified as iron slags (Houbrechts et al., 2011).

Macrofossil data were treated with multivariate regression trees (MRT; Birks, 2014) within the R environment (packages "mvpart" by Therneau et al., 2014 and "MVPARTwrap" by Ouellette and Legendre, 2013) in order to make zones based on the heterogeneity of the data. In addition, rate of change (RoC) was estimated for 5-year intervals by using the Chi-squared metric (iteration number = 1000) in R (package "RRatepol": Mottl et al., 2021). RoC peaks were identified based on general additive models (GAMs) fitted through the RoC scores and the associated age (non-linear trend method). A peak is considered

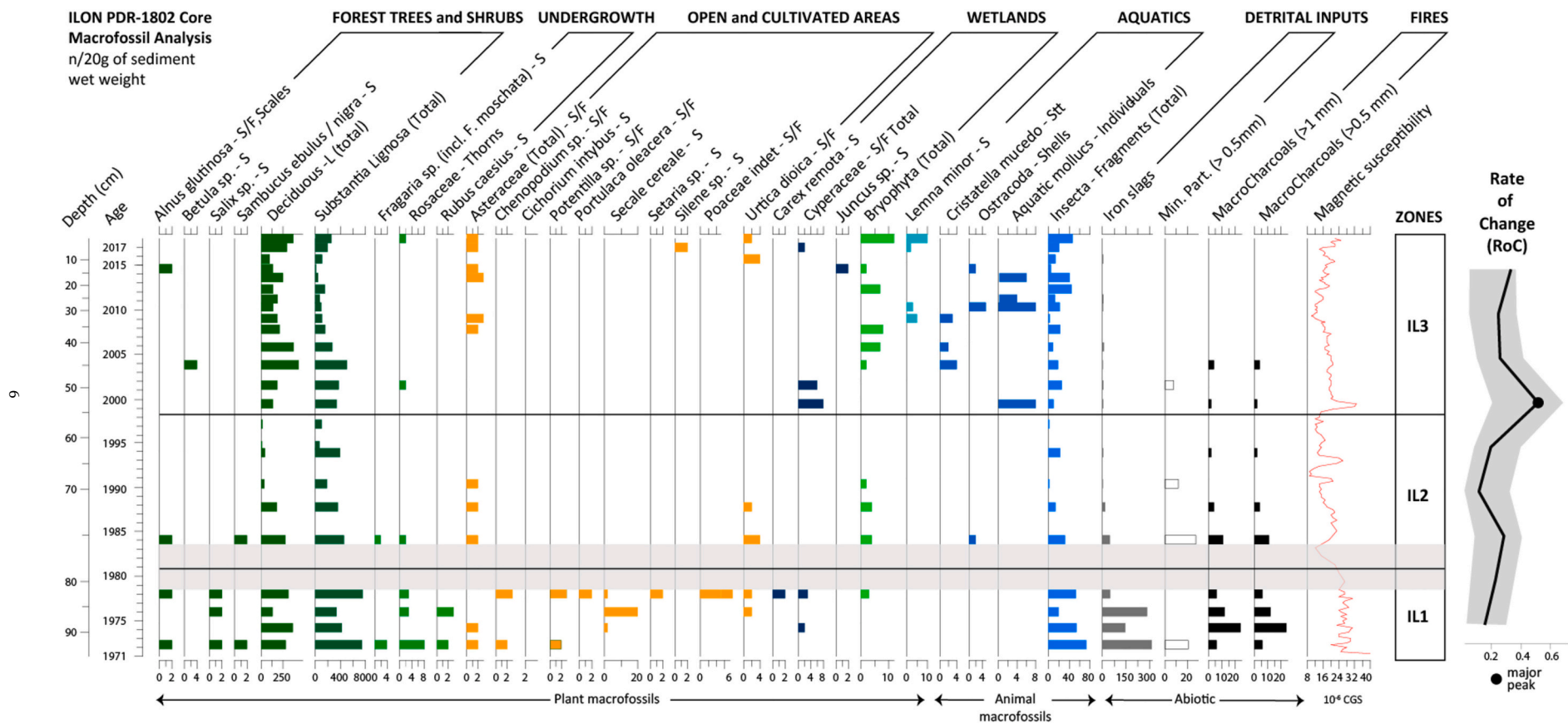


Fig. 4. Main macrofossil taxa extracted from the PDR-1802 core (ILON), magnetic susceptibility, and Rate of change (RoC). Abbreviations: F = fruits, L = leaves, S = seeds, Min. Part. = Minerogenic particles >0.5 mm (i.e. coarse sands), Stt = statoblasts. For the complete list of identified Mollusca species, see [Appendix 3](#). The IL1–IL2 limit is represented by a grey bar, in order to consider the macrofossil sampling resolution.

significant if it is twice the standard deviation of the model. These settings provide an indicator of compositional change that is independent of the sampling resolution. Finally, bar diagrams were plotted by using the “C2” software (Juggins, 2016; version 1.7.7).

2.4. Magnetic susceptibility (MS)

Volumetric magnetic susceptibility (χ) was measured by using a Bartington susceptibility meter (MS2E). This analysis was performed on cores, before sampling for macrofossils, to assess the magnetic level of sediments, giving an idea of the content in ferromagnetic (pure iron or iron oxides), paramagnetic (e.g., silicates) or diamagnetic (e.g., organic matter, water content) elements (Dearing, 1994). It can be used to identify erosion phases, detrital inputs and anthropogenic deposits along a core (Arnaud et al., 2005; Dearing, 1999; Jordanova et al., 2004). As the Rhône River Basin has been heavily industrialised, our hypothesis is that magnetic susceptibility (MS) peaks or trends may be linked to the record of iron slags transported by the river from industrial (stainless steel factories) or mining sources (Houbrechts et al., 2011). MS was measured every 0.5 cm on the PDR-1806 master core, and every 2 cm on the PDR-1802 core.

3. Results

3.1. Macro-remains from LIMO (PDR-1806; right bank of the Old Rhône River)

Based on MRTs, three zones of macrofossil assemblages have been identified on the PDR-1806 master core extracted from LIMO (Fig. 2): Lim1 (66–47 cm; 1956–1979), Lim2 (43–15 cm; 1986–2005), and Lim3 (11–3 cm; 2008–2016). Moreover, the change between zones Lim1 and Lim2 is also underlined by a significant peak in rate of change (RoC) defined on 5-year intervals (Fig. 2).

3.1.1. Zone lim1: Riparian woodland and lotic functioning (66–47 cm; 1956–1979)

Zone Lim1 is rich in wood fragments (*Substantia Lignosa*) and leaves (average = 1263#/20 g of sediment, $\sigma = 400$). Riparian taxa are mainly represented by black alder (*Alnus glutinosa*; Fig. 3A-B), and the undergrowth by strawberries (*Fragaria* sp.; Fig. 3C), brambles (*Rubus* section *rubus*; Fig. 3D) and gypsywort (*Lycopus europaeus*). The riverine vegetation is illustrated, among others, by the purple loosestrife (*Lythrum salicaria*). Seeds from close anthropized, notably cultivated, environments are also observed such as alfalfa (*Medicago sativa*), various Caryophyllaceae, including dwarf mouse-ear (*Cerastium pumilium*), lamb's-quarter (*Chenopodium album*), common purslane (*Portulaca oleracea*) and nettle (*Urtica dioica*; Fig. 3E). Seeds of cultivated exotic taxa are also present such as tansy leaf phacelia (*Phacelia tanacetifolia*) and tomato (*Solanum lycopersicum*) seeds. Mollusca remains represent a wide range of environments close to the coring site (see Appendix 3). In particular, the occurrence of the rheophile river limpet (*Ancylus fluviatilis*) may indicate flooding inputs. The hydrological connectivity with the main river branch is also underlined by the presence of fish vertebrae. Macro-charcoals are abundant (100 to 2840 fragments for 20 g of sediment), with a high degree of fragmentation (numerous small pieces <0.8 mm).

This zone is rich in iron slags (av. = 264#, $\sigma = 66$) with a maximum at 50 cm in depth, in the late 1970s (Fig. 3-J). Their presence correlates with positive and relatively stable magnetic susceptibility (MS) values (av. = 264×10^{-6} CGS, $\sigma = 4$). Small glass beads and shards, ceramic fragments and microplastics were also observed. This zone is also rich in minerogenic particles >0.4 mm (medium and coarse sands) deposited by floods (av. = 969#, $\sigma = 481$). All these particles may have been transported by the river into the studied side channel during floods. The maximum concentration of sands occurred at 50 cm in depth (late 1970s), as well as a peak in Mollusca remains. Fish vertebrae (*piscis spinae*) were also found during the same event, as well as at 66 cm in

depth (late 1950s).

3.1.2. Zone lim2: Terrestrialization (43–15 cm; 1986–2005)

Very few plant macrofossils were found in Lim2, and the change from Lim1 to Lim2 is underlined by a significant peak in rate of change (RoC; Fig. 2). Whilst tree and shrub remains are rarer than in zone Lim1 (av. = 500#, $\sigma = 152$), Bramble and purple loosestrife seeds are still found. Anthropized open environment plants are more present than in Zone Lim1, with the dominance of nettle, lamb's quarter and buttercups (*Ranunculus acris*). Among Gastropods, both aquatic prosobranch snails (*Bithynia tentaculata*) and pulmonated snails (*Galba truncatula*) are found, which suggests a succession of aquatic and dewatering phases. The accumulation of large macro-charcoals is limited between 31 and 22 cm in depth, with a maximum at 22 cm, suggesting a very local fire around 1998–2001. This zone has very few iron slags (av. = 10#, $\sigma = 5$), a decreasing magnetic signature (av. = 12×10^{-6} CGS; $\sigma = 4$), and the number of minerogenic particles is also low (av. = 74#, $\sigma = 46$).

3.1.3. Zone lim3: Aquatic to semi-aquatic environment (11–3 cm; 2008–2016)

Zone Lim3 is characterized by an increase in tree seeds, leaf and wood remains (av. = 1425#, $\sigma = 393$). Riparian taxa such as maple (*Acer* sp.), birch (*Betula* sp.), common hornbeam (*Carpinus betulus*) and black alder (*Alnus glutinosa*) are identified. Cyperaceae seeds are also found. Seeds from man-made environments are only represented by nettle. This phase is also marked by aquatic to semi-aquatic Bryophyta remains (*Seligeria*, *Philonotis* and *Thamnobryum alopecurum*). Animal remains characterized a regularly flooded environment, with of small freshwater crustacean resting eggs (ephippia of *Daphnia*) and ostracod shells (Fig. 3F-G), while insect remains (chitin and eggs) increased. Only *Galba truncatula*, an amphibious species that can survive long dry periods, is identified among Mollusca. Iron slags are absent and minerogenic particles are also very rare (av. = 28#, $\sigma = 35$). MS is still slightly positive and very stable, with an average of 14×10^{-6} CGS ($\sigma = 1$).

3.2. Macro-remains from ILON (PDR-1802; left bank of the Old Rhône River)

Based on MRTs, three zones of macrofossil assemblages were identified on the PDR-1802 core extracted from ILON (Fig. 4): IL1 (91–81 cm; 1971–1979), IL2 (77–57 cm; 1984–1997), and IL3 (53–1 cm; 1999–2018). In addition, the change between zones IL2 and IL3 is underlined by a significant peak in rate of change (RoC) defined on 5-year intervals (Fig. 4).

3.2.1. Zone IL1: Riparian woodland and lotic functioning (91–81 cm; 1971–1979)

Zone IL1 contains numerous riparian woodland macrofossils, with a maximum of 800 pieces of wood and >200 leaf fragments. Macrofossils from black alder (*Alnus glutinosa*), willows (including *Salix capraea* and *S. cinerea*), black and small elders (*Sambucus nigra* and *S. ebulus*) were found, accompanied by undergrowth taxa, such as strawberries (*Fragaria moschata*) and dewberries (*Rubus caesius*). Macro-charcoal pieces are frequent (up to 25#/20 g of sediment) and highly fragmented. Wetland and aquatic remains are rare: only sedges (Cyperaceae) are noticed (incl. *Carex remota*). Many taxa from open and anthropized environments are present, such as rye (*Secale cereale*), a widely diffused crop, and various Poaceae. Other herbs and/or common weeds in cultivated fields and open areas are represented by goosefoot (*Chenopodium* sp.), cinquefoils (*Potentilla* sp.), common purslane (*Portulaca oleracea*), and Asteraceae. Nettle seeds (*Urtica dioica*) are typical of nitrophilous environments. Animal macrofossils are mainly represented by undetermined insect remains. High concentrations of iron slags (up to 300#) associated with minerogenic particle peaks, and positive MS values (av. = 22×10^{-6} CGS; $\sigma = 3$), suggests flood inputs and a lotic functioning (Fig. 5).

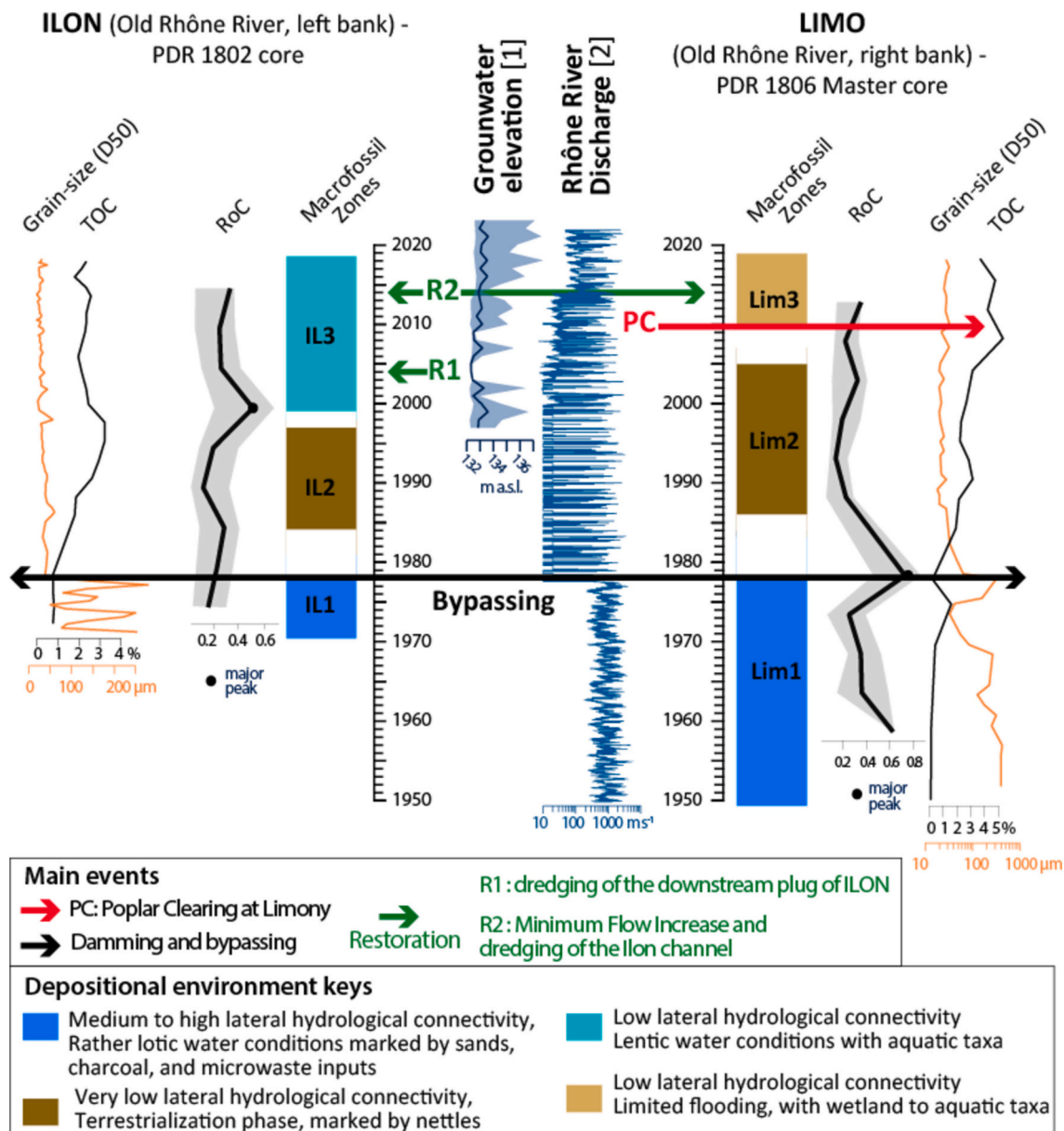


Fig. 5. Comparison of macrofossil zones and RoC on cores PDR-1806 and PDR-1802 (this work) with sedimentological data (grain-size and TOC – Total Organic Carbon, published by Vauclin et al., 2021b), [1] groundwater level (ADES piezometer BSS003ZFSK) and [2] the Rhône River discharge (based on hydro.eaufrance.fr and Compagnie Nationale du Rhône data; see also Noclin, 2024: 141) between 1950 and 2018.

3.2.2. Zone IL2: Terrestrialization (77–57 cm; 1984–1997)

Zone IL2 is poorer in macrofossils than zones IL1 and IL3. We still observe wood remains and leaf fragments as well as black alder, willow and strawberry seeds typical of a riparian forest, but the biodiversity is lower. The same applies to open and cultivated areas which are mainly represented by Asteraceae and nettles. Macro-charcoal, iron slags and minerogenic particles are very rare in this zone. All these elements indicate that the environment is no longer aquatic, but is rapidly filling in and becoming disconnected from the river.

3.2.3. Zone IL3: Lentic functioning (53–1 cm; 1999–2018)

The last phase offers high macrofossil concentrations, as illustrated by wood remains and leaf fragments (Fig. 4). Black alder and birch (*Betula* sp.) seeds indicated a riparian habitat. Sedges and rushes plant macrofossils complete the wetland picture. Cultivated companion plants are rarer but still present, with Asteraceae and nettles. This zone is marked by aquatic to supra-aquatic bryophytes, and by aquatic fauna

remains such as ostracods, and *Cristatella mucedo* (Fig. 3-I), a bryozoan living in colonies, in either lotic or lentic habitats. Aquatic plants such as duckweed suggest a lentic functioning and nutrient rich conditions (*Lemna minor*: Fig. 3-H). Zone IL3 also presents aquatic Mollusca, especially lentic species such as the prosobranch gastropods *Bithynia tentaculata* and *Potamopyrgus antipodarum*, while *P. antipodarum* and *Physa acuta* are exotic snails found in freshwater streams in Europe since the 19th century. Finally, iron slags, macro-charcoals and minerogenic particles are sporadic, suggesting limited detrital inputs.

4. Discussion

4.1. Environmental changes affecting side channels over time

In order to discuss ecological and hydro-sedimentary changes affecting side channels since the 1950s, Fig. 5 combines the macrofossil results with sedimentological data (median grain size - D50 and organic

carbon rate - TOC) published by Vauclin et al. (2021a, 2021b), as well as broader data such as groundwater elevation variations and changes in river discharge (see the caption of Fig. 5).

On each core, the first phases (Lim1 and IL1) are characterized by various taxa coming from the local riparian woodland, by amounts of macrocharcoals (highly fragmented) and industrial microwaste (mainly iron slags). Those accumulations coincide with sandy levels recorded on both sites (PDR1802 IL1 D50 = 135 μm ; PDR1806–1807 Lim1 D50 = 168 μm), and are a fossilized image of the material transported (and deposited) by the river in the depositional environment formed by side channels in the 1950s–1970s. The annual average discharge was about 1000 $\text{m}^3\cdot\text{s}^{-1}$ from 1950 to 1977, which explains the middle to high hydrological connectivity and such detrital deposits. It underlines that the studied side channels were frequently flooded and connected to the main stream, before the damming and bypassing of the Rhône River (Fig. 5). In both cores, positive even strong correlations (r comprised between 0.44 and 0.79) are observed between iron slags, macrocharcoals and magnetic susceptibility (Appendix 4). It suggests a common accumulation process, or even a common origin for these particles. The most probable source is the industrial valley of the Gier River, an upstream right-bank tributary of the Rhône River, where stainless steel factories developed since the mid-19th century (Périnaud et al., 2024). This Rhône River case is not an isolated one, as iron slags have already been identified in the sediments along the Loire (Gautier et al., 2009), and in Belgian rivers (Houbrechts et al., 2011). These elements have been used to estimate sediment transfer rates, but such “Anthropocene macrofossils” (i.e. iron slags and charcoal particles) seem also to be good indicators of the riverine ecosystem changes.

Plant macrofossils showed a fairly diversified riparian vegetation, with black alder, willow and hornbeam, and an undergrowth composed of wild strawberries and brambles. However, no remain could be clearly attributed to the poplar grove, which is a local well-known vegetation, monitored for a long time (Pont and Delaigue, 1995). Several hypotheses are possible to explain this lack of correspondence, such as a bias in conservation and/or a very local origin of macrofossil remains. Also, a large concentration of leaf fragments and small pieces of wood remains undetermined, but could refer to the surrounding poplar plots. Aquatic remains are rare in the 1950s – 1970s, probably due to the high connectivity of the side channels (lotic functioning). Finally, both cores offer a large diversity of open area taxa (Figs. 2 and 4), which is in line with the close presence of cultivated areas (cornfields) and meadows.

The upper limits of phases Lim1 and IL1 are well correlated and ended in 1979 (estimated age), which is 2 years after the bypassing of the PDR section (dam commissioned in 1977). The general policy of bypassing of the Rhône river is known to have caused a drop of the water level, dewatering and a terrestrialization of the river channels over several hundred kilometres in total along the river (Dépret et al., 2017). This change seems quite radical at LIMO side channel and is marked by a peak in the RoC.

Indeed, following the river bypassing, macrofossil phases Lim2 and IL2 are quite poor in taxa diversity despite a TOC increase on both sites (Fig. 5). Thus, this poor biodiversity is not linked to a lower preservation of organic matter. The comparison with sedimentological data rather suggests a change in the accumulation process, since the median grain-size (D50) decreases abruptly from sands to silts, and underlines a terrestrialization of the side channels (PDR1802 IL2 D50 = 39 μm ; PDR1806–1807 Lim2 D50 = 23.5 μm). The lack of iron slags, macrocharcoals and sands also supports this hypothesis, even if a combination of factors at various scales might be implied: disconnection from the Rhône River inputs, storage of sediments in the upstream dams, and de-industrialization resulting in less charcoals and iron slags transported by the river. For plant macrofossils, the riparian vegetation is always recorded and may include willows. The domination of nettle seeds began after the damming (1977), when the discharge delivered to the Old Rhône River decreased to $<30 \text{ m}^3\cdot\text{s}^{-1}$, except during floods (see curve [2] on Fig. 5). Their dominance could be linked to the oxidation of

nitrogen stored in the soil (nitrification) during the decades when the water table was low. Locally, nettle usually occupies Girardon groyne fields, also terrestrialized after the water drop caused by the bypassing of the river (Pont et al., 2008). Finally, to complete the broad environmental picture, this terrestrialization stage is also visible on past aerial photographs between 1981 and 1991 (Appendix 2). The same plant and abiotic macrofossil characteristics are found on both sites which further underlines the reliability of the macrofossil approach to reconstruct hydro-sedimentological and local vegetation successions based on fluvial sediment cores.

4.2. Restoration effects and macrofossil data

The macrofossil content of phases Lim3 and IL3 is typical of lentic water or temporary waterlogged conditions, with a low lateral hydrological connectivity (Fig. 5). The change is very clear on the ILON side channel, where it is a key point in the RoC curve. In particular, a rather high diversity of wetlands and aquatic plant or animal taxa is recorded in the sediment cores such as sedges, rushes, duckweeds, aquatic or semi-aquatic bryophytes, bryozoans, ostracods and freshwater Mollusca (Figs. 2–4). The close agreement between the taxa identified in the sediment record and in the 2008 survey data (data available on request from the RhônEco program) suggests that the cores provide a faithful representation of the dominant components of the flora and fauna, at least for the recent period. However, other local macrophytes do not appear in the macrofossil record, even though they usually provide easily identifiable seeds such as hornwort (*Ceratophyllum demersum*), pondweeds (Potamogetonaceae) or spiny water nymph (*Najas marina*). One hypothesis to explain the absence of such macrofossils is that the seeds were able to float and disperse downstream or upstream from the site. Thus, macrofossil records constitute a high-quality source for the presence of riparian woodland taxa and aquatic to semi-aquatic species, but they are most certainly non-exhaustive.

Notably, the timing of Lim3 and IL3 macrofossil phases differs, which can be discussed in the light of various regional or local events (Fig. 5). The return to lentic aquatic conditions at ILON is only possible after 2004, when the first restoration was carried out (event R1: dredging of ILON downstream plug). However, IL3 phase began a bit earlier, i.e. around 1999–2000. This step coincides with the beginning of a period of higher water levels, when the Rhône River discharge increased (see curve [2] on Fig. 5). Then, 2014 MIFI (event R2) ensured the continuation and consolidation of this new aquatic stage. In contrast, the LIMO side channel has only benefited from the 2014 MIFI, which affected the whole PDR sector (50 to 125 $\text{m}^3\cdot\text{s}^{-1}$), and other sectors along the Rhône River. In our opinion, it explains the longer duration of the terrestrial phase Lim2 compared to IL2. Indeed, Fig. 5 shows a gradual change between Lim2 (terrestrial phase) and Lim3 (limited flooding), which agrees with a diffuse effect of the MIFI. The delay observed between the beginning of the new aquatic phases Lim3 and IL3 could also be linked to the fact that the recovery of lotic river ecosystems is not immediate. Indeed, it may take decades to centuries to achieve, depending on the changes that can alter longitudinal, lateral and vertical connectivity in and between river channels at different points in time (Foster and Greenwood, 2016; Ward, 1989). Another event at LIMO, is the clearing of the poplar parcel surrounding the site, achieved in 2010, which leads to a TOC increase. In terms of macrofossils, the consequence is that the sediments are enriched in pieces of wood and leaves (Figs. 2 and 5). Thus, the macrofossil Lim3 phase is a combination of local (poplar clearing) and regional (MIFI) factors, both anthropogenically driven.

Finally, the upper part of the sediment records contains a diversity of wetland and aquatic taxa (plant and animal macrofossils). Remains of aquatic mosses, seeds, insect fragments, and micro-crustaceans such as ostracods and water fleas (*Daphnia*) are better preserved than in the lower sections of the cores. Concerning animal macrofossils, our study is limited in terms of identification and counting ($> 400 \mu\text{m}$). Interpretations of shifts in functional ecology therefore remain limited, as



Fig. 6. The Limony side channel covered by duckweed in 2019 (Credit: N. Noclin, 2019).

only large *Daphnia* ephippia were found based on the applied sieving, while their preservation could be linked to the nutrient or eutrophication state of the SC, as well as to presence/absence of submerged macrophytes and predatory fishes (Jeppesen et al., 2001). Duckweed seed accumulations refer to the current situation of these restored side channels, occupied by stagnant and eutrophic water (Fig. 6). As macrofossils are local, it only represents a fraction of biodiversity listed by the RhônEco monitoring program. Overall, the macrofossil results agree with the work of Janssen et al. (2021) on the vegetation river margins, who observed a greater biodiversity and the presence of pioneering riparian plants after restoration actions.

5. Conclusions and perspectives

This research proposes an application of macrofossil analysis, classically used in palaeoecology, to post-1950 sediment cores extracted from river side channels, in order to determine whether this method is reliable at several sites on a densely engineered (e.g. dams, bypassed reaches) and managed river. Such environments are challenging due to low organic matter levels (< 10 %) and occasional connections with the main river branch, which implies episodes of highly dynamic flooding.

Interestingly, the macrofossil records allowed a coherent history of the species habitats and biodiversity of the two sampled sites to be reconstructed. The analysis confirms a synchronous terrestrialization phase on the two cores and sites, after the abrupt reduction of the water discharge caused by the damming and bypassing of the river for navigation and hydroelectricity production. The macrofossil approach is therefore a valuable tool for contributing to the reconstruction of environmental changes affecting the various compartments of a river system. Finally, macrofossil data reveals the arrival of new wetland and aquatic vegetation, as a result of the channel restoration. This last point is crucial as it provides feedback on the development of ecological restoration in the medium term, as well as data on how these changes are recorded in the sediments. Among the identifiable indicators easy to identify, macrofossils from riparian woodland and undergrowth appear to be essential to interpretation of restoration effects. Quantifying the remains of wetland and aquatic species (incl. Sedges, rushes, duckweeds, and mosses), as well as aquatic fauna (*Daphnia* resting eggs, ostracod shells) also provides valuable information. The interpretation of micro-waste and macrocharcoal concentrations is more equivocal, as they may reflect local

discharges or fires, are often linked to detrital inputs and to the local to regional socio-economic context. Macrofossil analysis of side channel cores could thus become a tool for defining reference conditions to inform river channel restoration projects and for tracking their relative success over decadal timescales, as practised for other wetlands such as peat bogs. To go beyond the limits of analysing only the macrofossil content, in the future we plan to also perform palynological and eDNA analyses in order to reconstruct and model in a more complete way the evolution and response of species assemblages to the engineering projects over periods which are not usually covered by monitoring data.

CRedit authorship contribution statement

André-Marie Dendievel: Writing – original draft, Validation, Supervision, Methodology, Conceptualization. **Jérémy Riquier:** Writing – original draft, Validation, Resources, Conceptualization. **Brice Mourier:** Writing – original draft, Validation, Conceptualization. **Thierry Winiarski:** Writing – original draft, Validation, Conceptualization.

Declaration of competing interest

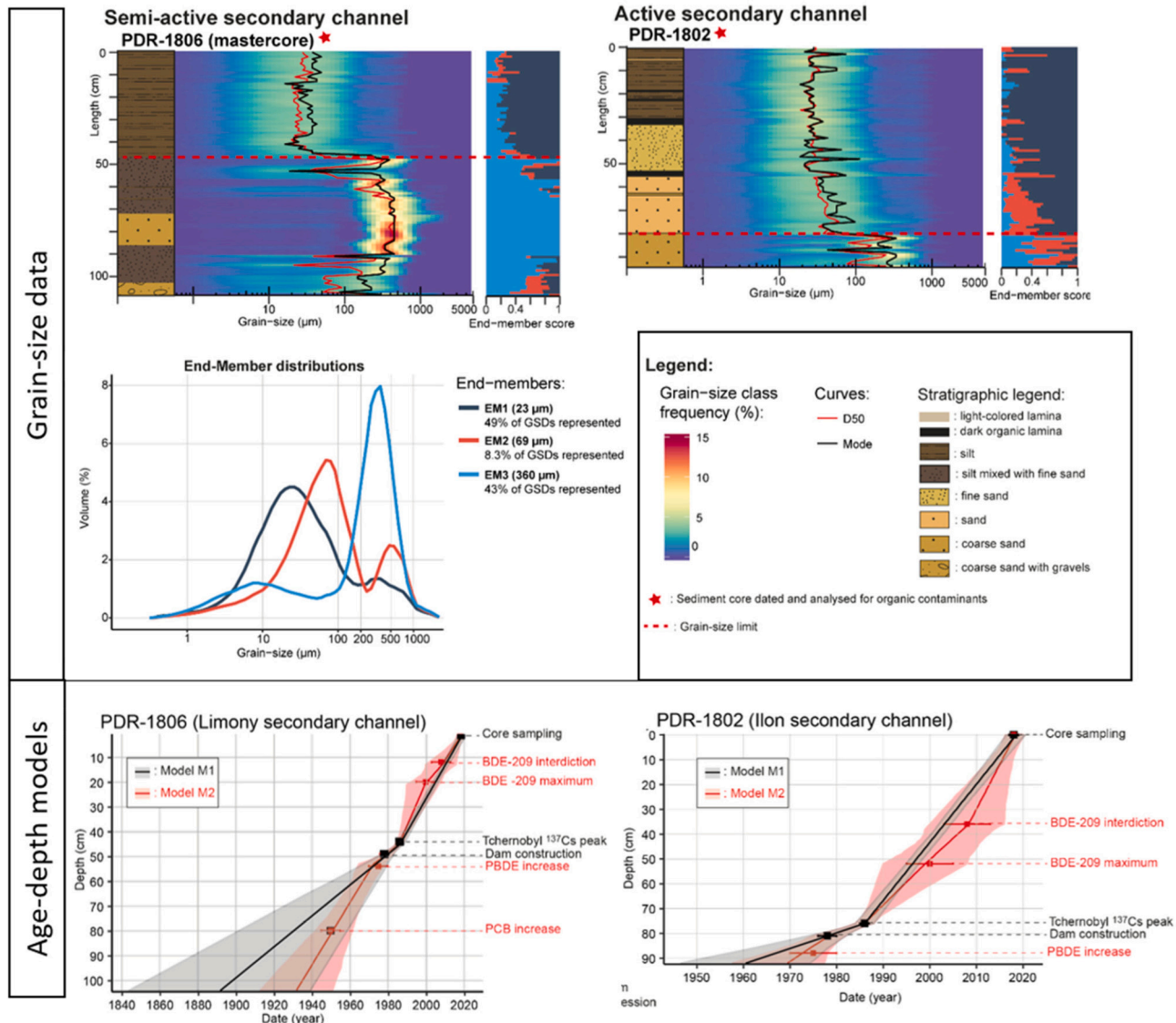
The authors declare that they have no conflict of interest.

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Appendix 1. Bypassing and restoration effects on side channel biodiversity, as recorded by river sediment archives

1.1. Grain-size data and age-depth models obtained for PDR-1806 (Limony) and PDR-1802 (Ilon) cores published by Vaulcin et al. (2021b)



Grain-size data and age-depth models obtained for PDR-1806 (Limony) and PDR-1802 (Ilon) cores published by Vaulcin et al. (2021b)

1.2. Coring site details

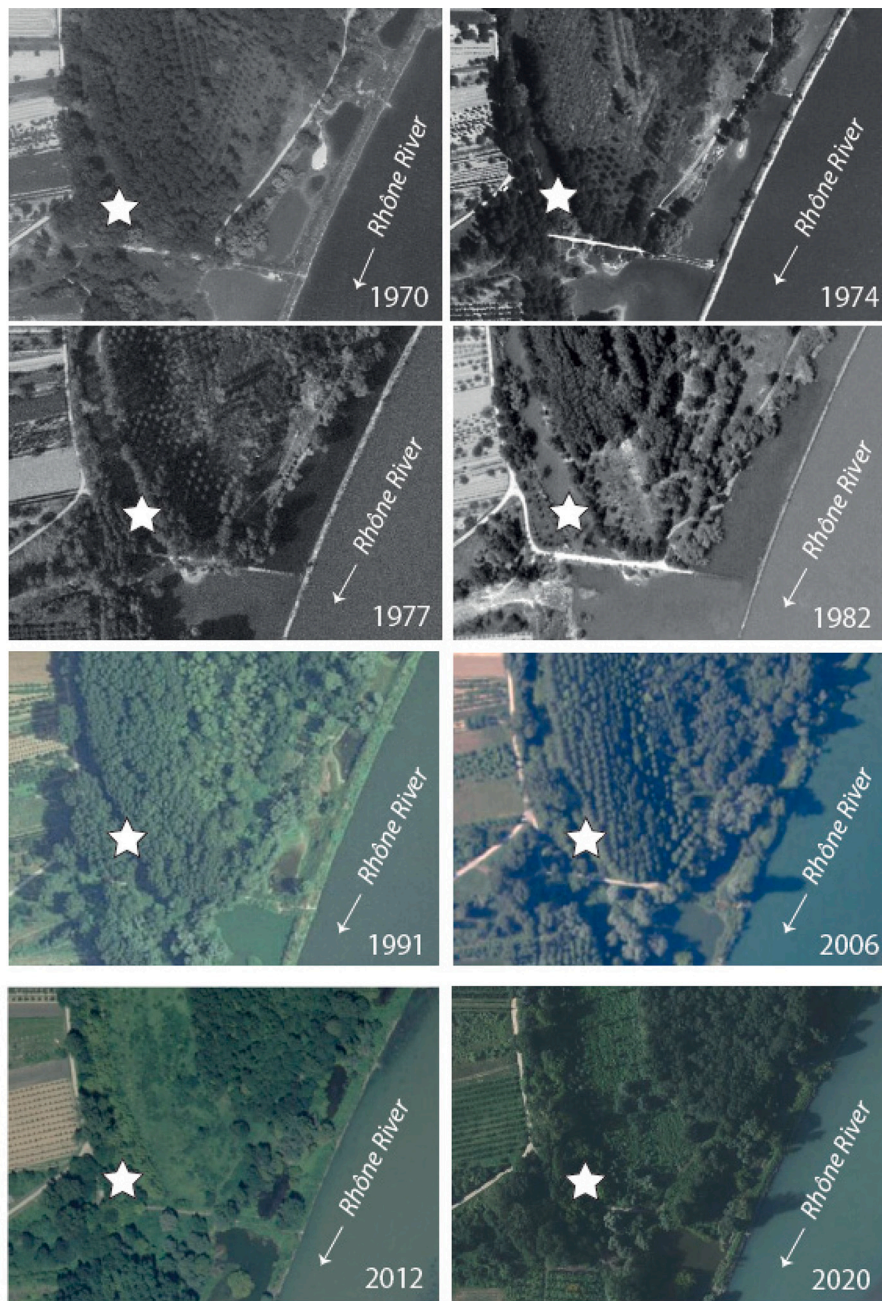
The Limony side channel (LIMO) is located on the right bank of the by-passed reach of the Rhône River (see Appendix 2.1). It was an active side channel in the 1860's, separated from the main channel by a small island. Both extremities of the channel were closed by submersible dykes during the Engineering Phase 1 (1880's). It is currently in a very advanced state of terrestrialization. Nowadays, this 650 m long side channel is connected to the main channel at its upstream end about 1.9 d.y⁻¹ (i.e. upstream overflow events leading to a lotic functioning) and 3.3 d.y⁻¹ at its downstream end (backflows, lentic conditions) according to Noclin (2024). The corridor of LIMO is occupied by a riparian shrubby vegetation, while poplar was cultivated for more than forty years next to the left side of the site, on a parcel cleared several times, which is a thicket since 2010 (see aerial photographs in the Appendix 2.1). The right bank presents fields and orchards since the 1970's according to the photo-based retrospective (Appendix 2.1). Two sediment cores were extracted from this site by using a COBRA-TT coring device. These cores were combined based on grain-size data in order to form a 108 cm-long core, called "PDR-1806 master core". Its bottom is estimated to date back to the beginning of the 20th century (at least) and present sand levels, while the chronology of the top 60 cm is well secured from 1965 to 2018 (Vaulcin et al., 2021b; see also Appendix 1.1).

The Ilon site (ILON) is part of a network of side channels located on the left bank of the by-passed reach called "Lône de la Platière" (PLAT). ILON is permanently connected at its downstream end to the PLAT, and disconnected from PLAT at its upstream end by an alluvial plug. Currently, the upstream end of ILON is flooded about 5.7 d.y⁻¹ a year on average (Noclin, 2024). The upstream extremity of PLAT was closed by submersible dikes

and groynes during the Engineering Phase 1 (1880's), which significantly decreased the water flow in ILON. Then, ILON underwent a gradual terrestrialization in the 1980s and 1990s following the water flow diversion of the Engineering Phase 2 (Vauclin et al., 2021b). Terrestrialized areas are clearly visible on aerial photographs between 1974 and 1991 (see Appendix 2.2). ILON was then restored in two steps. (i) In 2004, 200 m of the downstream end of ILON were dredged and reconnected to PLAT. (ii) In 2014, the remaining part of the channel (~750 m upstream) was also dredged to create a succession of large groundwater supplied pools. The ILON right bank presents poplar and box elder (*Acer negundo*) plots, while the left bank offers meadows and cornfields. Ash and poplar groves are found on the left bank margins as well. A 94 cm-long core (called "PDR-1802") was extracted from ILON in 2018 by using an UWITEC gravity corer for aquatic environments. The bottom of the sequence is dated back to the 1970's and continuously accumulated until 2018 (Vauclin et al., 2021b).

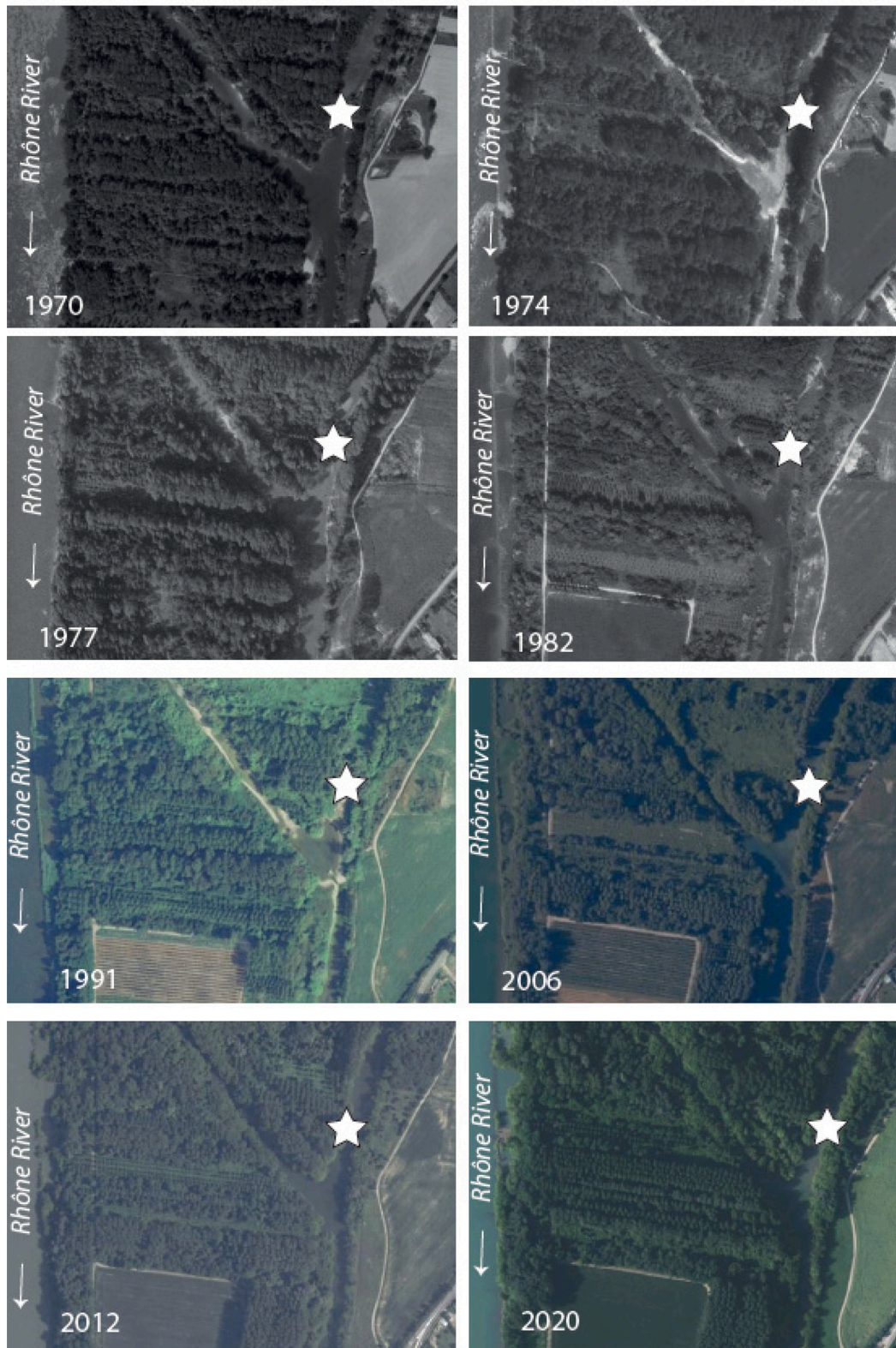
Appendix 2

2.1. Historical retrospective according to selected aerial photographs above LIMO



Historical retrospective according to selected aerial photographs above LIMO (Limony). The master core PDR-1806 is represented by a star. Source: <https://remonterletemps.ign.fr>.

2.2. Historical retrospective according to selected aerial photographs above ILON



Historical retrospective according to selected aerial photographs above ILON. The core PDR-1802 is represented by a star. Source: <https://remonterletemps.ign.fr>.

Appendix 3. Gastropod and Bivalvia inventory

Gastropod and Bivalvia inventory. Columns 1 to 11 present raw numbers of identified individuals, while columns 12 to 13 present the number of individuals normalised for 20 g of wet sediment.

Core	Sample	Age	1	2	3	4	5	6	7	8	9	10	11	12	13
			<i>Bithynia tentaculata</i>	<i>Potamopyrgus antipodarum</i>	<i>Valvata piscinalis</i>	<i>Ancylus fluviatilis</i>	<i>Galba truncatula</i>	<i>Physa acuta</i>	<i>Radix auricularia</i>	<i>Euglesa subtruncata</i>	<i>Euglesa sp.</i>	Aquatic taxa (sum)	Terrestrial taxa (not detailed)	Aquatic taxa / 20g	Terrestrial taxa / 20g
PDR1802	MR17	2013.6	1					1				2		6	
PDR1802	MR25	2011.2	1	1								2		4	
PDR1802	MR29	2010.3						1		1	1	3	1	8	3
PDR1802	MR53	1999.4		4								4		8	
PDR1806a	MR3>0.8	2016.2					1					1		1	
PDR1806a	MR19>0.4	2001					1					1	1	2	2
PDR1806a	MR43>0.4	1986	1									1		2	
PDR1806a	MR47>0.4	1978.4											2		6
PDR1807	MR48	1976.1				1						1	2	7	15
PDR1806a	MR51>0.8	1975.3			1							1		1	
PDR1807	MR50	1973.13						1	1			2		5	

Appendix 4. Correlation matrix between macrocharcoals, iron slags, coarse minerogenic particles (>0.5 mm), and MS (magnetic susceptibility)

Correlation matrix between macrocharcoals, iron slags, coarse minerogenic particles (>0.5 mm), and MS (magnetic susceptibility). Stars represent p-values: *significant (p-value < 0.05); ***very highly significant (p-value < 0.01).

PDR1086 master core (LIMO)	Macrocharcoals	Iron slags	MS	Coarse Minerogenic Particles
Macrocharcoals	1	-	-	-
Iron slags	0.793***	1	-	-
MS	0.439*	0.459*	1	-
Coarse Minerogenic Particles	0.728***	0.720***	0.361	1

PDR1802 (ILON)	Macrocharcoals	Iron slags	MS	Coarse Minerogenic Particles
Macrocharcoals	1	-	-	-
Iron slags	0.601***	1	-	-
MS	0.747***	0.605***	1	-
Coarse Minerogenic Particles	0.244	0.370	0.240	1

Data availability

Data will be made available on request.

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