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# Ecosystem-level effects of re-oligotrophication and N:P imbalances in rivers and estuaries on a global scale

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**Abstract**

Trends and ecological consequences of phosphorus (P) decline and increasing nitrogen (N) to phosphorus (N:P) ratios in rivers and estuaries are reviewed and discussed. Results suggest that re-oligotrophication is a dominant trend in rivers and estuaries of high-income countries in the last two–three decades, while in low-income countries widespread eutrophication occurs. The decline in P is well documented in hundreds of rivers of United States and the European Union, but the biotic response of rivers and estuaries besides phytoplankton decline such as trends in phytoplankton composition, changes in primary production, ecosystem shifts, cascading effects, changes in ecosystem metabolism, etc., have not been sufficiently monitored and investigated, neither the effects of N:P imbalance. N:P imbalance has significant ecological effects that need to be further investigated. There is a growing number of cases in which phytoplankton biomass have been shown to decrease due to re-oligotrophication, but the potential regime shift from phytoplankton to macrophyte dominance described in shallow lakes has been documented only in a few rivers and estuaries yet. The main reasons why regime shifts are rarely described in rivers and estuaries are, from one hand the scarcity of data on macrophyte cover trends, and from the other

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hand physical factors such as peak flows or high turbidity that could prevent a general spread of submerged macrophytes as observed in shallow lakes. Moreover, re-oligotrophication effects on rivers may be different compared to lakes (e.g., lower dominance of macrophytes) or estuaries (e.g., limitation of primary production by N instead of P) or may be dependent on river/estuary type. We conclude that river and estuary re-oligotrophication effects are complex, diverse and still little known, and in some cases are equivalent to those described in shallow lakes, but the regime shift is more likely to occur in mid to high-order rivers and shallow estuaries.

## 1 | INTRODUCTION

Pervasive degradation of freshwater ecosystems by human activities prompted efforts to reverse processes such as eutrophication, which is among the Earth's most severe drivers of ecosystem change (Ibáñez & Peñuelas, 2019). Eutrophication refers to the overproduction of organic material induced by anthropogenic inputs of P and N (Le Moal et al., 2019). Since the mid XX century many European and North-American freshwater lakes experienced water quality trends first in the form of increase (Cooke, 2007; Loizeau & Dominik, 2005) and then reduction of nutrient concentrations (e.g., total phosphorous and nitrogen) following a myriad of management actions such as the construction of wastewater treatment plants (WWTP), banning of P in detergents, ecosystem restoration (i.e., wetlands), or improvement in crop management (Bowes et al., 2011; Cozzi et al., 2019; Radach & Pätsch, 2007). As a result, cultural re-oligotrophication (also named re-oligotrophication or simply oligotrophication), here defined as the process of returning from eutrophic to oligotrophic conditions often with contrasting autotrophic communities (e.g., phytoplankton vs. macrophytes), was documented in lakes from a vast majority of high-income countries (Kronvang et al., 2005; Schindler, 2012; Stich & Brinker, 2010). However, situations toward nutrient enrichment (eutrophication) are still occurring in many low- to mid-income countries (Sardans et al., 2012a, 2012b), but information is only available in some countries such as India and China (Sarma et al., 2010; Ramesh et al., 2015; Duan et al., 2007; Qin et al., 2022). After extensive research in lakes, there also has been efforts to document fluvial and estuarine ecosystem responses to re-oligotrophication (Duarte et al., 2009; Hilt et al., 2011). Now, and despite a broad understanding on water quality trajectories and environmental controls (Dent et al., 2002; Ibáñez, Alcaraz, et al., 2012) and more recently on the main ecological responses (Bennett et al., 2021; Diamond et al., 2022), the timing, location, and magnitude of river and estuary re-oligotrophication, its nutrient-biological response relationships and potential drivers remain largely unknown.

Another aspect of river and estuary re-oligotrophication and associated ecological responses that has been neglected is the increase

in N to P ratio (N:P). Changes in N:P may induce shifts among primary producers hence favoring the dominance of certain groups of phytoplankton (Romero et al., 2013). Given the high spatiotemporal variability of river ecosystems and natural and anthropogenic drivers of flow alteration (Romero et al., 2021; Sardans et al., 2012a; Tong et al., 2020; Yan et al., 2016; Zhang et al., 2019), it is expected that this stoichiometric N:P imbalance has played a significant role in biological responses (Elser et al., 2009). Besides the widespread decrease in P due to management measures such as the installation of WWTP and the banning of detergents, and/or the increase in N due to an intensive use in N fertilizers, the increase in water N:P ratios can also occur naturally in rivers because of their high-water turnover (Peñuelas et al., 2013). As well, a global average pattern of rivers impounded by dams is to further increase the N:P ratios (Maavara et al., 2015). Therefore, the mechanisms linking oligotrophication, N:P imbalances, and global change drivers are complex and merit a comprehensive review.

Given the interconnected global change stressors and their acceleration affecting river ecosystems over the last decades (e.g., anthropogenic nutrient inputs, dam building, water extraction, land use change, warming, or atmospheric pollution) unexpected, abrupt shifts in ecosystem state and function, known as regime shifts, may occur similarly as those of shallow lakes (Scheffer et al., 1993). Despite the growing evidence that some large rivers have undergone critical transitions following oligotrophication trends (Ibáñez & Peñuelas, 2019), factors stabilizing and destabilizing these alternative stable states have become subjects of particular interest in river hydroecology to anticipate regime shifts in the opposite direction (e.g., re-eutrophication; Palmer & Ruhi, 2019). Some studies focused on multiple interacting factors to elucidate how chlorophyll-*a* (Chl *a*)—an ecosystem-wide indicator of trophic state—responded to a decrease in P (the main limiting factor of primary production in freshwaters). For instance, the top-down effect of fish and bivalves (e.g., control of phytoplankton via grazing; Minaudo et al., 2021), the bottom-up effect (e.g., control via nutrient limitation; Ibáñez, Alcaraz, et al., 2012), or legacy nutrient sources from historical agricultural sediments (Civan et al., 2018). This complexity, coupled with the fact that long-term (>20 years) river datasets suffer from

heterogeneous chlorophyll (Chl) observations as well as lack of contextual information, often results in inconsistent findings of nutrient-Chl relationships in the literature (Bennett et al., 2021). There is an urgent need to place individual case studies into a broader context and general comprehensive evidence based on available literature to outline how ongoing and future water management and restoration can benefit from a better knowledge of the consequences of re-oligotrophication process.

This review paper synthesizes the current understanding of the relationship between nutrient reduction trends, biological responses, and ecological consequences in rivers and estuaries, such as cascading effects and regime shifts. We provide comparisons with the analogous shifts that have occurred in lakes to advance our understanding of generalizations in critical transitions across lentic and lotic ecosystems. Our review also includes the concomitant increase in the N:P ratio since this ratio often has undesirable and less well-known biological and ecological consequences. By focusing on data and evidence from scientific literature, gray literature, and databases on water quality, we addressed the following interrelated questions:

1. To what extent is re-oligotrophication and stoichiometric N:P imbalance unfolding in rivers and estuaries? What are the limitations of available data? (*Section 2*)
2. What are the main effects of re-oligotrophication on biota and the whole ecosystem? (*Section 3*)
3. What are the main differences in the oligotrophication response of rivers, estuaries, and shallow lakes? (*Section 4*)
4. To what extent is the response of rivers and estuaries different as a function of watershed geochemistry? (*Section 5*)
5. What are the main feedbacks of re-oligotrophication with other global change factors such as warming and acidification, dams or invasive species? (*Section 6*)
6. What management measures regarding restoration, land use and water management can be proposed to correct the undesirable effects of river re-oligotrophication? (*Section 7*)

## 2 | TO WHAT EXTENT IS RE-OLIGOTROPHICATION AND STOICHIOMETRIC N:P IMBALANCE UNFOLDING IN RIVERS AND ESTUARIES? WHAT ARE THE LIMITATIONS OF AVAILABLE DATA?

Existing literature and recent reports show a decline both in P and N concentrations and an increase in N:P in rivers and estuaries over the last 30 years in high-income countries, mostly Europe and North America. Tables S1 and S2 refer to 71 study cases of rivers, groups of rivers, estuaries and groups of estuaries, based on 89 papers and reports, plus references therein, showing a compelling case of widespread re-oligotrophication. In many cases papers and reports refer to hundreds or thousands of rivers, estuaries or river stretches, such as the European Environment Agency (EEA) report based on data

from thousands of river sites, or some of the papers from United States (US) based on data from hundreds of river sites.

In rivers this trend is more pronounced for P than for N, implying that the N:P ratio is growing, a pattern generally observed in the European Union (EU) and US riverine ecosystems, with some exceptions such as some parts of the Mississippi basin (EEA, 2019, 2022; Oelsner & Stets, 2019; Stets et al., 2020). However, the extent and magnitude of re-oligotrophication and N:P imbalance is higher in the EU compared with the US, likely because of differences in river basin features (e.g., more acidic soils in US), human land uses (e.g., more sparse housing without wastewater treatment in US), and the different implementation of environmental policies (e.g., more strict nutrient targets in EU).

A study for the period 1992–2012 showed that most US river basins underwent a decrease in total P (TP), soluble reactive P (SRP), total N (TN), nitrate ($NO_3$), and ammonium ($NH_4$), except for river basins dominated by agriculture, where TP and SRP increased in most of them, TN and $NO_3$ remained rather stable and $NH_4$ clearly decreased (Stets et al., 2020). However, general declines in P have been reported in US river basins that have adopted heavy tile-drained practices (Kreiling & Houser, 2016). In the EU, $NO_3$ decreased 0.8% and SRP 1.8% per year on average over the period 1992–2015; the mean concentration of TP in lakes decreased 0.9% per year over the same period (EEA, 2019). As a result of these declining trends, SRP concentration in rivers halved along the period 1992–2012 and then leveled-off, while $NO_3$ decreased more slightly during the period 1992–2009 and then leveled-off (EEA, 2022). This is a consequence of the implementation of best management practices and reductions of agricultural nutrient inputs, improvements in wastewater treatment, and the reduction of phosphorus in detergents (Sardans et al., 2012b).

Literature concerning the trophic status of estuaries and bays is scarcer than in rivers but sufficient to show a growing number of cases where P and/or N have decreased in the last 20–30 years (Ibáñez & Peñuelas, 2019). The best documented cases (see Table S2) refer again to the US and the EU, such as Boston Harbor (Taylor et al., 2011), Tampa Bay (Greening et al., 2014), Chesapeake Bay (Lefcheck et al., 2018), San Francisco Bay (Glibert, 2010), Seine Bay (Romero et al., 2013, 2016), Ebro Estuary (Nebra et al., 2016), Danish coastal waters (Riemann et al., 2016), and Northern Adriatic coast (Mozetič et al., 2010). In most cases re-oligotrophication trends and effects in estuaries are not as marked than in rivers, likely because of the combination of less intense decrease in P concentration and the more important role of N in limiting primary production (which in turn has decreased less than P).

Much less information is available from the middle- and low-income countries. Yet, the general trend seems to be an increase in N and P leading to eutrophication in lakes, rivers, and estuaries during the last decades, meaning that the re-oligotrophication process is mostly occurring in high-income countries. Nonetheless, recent literature shows that the eutrophication process is being reversed in Chinese lakes from the most economically developed areas of the country (Tong et al., 2020), where nutrient enrichment started

earlier, but there is no current evidence of this happening in rivers and estuaries.

Regarding the response of river biota to P decline, the most basic and available variable is Chl (either total or *a*). Although existing datasets are quite limited across countries and along time (Bennett et al., 2021), there is much more data than for other variables such as phytoplankton biomass (or biovolume), phytoplankton composition, macrophyte biomass, etc. (in those cases data are very scarce). One of the most comprehensive available meta-analysis of world rivers showed positive responses of Chl *a* in the water column to TP and N (Bennett et al., 2021). The authors analyzed 105 studies comprising 439 nutrient-Chl pair effects between the years 1980 and 2017. They used a combination of databases, website searches, and gray literature. Among the open publicly available water quality databases are the Waterbase in Europe (EEA, 2020), the US National Water Information System (NWIS; USGS, 2022), the US Environmental Protection Agency's STOrage and RETrieval Data Warehouse (STORET; EPA, 2021), and the Global Freshwater Quality Database (United Nations Environment Programme, 2020). However, those databases rarely include estuaries; in most cases datasets from estuarine systems come from local or regional studies. Furthermore, most of the studies encompasses one visit at a year and focuses on few spatial stations across years (Ardón et al., 2021; Bennett et al., 2021). This make difficult to elucidate if declining P trends are linked to biological responses. A first examination of global databases (Waterbase, GEMStat) confirms that, indeed, in many cases the records are too short (i.e., after the 2000s) and the sample interval too long (i.e., less than 4 sampling points/year) to capture any meaningful annual trends. A preliminary NWIS exploration yielded a total of 152 sites with N, P, and Chl *a* data with at least six observations per year between the 1990s and 2010s.

In terms of identifying global nutrient and chlorophyll trends, North America (mostly US) is the region having more available records followed by Europe (mostly EU), while the main limitation is data scarcity in low- to middle-income countries. A few of these countries are increasing their water monitoring capacity and measuring nutrients in a regular way (i.e., China, India, Brazil, South Africa), although results are often unpublished or difficult to find and looking for the data in gray literature and non-published national databases is often unreliable and difficult to interpret. Even in high-income countries, access, interpretation, and comparability of water quality data (and nutrients, in particular) are frequently complicated for many reasons. For example, records of varying time spans and sampling frequency, inconsistently measured variables, units, or analytical procedures. Therefore, there is an overwhelming need to (a) consistently upload data and information to online repositories by participating countries, states, or agencies and provide clear protocols that may allow comparability of the records; and (b) invite other countries, states, and regions to use comparable monitoring schemes and protocols that will facilitate the use of this information to analyze long-term patterns (e.g., similar sampling frequency).

The lack of observational long time series data could be partly overcome indirectly by effect size relationships of key variables (e.g.,

Chl *a*–TP relationship). This may allow seeing the general association between variables, and then using a more restricted dataset with consistent temporal trends to predict the biological and ecological effects of oligotrophication. However, this approach results risky as it assumes that the ecosystem response to nutrients will be analogous in all the sites, not to mention differences in trend strength and direction between time periods (Ballantine & Davies-Colley, 2014). At this point, it is necessary to highlight two ideas. First, the need to identify environmental variables to group rivers and estuaries with similar characteristics where nutrient trends may follow similar patterns. Datasets such as the HydroATLAS (Linke et al., 2019), which presents a global compendium of hydro-environmental sub-basin and river reach characteristics may be very useful for this purpose. Second, data on primary producers could be obtained through remote sensing techniques, for instance to infer Chl values or macrophyte coverage from spectral signatures (Nelson et al., 2006). This would allow to obtain information from the past decades to elucidate what have been, for instance Chl trends in rivers and estuaries worldwide. This is already possible for large (mid- and high-order) rivers and estuaries using medium resolution images and open repositories (e.g., Copernicus or Landsat Programs from the European Spatial Agency and NASA, respectively), but this possibility has not been yet used to produce a consistent global dataset on Chl or macrophyte trends. Thus, remote sensing might fill gaps in long-term time series generating regular standardized products, through adequate processing data pipelines (e.g., Open Data Cube, Google Earth Engine, etc.).

The ability to compile a global database of biological trends following river and estuary re-oligotrophication may support monitoring schemes for adjustment and development of new biological indicators. Because biota integrates water quality conditions over time, different conclusions about nutrient shifts can be reached depending on which metrics or combination of them are used (Palmer & Febria, 2012). In a context of increasing and interconnected global change stressors, effective river monitoring requires community-curated long-term river biota databases that transcend political and administrative boundaries (Charles et al., 2021). Such tools could aid to find commonalities and differences across constituent states responsible of river and estuary ecological assessment.

## 3 | WHAT ARE THE MAIN EFFECTS OF RE-OLIGOTROPHICATION ON BIOTA AND THE WHOLE ECOSYSTEM?

The re-oligotrophication process is triggered by the decline in P, which in turn involves an increase in the N:P ratio, since N declines less than P (Ibáñez & Peñuelas, 2019). These stoichiometric changes trigger in turn cascading effects at ecosystem level, in some cases including ecosystem shifts. Given that re-oligotrophication of freshwater systems is commonly triggered by a decline in P (proportionally) faster than in N, this means that both nutrient decline and nutrient imbalance come together, so it is difficult to figure out

what are the specific effects of each phenomenon. This can mostly be disentangled through mesocosm experiments and models, rather than field data, and this issue deserves more research.

Despite recent research into ecosystem shifts in response to decreasing nutrient concentrations in rivers, many of the foreseen effects remain understudied (Diamond et al., 2022). The potential ecological consequences of re-oligotrophication involve cascading effects and changes in fundamental ecosystem properties such as species composition, primary productivity, food-web structure, stoichiometric ratios, food quality, habitat structure, nutrient dynamics, biogeochemical cycles, carbon storage, or greenhouse gas emissions (see Table 1 and Figure 1). As well, the effects of climate change (increasing temperature, acidification) as a multi-stressor effect on re-oligotrophication processes need to be investigated (Charlton et al., 2018), including the interactions of other global change effects (see Section 6).

Table 1 summarizes the main type of ecological effects of the re-oligotrophication process in rivers and estuaries. The main types of reported ecological effects (in lakes, rivers, and estuaries or in mesocosm experiments) and their causal links and main feedbacks can be summarized as follows (see Figure 1).

## 3.1 | Changes in phytoplankton and zooplankton biomass and composition

The most direct and easily measurable effect of re-oligotrophication in freshwaters (especially lakes, reservoirs, and large rivers) and estuaries is the decline in phytoplankton biomass (often measured as Chl *a* concentration in the water column) which reflects a decline in primary production (Abonyi et al., 2018; Pomati et al., 2012; Romero et al., 2016).

Moreover, the absolute and relative supplies of N and P in the environment have a major influence on the diversity of species at macro- and microscopic scales (Lee et al., 2017). Under sufficiently low P (below minimum requirements for a particular species) the extirpation of the less efficient primary producers (in terms of P needs) may occur, including the replacement by more efficient species (Elser et al., 2012). There are several studies showing a change in phytoplankton composition in rivers (see Table 1). In the Loire River, increases in phytoplankton functional diversity were documented in response to oligotrophication, potentially indicating enhanced ecosystem functioning (Abonyi et al., 2018; Diamond et al., 2022). As well, a functional shift involving the decrease in eutrophic planktonic taxa and the increase in benthic diatoms was observed in the middle section of the Danube River (Abonyi et al., 2018), as a result of a long-term decrease in phytoplankton biomass associated with an increase in species diversity. Single-celled eutrophic centric diatoms decreased in relative abundance, but flagellated, elongated, and filamentous forms increased. In some cases (Anneville et al., 2019) it has been shown an increase in total phytoplankton biomass despite phosphorus reduction, that was mainly caused by a particular phytoplankton assemblage which was better adapted to

the re-oligotrophicated environment characterized by relatively low phosphorus concentrations and warm water temperature, poorly controlled by zooplankton grazing.

Data from lake ecosystems show an increase in the species richness of both phytoplankton and zooplankton; for example, in Lake Zurich decreases in SRP concentrations since 1980 led to more than a doubling of phytoplankton species richness (from 40 to nearly 100) and zooplankton species (increasing from about 7 to 17; Pomati et al., 2012). There was also an increase in the number of phytoplankton functional groups.

## 3.2 | Changes in macroinvertebrate and fish communities

Changes in primary producers may impact on macroinvertebrates and fish abundance and composition (see Table 1), either directly (less or lower quality food leading to declines in fish and invertebrate biomass) or indirectly (new habitats created with the spreading of macrophytes, changes in substrate composition by the accumulation of organic matter, etc., favoring some invertebrate and fish species over others). Some authors even alert on the significant decline of river and coastal fisheries because of re-oligotrophication (Stockner et al., 2000).

## 3.3 | Macrophyte spreading and changes in macrophyte community

The effect triggered by the decline in phytoplankton and the increase in water transparency is the proliferation of submerged aquatic vegetation (Hilt et al., 2011; Ibáñez, Alcaraz, et al., 2012). This phenomenon has been seen in large rivers and some estuaries, including the Loire River (France; Diamond et al., 2022), Ebro River and Estuary (Spain; Ibáñez, Alcaraz, et al., 2012, Nebra et al., 2016), Danube River (Hungary; Abonyi et al., 2018), and Tampa Bay (US; Greening et al., 2014), among others (see Table 1). In the Loire River mean Chl *a* shifted from 0.08 to 0.01 µg L$^{-1}$ while macrophyte cover increased from 2% to 5% in average, up to 12% cover of the river channel in some areas (Diamond et al., 2022). The increase in SAV is a fundamental piece of a river ecosystem shift like previously described in shallow lakes.

## 3.4 | Regime shift

As mentioned, a regime shift similar to that observed in lakes has been observed in some rivers and estuaries during the last two decades. Lakes have been shown to undergo regime shifts, moving between alternative stable states in which the systems shift from one state to another, with fundamentally different characteristics in terms of functions, processes, species composition, and interrelationships. These states are considered stable over ecologically

**TABLE 1** Summary of reported ecosystem-level changes attributed to river and estuary re-oligotrophication (see Tables S1 and S2 for more information).

| Ecosystem-level effect | Type of effect | Drivers/mechanisms | Main references |
|---|---|---|---|
| Decline in phytoplankton | Primary producers | Decline in P triggers a lagged decline in phytoplankton (often measures as Chlorophyll) that can be quite abrupt when P decline reaches a certain threshold (catastrophic shift) | Abonyi et al. (2018); Derolez et al. (2019); Diamond et al. (2022); Floury et al. (2012); Hilt et al. (2011); Ibáñez, Alcaraz, et al. (2012); Kronvang et al. (2005); Longphuirt et al. (2016); Romero et al. (2013); Taylor et al. (2011); Van Nieuwenhuyse (2007) |
| Changes in phytoplankton community | Primary producers | Decline in P and/or increase in N:P trigger changes in community composition by eliminating or decreasing the abundance some species not adapted to oligotrophic conditions that are outcompeted by other species that are better adapted to the new conditions | Abonyi et al. (2018); Arroita et al. (2019); Burson et al. (2016); Cozzi et al. (2019); Lie et al. (2011); Liu et al. (2009); Ludwig et al. (2009); Minaudo et al. (2021); Mozetič et al. (2010); Zhao et al. (2005) |
| Macrophyte spreading | Primary producers | The decline in phytoplankton leads to an increase in water transparency that favors the growth of macrophytes in deeper areas of rivers and estuaries | Beck and Murphy (2017); Diamond et al. (2022); Greening and Janicki (2006); Hilt et al. (2011); Ibáñez, Alcaraz, et al. (2012); Kronvang et al. (2005); Lefcheck et al. (2018); Riemann et al. (2016); Ruhl and Rybicki (2010) |
| Changes in macrophyte community | Primary producers | Oligotrophic conditions first trigger the spread of some macrophyte species and then favors a change in community composition and an increase in diversity | Bakker et al. (2013); Kronvang et al. (2005); Riemann et al. (2016); Sand-Jensen et al. (2017) |
| Changes in zooplankton community | Secondary producers | The decline in phytoplankton and the change in community composition trigger the decline in zooplankton and often a change in community composition as well, favoring species more adapted to oligotrophic conditions | Kronvang et al. (2005); Mozetič et al. (2010) |
| Changes in macroinvertebrate and fish community | Secondary producers | Changes in primary producers may impact on macroinvertebrates and fish abundance and composition, either directly (less or lower quality food) or indirectly (i.e., new habitats with the spreading of macrophytes, changes in substrate composition by the accumulation of organic matter, etc.) | Arroita et al. (2019); Gilbert (2010); Ibáñez, Alcaraz, et al. (2012); Kronvang et al. (2005); Nebra et al. (2016); Riemann et al. (2016) |
| Changes in invasive and native species | Secondary producers | The shift to a macrophyte-dominated state may favor the presence and abundance of invasive species over native ones, that are adapted to conditions of higher water turbidity (suspended sediments or phytoplankton) and a free-flowing water column. The spread of macrophytes favors some invasive fish species and harms some native species such as freshwater mussels | Ibáñez, Alcaraz et al. (2012) |
| Cascading effects | Ecosystem structure/ function | Cascading effects may or may not involve an ecosystem shift from phytoplankton to macrophytes. The general sequence would be the decline in phytoplankton leading to the decline in zooplankton followed by the decline in fish populations, as well as the increase in other primary producers (macrophytes, benthic algae, macroalgae), which in turn can modify the river/estuary substrate, water chemistry, hydrology, ecosystem metabolism, and nutrient cycling | Derolez et al. (2019); Diamond et al. (2022); Ibáñez, Alcaraz, et al. (2012); Kronvang et al. (2005); Riemann et al. (2016) |

(Continues)

**TABLE 1** (Continued)

| Ecosystem-level effect | Type of effect | Drivers/mechanisms | Main references |
|---|---|---|---|
| Regime shift | Ecosystem structure/function | The regime shift involves a rapid transition from phytoplankton to macrophyte dominance due to higher water transparency, which in turn triggers cascading effects changing the abiotic and biotic components (see above). In some cases a regime shift from phytoplankton to benthic diatoms has been observed | Abonyi et al. (2018); Dent et al. (2002); Diamond et al. (2022); Hilt et al. (2011); Ibáñez, Alcaraz, et al. (2012) |
| Changes in ecosystem metabolism | Ecosystem structure/function | Changes in the food-web structure involve changes in the energy flow and the metabolic balance, changing the carbon cycle. The shift to a macrophyte-dominated state reduced the sensitivity of primary production to abiotic drivers, altered element cycling efficiency, flipped the net carbon balance from positive to negative, and weakened the temporal coupling between production and respiration | Arroita et al. (2019); Bernhardt et al. (2018); Diamond et al. (2022) |
| Changes in nutrient cycles | Ecosystem structure/function | Beside the changes in carbon cycle (see above), the oligotrophication process involves direct and indirect changes in P, N, and other elemental cycles. Changes in primary production and type of primary producers directly affect elemental cycles, while changes in substrate indirectly affect them | Elser et al. (2007); Minaudo et al. (2015) |
| Changes in food-web stoichiometry | Ecosystem structure/function | Changes in water stoichiometry involve changes in the stoichiometry of primary and secondary producers. According to the Growth Rate Hypothesis species with rapid growth rate require increased allocation to P-rich ribosomal RNA to meet the protein synthesis demands. Thus, fast-growing organisms tend to have biomass with low C:P and N:P ratios, raising their requirements for P from their environment or diet and making them poor competitors for this key resource | Acharya et al. (2004); Glibert (2010); Peñuelas et al. (2012); Sardans et al. (2012b) |
| Changes in substrate (sediments) | Abiotic conditions | The shift to a macrophyte-dominated state involves changes in the river/estuary bed due to reduced water velocity, causing the accumulation of finer sediments and organic matter. Macrophyte take most of nutrients from the sediment and this also changes sediment and water chemistry | Ibáñez, Alcaraz, et al. (2012) |
| Changes in water quality | Abiotic conditions | Changes in P and N:P trigger the oligotrophication effects on the ecosystem, which in turn trigger additional changes on water quality (less inorganic suspended sediment, different type of organic suspended matter and dissolved organic carbon, etc.). The shift to a macrophyte-dominated state may increase water temperature and dissolved oxygen concentration | Beck et al. (2018); Burson et al. (2016); Corman et al. (2015); Müller et al. (2014); Romero et al. (2021) |
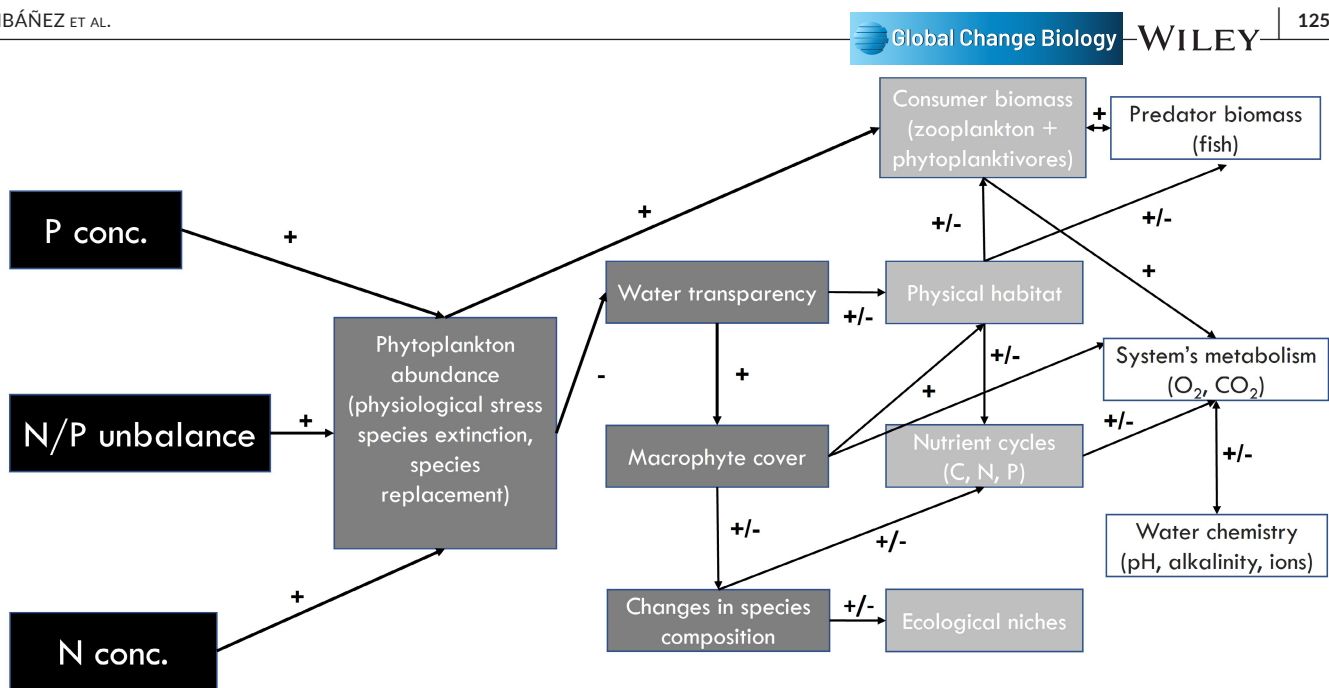
**FIGURE 1** Cascading effects of re-oligotrophication and N:P imbalance in aquatic ecosystems. Positive and negative feed-backs are depicted by the symbols + and -.

relevant timescales, for instance when a clear-water lake dominated by macrophytes shifts to a turbid, phytoplankton-dominated lake. Eutrophication drives the change to the turbid condition, which is resistant to change, in part due to the recycling or internal loading of P from the sediments to phytoplankton (Folke et al., 2004). Reducing nutrient inputs (oligotrophication), therefore, may not reverse the ecosystem conditions. Due to hysteretic dynamics, returning the system to a clear-water state requires that nutrients are reduced to levels lower than they were when the lake underwent the regime shift to a turbid state (Scheffer et al., 1993; Wilkinson et al., 2018). In lakes it has been shown that the collapse and recovery of aquatic vegetation by eutrophication and re-oligotrophication involves a decadal-long delay (Sand-Jensen et al., 2017).

While the re-oligotrophication process in rivers and estuaries is well documented in terms of nutrient and phytoplankton decline, the existing literature concerning a regime shift to a macrophyte-dominance state is still scarce both for rivers and estuaries. The first case described in the literature was the lower Ebro River (Spain) (Ibáñez et al., 2008), in which the collapse of phytoplankton was hypothesized to be either due to P decline or to the spread of invasive bivalves (zebra mussel) (Ibáñez, Caiola, et al., 2012). Results showed that P was by far the main driver of phytoplankton decline and the subsequent spread of macrophytes, while other factors such as damming leading to low suspended sediment and flood regulation were a prior necessary (but not sufficient) condition for macrophyte dominance. Figure 2 shows a conceptual model of ecosystems changes in the lower Ebro River as an example of what can be occurring in other similar cases. Another interesting case corresponds to the Spree River in Germany (Hilt et al., 2011), where the regime shift occurred over the same period than in the Ebro. The Spree case was used to build a model simulating the conditions for a regime shift

in flushed lakes, chains of lakes, and rivers, which is based on the classical model of regime shift in shallow lakes. The model predicts that abrupt changes between clear and turbid water states can also occur in lowland rivers, both in time and in space (Hilt, 2015). The most compelling case in terms of data availability to track the shift and the ecological effects of re-oligotrophication is the Loire River (France), since changes in macrophyte cover (in summertime) and many other parameters could be tracked for a long period (1997–2018) (Diamond et al., 2022). Regarding estuaries, the most compelling case of regime shift is the Lower Potomac River and Chesapeake Bay, where submerged aquatic vegetation (SAV) bed area and density class were mapped from aerial imagery acquired annually along 30 years (Lefcheck et al., 2018; Ruhl & Rybicki, 2010). Here the recovery of SAV was more progressive than in rivers and mostly triggered by N decline, tough P decline also played a role. More research is needed to elucidate potential differences in regime shift for the case of estuaries.

The regime shift from phytoplankton to macrophyte dominance observed in rivers and estuaries is thought to be equivalent to that observed in shallow lakes (see next section) but much more research is needed to know the implications of this shift on the ecology of lotic systems.

## 3.5 | Cascading effects

Overall, the biological and ecological effects of P decline and N:P increase are much more complex than the direct effects on limiting primary production and shifting primary producers from phytoplankton to macrophytes (Figure 1). The ecosystem shift to macrophyte dominance also causes structural cascading effects, such as changes
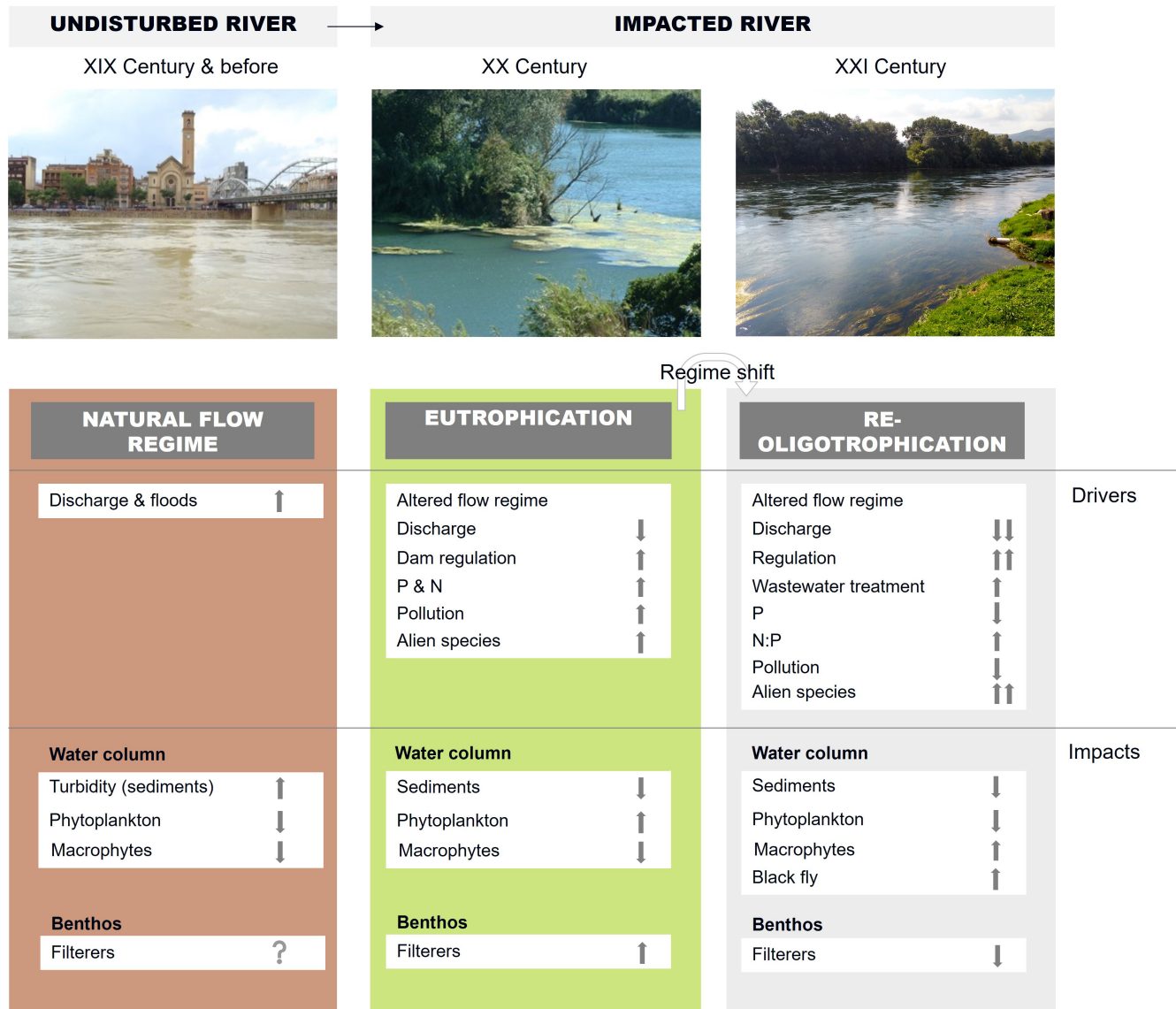
**FIGURE 2** Conceptual model of ecosystem changes in the lower Ebro River triggered by re-oligotrophication and other global change drivers (modified from Ibáñez et al., 2020).

in habitat type and the consequent functional effects such as changes in nutrient cycles (C, N, P, S) and ecosystem metabolism, as well as changes in food-web structure. When P becomes scarce, several connected effects have been reported including decreases in phytoplankton biomass and primary production, changes in species composition across the food-web, decrease in secondary production such as fisheries, decrease in food quality for consumers, physiological stress, etc. (Abonyi et al., 2018; Chételat et al., 2006; Friedrich & Pohlmann, 2009; Ibáñez, Alcaraz, et al., 2012; Stockner et al., 2000). Where P is unbalanced (N:P too high) changes in species composition, changes in food quality, and altered reproduction may occur (McCarthy et al., 2006; Peñuelas et al., 2013). Those are the main effects of the stoichiometric imbalance on phytoplankton (growth, reproduction, community structure) and their propagation on zooplankton and the whole food-web, altering both the food-web structure and the energy flow of the ecosystem.

## 3.6 | Changes in ecosystem metabolism

The shift to macrophyte dominance leads to changes in metabolic patterns of the ecosystem (e.g., oxygen dynamics and carbon dynamics) leading to changes in production/respiration patterns (e.g., daily cycles) and water chemistry (pH, alkalinity, ions, metals). A recent study from the Loire River in France (Diamond et al., 2022) found that the shift to a macrophyte-dominated state reduced the sensitivity of primary production to abiotic drivers, altered element cycling efficiency, flipped the net carbon balance from positive to negative, and weakened the temporal coupling between production and respiration. Despite the state shift in this ecosystem, changes in gross primary productivity and ecosystem respiration were minor and lagged the state changes by at least a decade.

Changes in oxygen concentration are mainly caused by changes in river ecosystem metabolism (primary production and respiration).

Metabolic rates of rivers are controlled by light, temperature, and hydrologic disturbance, while increasing nutrient availability can amplify the metabolic response (Bernhardt et al., 2018). Thus, the analysis of metabolic regimes of rivers through diurnal changes in dissolved oxygen may reveal changes in trophic status, including the possibility of detecting regime shifts (Bernhardt et al., 2018). Although theoretical advances linking river metabolism to changes in river ecosystems are currently progressing (Rüegg et al., 2021), empirical evidence on the effects of re-oligotrophication on rivers is still scarce (Bernhardt et al., 2018). As expected by the growth rate hypothesis, which predicts that higher growth rates are associated with higher P concentration and lower C:P and N:P ratios (Acharya et al., 2004), increases in water N:P ratios (due to higher P than N decrease) should have a strong impact on community structure favoring at the same time aerobic species and species with lower growth rates (Sardans et al., 2012b; Sterner & Elser, 2017). This phenomenon requires immediate research, especially to assess the potential impacts of the return to oligotrophic conditions but with remarkably high N:P ratios.

## 3.7 | Other ecosystem changes

The shift to macrophyte dominance also leads to changes in habitat structure (e.g., the spreading of macrophytes triggers changes in sediment features) leading to changes in species composition (e.g., the spread of macrophytes reduces the habitat of bivalves and favors alien fish species) and changes in biogeochemical cycles, for instance via the accumulation of organic matter in the sediment (Ibáñez, Alcaraz, et al., 2012; Murphy et al., 2018).

## 4 | WHAT ARE THE MAIN DIFFERENCES IN THE OLIGOTROPHICATION RESPONSE OF RIVERS, ESTUARIES, AND SHALLOW LAKES?

How re-oligotrophication affected ecological function and structure in lakes is well evidenced in the literature (Anderson et al., 2005), but far less is known about the consequences of nutrient reduction in rivers and estuaries (Ibáñez & Peñuelas, 2019). There are common ecological effects in all systems (i.e., phytoplankton and zooplankton decline), but it remains to be elucidated whether the theory of alternative states described for shallow lakes is fully applicable to all sort of rivers and estuaries. Under the alternative stable states model, the gradual internal feedbacks stabilizing the community within a "basin of attraction" are weakened by external forces or disturbances (Scheffer & van Nes, 2007; van Nes & Scheffer, 2004). Basins of attraction are modified by these external forces, and systems with "shallower" versus "deeper" basins of attraction will be more prone to cross critical thresholds in state variables that move the system into an alternative state (i.e., less resilience, sensu Holling, 1973). The result can be that dramatic nutrient reductions are needed to

drive changes in the ecosystem. For example, using a paleolimnological modeling approach, Qin et al. (2022) estimated that with an annual reduction of N and P of between 15% and 25% Lake Taibai (China) would take 10–20 years to shift from an algal dominated, turbid state, to a macrophyte-dominated, clear state.

Some differences should be expected in the response to oligotrophication between rivers, estuaries, and lakes, modulated by factors such as residence time, flood frequency and intensity, light penetration, or salinity. Under the assumptions of alternative stable states, rivers with larger deposition rates and less transport (such as dammed rivers with enough water column) would develop stronger positive internal feedbacks between submerged macrophytes and clear waters. This assumption would be violated in streams and small rivers, which are more open systems mainly controlled by external forcing (e.g., hydrologic regime; Dent et al., 2002) and have a shallow water column facilitating the dominance of phytobenthos over phytoplankton (Neal et al., 2006).

However, one of the few existing works on regime shifts in rivers (Hilt, 2015; Hilt et al., 2011) suggests that the response of primary producers to river re-oligotrophication would be similar to the response in shallow lakes, but in rivers there would be a more limited "phase space" for the shift between phytoplankton and macrophytes (and the reversal to phytoplankton) and this will largely depend on the water residence time. The lower the residence time, the more unlikely the shift, so the most favorable conditions would be in lowland rivers or rivers downstream of lakes or dams (Cottenie et al., 2001). Once the water residence time is adequate, other factors that might favor the transition from turbid to clear-water states in rivers involve the presence of macrophyte allelochemicals inhibiting phytoplankton (Mohamed, 2017), the increase on benthic substrate stability cause by riverbed encroachment, and the reduction of water velocity or increase in fine sediment deposition caused by macrophyte development (Ibáñez, Caiola, et al., 2012). In opposition, transitions from clear to turbid state could also be favored by the reduction of light penetration by phytoplankton or epiphyton coating when nutrients start increasing.

An important factor that modulates the different response of water bodies to oligotrophication is light penetration, which in part depends on water depth. Among others, this reason could explain why the classical alternative states between phytoplankton and macrophytes have been mostly described in shallow lakes. They are deep enough to allow for phytoplankton to dominate primary production and lake metabolism in eutrophic conditions but shallow enough to allow for the spread of macrophytes in most of the lake surface (and consequently becoming the dominant primary producers). This is more difficult to occur in deeper lakes (>10 m) since macrophytes can only grow in the shallow areas close to the shore. However, some works have shown that in deeper lakes the presence of macrophytes in the shore can also have a significant effect on phytoplankton decline (Hilt, 2015). For instance, a model predicted 15% less phytoplankton in 100 m deep oligotrophic lakes as compared to lakes without macrophytes (Sachse et al., 2014). In shallower water bodies (<1 m), phytoplankton is less abundant (small

water column), and macrophytes can receive enough light even in eutrophic conditions. Moreover, under shallow depth conditions emergent vegetation can take over and transform the shallow lake into a marsh.

Altogether the most favorable conditions for a shift between phytoplankton and macrophytes in rivers may occur in systems with a depth similar to shallow lakes, thus excluding streams (very shallow water column and high-water turnover) and very large rivers (>10 m deep), where not enough light for macrophyte development may reach most of the riverbed even under oligotrophic conditions. The non-linear relationship between water depth and surface of the bottom penetrated by light is modulated by the shape of the water body, and this could be at the base of the hysteretic behavior of the regime shift. In short, the shape of shallow lakes (or rivers and estuaries) that favors the new bottom surface of macrophyte colonization (as turbidity declines) increases rapidly in a particular depth range (i.e., stabilizing the "basin of attraction"). Thus, within this range a small increase in water clarity will generate a large new surface available for macrophyte colonization. In the case of deep lakes this process of generating new surfaces for macrophytes will be more gradual and with less total surface, likely causing a more progressive shift (less catastrophic) than in shallow water bodies.

In small river ecosystems (i.e., streams) less obvious alternate states might occur by involving other variables. For example, primary producer communities in streams could be dominated by different communities such as diatoms and cyanobacteria, bryophytes, filamentous algae, or macrophytes. This is the case downstream dams in mountain streams in which water residence time, substrate stability, and low nutrient concentrations favor macrophyte and bryophyte dominated communities as opposed to other primary producers (Goldenberg-Vilar et al., 2022).

Another differential factor of rivers compared to lakes is typically the occurrence of floods and associated high turbidity due to suspended sediment (Ibáñez, Caiola, et al., 2012). Frequent floods strongly reshape the riverbed and may prevent the establishment or spread of macrophytes even under oligotrophic conditions. Similarly, high turbidity causes light attenuation (that may also reduce the abundance of phytoplankton) or scouring of plant stands. In this sense, the growing number of highly regulated rivers worldwide favor more stable hydraulic conditions and clearer water for the development of macrophytes and other benthic primary producers (Grill et al., 2019; Ibáñez, Alcaraz, et al., 2012).

Regarding estuaries, their ecological response to re-oligotrophication also shows differential traits in comparison to rivers or lakes: first, the differences in response to hydro-morphology (and type of estuary); and second, to the nutrient load of the river in relation to the internal load of the estuary. Both components are in part related, since more mixed estuaries usually have more marine influence in proportion to the fluvial influence. The hypothesis is that the estuaries with more fluvial influence (river dominated, highly stratified) will show a quicker and stronger response to oligotrophication, and this response will be more related to the decreasing nutrient load from the river, and the critical nutrient will be P.

This is very clear with the example of the Ebro Estuary (a salt-wedge microtidal estuary), where the river re-oligotrophication process has caused the estuary to change from a hypereutrophic ecosystem with total anoxia in the lower layer most of the year to a mesotrophic–oligotrophic system with a well-oxygenated lower layer and a total recovery of the estuarine ecosystem in 10–20 years (Ibáñez, Alcaraz, et al., 2012; Ibáñez & Peñuelas, 2019). More mixed estuaries with less fluvial influence such as Chesapeake Bay have also shown a clear recovery because of the decreasing nutrients loads (Williams et al., 2010), but here the effect of N could be more relevant than P, although the upper sections appear to be more responsive because of the stronger fluvial influence. Interestingly, submerged aquatic vegetation has recovered because of decreasing nutrient loads (Lefcheck et al., 2018), but more research is needed to elucidate the complex ecosystem changes occurring in Chesapeake Bay in the last decades.

# 5 | TO WHAT EXTENT IS THE RESPONSE OF RIVERS AND ESTUARIES DIFFERENT AS A FUNCTION OF WATERSHED GEOCHEMISTRY?

The role of watershed geochemistry on river and estuarine response has not been investigated in a direct way. However, there are several studies that can shed light into the potential feedbacks between oligotrophication (due to P limitation) and watershed geochemistry. The main hypothesis is that alkaline river basins tend to be more oligotrophic than acidic ones. This also implies that the response to oligotrophication will be faster and stronger as the river chemistry is more alkaline/basic. The main reason is that phosphate precipitation increases with alkalinity and depends on the amount of calcium carbonate (phosphate co-precipitate with carbonates; Otsuki & Wetzel, 1972). Calcite also precipitates as gross primary production increases water pH, leading to P co-precipitation and indicating that P cycling is coupled with metabolism (Cohen et al., 2013). Actually, in karstic rivers photosynthesis and respiration of subaquatic vegetation are the dominant processes influencing in-stream diel variation of dissolved inorganic carbon and nutrients (De Montety et al., 2011; Nimick et al., 2011). A study carried out in montane streams of Arizona (Corman et al., 2015) found a strong negative correlation between water phosphate and calcium carbonate deposition rates, as well as a strong positive correlation with inorganic N, implying a positive relationship with N:P ratios. Reduced P in water may reduce biological N uptake, thus amplifying the stoichiometric signal of calcium carbonate deposition.

Research carried out in the last decades on the recovery of acidified lakes via liming has shown a re-oligotrophication process caused by P precipitation with carbonates and reduced P cycling during summer (Hu & Huser, 2014). Under more acidic conditions, P mostly precipitates with iron, but can also be re-dissolved more easily than in basic conditions. Some works have shown that eutrophication enhances acidification in lakes (Cai et al., 2011). The hypothesis could

be confirmed either with field data (comparing P values and trends in watersheds with contrasting alkalinity) or with laboratory experiments (looking at P precipitation dynamics).

# 6 | WHAT ARE THE MAIN FEEDBACKS OF RE-OLIGOTROPHICATION WITH OTHER GLOBAL CHANGE FACTORS SUCH AS WARMING AND ACIDIFICATION, DAMS OR INVASIVE SPECIES?

There are significant interactions with at least five factors of global change (acidification, increasing temperatures, air pollution, invasive species, and hydromodification by dam building) with clear potential links to P oligotrophication and N:P imbalance.

## 6.1 | Rising $CO_2$ and acidification

Rising carbon dioxide levels has been shown to produce effects on aquatic ecosystems, such as changes in production, community composition, and the ecological stoichiometry (Low-Décarie et al., 2015). Chemostat experiments with cyanobacteria showed an increase in biomass and an increase in C:N ratios that affected the nutritional quality of the phytoplankton (Verspagen et al., 2014), but nutrient imbalances may have pervasive effects across the foodweb. Acidification in freshwater ecosystems interacts with nutrients via re-dissolution of phosphate precipitates under more acidic conditions. This has been shown because of lake acidification via acid rain but may also be a consequence of acidification due to increasing $CO_2$ levels in freshwater. In order to reverse lake acidification, one management measure has been liming with carbonated materials, and this has been shown to cause oligotrophication via phosphate deposition (Hu & Huser, 2014).

## 6.2 | Global warming

An increase in temperature can also increase the co-precipitation of phosphate, but the relevance of this chemical process for an increase in a few °C should be further investigated. For instance, an experiment using marl lake water showed a change in phosphate co-precipitation from 45.1% at 12°C to 61.2% at 25°C under basic conditions (pH 9) (Otsuki & Wetzel, 1972). Global warming can also indirectly affect P dynamics through the stimulation of primary production and respiration, affecting P uptake and recycling (Stich & Brinker, 2010).

## 6.3 | Air pollution

Changes in atmospheric N and P emissions and deposition directly affect nutrient loads in rivers and estuaries. Interestingly the most

pristine rivers and lakes in US are undergoing a decrease in N loads and an increase in P loads (Stoddard et al., 2016), likely because of the effect of changing atmospheric deposition. While the global emissions of reactive N are increasing, the decline in N atmospheric deposition in US and Europe and their effects on ecosystems is well known (Eshleman et al., 2013). In contrast, P deposition trends are less known, but atmospheric P has recently been identified as a potentially important source of TP to alpine lakes and streams in Europe and North America (Camarero & Catalan, 2012; Stoddard et al., 2016 and references therein).

## 6.4 | Invasive species

The increasing abundance of invasive species in rivers and estuaries also interacts with the oligotrophication process in different ways. One of the most known interactions is the proliferation of invasive filter-feeders such as bivalves (Zebra and Quagga mussels, Asian clam, etc.), that can remove phytoplankton in large amounts, increasing water transparency. This phenomenon may interact with the decrease in phytoplankton caused by P scarcity, and both processes are found in many water bodies. However, when the dominant factor of phytoplankton decline is the increase in filter-feeders P may increase in the water column and the sediment. In cases like the Great Lakes the literature highlights the role of Zebra and Quagga mussels in increasing water transparency, but more recent studies also show a re-oligotrophication trend in which P limits primary production (Dove & Chapra, 2015; Evans et al., 2011). The rapid recovery of native species could also have a significant interaction with re-oligotrophication effects, for instance the recovery of freshwater mussels in rivers and lakes (Benelli et al., 2019).

## 6.5 | Dam construction and operation

Dam construction and operation change the nutrient fluxes in rivers in many aspects, while the hydrological changes can also affect the oligotrophication process and its ecological effects. In general, the presence of reservoirs tends to remove nutrients from the river that accumulate into the sediment or escape to the atmosphere (i.e., denitrification). The mass of total P (TP) trapped in reservoirs nearly doubled between 1970 and 2000, reaching $42\,Gmol\,year^{-1}$, or 12% of the global river TP load in 2000; but the current surge in dam building may imply that by 2030, about 17% of the global river TP load will be sequestered in reservoir sediments (Maavara et al., 2015). As well, worldwide N fixation in reservoirs was on the order of $70\,Gmol\,year^{-1}$, while denitrification and burial in reservoirs eliminated around $270\,Gmol\,year^{-1}$, equal to 7% of N loading to the global river network in year 2000 and predicted to double to 14% by 2030 (Akbarzadeh et al., 2019). According to Maavara et al. (2020) the growing number of dams decouple the riverine fluxes of N, P, and Si, and preferentially remove P over N in reservoirs while increase N:P ratios delivered to the ocean, raising the potential for P

limitation of coastal productivity. However, dam structure and operation can also enhance P removal during warm periods if the water is taken up from the hypolimnion in stratified reservoirs. Moreover, other mechanisms enhancing oligotrophication in reservoirs could be playing a role in rivers. A recent study in pre-Alpine lakes showed that contrary to the prevailing view, the P concentration of eutrophic lakes will decrease more than proportional to the reduction of their external P load, and faster than predicted by the linear (eutrophic state-based) models (Müller et al., 2014). Several potential mechanisms linked with more $CO_2$ capture and $O_2$ production and oxidative power linked to more clean waters and more photosynthetic activity can be argued to explain this phenomenon. In any case, this phenomenon could be also relevant for river re-oligotrophication and deserves further investigation to see how general these mechanisms in lakes and reservoirs can be.

# 7 | WHAT MANAGEMENT MEASURES REGARDING RESTORATION, LAND USE, AND WATER MANAGEMENT CAN BE PROPOSED TO CORRECT THE UNDESIRABLE EFFECTS OF RIVER RE-OLIGOTROPHICATION?

Reversing eutrophication by reducing P inputs to the rivers and estuaries is necessary but not sufficient to reach a good ecological status (sensu Water Framework Directive of the EU), since some undesirable effects such as a massive macrophyte growth have appeared in cases in which this phenomenon was not part of the reference conditions (i.e., pristine state). Restoring rivers involves also recovering hydromorphological functions, especially sediment transport and the hydrological regime, but also connectivity. A proper restoration strategy would indeed involve reducing eutrophication but also recovering riparian ecosystems, removing dams when possible (or increasing their connectivity), setting-up sediment by-pass systems in the reservoirs, managing invasive species in a more proactive way, etc. Under this "ideal" restoration approach macrophytes would not spread massively in most of cases because of higher water turbidity, higher peak flows, etc. At the same time, by recovering riparian ecosystems the N:P ratio would likely be more balanced, thus minimizing the undesirable effects of nutrient imbalance (i.e., changes in phytoplankton communities with cascading effects on aquatic the food-web).

With the joint challenges of increase in climate extremes, flow modification, and land-use transformation, studies that shed light into processes behind river re-oligotrophication are crucial for providing information on which of these are most influential measures with respect to N and P trends and stoichiometric imbalances. This is the only future pathway for designing restoration schemes and re-evaluating management practices to reduce the imbalances (i.e., move them closer to the Redfield reference values). In virtually all the cases described in the last decades, P is decreasing faster than N and the N:P ratio is often higher than 100 (Ibáñez & Peñuelas, 2019).

Thus, management measures should be mostly directed to further decrease N loads, which are often related to non-point sources coming from farming activities and to a lesser but still significant extent, urbanization (Miller et al., 2021).

For urban regions, the primary restoration method to decrease N loading is upgrading sewage treatment plants (Ator et al., 2020) but actions to reduce run-off from residential lawns can also be important (Pennino et al., 2016). In-stream restoration designs have thus far proven to be minimally effective in reducing nitrogen concentrations or downstream transport (Fanelli et al., 2019; Filoso & Palmer, 2011), although combined with watershed best management practices, this improves (Williams et al., 2017). While designs out of the channel or in the floodplain can sometimes result in reductions, they also tend to reduce phosphorus inputs through binding to retained sediments (Noe et al., 2019). Nutrient monitoring work by Kincaid et al. (2020) in Vermont USA, showed that N:P export from urban catchments varied such that ratios are highest in spring and near Redfield ratio in fall. They link this to differences in N and P transport dynamics during flow events combined with availability from source areas. They suggest the possibility of managing N:P ratios in urban streams by focusing carefully on stormwater retention to reduce N inputs to streams from springtime runoff combined with riparian replanting to reduce groundwater inputs during the summer baseflow periods. This reinforces the importance of restoring flow regimes, not just controlling events (Palmer & Ruhi, 2019).

For agriculturally dominated watersheds, two main types of measures are being discussed and implemented: the restoration of wetlands and riparian forests to remove N (and P) inputs to waterways, and the improvement of farming practices to reduce fertilizers and increase nutrient soil retention (Fennessy & Cronk, 1997; Mitsch et al., 2005; Stackpoole et al., 2019). There is extensive literature on restoration of these two types of ecosystems (wetlands and riparian ecosystems) and their effectiveness at reducing either N or P (Cheng & Basu, 2017) but few restoration projects have explicitly documented outcomes in a stoichiometric context. Because research has shown that denitrification can be carbon limited (O'Brien et al., 2017), some managers now routinely add some form of carbon (e.g., wood chips) as part of stream restoration projects; however, conditions required to maximize denitrification may also result in mobilization of phosphorus from the sediments (Duan et al., 2019). Finally, regardless of the land use, dam operation is another management option that can be relevant for this issue, both in terms of flow regime and water quality. Changes in flow regime such as the establishment of controlled floods could be relevant to control the spread of macrophytes in oligotrophic rivers, both due to the direct effect of peak flows on macrophytes and the indirect effect of higher turbidity and light attenuation. Changes in the release of water from the dam (from a different depth) could be also relevant to increase or decrease P inputs downstream, since hypolimnetic waters may contain higher P concentration.

As water resources are reallocated and natural flow regimes altered (i.e., dams), we might expect an increase in lowland rivers dominated by interconnected river–lake systems (Palmer & Ruhi, 2019).

If a local river regime shift occurs upstream, propagules and energy can permeate through the whole river due to a domino effect (Rocha et al., 2018). Therefore, any restoration measure aimed at reducing local nutrient load, improving hydrological connectivity and biochemical fluxes should start upstream. A critical challenge in river re-oligotrophication in regard to restoration and management is the link from organismal to ecosystem-level processes. For instance, several studies have highlighted the importance of propagule availability and dispersal for the establishment of macrophytes (Bakker et al., 2013). Yet, there is virtually no experience in river restoration for maintaining clear waters. To partially overcome this, long-term monitoring programs can benefit from measuring macrophyte coverage that would yield early warning signals of state shifts, and therefore, inform on which ecological stressors are of most concern to reduce or restore toward river re-oligotrophication.

# 8 | CONCLUSIONS

- The re-oligotrophication of rivers and estuaries is a widespread process in high-income countries that was preceded by the re-oligotrophication in lakes and anticipates a similar process in middle-income countries like China.
- The re-oligotrophication process is very often accompanied by an imbalance of the N:P ratio which tends to increase due to a stronger decrease in P in regard to N.
- There are data limitations to confirm the extent, pace, and consequences of the re-oligotrophication process, even in high-income countries. Consistent data series covering the last decades are limited in terms of nutrient trends and scarce in terms of chlorophyll trends, not to mention biological variables such as phytoplankton or macrophyte trends.
- The ecological effects of P decrease and N:P increase in fresh waters are pervasive and trigger cascading effects that change the species composition, productivity, metabolism, nutrient cycles, trophic network, physical habitat, and water chemistry of rivers, estuaries, and coastal areas. However, it is difficult to elucidate what are the effects attributable to P decline and to N:P imbalance.
- The re-oligotrophication process triggers in some cases an ecosystem shift from phytoplankton to macrophyte dominance in rivers and estuaries which is equivalent to the classical shift described in shallow lakes. However, in most pristine rivers macrophytes did not dominate primary production due to higher water turbidity and peak flows. The scarcity of data makes difficult to know the extent and pace of this process.
- Is seems that the ecosystem shift takes place in rivers and estuaries showing more similar features to shallow lakes: low water turnover and low turbidity, enough water column for phytoplankton or macrophyte dominance, light penetration to the bottom, etc.
- Alkaline river basins tend to be more oligotrophic than acidic ones. This also implies that the response to re-oligotrophication will be faster and stronger as the river chemistry is more alkaline/basic, since phosphate precipitation increases with alkalinity and depends on the amount of calcium carbonate.
- There are significant interactions with at least five factors of global change (acidification, increasing temperatures, air pollution, invasive species, and hydromodification by dam building) with clear potential links to P oligotrophication and N:P imbalance.
- Integrated river basin management and ecosystem restoration are key to avoid the undesirable effects of re-oligotrophication and N:P imbalance. Restoration of wetlands and riparian habitats is fundamental to reduce non-point N sources.

## CONFLICT OF INTEREST

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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## SUPPORTING INFORMATION

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