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Eco-Evo-Hydraulics: Integrating Fish Evolution Into Ecohydraulics for Conservation

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Abstract Riverine fish conservation in eco-hydraulics is often based on restoring or regulating river habitat to a semi-natural state. For example, ecohydraulic projects support fish populations by increasing river connectivity through fishways, and by maintaining or restoring natural flow variance to enhance habitat quality and availability. However, the application of these concepts is challenging due to climate change and human perturbations that can modify the riverine environment in unpredictable ways. To address these challenges, we propose broadening eco-hydraulics to eco-evo-hydraulics by incorporating the evolutionary dynamics of fish populations into eco-hydraulics. We argue that this may improve the resilience and resistance of fish populations to future climate and human perturbation. Moreover, the evolutionary response of fishes to perturbations also alters their capability to "zoogeomorphically engineer" their physical environment, with associated feedbacks such as changes in sediment mobilization. Thus, understanding such hydro-evolutionary feedbacks can improve the long-term prediction of river hydraulics. In this position paper, we explore the interactions between hydraulics, hydrology, and rapid evolution based on a literature review to identify gaps and opportunities that need joint efforts from water resources engineers and evolutionary biologists. We propose the concept of eco-evo-hydraulics with hydro-evolutionary feedbacks to encapsulate the interactions between the three disciplines, and suggest research avenues for the future. Finally, we suggest potential managerial strategies based on the eco-evo-hydraulic concept for local and basin-wide fish conservation. We aim to fill the gap between water resources management and evolutionary biology to provide a new theory for fish conservation.

Plain Language Summary Protection of river ecosystems usually focuses on management of river habitats, often within the environmental flow paradigm. This approach requires good understanding of the historical river environment, which is challenging because of climate change and human perturbation. In our paper, we propose a new and more flexible strategy that overcomes this uncertainty by considering the resilience of a fish population based on its ability to adapt to different stresses. We also found that changes in the river environment and river life mutually influence each other, but this interaction has been largely ignored. We explore the interplay between hydraulics, hydrology and -evolution, and suggest how these interactions can be integrated to develop conservation plans in basin-wide water management.

Key Points:

- Human disturbance in hydraulic and hydrological processes impacts fish evolution
- Fish evolutionary responses feedback to hydraulic and hydrological processes
- Hydro-Evolutionary Feedbacks is proposed to integrate eco-evolutionary dynamics into water resources management

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1. Introduction

Hydraulic structures are built to control flow regimes and generate socio-economic growth (Brown & Lall, 2006). Weirs and dams along rivers serve the purpose of lifting upstream water levels as a stable water resource for human activities and to modify the magnitude and timing of flow downstream to mitigate flooding (Itsukushima, 2023; Mallen-Cooper & Zampatti, 2018). However, the construction of weirs, dams and other hydraulic barriers fragments rivers (Belletti et al., 2020) and alters the physicochemical characteristics of riverscapes (Chapman et al., 2014) and habitat suitability for aquatic organisms (Katopodis & Aadland, 2006), which in turn results in the loss of native biodiversity (Deflem et al., 2022; Raeymaekers et al., 2008; Zarri et al., 2022). Facing the rapid growth of the human population and more complicated extreme weather patterns, higher demands on water infrastructure for flood/drought control are exacerbating the conflict between socioeconomic developments

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and the conservation of fish and other aquatic life (Bertola et al., 2023; Willems et al., 2012). A recent examination of the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species pointed out that 26% of freshwater fishes are threatened with extinction, where dams and water extraction account for 46% of fish biodiversity loss (Sayer et al., 2025).

In contemporary water resources management, fish conservation primarily focuses on how to reduce human perturbations to fish habitats and how to restore or regulate river habitats (Katopodis, 2022). For example, in eco-hydraulics, Katopodis (2005) indicated that "healthy fish populations depend on habitat connectivity, on suitable habitat features which differ between species and life stages, and on river flow regimes which provide sediment, groundwater and nutrient circulation that sustain ecological integrity." Habitat-based management strategies can integrate environmental change into water resources management whenever a biologically meaningful quantitative relationship can be found between ecological and hydraulic or hydrological processes (Katopodis, 1992, 2022). As such, adaptive management strategies can be applied to minimize uncertainties from climate change and human activities through continuous monitoring of the habitats, updating knowledge and adjusting regulations to conserve river ecology (Holling, 1978; Katopodis, 2022; Walters, 1986). However, effective adaptive management requires informative monitoring coupled with a holistic understanding of dynamic river systems, both of which remain challenging to achieve. For example, it is costly and usually not feasible to change the design (geometry, size, and slope) of fishways after they have been installed. Also, it is undeniable that highly effective fishways for all fish species do not exist at this time (Hershey, 2021), although nature-like fishways that mimic a natural stream have the potential to realize this (Katopodis & Williams, 2012). Overall, new theories are required in eco-hydraulics to minimize the management uncertainty.

Faced with these challenges, we drew inspiration from natural rivers, where barriers and diverse habitat types occur naturally. This prompted us to ask: can fish conservation in eco-hydraulics be informed by understanding how fish adapt to the river? To explore this idea, we advocate combining eco-hydraulics with evolutionary biology, which investigates the origin of species and the processes by which they evolve and adapt under natural selection (Darwin, 1859).

Recent studies have found that fish ***evolution*** has been observed within the typical lifespan of an engineering project (Cai et al., 2025; Hendry, 2017; Hendry & Kinnison, 1999; A. J. Jensen et al., 2022). For example, Atlantic salmon (*Salmo salar*) decreased to one-third in body mass in 30 years after river regulation in River Eira, Norway, and this decrease was associated with genetic changes (A. J. Jensen et al., 2022). The blacktail shiner (*Cyprinella venusta*) in Claiborne Lake reservoir, U.S.A., showed morphological changes related to head size, body depth, and length of dorsal fin base only 1 year after dam closure (Haas et al., 2021). These evidences support the argument to consider fish evolution in engineering design for conservation purposes. At the same time, studies also found that the ecological impacts from intraspecific variance (variance within a species) and interspecific variance (species effects) are comparable in magnitude (Des Roches et al., 2017), which supports the importance of analyzing how fish evolution alters the hydraulic and hydrological environment (Dong et al., 2024). Moreover, the evolutionary response of fish species to human perturbation has been found to link with river fragmentation (Deflem et al., 2022) and pollution (Calboli et al., 2021). Evolutionary response is used here to encompass genetic ***adaptation***, plastic responses (***plasticity***) with heritable components, and their interactions, unless explicitly stated otherwise. A recent study indicated that the hydraulic regimes in the Demer, Belgium, a highly regulated system, lead to genetic changes in the populations of three-spined stickleback (*Gasterosteus aculeatus*) (Cai et al., 2025). The genetic impacts of flow regimes have not been a central focus of research due to the limited integration between water resources management and evolutionary biology. Bridging these two fields now is therefore both timely and important.

Through a comprehensive review of evolutionary biology, hydraulics and hydrology, we summarize current research in each field and propose the novel concept of hydro-evolutionary feedbacks to bridge these disciplines and extend eco-hydraulics into eco-evo-hydraulics (Figure 1). While establishing this framework, we observed that there are plenty of overlapping terminologies that are used in both evolutionary biology and eco-hydraulics. We list the glossary in Appendix A and highlight (bold and italic) the meaning of terms in each discipline to avoid misunderstanding. For example, adaptation in eco-hydraulics generally refers to whether fish can survive in a hydraulic environment and maintain their population dynamics (e.g., population size) (Katopodis & Aadland, 2006). Or it refers to the modifications of the fishway design parameters to suit a particular dam in a generic sense (Katopodis & Williams, 2012). In evolutionary biology, however, adaptation refers to the ***phenotypic***

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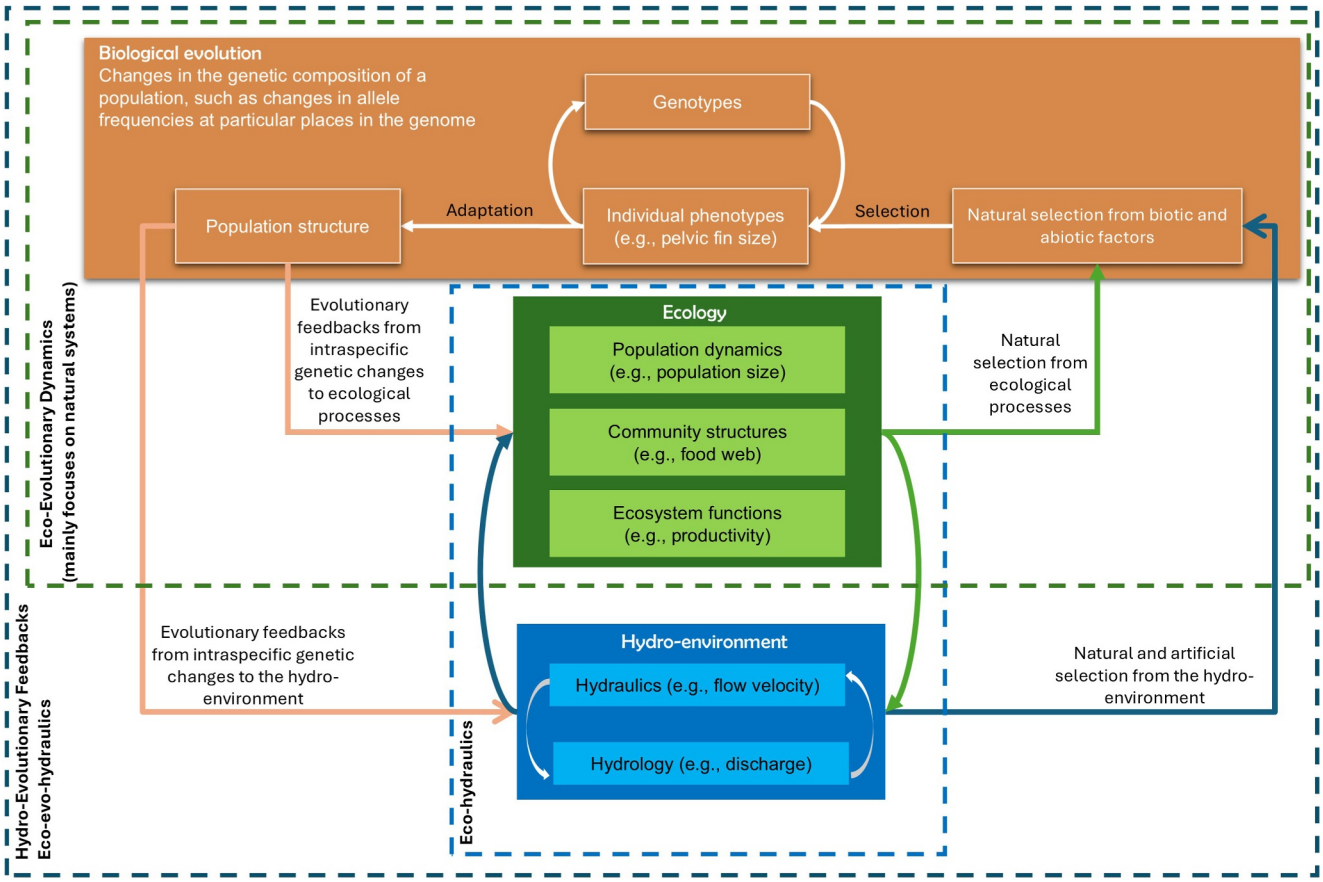

Figure 1. Demonstration of how evolutionary biology links to eco-hydraulics and how to connect hydro-evolutionary feedbacks to build eco-evo-hydraulics.

change that improves population fitness (e.g., reproductive or survival rate) and that has a genetic (***genotype***) basis. Accordingly, when the carrying capacity of the environment increases (e.g., more resources), leading to an increase in population size, eco-hydraulic engineers conclude that the fish adapted to the environment. While for evolutionary biologists an increase in population size is only indicative for ongoing adaptation when the increase is the result of increased population fitness (i.e., a higher survival rate or reproductive rate). The second example is ***evolution***. In hydraulic engineering, the word "evolution" may refer to a change in river morphology, whereas in this paper, we adhere to the biological definition of evolution as a change in the genetic composition of a population, usually ***allele*** frequencies at particular places in the DNA sequence (Hendry, 2017). Evolution can be measured by the changes of the average and intraspecific variance of a population property (e.g., heritable ***phenotype***) (Haldane, 1949).

The paper is structured as follows: First, following a review of two main research areas in ecohydraulics (river connectivity and environmental flow regime), we discuss why it is a challenge to use current theories to guide water resources management under the stress of climate change. Second, we introduce concepts, methods and applications in evolutionary biology, especially in adaptive evolution and population genetics, to discuss why an evolutionary perspective can improve the efficacy of fish conservation in eco-hydraulics. Third, we propose our new hydro-evolutionary feedbacks (Hydro-Evo) theory and discuss the feedbacks and interactions among hydraulics, hydrology, ecology and evolution. Finally, we demonstrate how to use the Hydro-Evo theory to guide eco-hydraulics in fish conservation.

This review paper was first drafted in 2021. Initially, literature was searched from the Web of Science database on 13th September 2021, with broad keywords: TS = ((Hydrology OR Hydraulics) AND (Ecology OR Evolution)), with the aim of finding connections in interdisciplinary studies. In total, 10,667 records were found. Research increased exponentially after 1997, but most of the studies did not directly connect with eco-hydraulics because the word "evolution" is also used to describe river morphological change. Therefore, another keyword, "fish,"

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was added for papers published after 1997. All the search records' abstracts were reviewed, and some representative studies were selected for presentation herein. Despite the use of a broad set of keywords, some well-known studies in either biology or hydraulics were not present in the search results. We added some studies based on our experience, suggestions from other experts, and cross-checking reference lists in other publications. Finally, we continued to track the newly published literature since 2021. On 22nd Oct 2025 we searched the Web of Science database again. We found 6,690 records in the Web of Science Core Collection, and 71,177 records in the Web of Science All Collection. Only 468 records related to fish were published after the year 1997 in the core collection. This points to the limited research effort in this field. We summarized the timeline of some milestone studies in eco-hydraulics, and listed those emerging topics that started to appear in the database (Figure 2). Due to the large body of literature, we only listed the earliest and most accessible studies in Figure 2. For example, in fishway design, we listed references related to the Denil fishway because its progress represents our understanding of how fish behave at hydraulic barriers, but we did not list research on other types of fishways (e.g., pool and weir fishway and vertical slot fishways (Katopodis & Williams, 2012)). Nevertheless, these unlisted studies have also made significant contributions and continue to exert a strong influence on current eco-hydraulics research.

2. Historical Perspective

Since the last century, two main areas of research have focused on conserving riverine fisheries (Figure 2). In the first research area, hydraulic studies have focused on mitigating river disconnectivity to avoid fish stock declines due to dam construction (United States Congress Office of Technology Assessment, 1995). The construction of fishways and their legal regulation can be traced back as early as the 18th century (Clay, 1995; Katopodis & Williams, 2012; Massachusetts governmental laws, 1887), but the determination of engineering design criteria was established by the early 20th century, presented by the Denil fishway (Denil, 1909) and the following studies from the Committee on Fish-Passes, British Institution of Civil Engineers (1942), McLeod and Nemenyi (1941), and Collins and Elling (1960). Later, the 30 years of research on fish behavior in response to fishway designs by the Bonneville Fisheries-Engineering Research Laboratory turned out to be a milestone (Katopodis & Williams, 2012; United States Congress Office of Technology Assessment, 1995) (Figure 2). More recent studies have considered the operation of river barriers in a broader context, which includes the spatio-temporal variance of chemical, hydraulic/hydrological (the distinction between these terms will be explained in Section 5.1), and socio-economic factors on a cross-border or international scale (Flecker et al., 2022). The conservation scope has been extended from protecting the connectivity of a single species to considering community structure, such as the interaction between native (e.g., salmonids and eels) and invasive species (e.g., zebra mussels, lampreys, and gobies) with quantitative (Bergman et al., 2022; Castro-Santos, 2004) and evidence-based approaches (Silva et al., 2018).

The second main area of research in conserving riverine fisheries focuses on the association between river habitat suitability and fish population size and community assembly (Figure 2). Since the last century, researchers have realized the value of ecology when solving practical problems in water management, such as understanding how water ions (Coker, 1925), nutrients (Holden & Green, 1960), salinity (Tyler, 1971), oxygen and temperature (Hendricks, 1993), flooding (Beumer, 1980; Gehrke et al., 1995), water level (Mitsch et al., 1991), bed morphology (Death & Winterbourn, 1994), and temporal flow variance (Poff et al., 1997) affect population size and community composition (Figure 2). One major milestone in advancing stream ecology from a descriptive (classifications and conceptual models) to a predictive discipline was the introduction of the river continuum concept by Vannote et al. (1980), which transits the analysis of the river system from discrete stream classification (Horton, 1945) into a continuum-oriented object along a longitudinal gradient of environmental factors (e.g., availability of food resources) (Doretto et al., 2020). Ecologists started to integrated both the discontinuities (lakes and tributaries) and continuities into predictive models, considering the heterogeneity of river nutrient concentration, substrate composition, sediment transportation and organic matter availability associated with the local environment (Montgomery, 1999; Townsend, 1989). By the mid-1990s, the study of ecology associated with hydraulic environments generated the interdisciplinary field of eco-hydraulics (Biggs, 1996; Fjellheim, 1996; Leclerc et al., 1996; Scarlatos, 1996; Stalnaker & Bovee, 1996). Initially, eco-hydraulic studies only used minimum flow as an indicator to control habitat quality. This situation was then improved by the natural flow regimes theory, which emphasizes that the flow dynamics, including magnitude, frequency, duration, timing, and rate of change, are all important in sustaining biodiversity and ecosystem integrity in rivers (Poff et al., 1997). The

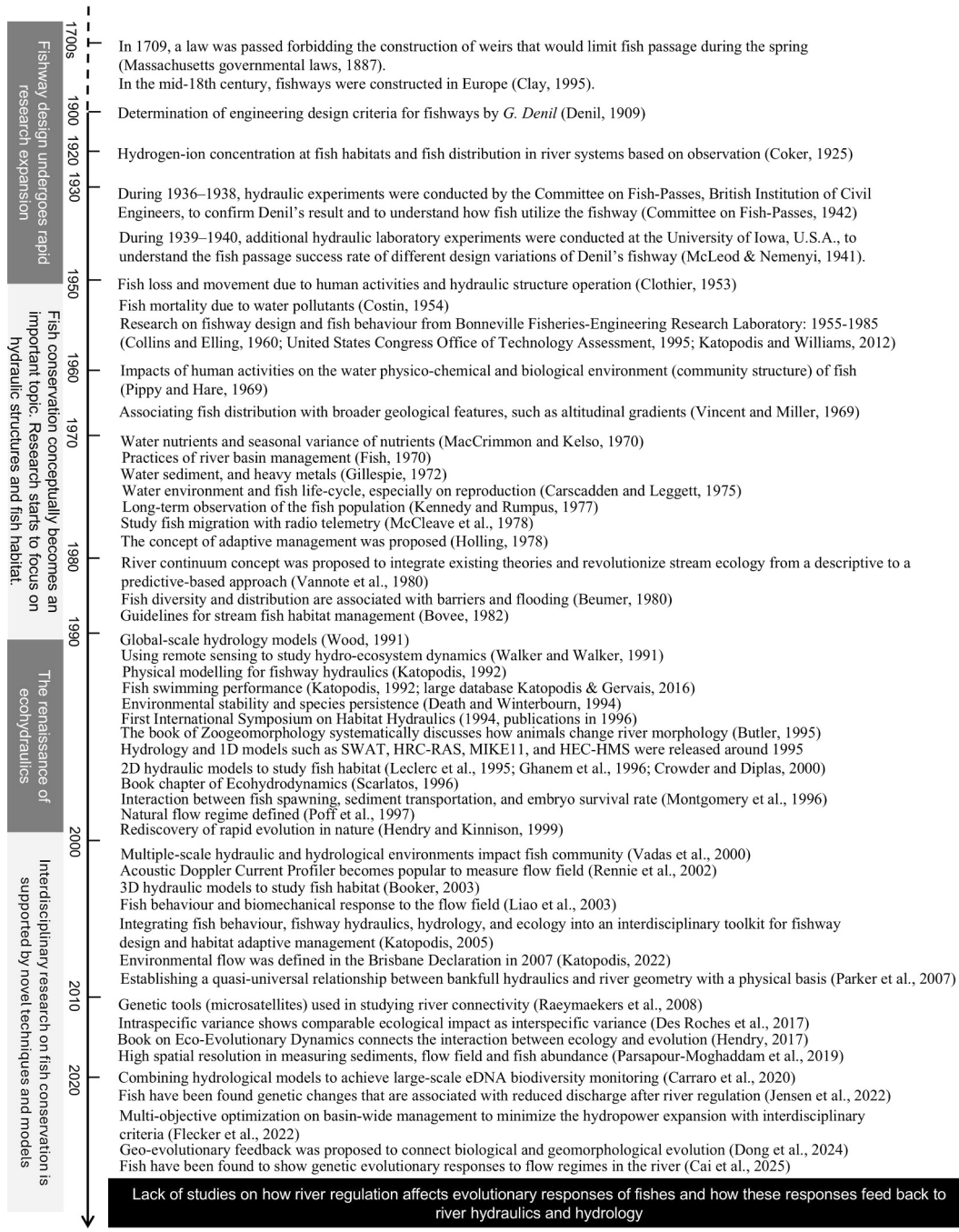

Figure 2. Timeline of the progress of eco-hydraulics for freshwater fish conservation (Beumer, 1980; Booker, 2003; Bovee, 1982; Butler, 1995; Cai et al., 2025; Carraro et al., 2020; Carscadden & Leggett, 1975; Clay, 1995; Clothier, 1953; Coker, 1925; Collins & Elling, 1960; Committee on Fish-Passes, 1942; Costin, 1954; Crowder & Diplas, 2000; Death & Winterbourn, 1994; Denil, 1909; Des Roches et al., 2017; Dong et al., 2024; Fish, 1970; Flecker et al., 2022; Ghanem et al., 1996; Gillespie, 1972; Hendry, 2017; Hendry & Kinnison, 1999; Holling, 1978; A. J. Jensen et al., 2022; Katopodis, 1992; Katopodis, 2005; Katopodis, 2022; Katopodis & Gervais, 2016; Katopodis & Williams, 2012; Kennedy & Rumpus, 1977; Leclerc et al., 1995; Liao, 2003; MacCrimmon & Kelso, 1970; Massachusetts governmental laws, 1887; McCleave et al., 1978; McLeod & Nemenyi, 1941; Montgomery et al., 1996; Parker et al., 2007; Parsapour-Moghaddam et al., 2019; Pippy & Hare, 1969; Poff et al., 1997; Raeymaekers et al., 2008; Rennie et al., 2002; Scarlatos, 1996; United States Congress Office of Technology Assessment, 1995; Vadas et al., 2000; Vannote et al., 1980; Vincent & Miller, 1969; Walker & Walker, 1991; Wood, 1991).

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natural flow regime theory developed into the environmental flow theory, which guides water resources management by taking into account human alterations to the natural flow (Poff, 2018; Poff & Matthews, 2013). Nowadays, the field of eco-hydraulics has not only included flow regimes in planning but also river morphodynamic (e.g., zoogeomorphology/biogeomorphology/ecosystem engineering), ice-dynamic and thermal aspects, as well as socio-economic-environmental criteria (Flecker et al., 2022; Katopodis, 2022; Parker et al., 2007; Rice, 2021; Yang et al., 2024). In the year 2024, the 15th International Symposium on Ecohydraulics and Fish Passage (ISE-FP 2024) was held, the first joint conference by the International Symposium on Ecohydraulics (hosted by the International Association for Hydro-Environment Engineering and Research) and Fish Passage Conference (hosted by a joint committee of the American Fisheries Society and American Society of Civil Engineers' Environmental and Water Resource Institute), further emphasizing the importance of joint research between fish passage design and habitat management.

From a historical perspective, the establishment and development of eco-hydraulics have always involved interdisciplinary research (Flecker et al., 2022; Katopodis, 2005) (Figure 2). In the last century, studies connected fish behavior and fishway hydraulics, as well as fish distribution and water physico-chemical conditions. Eventually, this research jointly connected fish passage, habitat suitability, and river morphodynamics together to create a field named eco-hydraulics. Physical hydraulic modeling on various fishway types (Katopodis, 1992), innovative fish swimming performance assessment (Katopodis, 1992; Katopodis & Gervais, 2016), habitat restoration (Katopodis & Aadland, 2006), as well as development of numerical 2D hydraulic models to study fish habitat in the mid-1990s (Crowder & Diplas, 2000; Leclerc et al., 1995), including the open access RIVER2D www.river2d.ca.(Ghanem et al., 1996; Katopodis, 2005), further advanced the field of eco-hydraulics. At the same time, the hydraulic impacts from river biota emerged in the 1990s, when zoogeomorphology was established to connect how aquatic species affect river morphology, as well as how the changes in river morphology affects aquatic organisms (Butler, 1995; Montgomery et al., 1996; Rice et al., 2019). Around 2000, rapid evolution was rediscovered (Donihue et al., 2018; Endler, 1980; Grant, 1986; Hendry et al., 2000; Hendry & Kinnison, 1999), and evolutionary processes were found to have significant ecological impacts, which still require further investigation (Blanchet et al., 2020; Des Roches et al., 2017). At present, how human perturbations in river affect river biota, and how the evolution of river biota feeds back into river hydraulics and morphodynamics, needs to be addressed and integrated into model prediction. Understanding these evolutionary feedbacks and their consequences for resilience of aquatic communities is necessary for river ecosystem conservation when designing and managing river infrastructure. In this review paper, we extend a broad definition for eco-hydraulics, namely the study of interactions between hydraulics, morphodynamics and ecology, by incorporating evolution to establish the field of eco-evo-hydraulics.

3. Population Genetics as a Tool to Link Eco-Hydraulics and Conservation Biology

Although both water resources management and conservation biology study fish passage and connectivity, there are important thematic differences. Water resources management mainly focuses on the design of a fishway and evaluates its attraction efficiency, passage efficiency and passage time to measure the successful rate of fish passage through a barrier (Hershey, 2021; Noonan et al., 2012; Williams et al., 2012). Fish passage studies initially focused on economically important species, such as salmon and trout and have been gradually extended to non-salmonid species (Bravo-Córdoba et al., 2021; Hershey, 2021; Katopodis, 2005; Katopodis & Williams, 2012; Prunier et al., 2023), but also to other issues such as the control of invasive species (Bergman et al., 2022; Deflem et al., 2022). In contrast to these very fine-scale and species-specific ecohydraulic studies, studies on riverine connectivity in conservation biology take a more holistic approach (Belletti et al., 2020; Jumani et al., 2020; Zarri et al., 2022). First, conservation scientists question the performance of a fishway to the whole community, where they found the passage rate of salmonids to be significantly higher than that of non-salmonid species (Noonan et al., 2012). Second, connectivity is usually defined on a larger scale, such as the ***migration*** of fish on a basin-wide scale (Cote et al., 2009). Several river connectivity indices have been developed to measure the longitudinal connectivity of rivers for fish passability, which is defined as the probability of fish being able to cross a barrier in both the upstream and downstream direction (Cote et al., 2009), such as the dendritic connectivity index (DCI) (Cote et al., 2009). DCI is calculated from the number of barriers and fish passibility between two random points in the river system. These indices have been used to assess bidirectional upstream and downstream passage for potadromous fish (migrating within freshwater) and diadromous fish (migrating between marine and freshwater). River connectivity indices can be applied for multiple species, but

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because of data limitations, some assumptions are made about fish behavior, such as whether or not fish disperse across barriers, as well as overall ***dispersal*** distance and reproductive rates in a new habitat. As a result of the large number of assumptions, environmental risk assessment based on a deterministic model includes a high degree of uncertainty in the input variables, which may complicate model interpretation. The limitations in estimating fish behavior in risk assessment represent a significant drawback in water resources management.

Measuring dispersal, such as via fish movement under various flow conditions (Akanyeti & Liao, 2013; Blondel et al., 2020; Liao, 2003; Tudorache et al., 2008), and integrating fish movement as well as swimming-associated traits into hydrodynamic modeling (Bergman et al., 2023; Katopodis & Gervais, 2016; Sciascia et al., 2022; Zielinski et al., 2018), remain a challenge, especially for transiting through areas with high water velocities and turbulence, such as the Fraser River Canyon (B.C., Canada; Hinch & Bratty, 2000). Capture-recapture methods (Pépino et al., 2012), acoustic cameras (Martignac et al., 2015), and telemetry (Cayuela et al., 2018; Crossin et al., 2017; Halfyard et al., 2017) are used to evaluate the impact of water resources management on connectivity. Capture-recapture methods have the advantage of surveying long-lived species at a broad range at a relatively low cost; however, capture-recapture methods can be expensive in terms of both labor and time. Acoustic cameras can provide an efficient count of fish dispersal but with limited ability for recognizing fish species (Martignac et al., 2015). Current AI image processing techniques may assist fish recognition and improve this method (Chai et al., 2023). Telemetry, such as acoustic telemetry, can provide comprehensive information about fish trajectory, environment, behavior, and physical state (Crossin et al., 2017). However, because of battery life and sensor size, telemetry cannot be applied throughout the life span of long-lived species or in very small (<65 mm; Bergman et al., 2022) fish (Cayuela et al., 2018). There are emerging methods to study fish egg dispersion with a Lagrangian model, which provides a powerful tool for studying hydraulic impacts on fish at microhabitat scale (G. Li et al., 2023). However, this simulation method cannot be scaled to the basin-wide level because of high computational cost. An alternative method is to use genetic markers (BOX 1), which can be used for ecological and demographic purposes, to evaluate population size and track dispersal, but also for evolutionary purposes to measure population genetic diversity, evaluate evolutionary responses and other information that can be easily used in river management on a basin-wide scale (Deflem et al., 2022; A. J. Jensen et al., 2022; Raeymaekers et al., 2008). For instance, river connectivity can be estimated by comparing the genetic similarity between populations, for example, upstream versus downstream of a barrier (Prunier et al., 2023; Raeymaekers et al., 2009). Genetic markers can be applied to survey large basin areas. As an example, Prunier et al. (2020) developed a genetic-based index (the F_{INDEX}) that evaluates river fragmentation induced by a single barrier by combining observed genetic differences and computer simulations, which standardizes the impacts of population size and the age of a barrier. Prunier et al. (2023) applied this indicator to 11 weirs in France, before and after fishway restoration or barrier removal, for two genera of cyprinids. They found that the indicator provides a good evaluation of river restoration, providing an operational tool for managers.

BOX 1 Genetic markers and DNA sequencing techniques for population and conservation genetics

Genetic markers are specific regions in the ***genome*** that can be used to identify individuals and species, describe their relatedness and study inheritance patterns. In fish conservation, we introduce two types of markers: ***microsatellites*** and ***single nucleotide polymorphisms (SNPs)***.

Microsatellites are repetitive segments of DNA scattered throughout the genome (Hamilton, 2021). The number of segment repetitions in the microsatellite is used to estimate polymorphisms, and it varies among individuals and populations (Guillemaud et al., 2010; Marchetto et al., 2010). A single microsatellite marker can hence support tens of different variants (alleles), which makes them very informative for analyzing fine-scale population structure, relatedness estimation or studying connectivity with a limited number of ***loci*** (DeFaveri et al., 2013). These characteristics make microsatellites suitable for inference of ***gene flow***, ***genetic drift*** and population genetic structure. As a result of these properties, microsatellites became one of the most popular methods for assessing population genetic information (Morin et al., 2004). However, it is questionable that microsatellites can be used to study whole-genome diversity (Väli et al., 2008). Most microsatellites are distributed in regions that do not code for a specific phenotype and are not under direct selection. They are therefore so-called "neutral" genetic markers (DeFaveri et al., 2013). However, current thinking is that very few genetic markers in the genome

behave truly in a neutral manner (Charlesworth et al., 1994; Jenner et al., 2022; Kern & Hahn, 2018). For example, microsatellite ***locus*** *stn321* is associated to body shape in three-spined stickleback (Bolnick et al., 2009). Nonetheless, it could be risky to apply a limited number of microsatellite loci in studying connectivity. Moreover, because of the decreasing cost of genotyping, microsatellite markers have lost their advantage in low expense. Instead, for the price of 20 microsatellites, researchers can get tens of thousands of SNPs with reduced representation sequencing (Table B1), which can provide a better resolution for the analysis of population genetic structure (discussed below). An alternative method of genotyping microsatellites is to read the number of repeats directly through next-generation sequencing (NGS) (Lepais et al., 2020), which allows the use of microsatellites at a low cost (13–20 euro for 30–50 microsatellites per sample).

SNPs are substitutions of a single nucleotide at a specific position in the genome that are present in a sufficiently large fraction of the population (Wright, 2005). SNPs are located in both protein-coding and non-coding regions. There are plenty of SNPs in coding regions that behave almost neutrally, and SNPs outside coding regions could impact fitness directly (via regulation) or link selection and genetic draft (the effect on a locus by selection on linked loci) (Garcia-Elfring et al., 2021; Hall et al., 2022; Nielsen, 2005). Hence, SNPs can not only identify population structure but are also used to study dispersal. SNPs have mostly replaced microsatellites as an alternative genetic marker. Because SNPs occur in very high numbers along the genome, they have the advantage of providing a finer resolution for analyzing population structures and estimating genetic diversity (Marandel et al., 2020; Vignal et al., 2002). Therefore, SNPs can be used to study both neutral and adaptive ***genetic divergence***. For example, using SNPs, Ishikawa et al. (2019) identified the gene *fads2*, which increases the three-spined stickleback's ability to produce the omega-3 fatty acid docosahexaenoic acid (DHA) in a freshwater environment lacking DHA, and helps marine stickleback to colonize freshwater systems. Similarly, the SNPs method detected the aryl hydrocarbon receptor (AHR) signaling pathway (*AHR2a, AHR1a, AIP, and CYP1A*) that shows an important role in the tolerance for polychlorinated biphenyl, halogenated aromatic hydrocarbons and polycyclic aromatic hydrocarbons in populations of Atlantic killifish (*Fundulus heteroclitus*) (Reid et al., 2016).

Genetic sequencing has become increasingly less expensive over the last decade, which has made it feasible to assess genetic characteristics and ***evolutionary potential*** for applications in conservation and natural resources management (Thompson et al., 2023). The diversity of questions addressed and sequencing methods available requires sound planning. Based on our experience, Table B1 provides an overview of the advantages and disadvantages of some widely used sequencing methods, focusing on microsatellites or SNPs as genetic markers, and their estimated cost to assist water resources managers with time and budget planning. It is a challenge to provide a general cost because the total cost of sequencing is associated with multiple steps, including DNA purification, library preparation, reagents, sequencing in-house or outsourced to companies, sequencing countries/areas, target species, sample size, the length of genomes, sequencing coverage (how many bases sequenced) and other costs. For example, the cost for whole genome sequencing of an individual water flea *Daphnia sp*. ranges from 56 to 116 euro according to the setup (based on experience). Thus, the aim of Table B1 is only to provide a rough magnitude of cost for those who are encouraged by this paper and would like to consider adding genetic markers in their assessment. Considering the massive construction, operation and maintenance cost of an engineering project, the biological sequencing cost is marginal and worth considering in impact assessments. Moreover, we add environmental DNA (eDNA) meta-barcoding in Table B1. Environmental DNA is the DNA that can be detected in environmental sources, such as water bodies, where DNA is released by living and dead organisms, as well as shed material (URycki et al., 2024). With the help of hydrological and hydraulic models, eDNA analysis can better trace the contribution of eDNA sources from different spatial-temporal locations and better understand the release dynamics (URycki et al., 2024). Meta-barcoding techniques are frequently adopted in natural resources management to identify taxa within the same sample (Carraro et al., 2020) and have been used as emerging tools to estimate the ecological impacts of river infrastructures from eDNA (Nowak et al., 2023). Environmental DNA, in theory, has the potential to detect intraspecific variance, which can provide insights into population structure and the detection of candidate genes (Andres et al., 2023). Since 2020,

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several emerging studies have tested this potential. For example, Andres et al. (2021) demonstrated that eDNA can reveal population structure through detecting microsatellite markers and M. R. Jensen et al. (2021) attempted to capture whale shark mitochondrial and nuclear DNA through eDNA. Lately, in a study on the common frog (*R. temporaria*), the Hybridization Capture Using RAD Probes (hyRAD) approach has proven particularly effective in capturing SNPs from environmental DNA based on probes designed from the Reduced Representation Sequencing (RRS) method (Manel et al., 2025). Looking ahead, if functional candidate genes linked to adaptation to human-induced perturbations can be identified, eDNA assays could be specifically designed to target variation in those genes. Such an approach could provide a promising and efficient tool for monitoring adaptive variation in natural populations.

In addition to the sequencing cost, sampling (e.g., electrofishing or fish trapping) and logistic costs (e.g., transport and storage) also need to be considered. Sampling and transportation in remote areas such as the Amazon tributaries or Arctic rivers can be exceptionally costly. Logistically, a small fin clipping stored in analytical grade ethanol can be kept at room temperature, which saves the cost and space for transportation. It should be noted that, in some countries, carrying ethanol might also be complicated due to local regulations. Research ethics should be followed when doing experiments on animals. If sequencing must be done during remote sampling, the nanopore ONT MinION tool, which is a hand-sized portable device that allows sequencing in the field, can be used (Runtuwene et al., 2019). The sequencing accuracy of MinION without combining other high-accuracy sequencing techniques is currently not enough to be used to identify SNPs, but it can be used to detect the presence of some species (Jain et al., 2016). Further information about cost estimation with MinION for biodiversity assessment can be found in Pomerantz et al. (2018).

4. Broadening Regime-Based Methods for Water Resource Management Through Integrating Evolutionary Potential: Hydro-Evolutionary Feedbacks

Although environmental flow is a valuable concept in water resources management, it is challenging to apply when facing the uncertainty resulting from growing human perturbation and climate change. First, in the majority of regulated rivers, we lack historical data or cross-legislative boundary data to define what a "natural regime" is (Flecker et al., 2022; Katopodis, 2022; Maaß et al., 2021). Second, human activities facilitate the spread of invasive species and disturb community structures and ecosystems, leading to unanticipated impacts. For example, topmouth gudgeon (*Pseudorasbora parva*) is an invasive species from Southeast Asia into Europe. Because it has a similar function to native cyprinid fishes and a propensity to form large populations (Britton, 2023), it competes with native species and shifts the native species to new habitats. Third, because of the growing human population, it is challenging to predict the environmental flow that might fit with human demands. At the same time, climate change is disturbing flow regimes (Bertola et al., 2023), changing water temperatures (Justice et al., 2017; Mimeau et al., 2024), and altering fish life-history traits (Stanislawek et al., 2025). As a consequence, the uncertainty brought by climate change makes the planning of regional hydrology and hydraulic infrastructure for social-economic rewards (power generation, water supply, irrigation and flooding control) more difficult (Flecker et al., 2022; Katopodis, 2022). In addition, researchers have also realized the importance of meta-ecology and the connections between populations, communities and ecosystems (Angeler et al., 2023; Warmuth et al., 2025). Hence, environmental flow regime theory should be extended to understand the uncertainty in the changing river environment at a large spatial scale (Bertola et al., 2023; Poff, 2018; Poff & Matthews, 2013).

We propose adding a focus on evolutionary dynamics to enhance river organisms' resistance and resilience against future challenges to the "regime-based" approach. Resistance refers to the ability of a population to maintain the same state for properties such as population size, intraspecific frequency distribution of heritable phenotypes, and genetic diversity when ecological stress is added (a high percentage is more likely than 100% maintaining the same state). Resilience is defined as the ability of a population to recover to the prior state after exposure to ecological stress (Blondel et al., 2021) (a high percentage is more likely than 100% recovery to the prior state). Both resistance and resilience are part of the "***adaptive capacity***" of a population, which is the ability

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of a species to adapt to future environments (Blondel et al., 2021; Nicotra et al., 2015). One might suppose that such capacity is irrelevant to contemporary watershed management, assuming that evolution is a process that requires long time scales far beyond those considered in water management plans. In reality, however, dramatic evolutionary responses to ecological stress can take place in less than a decade—a phenomenon often called "rapid evolution" or "contemporary evolution" (Endler, 1980; Grant et al., 2017; Hendry & Kinnison, 1999). Life history, evolutionary potential, and ***plasticity*** are three main aspects of adaptive capacity (Nicotra et al., 2015). For instance, if a population (a) has a fast reproductive rate (life history), (b) has an above average genetic diversity and genotypes associated with the functional traits to adapt to the new environment (evolutionary potential), and (c) has the ability to change its genetic expression to adapt to the new environment (plasticity), the adaptive capacity of this population is considered high (Nicotra et al., 2015). In practice, adaptive capacity, or more specifically, evolutionary potential, has been broadly applied in conservation (Steeves et al., 2017), through quantitative standards such as ***effective population size*** (N_e) (Hoban et al., 2020; Lowe et al., 2017; Thompson et al., 2023; Waples, 2025) and ***genomic offset*** (Fitzpatrick & Keller, 2015; Jacquemart et al., 2025; Razgour et al., 2019; Rellstab et al., 2021). In Section 6, we will further discuss how to use these two standards in river conservation. The logic of the N_e is that a large population increases the likelihood that a population has and maintains the variant(s) of the gene(s) that could facilitate adaption to the future environment. N_e can be estimated from proxy data, such as population size (Hoban et al., 2022); thus, it has the advantages of immediate and broad fit to policy making when genetic and demographic data are hard to obtain (e.g., Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2024)). In contrast, genomic offset is based on a clear understanding of the genetic mechanisms underlying adaptation, and it can be used to better understand the interplay between genetic change and environmental change. This includes steps such as (a) a gene-environment association study to identify which genes associate with environmental stress; (b) a model to build a predictable relationship between environmental and genetic changes (e.g., gradient forest method (Fitzpatrick & Keller, 2015)); (c) a model to predict future environmental change and species distribution (e.g., ecological niche models (Rellstab et al., 2021)); (d) predicting allelic frequency change in the new environment; and (e) quantifying the maladaptation of the population in the future environment based on the predicted discrepancy between future genotype and current genotype.

Even though the importance of genetic diversity and evolutionary potential has been recognized for decades (Boag & Grant, 1981), applications in natural resources management are limited to a few flagship species (Heuertz et al., 2023). This "application gap" is partially due to the lack of a bridge between natural resources managers and evolutionary researchers (Cook et al., 2021). Water resources management is no exception. Here we introduce the new concept of hydro-evolutionary feedbacks (Hydro-Evo) to explain how its three pillars (hydraulics, hydrology and evolution) interact. The explanation of Hydro-Evo is available in Section 5. To this end, we demonstrate how incorporating evolutionary potential into collective guidelines could lead to a promising solution for basin-wide water resources management and engineering design.

5. Interactions Between Evolution, Hydraulics and Hydrology

Rapid evolution implies that environmental change and evolutionary responses can happen within the life-cycle (all stages) of a hydraulic infrastructure. Rapid evolutionary responses might then feed back to influence river hydraulics (Govaert et al., 2019). For instance, river regulation may lead to reduced waterflow, and low flow can select Atlantic salmon (*Salmo salar*) populations for reduced body size (A. J. Jensen et al., 2022). This effect on body size might be associated with a restriction on the chance of large salmon to access spawning ground (Carlson et al., 2011). Moreover, large fish might also suffer a higher mortality rate from strikes when they pass a hydraulic infrastructure (Cox et al., 2023). When salmon reproduce in freshwater, females move bed substrates to build redds to lay their eggs, which alters the sediment mobility and transport (Hassan et al., 2008; Rennie & Millar, 2000). The movable particle size has been found to be associated with fish body size, where bigger fish can move larger sediment to access more areas for spawning (Riebe et al., 2014). Thus, evolutionary changes in Atlantic salmon body size might affect sediment transportation. Cases such as this, where ecology (environment) modifies evolutionary processes and the resulting evolutionary response feeds back to environment, are encompassed by a relatively new scientific field named ***eco-evolutionary dynamics*** (Hendry, 2017). Recently, eco-evolutionary dynamics theory has inspired geoscientists to consider geo-evolutionary feedbacks that connect rapid evolution with landscape change by extending the scope of the zoogeomorphic engineering processes (Dong et al., 2024). In this section, we further integrate eco-evolutionary dynamics into eco-hydraulics by analyzing the

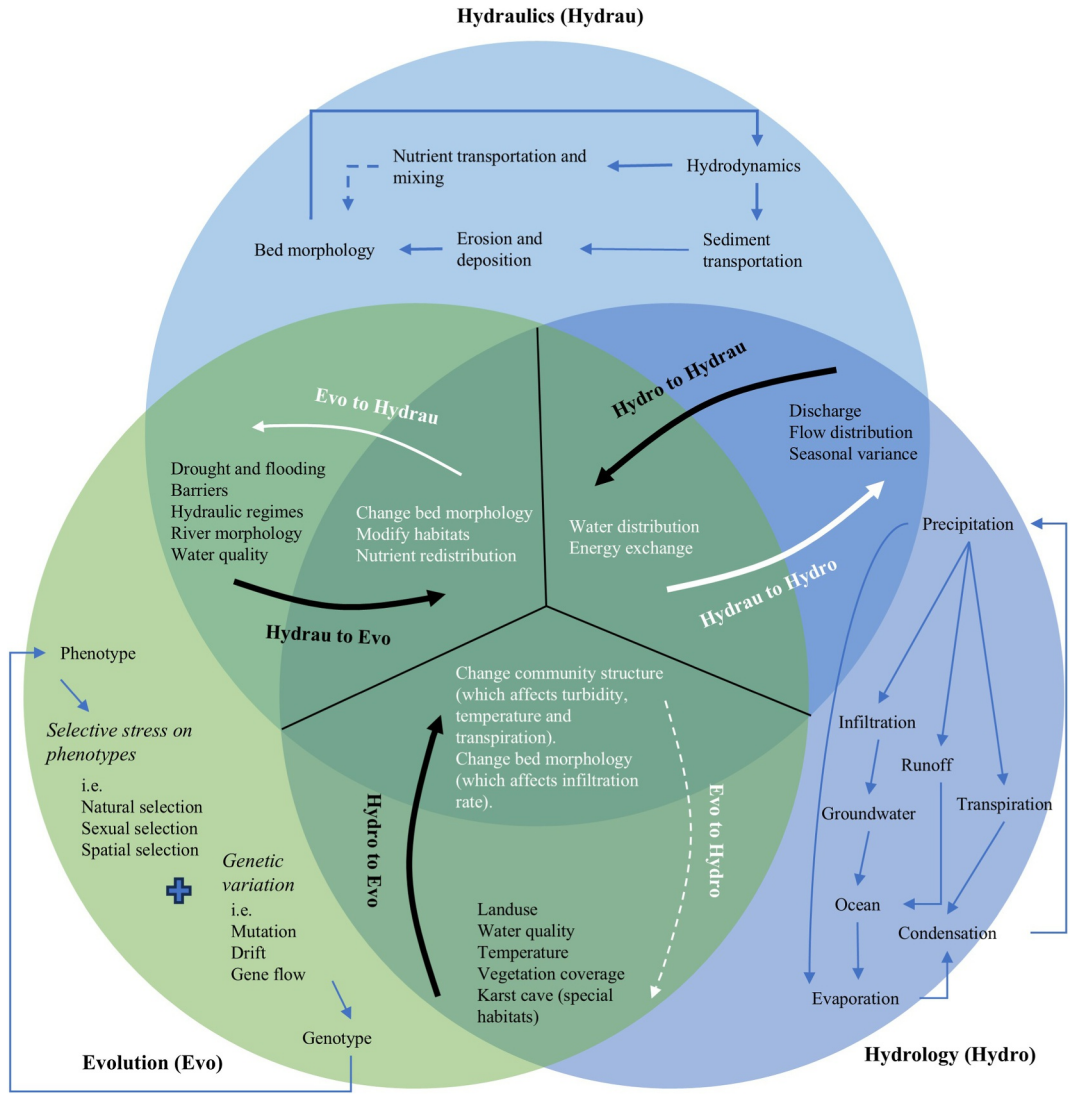

Figure 3. Hydro-Evolutionary Feedbacks describe the reciprocal interactions among evolution, hydraulics, and hydrology. Within each circle, blue arrows indicate internal dynamics among processes (with dashed lines representing indirect effects). In each of the overlapping regions, we list variables from the literature that are currently known to mediate the interactions between two out of three fields. Variable colors (black or white) correspond to the color of the associated feedback. Dashed arrows represent indirect effects, whereas solid arrows represent direct effects. A thick black or white arrow indicates that at least one study has documented the interaction, while a thin black or white arrow reflects a hypothesized link. For example, fish length is expected to influence sediment mobilization (Evo to Hydrau), but no study has yet analyzed how selection-driven changes in fish size might alter sediment dynamics.

feedbacks between hydraulics (including zoogeomorphology), hydrology, and evolution based on a structured literature review that demonstrates how different pillars link to each other from a Hydro-Evo perspective (Figure 3). This framework aims to extend eco-hydraulics into eco-evo-hydraulics in order to stimulate further interdisciplinary research, especially for future applications in water resources management.

5.1. Interactions Between Hydraulics and Hydrology

The closely related topics of hydraulics and hydrology study the movement of water (Figure 3). A key difference is that hydrology focuses on the amount of water transported between water bodies, such as the transportation from oceans, seas or lakes to land through evaporation and precipitation with runoff to streams and rivers. Hydraulics instead focuses on the water movement in river channels, such as flow velocity, sediment transportation, and bed morphological changes. Hydrology thus usually focuses on the water cycle over larger spatial and

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temporal scales than hydraulics. A hydrological model estimates the catchment runoff flows based on a long-term time series of meteorological input, whereas a hydraulic model uses a runoff discharge hydrograph as input to predict the area of floodplain inundation and the velocity distribution for a specific event, such as a historical flood or a synthetic event (e.g., a designed rainfall) with a given frequency of occurrence (e.g., the 100-year return period event). Water physico-chemical conditions are then linked to both hydraulics and hydrology. Within the Hydro-Evo feedbacks, the impacts of physico-chemical conditions on evolutionary change in aquatic organisms can be classified as hydraulic impacts or hydrological impacts. If the local flow field and water movements within the channel are the driving force of physico-chemical conditions, it is classified as hydraulics, such as the fate and transport of contaminants due to advection and diffusion processes. If the dominant factor is driven by watershed processes, it is classified as hydrology, such as input of agricultural or industrial pollutants by overland runoff. Herein, for purposes of classification, bulk water temperature and chemistry are considered a function of hydrological processes.

5.2. Interactions Between Hydraulics and Evolution

5.2.1. Hydraulics-to-Evolution

In this section, we focus on human-induced changes in flow regime and their consequences for fish evolution (Figure 3). Three factors are considered in hydraulics: river connectivity, flow field, and sediment transportation.

Connectivity: Hydraulic structures decrease genetic diversity and gene flow by limiting the movement of fish between upstream and downstream populations (Raeymaekers et al., 2008, 2009; Zarri et al., 2022). The reduced connectivity promotes genetic differentiation between populations and reduces genetic diversity within populations (Roberts et al., 2013). The reduced connectivity not only affects diadromous fishes that migrate between marine and freshwater, but also potamodromous fishes that migrate within freshwater for reproduction, feeding and seeking refuge. For example, in large tropical river basins, such as the Amazon, Congo and Mekong, where potamodromous fishes constitute a larger proportion of the fish fauna, a major question is how river barriers, seasonal connectivity and extreme events (e.g., flood pulses) affect river connectivity (Herrera-R et al., 2024). Genetic diversity within a population is usually linked to population size (more specifically, the effective population size), where genetic drift can significantly reduce genetic diversity in a small population (Hamilton, 2021). On a basin-wide scale, gene flow among (sub)populations can be substantial, such that local populations are genetically not independent units. The concept of effective meta-population size was introduced to accommodate this situation (Palstra & Ruzzante, 2011; Wright, 1943). Simulations of meta-population size at different gene flow scenarios show that genetic differentiation among subpopulations can reduce effective meta-population size, and that asymmetric gene flow among populations can also reduce the effective meta-population size (Palstra & Ruzzante, 2011). This implies that fishway design should consider both directions of fish movement in order to maintain the meta-population size at a sustainable level, as has been advocated in the literature on fish passage for a long time (e.g., Katopodis & Williams, 2012).

Biologists highlight that powerful river rapids can represent a barrier to gene flow and further affect fish genetic structures. They suggest adding hydraulic and hydrological simulation or monitoring to study the altered river connectivity due to flow regimes and river morphology (Kurata et al., 2022; Stokes et al., 2023). Also, low river flow, a typical feature of dams, can reduce river connectivity and lead to ***inbreeding depression*** of upstream populations (Pavlova et al., 2024).

Flow field: Hydraulic structures such as dams also alter hydraulic habitats by changing the upstream lotic environment (flowing water) to a lentic environment (standing water) (Maaß et al., 2021), harming rheophilic species (Katopodis & Aadland, 2006). Besides, hydropower development and operation are also expected to disturb river habitat that threatens endemic fish at different life stages (Luo et al., 2025). There are other natural barriers, such as debris from trees that can form barriers to generate pools and bars to create habitat for some species (Abbe & Montgomery, 1996). Also eco-engineers, such as beavers construct dams that affect hydraulic habitat (Ecke et al., 2017). Many studies have documented phenotypic differences between fish populations naturally occupying adjacent habitats with different flow conditions (Dermond et al., 2019; Izen et al., 2016; Langerhans & Reznick, 2010). Subsequently, studies have shown rapid divergence in fish morphology following dam construction (Haas et al., 2021; Zarri et al., 2022). However, it is important to investigate whether such phenotypic changes have a plastic, genetic or epigenetic basis. A. J. Jensen et al. (2022) revealed a decrease in body mass of Atlantic salmon with river regulation through a reduced discharge on a decadal timescale. This

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change could be partly explained by changes in allelic frequency at two loci in the region of the *vgll3* and *six6* genes. Although this study shows that human regulation in discharge can affect fish body mass, discharge itself is not an effective parameter that supports engineering design without other hydraulic variables (e.g., channel morphology). Studies that can be integrated into engineering design are still missing.

Another challenge in combining evolutionary studies with engineering design is to disentangle flow field effects from other aspects of environmental change. For example, the habitat choice of a fish has a significant correlation with fish morphology (Jacobson et al., 2017), but also predator-prey interaction may have an impact (Sass et al., 2006). That is to say, the observed phenotypic change after impoundment might also be explained by the changes in community structure (Haas et al., 2021). Additionally, we still do not have a full understanding of fish behaviors and the underlying genetic or epigenetic mechanisms that enable fish to adapt to different flow conditions. Recently, studies have shown that genetic differences related to the fish sensory system are present in different hydraulic environments (Cai et al., 2025). In addition, the variation in gene expression related to fish behavior under different flow conditions (Kakakhel et al., 2025) suggest more complicated molecular mechanisms behind fish adaptation to different hydraulic environments. Many studies observed that a range of behavioral responses of fish help them pass river obstacles (Podgorniak et al., 2015, 2016) and adapt to the changes in flow fields. For example, some fish individuals are more efficient in exploring and using different river shelters (Hockley et al., 2014; Sommer-Trembo et al., 2024), or gaining advantages by performing the Karman gait (Liao, 2003), a body kinematic behavior of fish to swim in a vortex street. Understanding the evolutionary response in fish behavior and how fish behavior changes might feed back to the local hydraulic and hydrological environment would benefit fish passage design and provide practical guidelines in river structure operation. Revisiting the previous example, reduced body mass may also lead to reduced swimming speed and endurance with implications for fish migrations (Katopodis & Gervais, 2016). Genotypic and phenotypic data at a fine spatial (Haenel et al., 2021; Izen et al., 2016; Maciejewski et al., 2020) and temporal resolution (Haas et al., 2021; A. J. Jensen et al., 2022) need to be collected in order to minimize the confounding impacts from other non-target variables.

Sediment transportation: Anthropogenic activities, such as agriculture and urbanization, increase suspended sediment (Courtice & Naser, 2020; Hornung & Reynolds, 1995; Parker et al., 2007) and may change groundwater flow, water quality or ice regimes that can be detrimental for fish (Katopodis & Aadland, 2006). River barriers can reduce sediment transportation downstream and trap sediment upstream (Maaß et al., 2021). This process can alter bed morphology (Parker et al., 2007), change fish habitat suitability (Katopodis & Aadland, 2006), and alter turbulent flow characteristics that affect habitat quality and availability (Reggad et al., 2025). Sediment can affect fish distribution by changing bed morphology and affecting fertilization and feeding rates (Chapman et al., 2014; De Robertis et al., 2003; Hassan et al., 2008; Parker et al., 2007), as well as spawning habitat suitability (Rahman et al., 2025). For example, when the scour depth at a redd site exceeds the depth of egg burial, salmon embryos can be swept out (Montgomery et al., 1996; Rennie & Millar, 2000), and the gravel size acts on the evolution of salmon egg size (Quinn et al., 1995). Studies have found that fish show habitat preference based on sedimentation. For example, juvenile yellow perch (*Perca flavescens*) utilize a habitat in which sediment deposition occurs (Parsapour-Moghaddam et al., 2019). However, it is still unclear how fish adapt to sediment deposition. Sediment concentration could also potentially select fish for their visual properties and decision-making capacities, such as the function of their tectum (Barker & Baier, 2015). In addition, dams also impede nutrient load via reducing sediment transportation, which further alters the biogeochemical cycle in the river and influence downstream river sections (Maavara et al., 2020).

5.2.2. Evolution-to-Hydraulics

To date, there is limited empirical evidence quantifying evolutionary feedbacks from fish evolution to hydraulic processes, as well as the magnitude by which hydraulic conditions can be altered as a consequence of evolutionary change. However, accumulating indirect evidence suggests that such feedbacks are plausible. Here, we explore this question based on mechanistic reasoning and empirical observations from related studies.

In this section, we turn our focus to whether fish evolution can feedback to alter human-induced changes in flow regime. The first step is to establish that fish—irrespective of any rapid evolution—influence hydraulics. Depending on the size and abundance of fish, a large number of fish might change the river flow regime while they swim or perform as an obstacle (Trinci et al., 2017), but these direct impacts could be small. Instead, some

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fish species can significantly change bed morphology and river habitat to impact hydraulics (zoogeomorphology/biogeomorphology/ecosystem engineers; herein defined as zoogeomorphic engineering) (Butler, 1995; Jones et al., 1994; Viles, 1988). For example, Atlantic salmon, sea lampreys (*Petromyzon marinus*), three-spined stickleback (*Gasterosteus aculeatus*), smallmouth bass (*Micropterus dolomieu*), stoneroller (*Campostoma anomalum*), and chub (*Nocomis spp.*) can modify sediment transportation and change bed morphology during nest building (Albertson & Allen, 2015; Dhamelincourt et al., 2022; Hassan et al., 2008; Rice et al., 2019; Östlund-Nilsson et al., 2007) (Figure 3). This form of zoogeomorphic engineering may, in turn, influence local flow regimes by altering bed morphology. The extent to which evolutionary changes in fish populations modulate this geomorphic feedback warrants further investigation.

Water resource regulation generates fine sediment (Courtice & Naser, 2020), and finer grain size can induce negative selective stress on salmon egg size, which leads to a smaller body size of salmon (Quinn et al., 1995). Besides, river regulation can select Atlantic salmon for a smaller size (A. J. Jensen et al., 2022). These smaller fish likely have a different impact on bed morphology and river habitat than bigger fish. This potentially heritable phenotypic change related to body size could further reduce the capacity of salmon to impact sediment transportation. Other examples, such as benthic feeding by *cyprinid* fishes (e.g., barbel (*Barbus barbus*), common carp (*Cyprinus carpio*)), common bullhead (*Cottus gobio*) and other species can disturb the surface layer to change grain orientation or flip clasts, and even whole-grain displacement by large fish (Pledger et al., 2014; Rice et al., 2019). The selection of fish size might indirectly feed back to river hydraulics through zoogeomorphic engineering processes. For example, Atlantic salmon can change the local bed grain size when building a redd. The small local dune-like form of a redd may increase the local grain mobility owing to the convective acceleration over the crest at the tail-spill (Rennie & Millar, 2000). Further, the size of salmon influences the size of the redd they construct (Riebe et al., 2014), which should then influence the near-bed velocity field. Hence, any rapid evolution of salmon size, which is common (Oke et al., 2020), might feed back to hydraulics through changes in the size of redds they construct. In shallow creek mouths, large Atlantic salmon usually cannot pass (Carlson et al., 2011), and this selective stress can change the evolutionary dynamics of salmon. The changing size of salmon would also change the number of eggs produced (Carlson et al., 2011; Oke et al., 2020). Salmon are philopatric which means that they return to their natal sites to breed (Hendry et al., 2003). Thus, the reduced salmon size in a year will further impact the salmon that return to the natal site, which would affect sediment transportation in the future.

Another potentially important, however indirect, feedback from evolution to hydraulics is from those fish that play a role as ecosystem engineers to influence the river community through nutrient flow (Moore, 2006). Ecosystem engineers are defined as "organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (Jones et al., 1997)." Examples include flannelmouth characin (*Prochilodus mariaei*) fish that play a critical role in organic carbon transportation (Taylor et al., 2006), and Pacific salmon (*Oncorhynchus nerka*) that die upstream and hence fertilize the otherwise oligotrophic rivers with nutrients (Holtgrieve et al., 2010). Macrophytes benefit from organic carbon, as it can attenuate UV-B radiation, bind heavy metals and provide carbon dioxide when it breaks down (Reitsema et al., 2018). Macrophyte coverage in rivers influences hydraulics by increasing flow resistance. Therefore evolutionary change in populations of flannelmouth characin and other fish might potentially lead to changes in macrophyte cover that subsequently alter river hydraulics.

5.3. Interactions Between Hydrology and Evolution

5.3.1. Hydrology-to-Evolution

Discharge affects several hydraulic factors such as river connectivity, water depth and velocity (Manning's equation)—and, thus, hydrology influences fish evolution via the above processes (Figure 3). Various studies show that fish (and other aquatic species) that regularly experience flooding events are adapted to such disturbances (Blondel et al., 2021; Poff et al., 1997; Weese et al., 2011). Floodplains are considered to provide fish with a fertile ground for food (phyto- and zooplankton) and higher temperatures favor larvae growth (Balcombe et al., 2007; King et al., 2003). Under climate change, the frequency and magnitude of these hydrological events are likely to induce an evolutionary response from fish species (Bertola et al., 2023; Lee et al., 2023; Whitfield, 2012; Willems et al., 2012).

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The second important component is related to the physico-chemical-biological factors associated with hydrological changes. Hydrological environments affect river temperature and oxygen levels, which might affect fish tolerance to these variables (Eliason et al., 2011; Maciejewski et al., 2020; McKenzie et al., 2020). Furthermore, nutrients can affect the amount of fish food availability by impacting primary productivity (Holden & Green, 1960). Finally, high nutrient levels result in algal blooms, which significantly reduce the concentration of dissolved oxygen and increase fish mortality rate.

Most fish are ectothermic animals that depend on ambient water temperature to regulate their body temperature. Under ongoing global warming, elevated water temperatures are expected to impose strong selective pressures on fish growth rate and body size (Stanislawek et al., 2025). In addition, climate-associated stressors such as drought and hypoxia are expected to alter fish genetics, traits, abundances, and community structure (Abdelnour et al., 2024; Crispo & Chapman, 2010). For example, compared to three-spined sticklebacks, the closely related nine-spined sticklebacks (*Pungitius pungitius*) are better adapted to low-oxygen environments (Lewis et al., 1972).

Industrial and agricultural pollution select fish that are tolerant to pollutants (Reid et al., 2016; Vega-Retter et al., 2024), and the pollutant emission from industrial and agricultural activities into rivers is considered in hydrological models (Keller et al., 2023). Pollutants can have important evolutionary consequences. For example, specific genomic regions were associated with high mercury load in three-spined stickleback (Calboli et al., 2021).

There are also ecological pathways for hydrology that affect the evolutionary dynamics of aquatic organisms indirectly. For instance, changes of hydrological factors alter community structure (Zhang et al., 2012), thereby affecting fish abundance, distribution and reproduction. Groundwater movement transports nutrients (Ingram, 1967) and impacts vegetation distribution. All of these changes are strongly influenced by hydrology and can modify the evolutionary trajectories of aquatic organisms.

5.3.2. Evolution-to-Hydrology

Evolutionary feedback to hydrology is typically indirect, as aquatic organisms at a single location are unlikely to influence the hydrological cycle at large spatial scales. Compared with the Evolution-to-Hydraulics pathway, the Evolution-to-Hydrology pathway has received considerably less attention. A major challenge in studying this process lies in quantifying how evolutionary adaptations to local habitats may scale up to influence hydrological dynamics across broader spatial and temporal scales. Although establishing such connections is difficult, we argue that these feedbacks may nonetheless exist and warrant further investigation.

The evolution of aquatic organisms could change bed morphology and nutrient distribution in the river, impacting the local habitat (Dong et al., 2024). Different from Evolution-to-Hydraulic feedback, here, the bed morphological changes (changed bed substrate) link to the hydrological cycle through the groundwater-surface water transition, which is within the study scope of hydrogeomorphology. Additionally, fish evolution may influence nutrient fluxes across rivers, catchments, adjacent terrestrial systems, and even between marine-terrestrial ecosystems (Bassar et al., 2010; Dong et al., 2024; Helfield & Naiman, 2001; Quinn et al., 2000), potentially altering vegetation abundance and, in turn, affecting evapotranspiration rates (Figure 3). For example, during the whole life cycle of a fish, its activity redistributes biomass and nutrients, which could impact the mass and energy flux in different watersheds. Even small evolutionary changes in the life cycle of local fish populations may accumulate over time, potentially leading to hydrological consequences at broader spatial and temporal scales.

Besides, when considering metapopulations (Fronhofer & Altermatt, 2017; Warmuth et al., 2025), evolutionary change through changes in the level of gene flow among subpopulations might impact the basin's hydrological processes that interact with communities and ecosystems. At the community level, the evolution of population-specific traits may affect predator-prey interaction, which may impact water turbidity and affect water temperature and evaporation rate from varied population sizes (Gu et al., 2023). At the ecosystem level, studies have found that intraspecific diversity impacts ecological system functions (production and decomposition) that may link to the hydrological cycle (Blanchet et al., 2020; Des Roches et al., 2017; Raffard et al., 2021; Whitham et al., 2003). Overall, feedback from evolution is more likely—or at least more easily studied—for hydraulics than for hydrology.

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6. Applying Evolutionary Potential to Water Resources Management

Water resources management has traditionally taken a static view where a system, for example, urban flooding management, is considered stable throughout the whole life cycle, which is known as "fail-safe" (Ahern, 2011; Kim et al., 2017). This "fail-safe" concept assumes a system that is resistant to all the disturbances from the environment, where resistance means the ability of a system to avoid displacement from its original state after being exposed to perturbation (Pimm, 1984). However, this static viewpoint has been questioned for not considering the uncertainty of the future environment, and thus, a concept of "safe-to-fail" has been born to guide engineering design with the consideration of system failure and re-establishment (Ahern, 2011). "Safe-to-fail" emphasizes the dynamics of a system and focuses on system resilience (Leandro et al., 2020; Moura Rezende et al., 2019; Sharifi, 2016), where resilience means that a system has the tendency to return to the original state following an initially strong displacement (Blondel et al., 2021; Pimm, 1984). The Hydro-Evo Feedbacks can be easily integrated into resilience-based water resources management. When a population is under environmental stress, it might undergo a period of decline, but eventually, it might be capable of adapting and recovering. Implementing this perspective can take the form of considering genetic diversity and evolutionary responses, as we will now discuss.

6.1. Potential Managerial Strategies Based on Genetic Diversity

The key parameter determining evolutionary adaptation is the additive genetic variance in fitness (Hendry et al., 2018), which is exceedingly hard to measure in natural populations. Genetic diversity (e.g., allelic richness or ***heterozygosity***)—or even phenotypic variation—becomes a proxy to evaluate adaptive capacity (Pearman et al., 2024). The underlying logic behind enhancing genetic diversity is that (a) high genetic diversity increases the probability that some individuals in a population possess a combination of genes that allows them to adapt and survive novel environmental stress; and (b) a large population size facilitates adaptation to a new environment and avoids the possibility of extinction due to genetic drift faced by small populations. In practice, genetic diversity indicators, such as (a) the number of populations with effective population size above versus below 500 (N_e 500 indicator), and (b) the proportion of populations maintained within species (PM indicator), are increasingly being applied to natural resources management (Convention on Biological Diversity, 2024; Hoban et al., 2020). Reporting these genetic indicators (N_e 500 indicator and PM indicator) to the Convention on Biological Diversity (CBD) has been accepted by 196 parties during the fifteenth meeting of the Conference of the Parties (COP 15). When demographic data and DNA data are hard to access, N_e could also be estimated by proxy data using $N_e/N_c = 0.1$ (Hoban et al., 2023), where N_c is the census size. It is straightforward to connect the census size to the existing adaptive management in eco-hydraulics, where the population size is monitored. As a result, there is no extra material cost associated with calculating N_e, which allows a broader application in understanding which species are more vulnerable to human perturbation in the river system. However, the reliability of this proxy varies substantially among taxa, ecological contexts, and life-history traits (Harribey et al., 2025; Waples, 2025). While the $N_e/N_c = 0.1$ approximation performs reasonably well for several species, it requires careful evaluation of fish life-history traits. Marine fish species with large census sizes and weak genetic structure often exhibit extremely low N_e/N_c ratios ($10^{-3} \sim 10^{-8}$) (Hauser & Carvalho, 2008). In contrast, some studies suggest that bony freshwater fish may have substantially higher ratios, with reported averages around 0.389 (Hoban et al., 2020; Paz-Vinas et al., 2024). There are still some practical questions that have not been solved related to how to provide the best estimation of effective population size (Geue, Bertola, et al., 2025; Geue, Vejlgaard, et al., 2025). Empirical validation of species-specific N_e/N_c ratios remains essential for developing practical freshwater conservation guidelines.

The required frequency of monitoring depends on the generation time of the vulnerable species; thus, we cannot provide a general guideline. That said, monitoring should be relatively frequent during the operation period of a hydraulic structure (e.g., at least every 5 years) and monitoring should continue following decommissioning of the structure (e.g., every 10 years).

Genetic diversity certainly varies among fish populations—even within a single watershed. For example, the lower genetic diversity found in headwaters in some species might be explained by the combined effects of downstream-biased dispersal, increased downstream habitat availability and only rare upstream-directed colonization (Paz-Vinas & Blanchet, 2015; Paz-Vinas et al., 2013). Hydraulic barriers or poorly designed structures, such as weirs or culverts, at the headwater may further reduce upstream connectivity and gene flow. Isolated upstream populations at low effective population sizes lose genetic diversity through genetic drift (Zarri

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et al., 2022, 2025). Thus, in headwaters, countering the negative impact of humans can involve strategies, such as removing unnecessary barriers, building fishways for large dams and avoiding building new barriers (Zarri et al., 2022, 2025). Alternatively, nature-based solutions can be implemented to delay runoff and increase storage and groundwater recharge. These solutions include vegetation strips, pools, vegetated micro-depressions, blocked drainage ditches, renaturalized upstream river reaches, and small river bed steps. Water can also be harvested in built-up areas, for example, by storing rooftop water (Willems et al., 2012). With respect to hydropower, hydrokinetic river turbines can be implemented to avoid building hydraulic barriers (Kirby et al., 2023). On the other hand, in downstream areas, increased habitat availability (Lague et al., 2005) that could increase effective population size may counterbalance genetic drift. High genetic diversity can also support the resilience of fishes to climate change. For diadromous fish such as Atlantic salmon, downstream large dams have significant impacts, and fishways are required to increase connectivity in both directions (Katopodis & Williams, 2012).

6.2. Potential Managerial Strategy Based on Evolutionary Responses

Evolutionary responses occur when fish populations quickly respond to the changing environment. Blacktail shiner (*Cyprinella venusta*) showed phenotypic changes shortly after impoundment, including reduced head size, increased body depth and a decline in the length of the dorsal fin base (Haas et al., 2021). Atlantic salmon reduced body mass in order to adapt to river regulation (A. J. Jensen et al., 2022). There is no doubt that incorporating such information could benefit future water resources management, but it will take time and more research to develop applications.

One challenge is the difficulty of identifying the key hydraulic changes that impose selection on particular fish traits. The majority of studies on the impacts of water resources management are generally linked to the change of habitat before and after management, and its impacts on fish morphology, life history, migration, and behavior (Zarri et al., 2022). However, there is a lack of information on the specific design parameters and their impact on fish evolutionary responses. For example, what is the threshold to operate the hydraulic regime that minimizes human-induced selective stress? What kind of selection pressures are associated with river engineering design, such as bed roughness, bed load, channel cross-sectional shapes, width-depth ratio, turbulence, specific discharge and sinuosity (Cai et al., 2025; Katopodis & Aadland, 2006; Reggad et al., 2025)? How do we evaluate the potential selection pressures induced by the whole life-cycle of a hydraulic project and its further feedbacks in Hydro-Evo?

A second challenge relates to identifying specific genetic responses. One approach is to measure the amount of adaptive genetic variance (e.g., the total number of ***genetic outliers***) associated with specific hydraulic variables through methods such as ***gene-environmental association studies*** or by assessing ***genomic offset*** (Rellstab et al., 2015, 2021). By proper design of the environmental contrast/gradient (e.g., collecting samples in areas that have different flow fields), the number of genetic outliers associated with target environmental variables is indicative of the selective stress of the variables. Gene–environment association studies on river hydraulic regimes remain uncommon. Cai et al. (2025) identified genes associated with different hydraulic regimes in three-spined stickleback. Those genes are, related to the sensory system; however, further studies are needed to test whether this result is generalizable. Because the same species may show non-parallel evolution, that is, different evolutionary responses to the same environmental stress (Bolnick et al., 2018), using the number of genomic outliers to evaluate the environmental impacts on fish evolution may be inaccurate. Nonetheless, it is a reasonable starting point to use the number of genetic outliers between populations of similar lineage to assess the impact of a particular environmental variable. Compared to traditional methods that measure population size, survival rate and reproduction, population genomic studies assessing evolutionary responses can measure more subtle hydraulic impacts, which do not cause a high mortality rate but increases the ***genetic load*** of fish populations. Debate is ongoing as to how to effectively capture adaptive genetic variance because the value of this genomic offset indicator is sensitive to species, location, and environmental parameters of interest.

Despite these challenges, existing knowledge can be useful right away. Headwater populations are often small and isolated, and they often form unique populations from a genetic point of view (Finn et al., 2011; Van Houdt et al., 2005). These unique populations (subject to genetic drift) are often the genetic fuel for selection in more downstream populations (Finn & Poff, 2011). So, headwater populations, even if they are not diverse, can be very important for the adaptive capacity of more downstream populations. Thus, such populations deserve special consideration. Further, intensive hydraulic disturbances—especially given climate change—are expected to induce stronger effects than natural disturbances (Grant, 1986; Oz et al., 2014; Zarri et al., 2022). In such cases,

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we might expect that a population previously exposed to a similar stress—whether natural or anthropogenic—will be better able to cope with that stress, including through rapid evolution (Abdelnour et al., 2024; Blondel et al., 2021). Therefore, when planning a hydraulic structure, a survey of historical natural disasters should be conducted on the fish demographic history. Conducting genetic sequencing and identifying local adaptive loci will generate an extra cost compared to using the N_e proxy data, but it enables better prediction of fish adaptation as well as their evolutionary responses. Compared to the project cost of constructing a fishway, where costs per meter of head range from US$206,060 for nature-like by-pass channel fishways to US$1.6 million for a fish elevator (Bruch & Haxton, 2023), the cost of sequencing is marginal (Table B1).

In practice, water resources management strategies should incorporate a Hydro-Evo perspective and apply strategies, such as:

1. Monitoring genetic diversity (such as through N_e) of fish populations in river systems, especially at human-regulated reaches, to identify species and populations that require immediate action.
2. Providing a river refuge as a cushion for fish populations to adapt to the perturbations of an engineering project. The hydraulic structure should apply adaptive management to minimize the evolutionary impact during its operation.
3. Conducting genetic monitoring during the whole life-cycle of a hydraulic structure to track the evolutionary responses from design to post-decommissioning to understand the evolutionary impacts of an engineering project in its life-cycle.
4. Conducting spatial gene-environmental association studies that examine the relationship between environmental stresses and evolutionary responses.
5. Evaluating the consequences of building new hydraulic infrastructure based on simulations from biophysical models and field experiments to assess fish dispersal, fitness and associated genetic change.
6. Constraining the design and construction of hydraulic infrastructure based on its impacts on genetic variance, and aiming to find a balance in sustainable socio-economic benefits and conservation.
7. We also suggest monitoring the evolutionary response of fish to the changes in hydraulic and hydrological environment over time.

7. Limitations and Future Perspectives

Conserving fish species based on environmental flow is widely used in water resources management. However, this concept has been challenged by the increasing uncertainty of climate change and rapid human development. In this article, we argue that river regulation not only reshapes hydraulic, hydrological and geomorphological processes but also imposes selective pressures on fish populations. Fish evolutionary responses may, in turn, influence hydraulic, hydrological and zoogeomorphic engineering processes, generating hydro-evolutionary feedbacks within river systems. By explicitly integrating evolutionary theory into eco-hydraulics, we propose eco-evo-hydraulics as a conceptual extension aimed at improving long-term sustainability in water resources management under accelerating global change.

Despite the conceptual framework outlined here, empirical evidence for hydro-evolutionary feedbacks remains limited. Most existing studies focus on salmonids and temperate natural river systems, leaving tropical, Arctic, and highly regulated rivers comparatively understudied. Moreover, current discussions of evolutionary responses related to zoogeomorphological effects are largely based on the relationship between fish body size and spawning or feeding activities involved in zoogeomorphic engineering processes, and may therefore not fully capture the broader diversity of zoogeomorphic engineering mechanisms. In addition, an important yet underexplored question in this paper is how river regulation–induced evolution interacts with other selective pressures, such as global warming, as this topic has not been thoroughly examined due to the limited number of empirical studies. Additionally, quantitative estimates of the strength, spatial extent, and temporal persistence of evolutionary feedbacks to flow regime, sediment transport, and channel morphology are still scarce. These limitations reflect not only gaps in available data, but also the methodological challenges of detecting evolutionary change and linking it to riverine processes.

Future research should prioritize several key directions. First, we need to clarify the magnitude (how strong is the selective stress?), mechanism (which traits/pathways are under selection?), parallelism (are selective pathways parallel among populations and across taxa?), and by which spatial-temporal scales river regulation and operation drives evolutionary change in wild fish populations. Second, identifying and quantifying evolutionary feedback

pathways will be essential for assessing their relative importance compared with other physico-chemical (nutrient flux) and ecological (community structure and fish abundance) drivers of zoogeomorphic engineering processes. Third, improved approaches are required to estimate adaptive capacity and evolutionary potential in management contexts. Although monitoring indicators such as N_e provide a promising bridge between evolutionary potential and managerial policy, appropriate sampling schemes and estimators require further refinement before they can be reliably applied in river systems. Finally, integrating evolutionary dynamics into hydraulic modeling and river design frameworks will be crucial for translating theory into practice. Although incorporating ecological processes into hydraulic models is already challenging, accounting for evolution may ultimately improve ecological predictions because metrics such as genetic offset could help to evaluate whether fish populations are likely to maintain adaptive potential under changing environmental regimes.

In summary, the central message of this study is that riverine organisms are not evolutionarily static components of a managed system. They evolve under anthropogenic regulation, and these evolutionary changes can reshape ecological interactions, and geomorphic processes over time. Recognizing and incorporating these dynamics is fundamental to improving risk assessment, conservation planning, and the long-term resilience of regulated river systems.

Appendix A: Glossary

Terminology	Definition	Source
Adaptation	Phenotypic change that improves fitness and has a genetic basis.	Hendry (2017)
Adaptive capacity	The ability of a species to adapt to future environments.	Nicotra et al. (2015)
Allele	A variant or alternative form of the DNA sequence at a given locus.	Hamilton (2021)
Dispersal	Permanent movement away from an origin and long-term settlement at a new location.	Lowe et al. (2017)
Eco-evolutionary dynamics	Interactions between ecology and evolution that play out on contemporary time scales.	Hendry (2017)
Effective population size (Ne)	The size of an ideal population that would experience the same amount of genetic drift as the observed population.	Waples (2025)
Evolution	Changes in the genetic composition–usually allele frequencies at particular places in the DNA sequence–of a population	Hendry (2017)
Evolutionary potential	The ability of populations to evolve in response to environmental changes.	Steeves et al. (2017)
Genetic divergence	Fixed genetic differences that accumulate between two completely isolated lineages that were originally identical when they separated from a common ancestor.	Hamilton (2021)
Genetic drift	Change in gene frequencies over time owing to random differences in the survival and fecundity of individuals, as well as to binomial sampling of alleles during meiosis.	Lowe et al. (2017)
Gene flow	Movement of genes from one population to another. In population genetics theory, gene flow is represented by migration rate (m) the proportion of individuals in a focal population that are immigrants.	Lowe et al. (2017)
Genetic load	Reduction in mean fitness of a population due to the accumulation of unfavorable alleles, relative to an idealized population composed of optimal genotypes.	Hoffmann et al. (2021)
Genetic outliers	In this review paper, we define genetic outliers as genetic loci that exhibit variation statistically significantly associated with environmental variables, show significant differences among populations, or differ markedly from the average or expected genomic patterns (for example, loci with F_{ST} values much higher or lower than the genome-wide mean). Such loci are often	Capblancq and Forester (2021) and Rellstab et al. (2015)

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Table
Continued

Terminology	Definition	Source
	considered candidate genes under selection. However, in some cases, neutral loci may also display significant differences between populations and may similarly show significant correlations with environmental variables.	
Genome	The genome is the entire set of DNA instructions found in a cell.	National Human Genome Research Institute (2023)
Genomic offset	The distance between the current and required genomic composition in a set of putatively adaptive loci under a future/changed environment. The latter can be understood in a spatial or temporal perspective.	Rellstab et al. (2021)
Genotype	The set of alleles possessed by an individual at one locus; the genetic composition of an individual at one locus or many loci	Hamilton (2021)
Gene-environmental association studies	The main goal of gene-environmental association studies is to test whether a specific allele or locus genotype is associated with a specific environmental factor, while controlling for neutral genetic structure.	Rellstab et al. (2015)
Heterozygosity	Having inherited different versions (alleles) of a genomic marker from each biological parent.	National Human Genome Research Institute (2023)
Inbreeding depression	Inbreeding depression is, when mating partners are too closely related, the reduced survival and fertility of offspring of related individuals.	Charlesworth and& Willis (2009)
Locus	(plural: loci) Literally "place" or location in the genome.	Hamilton (2021)
Microsatellite	Microsatellite, as related to genomics, refers to a short segment of DNA, usually one to six or more base pairs in length, that is repeated multiple times in succession at a particular genomic location. These DNA sequences are typically non-coding. The number of repeated segments within a microsatellite sequence often varies among people, which makes them useful as polymorphic markers for studying inheritance patterns in families or for creating a DNA fingerprint from crime scene samples.	National Human Genome Research Institute (2023)
Migration	Temporal movement away from an origin and settlement at a new location.	Hendry (2017)
Phenotype	The morphological, biochemical, physiological, and behavioral attributes of an individual; synonymous with character and trait.	Hamilton (2021)
Plasticity	Ability of an individual genotype to express different values of a given phenotypic trait in different environmental conditions. This term also includes the particular case of transgenerational plasticity, which describes the ability of an individual genotype to produce different offspring in different environmental conditions.	Rey et al. (2016)
SNPs	A single nucleotide polymorphism (abbreviated SNP) is a genomic variant at a single base position in the DNA. Scientists study if and how SNPs in a genome influence health, disease, drug response and other traits.	National Human Genome Research Institute (2023)

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Appendix B: Comparison of Sequencing Methods

Table B1
Advantages and Disadvantages of Different Sequencing Methods, Including the Estimated Cost per Sample (Typically an Individual Fish)

Experimental methods	Special steps	Estimated cost	Advantage	Disadvantage	References
DNA microsatellite	Primer development and testing	1. 5,000 euro for development; 2. 2–12 euro per locus per sample when genotyped using electrophoresis.	1. Easy data analysis; 2. Data resolution suffices to evaluate connectivity on a large scale.	This approach requires specialized developmental steps.	Y. Li et al. (2002)
SNP mining through Reduced Representation Sequencing (RRS)	1. High molecular weight (HMW) DNA; 2. Calculate coverage if genome is known	40 euro/sample	1. Cheap compared with WGS; 2. Might yield enough loci to infer environmental impacts and adaptation; 3. Might yield enough loci to study fish population structure within a river or on a basin scale.	This approach provides lower resolution for identifying loci under selection than whole-genome sequencing.	Altshuler et al. (2000)
Whole genome sequencing (WGS)	HMW DNA	50-250 euro/sample	Whole-genome sequencing provides high accuracy and enables detailed detection of adaptive loci and signatures of selection.	Expensive	Baym et al. (2015) and Ekblom and Wolf (2014)
Whole genome pool sequencing (Pool-seq)	Equimolar the DNA contribution from each sample	700 euro to 1000 euro/pool/ 20 samples in a pool	1. Can allow whole genome sequencing on a limited budget; 2. Yield enough loci to infer environmental impacts and adaptation; 3. Yields enough loci to study fish population structure within a river or on a basin scale.	1. Uncertainty of the DNA quality of each individual in a pool, and some individuals can over-represent other samples; 2. Cannot identify individual's genotype and track individual's migration; 3. Lack of the ability to study genome rearrangement.	Ferretti et al. (2013)
DNA barcoding of environmental DNA	Precautions during sampling and lab analyses	230 euro/sample	1. Non-invasive method; 2. Can be used to detect community abundance and estimate population size; 3. Analysis can be conducted in the field using compatible third-generation sequencing platforms.	Contamination issues	Andres et al. (2021)

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

This review paper is based entirely on review of published literature. As such, no data were used to generate this paper.

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