The Evolutionary Consequences of Dams and Other Barriers for Riverine Fishes

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Dams and other anthropogenic barriers have caused global ecological and hydrological upheaval in the blink of the geological eye. In the present article, we synthesize 307 studies in a systematic review of contemporary evolution following reduced connectivity and habitat alteration on freshwater fishes. Genetic diversity loss was more commonly observed for small populations impounded in small habitat patches for many generations behind low-passability barriers. Studies show that impoundments can cause rapid adaptive evolution in migration timing, behavior, life history, temperature tolerance, and morphology, as well as reduce phenotypic variance, which can alter adaptive potential and ecological roles. Fish passage structures can restore migratory populations but also create artificial selection pressures on body size and migration. The accelerating pace of dam removals and the paucity of data for fishes other than salmonids, other vertebrates, invertebrates, and tropical and southern hemisphere organisms highlights the urgent need for more studies on the rapid evolutionary effects of dams.

Keywords: dams, selection, reservoir, genetic diversity, evolution

The installation of dams has reshaped freshwater ecosystems across the globe. Dam-induced disturbance compounds other environmental changes wrought by climate change, eutrophication, and landscape changes (Fuller et al. 2015). Despite these adverse consequences, dam construction is accelerating in the developing regions of tropical South America, Asia, Eastern Europe, and Africa and is expected to severely fragment 89% of global river flows by 2030 (Zarfl et al. 2014, Grill et al. 2019). Although the ecological impacts of dams have been subject to close examination for many decades, the evolutionary effects were not well studied until recently (figure 1a) and continue to receive less attention than the ecological consequences. Anthropogenic pressures can cause rapid evolution in affected populations, sometimes causing intraspecific differentiation that has been demonstrated to create ecological effects of comparable magnitude to those seen among separate species (Hairston et al. 2005, Post et al. 2008, Des Roches et al. 2018). An understanding of rapid evolutionary processes is critical for ecologists and managers alike, because humans disrupt patterns of natural selection and phenotypic evolution, potentially leading to undesirable outcomes such as fisheries collapse or altered ecosystem stability (Darimont et al. 2009, Fugère and Hendry 2018).

Dams and other barriers have strong ecological effects, and these effects frame the potential for evolutionary change. Barriers decrease population connectivity by physically blocking the movement of fishes, although smaller barriers may allow passage to a subset of the population. These connectivity changes can alter community dynamics by blocking access to upstream habitat for ecologically important species, such as key predators (Flecker et al. 2010). Furthermore, the physical and chemical environment can be altered both upstream and downstream of barriers. Stream barriers can alter channel geomorphology, reduce discharge, decouple the natural correlation between discharge and temperature, and affect the magnitude, frequency, and duration of floods (Ligon et al. 1995, Poff et al. 1997, Stanford and Ward 2001, Olden and Naiman 2010, Zarri et al. 2019). When dam construction changes the river into a lentic environment, it can increase water depth, clarity, sediment deposition, sediment retention, and pelagic production, while also reducing fish diversity and creating habitat for lentic fishes, macrophytes, and plankton (Freedman et al. 2014, Olden 2016, Arantes et al. 2019). Finally, barriers modify biogeochemical cycles and impede the flow of nutrients downstream (Maavara et al. 2015, 2020), in addition to blocking migratory vertebrates from transporting nutrients to the upper reaches of the watershed (Pringle 1997, Friedl and Wüest 2002, Greathouse et al. 2006, Flecker et al. 2010, Childress et al. 2014). In short, dams act as barriers to population connectivity and alter the physical and biological environment.

BioScience XX: 1–18.
https://doi.org/10.1093/biosci/biac004

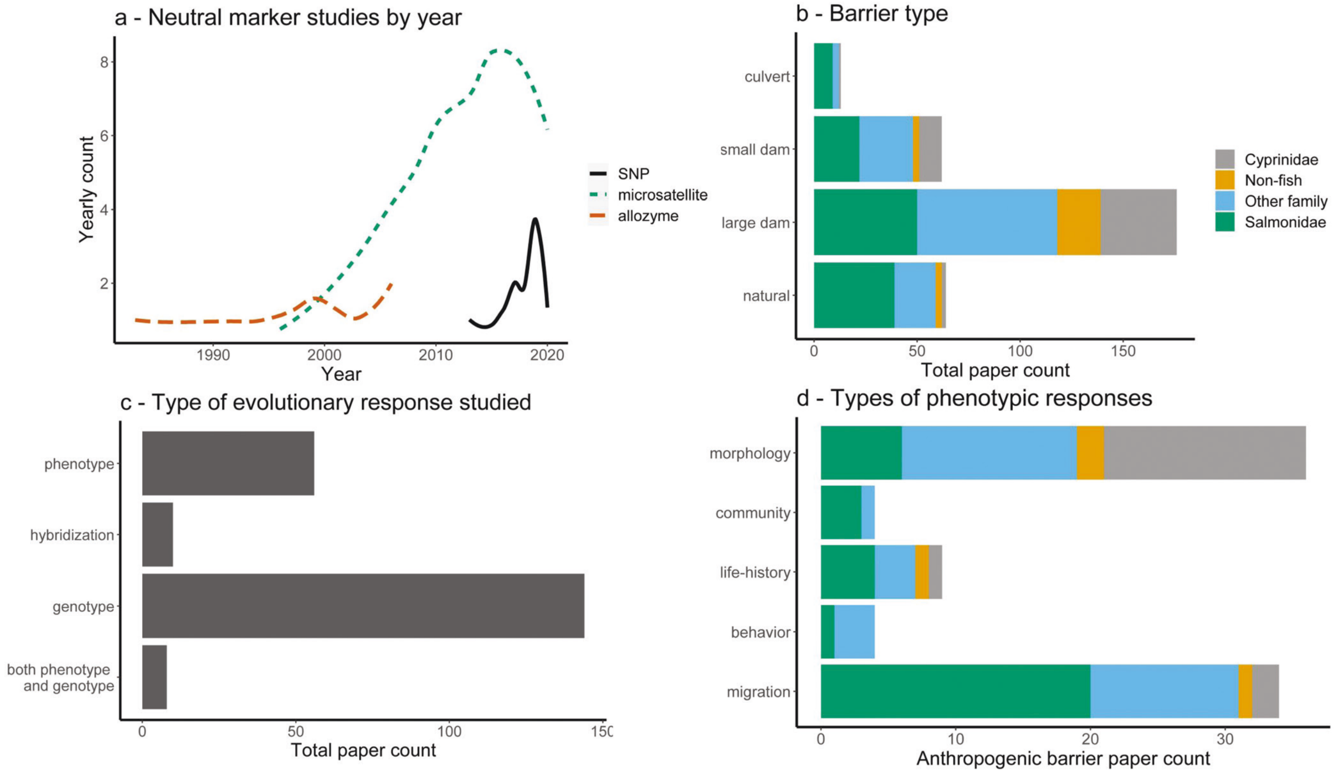


Figure 1. Classification of studies regarding the evolutionary consequences of anthropogenic barriers for fishes. (a) Yearly count of studies using different types of neutral markers, indicating prevalence of microsatellite studies for the last two decades and SNP studies becoming more common in the last 5 years. Note that mitochondrial DNA studies were not included in this graph (see the supplemental material). Different types of SNP studies include RAD (6 studies on fishes), SNP panels (10), genomic SNPs (1), and microhaplotype (1). (b) Barrier type, including natural barriers, colored by fish family. (c) Number of papers binned into evolutionary response, dominated by genotype and phenotype studies, with few studies combining both. (d) Common phenotypic responses colored by fish family.

The pervasive impacts of dams on aquatic ecosystems raises the question *What are the evolutionary consequences of dams and other anthropogenic barriers on freshwater fishes?* Portions of this question have been addressed in recent symposia (Ross 2015), as well as in reviews on Pacific salmonids (Waples et al. 2008), fragmentation in response to dams (Gido et al. 2016), and fish passage (McLaughlin et al. 2012). In the present article, we compile all these pieces in a systematic review while bringing in new findings made possible by the genomic revolution. In particular, the exponential decrease in sequencing and computation cost has facilitated studies of nonmodel organisms using techniques including whole genome analysis, transcriptomics, reduced representation sequencing such as RADseq, and targeted genotyping of genome-wide markers. The evolutionary impact of stream barriers is multifaceted and highly context dependent, but studies generally involve two major classes of evolutionary response: altered genetic connectivity in response to fragmentation and adaptation to altered habitat. We preface these sections with a discussion on riverscapes and how different barrier types and location in the watershed mediate evolutionary outcomes. Finally, we examine evolutionary restoration and selective filters imposed by barrier mitigation strategies, including fishway installation, barrier removal, and fish translocation.

We used the Web of Science and a search protocol from the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) to structure our review (Moher et al. 2015). Our search of relevant keywords identified 2,383 studies, which, on the basis of first- and second-pass eligibility criteria to retain studies on the evolutionary consequences of natural and anthropogenic barriers for aquatic organisms (see the supplemental material), were narrowed by two reviewers to 307 studies. On the basis of our search results, we focus on fishes, which were the subject of 90% of the studies in our data set. Other taxa included herpetofauna (4%), invertebrates (5%), and plants (1%), and there was insufficient information to evaluate whether the findings discussed are generally applicable to these understudied taxa. Finally, the studies included in our review extensively cover northern latitudes (81%), whereas fewer studies took place in the tropics (13%) and in southern latitudes (6%; see the supplemental material). Definitions of terms are available in table 1.

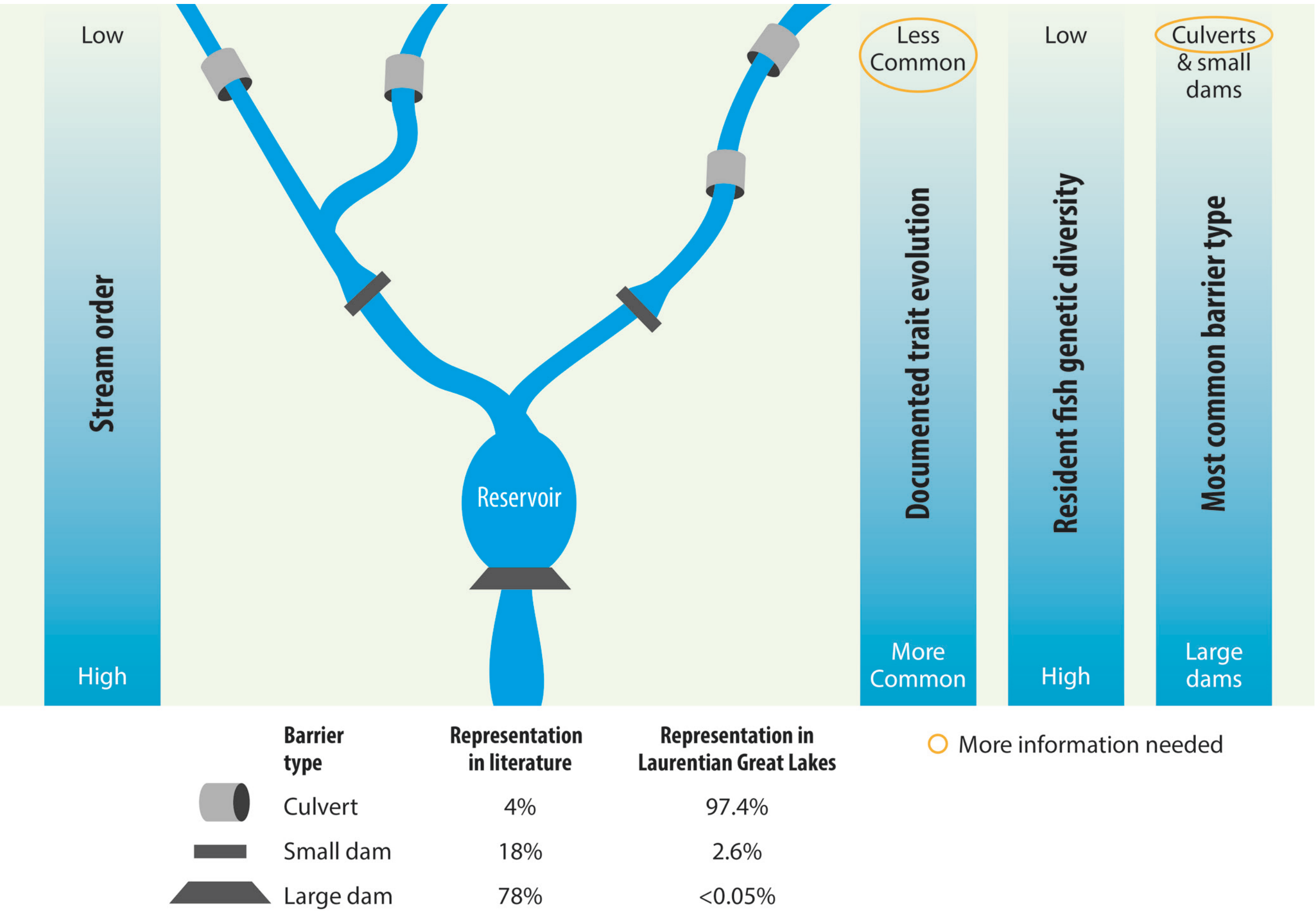
Table 1. Definitions.

Term	Definition
Adaptive loci	Genetic variants that influence individual phenotype and fitness
Allele	One genetic variant at a particular locus
Anadromy	Migration from the ocean to freshwater for spawning
Barrier passability	The probability that an individual can overcome a barrier
Common rear (common garden)	To raise different populations in the same environment and decouple the genetic and plastic contributions to a trait
Culvert	Anthropogenic structure that allows a stream to cross under a road
Dispersal	Movement and settling in a new location from birth place, which potentially leads to gene flow
Effective population size	The size of an ideal population that loses genetic diversity at the same rate as the actual population under study, loosely thought of as the number of breeding individuals per generation
Gene flow	Movement of individuals followed by successful reproduction
Genotype	Set of alleles an individual has at a single locus or several loci
Heritable	A trait that, at least in part, is genetically determined by a parent
Heterozygosity	Proportion of individuals with multiple alleles at a locus
Hybridization	Reproduction between two distinct populations or species
Lentic	Nonflowing water, such as in a reservoir or lake
Locus	A physical region in the genome that can have distinct alleles and therefore show variation among individuals
Lotic	Flowing water, such as in a river
Migration	An adaptation to spatiotemporally fluctuating resources, where individuals move to spawn or feed, followed by death or a return to adult habitat
Neutral locus	Locus that is not under selection, used to assess connectivity
Plasticity	The expression of several different phenotypes by a single genotype
Phenotype	Observable traits that are the product of an individual's genotype and environment
Population structure	Genetic differences among populations that indicate levels of connectivity and time since divergence
Resident	An individual that does not migrate to complete its life cycle
River order	Measurement of stream location in watershed, where low numbers indicate upstream streams and high numbers indicate downstream rivers
Riverscape	The elements of a landscape that include or affect the river environment, integrating longitudinal, lateral, vertical, and temporal connectivity
Natural or anthropogenic selection	The process of adaptation, where individuals expressing certain traits disproportionately reproduce, leading to evolution

Barrier type, passability, and location within riverscapes

The riverscape concept integrates all aspects of a landscape that are connected to fresh water through longitudinal, lateral, vertical, or temporal links (Fausch et al. 2002). Furthermore, this concept provides an appropriate place to understand the degree to which in-stream barriers alter connectivity, primarily in the longitudinal and temporal axes. Measurements of connectivity across the riverscape are grounded in metrics such as the Dendritic Connectivity Index (Cote et al. 2009) but have expanded to include advances in resistance pathways (Zeller et al. 2012) and graph theory (Eros et al. 2011). There are many barriers to movement across riverscapes, including distance, resistance due to unfavorable habitat, and local adaptation along ecological gradients (Orsini et al. 2013, Davis et al. 2018), but we focus on anthropogenic barriers because they present a distinct and pervasive evolutionary disturbance.

Passability is central to understanding the evolutionary consequences of barriers because the degree of isolation strongly affects the risk of genetic diversity loss and inbreeding (Frankham et al. 2002). Passability is affected by barrier height, barrier type, direction of passage, river flow, location within watersheds, and fish traits. The most common barrier types are culverts, then low-head dams with small or nonexistent water storage capacity, then large dams with reservoirs (Rosenberg et al. 2000). In the basin of the Laurentian Great Lakes, culverts are 38 times more common than all other barrier types combined (Januchowski-Hartley et al. 2013). High barrier density decreases habitat patch size, which tends to reduce population size and accelerate genetic drift within populations, whereas multiple barriers between populations appear to additively reduce connectivity (Jager 2005a, 2005b, Raeymaekers et al. 2008, Whiteley et al. 2013). Although culverts typically have higher passability than dams, poorly designed culverts can be substantial



Barrier type	Representation in literature	Representation in Laurentian Great Lakes
Culvert	4%	97.4%
Small dam	18%	2.6%
Large dam	78%	<0.05%

Figure 2. Conceptual diagram of evolutionary response to anthropogenic barriers. Note increased rates of documented trait evolution in response to larger dams, but greater fragmentation and reduced genetic diversity of resident species in upper watersheds. Bars represent change from upper watershed to lower watershed in trait evolution, genetic diversity, and barrier type. In the Laurentian Great Lakes, culverts are much more common than small dams, which are much more common than large dams (Lehner et al. 2011, Januchowski-Hartley et al. 2013). Upper watersheds, experience higher fragmentation and reduced patch size, but by barriers that commonly have greater rates of passability. Habitat is not altered to the same degree as experienced in lower watersheds and larger dams, and trait evolution appears to be rarer in upper watersheds. In contrast, mainstem rivers typically are less fragmentated with larger patch sizes, but barriers can be completely impassible and trait evolution is more common given the high degree of habitat alteration.

barriers to movement when too narrow, too long, or with a downstream overhang and waterfall; therefore, many culverts are completely impassible to most individuals moving upstream (Nislow et al. 2011, Macpherson et al. 2012, Januchowski-Hartley et al. 2013, Wood et al. 2018). Large dams typically cause greater fragmentation and phenotypic divergence than smaller dams or, if they create a reservoir, alter upstream or downstream habitat or are built on rivers that have long-distance migratory fish species (Fluker et al. 2014, Smith et al. 2019). In the Great Lakes, small dams are 18 times more common and impound three to four times as much water as large dams, although they receive less attention in the evolutionary literature (figure 2; Rosenberg et al. 2000). Low-head dams include weirs, diversions, or watermills and typically release water over the barrier, causing widespread fragmentation of species that cannot jump over them (Blanchet et al. 2010). Drastically reduced water flow can make even small barriers impassible (Dehais et al. 2010, Bohling et al. 2019). Recent studies have shown that hydropeaking dams, which release flow on the basis of energy demand and cause river discharge to fluctuate dramatically and at high frequencies, can reduce fish effective population size and genetic diversity trajectories more than run-of-the-river or bypass dams, which do not have an upstream storage reservoir (Valenzuela-Aguayo et al. 2020, Peek et al. 2021). Large dams without fishways block upstream passage for most species, whereas downstream passage can be possible for early life-stage individuals with an increased risk of

Box 1. All study designs are not created equal.

The physical structure of a watershed present challenges when trying to implement a repeatable study with true replication. Riverscapes display a branching dendritic layout, high habitat heterogeneity, and a predictable change in abiotic and biotic environments from the upper watershed to the mainstem (Vannote et al. 1980, Poff et al. 1997, Fagan 2002, Fausch et al. 2002, Benda et al. 2004). At first glance, the most appropriate way to assess the evolutionary impact of a dam may be to compare populations upstream and downstream of a dam. However, population size and genetic diversity for many species are positively correlated with river order even without a dam, whereas phenotypes such as individual swimming performance can differ predictably with flow regime. Furthermore, when estimating population-level characteristics, the analysis of a single population below the barrier and a single population above the barrier does not provide replication. The addition of several populations spaced evenly above and below the barrier can allow better estimation of connectivity impacts by comparing gene flow across fragmented and free-flowing reaches. However, these findings may be confounded if genetic diversity decreases in lower river orders because of decreased effective population size, even in free-flowing watersheds. The literature suggests that the strongest inference for assessing connectivity impacts from barriers comes from multiple comparisons of a fragmented and free-flowing watershed, where evenly spaced populations of the same species along the adjacent watersheds can be corrected for river order. Helpful factors in determining the distance between sampling sites include the predicted granularity of population structure and the density of barriers, while being constrained by funding and time. Furthermore, this approach allows the comparison of barriers across spatial scales, from the isolated reach to entire watershed. However, this begins to present challenges around sampling effort, habitat differences, trophic structure, or water quality, so study watersheds must be chosen with care.

Although comparisons of fragmented versus free-flowing watersheds are robust to natural changes in genetic diversity, other study designs can be effective in examining the genetic consequences of anthropogenic barriers: above or below the barrier, several populations across a single fragmented watershed, before and after the installation or removal of a barrier, and reservoir versus upstream river populations (figure 3). Examining multiple populations within fragmented watersheds is effective for quantifying the impact of different barrier types across different species, but studies need to assess whether genetic diversity naturally decreases with decreasing river order for their focal species. We found few before-and-after studies (figure 3), which are effective in assessing phenotypic impacts of barrier installation, fishway installation, or barrier removal. Historical collections provide the most robust but underused opportunity to examine evolutionary responses to barrier installation and removal, although degraded DNA in archived samples can present challenges for robust genomic analysis. Furthermore, they are the only pathway to quantifying genetic changes in response to very old dams where we otherwise have no way of knowing the original genetic characteristics; modern comparisons cannot show what has been lost or changed over centuries (Gustafson et al. 2007).

mortality due to power generation turbines and unfavorable conditions below hydroelectric dams.

Culverts are more common in headwater reaches where streams are relatively small, whereas larger barriers are more common where there is sufficient water flow to generate mechanical or electrical power, divert and distribute water, or a need for flood control (figure 2). Genetic diversity can covary with river order, because gene flow and effective population size of nonmigratory species typically decreases farther upstream or at higher elevations (Narum et al. 2008, Dehais et al. 2010, Haxton et al. 2015, Winans et al. 2015, Blanchet et al. 2020). Well-designed studies (box 1) that control for natural reductions in genetic diversity farther upstream suggest that barriers in upper tributaries can be more harmful for resident species, because they impound smaller and lower-diversity populations that can become inbred (Heggenes and Røed 2006, Whiteley et al. 2010, Haxton et al. 2015, Pavlova et al. 2017, Coleman et al. 2018). Although culverts typically have higher passability than dams, lower flows in small streams may make barrier passability more challenging, and even reduce allelic richness of upstream populations as much as natural waterfalls (Raeymaekers et al. 2008, Torterotot et al. 2014). However, patch size remains a crucial predictor in genetic diversity loss, with large patches above barriers harboring larger populations and greater genetic diversity compared to smaller patches (Whiteley et al. 2013). Furthermore, migratory species can move into upper tributaries during spawning migrations, resulting in seasonally fluctuating patterns of genetic diversity. In some species, morphological and physiological phenotypes vary predictably with flow regime (Langerhans 2008), suggesting that river order may drive trait expression. Despite being more abundant than dams, culverts are vastly understudied in the evolutionary literature (figures 1b and 2), which is an important knowledge gap given the natural decrease of genetic diversity in the headwaters and risk of inbreeding leading to local extinction.

Dams as barriers: Shifting genetic diversity in response to altered connectivity

The alteration in connectivity caused by dams diminishes gene flow, which can reduce effective population size and genetic diversity. Genetic diversity is a crucial predictor of population persistence, because reduced diversity can result in inbreeding depression, reduced fitness, or extirpation several decades after fragmentation (Frankham et al. 2002, Vera-Escalona et al. 2018). Genetic diversity at neutral loci is loosely but not always correlated with adaptive potential and diversity at adaptive loci (Messer et al. 2016, Kardos et al. 2021). Decreases in genetic diversity at neutral

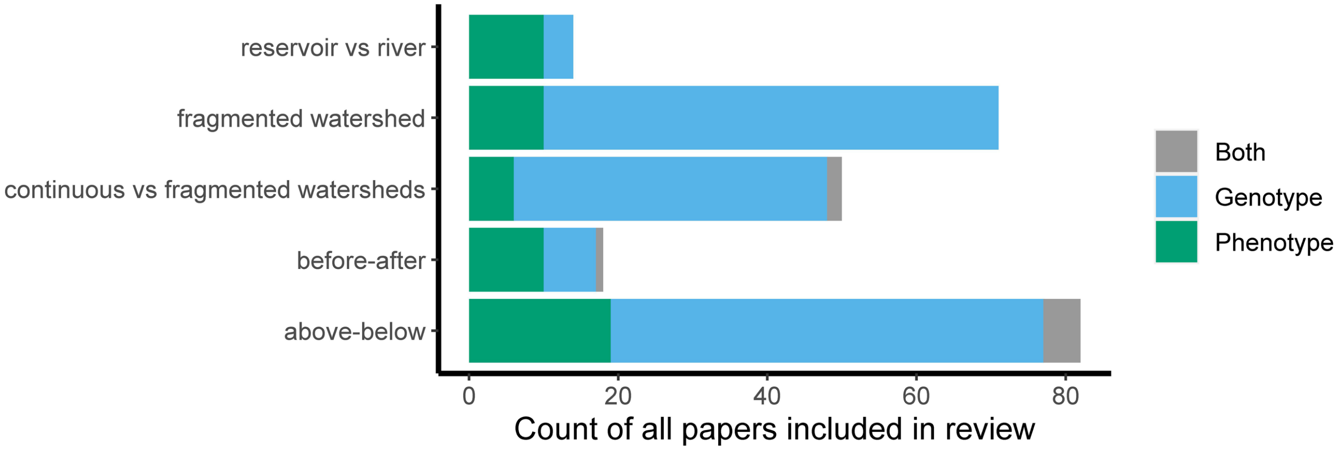


Figure 3. Frequency of different study designs used to examine the evolutionary impact of barriers, colored by whether papers examined phenotypic outcomes, genetic outcomes, or both. Note the low numbers of studies before and after barrier installation or removal and the intermediate number of studies on continuous versus fragmented watersheds, which are commonly the most robust comparisons.

loci indicate the sensitivity of a population to reductions in both connectivity and the number of breeding individuals per generation. The majority of the studies we examined included a genetic component (figures 1c and 3), primarily measured by microsatellite and, in more recent years, small panels of single nucleotide polymorphisms (SNPs), genome-wide SNPs generated with restriction-site associated DNA (RAD) studies, and gene expression (transcriptomes) studies. In this section, we synthesize the 152 studies in our data set that expressly measure how anthropogenic barriers alter genetic connectivity, population differentiation, and reductions in genetic diversity, as well as the species and barrier features that mediate these responses. Where applicable, we include studies on natural barriers to understand the potential long-term genetic implications.

Anthropogenic barriers reduce genetic connectivity of species that disperse or migrate over long distances, unless they are capable of moving across the barrier (Bessert and Ortí 2008, Blanchet et al. 2010). The largest and least passable natural barriers cause the greatest genetic isolation (Kelly and Rhymer 2005, Deiner et al. 2007, Buonaccorsi et al. 2017, Bohling et al. 2019). Anthropogenic and natural barriers are typically more passable when fish are traveling downstream, whereas upstream passage may only be possible during high flows (Raeymaekers et al. 2009, Junker et al. 2012, Peacock et al. 2016, Kelson et al. 2020). This asymmetrical passage can create a system of one-way valves allowing only downstream gene flow, which studies on natural barriers have shown to isolate upstream populations and reduce the effective population size of the metapopulation (Hänfling and Weetman 2006, Gomez-Uchida et al. 2013, Bowersox et al. 2016). Over the long time periods represented by natural barriers, reduced and unidirectional gene flow causes a cumulative increase of genetic diversity below each waterfall, with the highest diversity found in anadromous populations connected to the ocean (Crispo et al. 2006, Junge et al. 2014, Sandlund et al. 2014, Harris et al. 2015, Reis et al. 2015, Erin et al. 2019). When river fish populations have larger populations downstream and greater allelic richness, dams can prevent the flow of alleles into upstream populations (Kitanishi et al. 2012).

Barriers can increase genetic differentiation by decreasing the homogenizing forces of migration and dispersal, while also accelerating genetic drift, which causes population divergence. For populations with high to moderate dispersal or migratory distance, dams can rapidly increase genetic differentiation (Bessert and Ortí 2008, Leclerc et al. 2008). However, populations subdivided by natural barriers with low passability are already differentiated and may be slower to respond to barrier installation (Leblois et al. 2006, Landguth et al. 2010). Finally, recent population extirpation and subsequent reestablishment events will alter measurements of genetic divergence, because not enough time has passed for populations to become differentiated (Kitanishi et al. 2012, Mcbride et al. 2014).

Although population connectivity is commonly reduced within a single generation, it can take several generations for genetic population structure to respond to reduced gene flow (Deiner et al. 2007, Cayuela et al. 2018). Genetic differentiation may only occur after many generations of impoundment, or more quickly if effective population sizes (N_e) are small (Hoffman et al. 2017). In a recent large study, Ruzich and colleagues (2019) found that genetic differentiation did not increase after 20 generations of impoundment for four fishes with high N_e (over 3,275). However, genetic differentiation did increase for smallmouth bass (*Micropterus dolomieu*), a predatory species with high spawning site fidelity and a lower N_e (237) than the other species. Low N_e causes populations to drift faster, losing allelic diversity at a greater rate and stochastically shifting allele frequencies (Frankham et al. 2002, Whiteley et al. 2013, Argentina et al. 2018). If large N_e is retained upstream of dams, however, genetic diversity can remain high (Kitanishi et al. 2012). Well-designed studies (box 1) examining genetic diversity loss should therefore consider the number of impounded generations weighted by dam passability, the number of barriers, dispersal capabilities of the species, and estimated changes in patch size that can drive N_e (Kelly and Rhymer 2005, Cote et al. 2009, Whiteley et al. 2013, Rodeles et al. 2021).

Dams can further reduce genetic diversity of populations if effective population size decreases to the point of inbreeding. Lotic species are more susceptible to reductions in population size and genetic diversity in the reservoir, whereas lentic species may experience population growth and increased genetic diversity (Smith et al. 1983, Whiteley et al. 2013, Farrington et al. 2014, Camak and Piller 2018). Populations experiencing bottlenecks or founder effects due to recent recolonization of habitat above waterfalls, as well as reduction in effective population size due to low-quality or limited habitat, can show reduced allelic richness and expected heterozygosity (Neville et al. 2006). Impounded and upstream populations generally have lower genetic diversity than populations below dams, although populations directly below large hydropower dams have shown reduced genetic diversity as well (Raeymaekers et al. 2008, Pavlova et al. 2017, Ackiss et al. 2019). Reduced genetic diversity could result from a selective sweep, because strong selection can diminish the number of breeding individuals per generation (Corbett-Detig et al. 2015).

Dams altering habitat: Phenotypic adaptation

Although barriers reduce genetic connectivity and diversity, adaptive evolution can improve individual fitness, increasing survival and reproduction where habitat has been perturbed. Selection has the potential to act on a diverse suite of heritable phenotypes that alter fish survival, migration, or reproduction in impounded watersheds (Waples et al. 2008). The magnitude of adaptive evolution increases with the strength of selective pressure, the number of generations since impoundment, and the heritability of the trait under selection. The reduction of gene flow or genetic diversity can inhibit adaptive evolution, because evolution over short time scales acts on existing genetic variation rather than new mutations. Over long time periods, however, studies examining natural barriers indicate that both selection and drift play a role in shaping phenotypes. We included the common-rearing studies (3 out of 64 studies, 5%), which can account for and quantify incomplete inheritance, while also including relevant studies on field observations (61 out of 64, 95%), which cannot differentiate between plastic and heritable changes. Where relevant, we include additional common-rearing studies on natural barriers and nonfishes (n = 13 studies). Assessing the relative importance of evolution, plasticity, and the evolution of plasticity is critical for understanding evolutionary trajectories and ecological implications (Govaert et al. 2016). Although the number of studies that examine both genetic and phenotypic outcomes of barrier installation is limited (figures 1d and 3), we include them where relevant. We discuss changes in the mean and variance of traits that commonly appeared across the 64 phenotypic studies in our systematic review: migration, behavior, life history, community-induced shifts, species hybridization, and morphology (figure 1d).

Barriers can alter selection on migratory and reproductive phenotypes, underlain by adaptative genomic regions. Recent studies have uncovered that complex phenotypes can be controlled, or at least strongly influenced, by surprisingly small genomic regions (Barson et al. 2015, Thompson et al. 2020). The 33 studies we reviewed on migration or reproduction were primarily based on several well-studied salmonid systems (figure 1d). Dams can trap anadromous individuals upstream, and populations either shift toward residency (Yamazaki et al. 2011) or, if the reservoir habitat is extensive, freshwater migrations (Hecht et al. 2013, Pearse and Campbell 2018, Abadıa-Cardoso et al. 2019, Larson et al. 2020). If individuals are able to outmigrate down and over the barrier, upstream populations can lose migratory alleles and phenotypes over time (Morita et al. 2000, Morita and Yamamoto 2001, Pearse et al. 2009, Phillis et al. 2016, Leitwein et al. 2017, Fukushima et al. 2019). The frequency of alleles associated with migration in California steelhead were reduced by 31% above impassible natural barriers and 18% above impassible anthropogenic barriers, indicating that freshwater residency can evolve rapidly (Pearse et al. 2014, Apgar et al. 2017). However, migratory capacity may not disappear entirely: Landlocked sockeye salmon (*Oncorhynchus nerka*) resumed anadromy following experimental water releases 90 years (25 generations) after impoundment (Godbout et al. 2011, Samarasin et al. 2017), and genetic diversity at migratory loci was maintained in steelhead (anadromous *Oncorhynchus mykiss*) above the Elwha River and Glines Canyon Dams (Fraik et al. 2021). Common-rearing studies indicate greater downstream movement during darkness, growth rates, and earlier maturation rates below waterfalls, as well as a loss of osmoregulatory capacity above waterfalls (Northcote 1981, Eliassen et al. 1998). Below barriers, migration can be delayed if outmigrating juveniles have to pass through reservoirs, whereas growth can be reduced by cold reservoir releases (Angilletta et al. 2008, Williams et al. 2008, Waples et al. 2017). Because of these compounding factors, fall-run Chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River (United States) have evolved to outmigrate at age one instead of as young-of-the-year (Connor et al. 2005, Hegg et al. 2013). Tolerance to cold temperatures directly below dams appears to be a common phenotypic response, although responses indicate high levels of plasticity under the short time scales imposed by dams (King et al. 1985, Catenazzi and Kupferberg 2017), and adaptation to altered temperature regimes within reservoirs has yet to be elucidated.

Behavioral syndromes that increase individual propensity to move upstream through barriers may also be acted on by passable barriers. Brook trout (*Salvelinus fontinalis*) with larger and more streamlined bodies have higher attempt and success rate at passing culverts, indicating that passage may be influenced by suites of morphological and behavioral traits that together function as migratory syndromes (Goerig et al. 2020). Upstream movements of European eel (*Aguilla anguilla*) across small dams selected for larger individuals with greater endurance and anaerobic capacity that also expressed genes related to cognition (Podgorniak et al. 2015, 2016, 2017). Only four studies in our data set robustly examined behavioral selection (figure 1d) in fishes following impoundment but advances in transcriptomics may provide alternatives to challenging field assays in future studies.

Reservoirs create novel habitat for riverine species that can alter selection on life-history traits such as body size, maturation, and fecundity (*n* = 8 studies). In the early years following impoundment, reservoirs commonly exhibit a trophic upsurge and increase in fish richness, but richness appears to decrease as the reservoir ages (Agostinho et al. 2008). Plastic shifts include reduced lifespan and maximum body size, and increased reproductive effort following impoundment, whereas size and age at maturity tend to increase with reservoir size (Donchelle and Panfili 1998, Mérona et al. 2009). These results corroborate those found across many fish communities globally, which indicate reservoirs are disturbed habitats where high-fecundity individuals thrive (Arantes et al. 2019). These pioneer strategies likely peak in early years of a reservoir before fish populations reach high densities.

Changes in community composition and subsequent changes in competition or predation above barriers can also drive evolution (*n* = 4 studies), and studies of natural barriers provide information on the long-term adaptive consequences (*n* = 13 combining all organisms across natural and anthropogenic barriers). Decreased predator threat for long periods of time above barrier waterfalls can also relax selection on pleon size and rostrum length in amphidromous shrimp, boldness, sexual signaling, plate count and spine length in threespine stickleback (*Gasterosteus aculeatus*), and delay senescence and maturation through altered sexual selection in Trinidadian guppies (Endler 1990, Kristjánsson et al. 2002, Brown and Braithwaite 2004, Bryant and Reznick 2004, Olsen and Vøllestad 2005, Ocasio-Torres et al. 2015). However, phenotypic drift can also occur over protracted isolation above natural barriers, which likely altered lateral line, vertebra, and fin ray meristics, as well as coloration in *Oncorhynchus* species (Currens et al. 1990, Takahashi et al. 2016). Field observations of white-spotted char (*Salvelinus leucomaenis*) showed faster growth and earlier maturity above small dams, where residents don't compete with large anadromous char below the dam. However, in common-rearing experiments, char from above barriers grew more slowly and matured later than char from below barriers (Conover and Schultz 1995), suggesting relaxed selection on growth rate when competition is lessened above the barrier, as opposed to below-barrier environments where the growth rate is more correlated with fitness (Morita et al. 2009). The same pattern was observed for sticklebacks above and below barrier waterfalls, where common-reared growth rates were greater in populations experiencing interspecific competition (Olsen and Vøllestad 2005). Other common-rearing studies suggest strong community effects for populations trapped above waterfalls, such as increased carotenoid sequestering, and decreased parasite resistance (Craig and Foote 2001, Erin et al. 2019). Common-rearing experiments are essential to understand competition-induced phenotypic change, because countergradient selection may mask cryptic evolutionary changes.

The reduction of flow variation and available habitat by impoundment can decrease phenotypic diversity. In California Chinook salmon, anthropogenically reduced flow magnitude and variance stabilizes selection on intermediate emigration times and sizes, in contrast to the natural environment, which balances selection on several emigration phenotypes (Sturrock et al. 2020). Fall-run Chinook salmon enter the watershed late in the season when they are reproductively mature and spawn farther downstream, whereas spring-run Chinook enter when premature, migrate to upper tributaries, and spawn after developing gonads over the summer (Quinn et al. 2016). Spring-run spawning habitat has been extensively compressed by dams, which has resulted in hybridization between spring- and fall-run fish (Kinziger et al. 2008, Thompson et al. 2019). In some cases, allelic richness is driven more by introgression between resident and anadromous ecotypes rather than by barriers, and transcriptomic studies corroborate that widespread loss of these highly migratory phenotypes can reduce the adaptive genetic diversity and gene expression of affected populations (Rougemont et al. 2020, Thompson et al. 2020), as well as a valuable source of early spring protein historically relied on by Native American tribes. The extent to which stabilizing selection acts on phenotypes beyond those linked to migration is unknown.

Dams can also alter phenotypic diversity by creating an environment for novel species hybridizations, whereas alternative life histories or species may evolve over longer time periods. Although we found few studies testing hybridization (*n* = 14; figure 1c), genetic and morphological analyses document hybridization in minnows (Cyprinidae) and riparian toads following anthropogenic barrier installation (Balon 1992, Sullivan et al. 2015, Guivier et al. 2019). Small dams are also used as a conservation tactic to prevent hybridization by invasive species, which include trout, mosquitofish, lamprey, or carp (Davis et al. 2006,

Box 2. Rapid evolution of migratory alewife (*Alosa pseudoharengus*) following impoundment catalyzes an ecoevolutionary feedback loop.

The alewife is an important zooplanktivorous fish found along the Atlantic coast and in lakes across eastern North America. There are two life-history forms of alewife: the ancestral migratory (anadromous) form that moves between marine and freshwater ecosystems and the evolutionarily derived resident (landlocked) form that resides in freshwater. In many coastal watersheds, dams built by European colonists (1630–1800) isolated individuals from anadromous ancestors creating landlocked populations (Palkovacs et al. 2008, Twining and Post 2013, Twining et al. 2013). Landlocked populations in Connecticut are genetically isolated and independently derived from anadromous runs, which have significantly higher genetic diversity and continue to exchange genes with neighboring anadromous runs (Palkovacs et al. 2008).

The repeated evolution of the resident phenotype has resulted in parallel evolution across several traits. Landlocked alewife remain in freshwater year round, have smaller gape and narrower gill raker spacing, are not size selective when foraging on small-body prey, forage exclusively in open water, and are more fusiform in body shape. Anadromous alewife are typically present in freshwater for half the year (May–October for young of the year), have larger gape and wider gill raker spacing, are always positively size selective and forage across near-shore and open-water habitats (Post et al. 2008, Palkovacs and Post 2009, Schielke et al. 2011, Jones et al. 2013, Palkovacs et al. 2014). Landlocked populations have reduced fecundity, smaller adult body size, and earlier age at maturity (Graham 1956), and spawn later in the year than anadromous alewife (Littrell et al. 2018). Landlocked alewife have also partially lost the ability to osmoregulate in seawater; it is mediated through changes in ion regulation in their gills (Velotta et al. 2014).

These phenotypic differences have altered the ecological role of these two alewife forms such that landlocked and anadromous alewife have very different effects on community structure and ecosystem function (Post et al. 2008, Palkovacs and Post 2009, Walters et al. 2009, West et al. 2010, Twining et al. 2013, Weis and Post 2013). Lakes with landlocked alewife are dominated by small-body zooplankton (Brooks and Dodson 1965, Post et al. 2008). Lakes that receive seasonal migrations of anadromous alewife are dominated by large-body zooplankton in the spring and early summer, and small-body zooplankton in late summer and autumn (Post et al. 2008, Howeth et al. 2013). These ecological changes in turn altered the adaptive landscape for alewife, creating an ecoevolutionary feedback, which is the cyclical interplay between the evolution of phenotypic and ecological changes that feeds back to cause continued ecological and evolutionary changes (Palkovacs and Post 2008).

The construction of dams initiated an ecoevolutionary feedback between alewife and the zooplankton community, which propagated through the food web. Differences in alewife predation have, for example, driven evolution in *Daphnia ambigua* (Walsh and Post 2011, Walsh et al. 2012, 2014), the dominant grazer in lakes, and that evolution has altered consumer–resource dynamics between *Daphnia* and algal primary producer biomass (Walsh et al. 2012). The whole-lake changes caused by alewife evolution also caused shifts in the foraging morphology and efficiency of bluegill (*Lepomis macrochirus*), a common competitor (Huss et al. 2014), the habitat use and lipid storage of chain pickerel (*Esox niger*), the native top predator (Brodersen et al. 2015), and the growth and trophic ontogeny of young-of-the-year largemouth bass (*Micropterus salmoides*) (Boel et al. 2018). The installation of dams were the catalyst for these changes in the coastal ecosystems, but they may also emerge in the Laurentian Great Lakes where alewife have invaded (Smith et al. 2020). Ecoevolutionary feedbacks require a specific set of traits and ecological conditions to occur but may be more widespread in novel impounded environments than is currently understood.

McLaughlin et al. 2012, Ardren and Bernall 2017). The evolution and maintenance of alternative life histories can be influenced by significant natural barriers: Siletz Falls, in Oregon (United States), for example, is a selective barrier to fall-run Chinook salmon that spawn below it, whereas spring-run Chinook can pass the falls to spawn upstream (Davis et al. 2017). Both drift and selection can play a role in speciation above natural barriers (Ostberg et al. 2009, Dias et al. 2013, Castro et al. 2014), but we found no evidence of speciation in response to anthropogenic barriers likely because of the generally short timeframe such barriers have been in place.

Morphological evolution is a well-documented response to impoundment, particularly in large reservoirs (n = 34 studies; Ross 2015). Morphological trait shift following impoundment is primarily informed by studies on cyprinids (figure 1d). Field observations and common-rearing studies indicate that the lentic reservoir environment generally selects for deeper-bodied fish with smaller heads, larger fin bases, increased caudal depth, and reduced shape variation when compared with lotic environments (Bianco 2002, Pamponet et al. 2008, Franssen 2011, Aguirre et al. 2013, Franssen et al. 2013, Cureton and Broughton 2014, Eagderi et al. 2014, Gaston and Lauer 2015). These intraspecific shifts coincide with previously documented trait-based community shifts following impoundment (Arantes et al. 2019). Reservoir morphologies appear to allow for faster turning speed and predator escape in lentic environments, whereas a fusiform body shape is better for maintaining position in a flowing river. Other *in situ* responses of populations in reservoirs include altered eye size and increased caudal spot size for predator avoidance (Aguirre et al. 2013, Geladi et al. 2019). Flow- and predator-induced plasticity contributes to morphological changes, whereas responses can be site and species specific. Downstream morphological shifts include sensory adaptations to clearer water and niche partitioning to compensate for increased competition through jaw morphology shifts (Morita and Suzuki 1999, Dieterman and Galat 2005). Morphological differentiation between river and reservoir increases with the number of barriers separating populations and when reservoir habitat is markedly different from the river habitat (Poulet 2008, Franssen et al. 2013, Santos and Araújo 2015, Radojković et al. 2018). The selection strength and rate of morphological change appear to be greatest when populations are first impounded, but then slow as the population adapts to directional selection (Cureton and Broughton 2014, Haas et al. 2021, but see Haas et al. 2010). It remains to be seen whether morphological evolution can be reversed when barriers are removed.

Barrier mitigation

Barrier mitigation involves conservation-oriented actions, such as fishway construction, barrier removal, or stocking to diminish or eliminate the negative impacts of barriers. Fishways have important implications for connectivity and can create selective filters on the phenotypes affecting passage (McLaughlin et al. 2012). Limited evidence discussed below indicates that barrier removal rapidly restores genetic connectivity, although genetic rescue and conservation hatcheries can also be effective under some circumstances.

Fishways can make barriers passable but also act as a selective filter on migratory phenotypes and body size. Not all fish species can pass fishways effectively, because they are often designed for migratory North American salmonids (Compton et al. 2008, Wilkes et al. 2019, Matica 2020). Poorly designed fishways do not fully reconnect populations and can increase the cost of migration, possibly favoring selection for residents life-history traits in salmonids (Jager et al. 2016, Underwood et al. 2016, van Leeuwen et al. 2016, Haraldstad et al. 2019, Landsman et al. 2020, Lothian et al. 2020). For example, summer steelhead were historically the only run that could pass a large natural barrier because of low summer flows, but a fishway allowed winter steelhead to pass and hybridize with summer steelhead, nearly causing extirpation of the run (Hemstrom et al. 2018). Furthermore, climbing amphidromous gobies (subfamily Sicydiinae) with larger sucking disks have a greater likelihood of passing dams than those with smaller disks, whereas brook trout with more streamlined bodies had more attempts and greater success at passing a culvert (Goerig et al. 2020, Lagarde et al. 2020). Only large brown trout could pass a waterfall on the River Gulbrandsdalslagen (Norway), but a fishway relaxed this selection on body size, quickly reducing somatic growth rate and size at maturity (Haugen et al. 2008). Other examples include selection for larger lampreys through five dams on the Snake River (Washington, United States) but selection against larger Atlantic Salmon in the Penobscot River (Keefer et al. 2009, Maynard et al. 2017). Fishways appear to stabilize selection on intermediate trait values determined by species characteristics and fishway design, and no robust studies have yet documented a fishway allowing nonselective passage.

Barrier removal appears to be the best method for reconnecting fragmented populations. Demographic connectivity appeared to be quickly restored following removal of both large dams and culverts (Quinn et al. 2017, Wood et al. 2018), and the restoration of genetic connectivity may only take a few generations (Neville and Peterson 2014, Neville et al. 2016, Nathan et al. 2018, et al. 2021). However, large fluctuations in population size or gene flow following barrier remediation can result in stochastic swings in allelic fixation and richness (Neville et al. 2016). Migratory individuals can boost the effective number of spawners in resident populations to quickly restore previously impounded populations (Weigel et al. 2014). Prioritizing the barriers to remove is a key factor when attempting to rescue and preserve anadromous populations: Modeled predictions suggest that restoring anadromous genotypes may be significantly more cost-effective when several smaller barriers are removed instead of a single large one (Apgar et al. 2017). Barrier prioritization may be a pathway to rapid evolutionary restoration, but it remains to be seen whether phenotypic adaptations that have evolved in response to impoundment are maladaptive in restored rivers.

Although stocking can maintain fisheries yields and reintroduce extirpated populations (Bowersox et al. 2016), negative genetic effects often manifest because of reduced effective population size and altered selection patterns. Dams increase genetic differentiation between populations, but stocking reduces differentiation, and both commonly decrease effective population size and genetic diversity (Small et al. 2007, Heist and Mustapha 2008, Pearse and Garza 2015). Conservation barriers can effectively block introgression by hatchery fish and retain wild alleles above barriers, although such barriers may curtail the effective population sizes of above-barrier wild populations (Sato et al. 2010). Although many correctly assume that hatchery fish will introgress with native populations, with negative genetic outcomes, hatchery populations occasionally do not interbreed, likely because of differences in spawning time, low reproductive success, or low offspring survival (Deiner et al. 2007, Weigel et al. 2014, Kelson et al. 2015, Bohling et al. 2019). For a review of the ecological and genetic effects of stocking, see Araki and Schmid (2010). The recently initiated stocking of brown trout into the Pasvik River in Norway and Russia led to high heterozygosity but low allelic diversity, an indicator of stocking-induced outbreeding but also an early warning sign of pending genetic diversity reduction (Klütsch et al. 2019). In-basin conservation hatcheries designed to reconnect fragmented populations without decreasing effective population size could be useful in counteracting dam-induced divergence.

Takeaways and future directions

Dams and culverts have the potential to cause rapid evolution by altering aquatic connectivity and habitat. As was expected from population genetic theory, connectivity impacts are particularly severe with low barrier passability, reduced habitat patch size, small effective population size, highly migratory species, or when impoundments have been in place for many generations. Headwater populations are likely more susceptible to fragmentation and diversity loss because of reduced effective population sizes and high occurrence of culverts (figure 2). We find both plastic and heritable phenotypic shifts in traits underpinning migration ($n = 22$ papers), behavioral syndromes ($n = 4$), life history ($n = 17$), and morphology ($n = 42$), as well as altered patterns of hybridization ($n = 14$). Below barriers, trait shift can also occur because of changes in river flows, turbidity, or temperature. Furthermore, the homogenization toward reservoir habitat, reduced variation in downstream river flow, and reduced connectivity to upstream habitat appears to widely reduce trait variation and genetic diversity of adaptive loci.

Decreasing intraspecific diversity is a conservation concern, because it can reduce the stability of the system (Schindler et al. 2010). Barrier mitigation strategies such as fishways and stocking can be effective, but prioritized dam removals are the only way to truly restore traits and genetic variation (Apgar et al. 2017). Fishways can restore connectivity, but if they are not well planned, they may cause migration delays or act as selective filters on behavior, body size, or morphology. Hatcheries can boost fish population size and homogenize populations across barriers but can also dramatically decrease genetic diversity and erode local adaptation. Dam removal offers a better option for evolutionary restoration and, although studies have only recently begun to emerge, preliminary evidence suggests that renewal of genetic diversity may take several generations after connectivity is restored. It remains to be seen whether phenotypic adaptations to impoundments persist when the barrier is removed.

We identified several biases in the literature that may have affected the strength of our inference across species, latitude, and barrier types. First, our review likely suffered from publication bias, where only studies in which evidence of evolution was found have been published. This likely affects the adaptation and barrier mitigation findings more than those on genetic diversity. Next, few phenotypic studies used common-rearing techniques (3 out of 64 studies) to decouple plastic from genetic effects. Most studies documented only field observations (61 out of 64), which reported interesting phenotypic divergence but were unable to determine whether observed shifts were heritable. We also found strong latitudinal and taxonomic bias. Most studies were from north temperate ecosystems (supplemental figure S2), which have different species assemblages, flow regimes, and frequency of barrier types than tropical ecosystems. This bias is of particular concern, because rivers in Asia, Africa, and South America are becoming heavily fragmented with little to no representation in our evolutionary literature base (Grill et al. 2019). Although neutral evolutionary impacts likely remain the same across latitude, adaptive responses may be different in tropical ecosystems because of different taxa and river flow characteristics. A consequence of this latitudinal bias is greater representation of particular fish families, such as salmonids, cyprinids, and percids (figure 1). Furthermore, understudied taxa such as plants, herpetofauna, aquatic invertebrates, and plankton have terrestrial adult life stages or resistant dormant stages, which may not be as affected by damming. Finally, we found biases in the barrier type and study design. Many studies focused on large dams, even though small dams and culverts were much more numerous across the landscape (figure 1b). As was discussed in box 1, studies comparing fragmented with free-flowing watersheds can quantify the predictable reductions in genetic diversity in upstream reaches.

Methodological advances may address these gaps in the literature while providing opportunities for future research. First, population genetic theory predicts that reduced genetic diversity diminishes adaptive potential, but this question has not been examined in populations that experienced dam-induced selection pressure while experiencing genetic diversity loss. In a similar theme, some studies have alluded to strong selection around dams leading to reductions in genetic diversity, but this has not been robustly addressed. Whole-genome sequencing, particularly low-coverage approaches used to estimate allele frequencies across populations (Lou et al. 2021), can address these questions by examining neutral markers and also allow high-resolution scans for signatures of selection. It is important to conduct such studies on individuals for which abundant phenotypic data are available for subsequent genome-wide association studies. Next, the paucity of common-rearing studies handicaps robust analysis, particularly when counter gradient selection masks cryptic evolutionary changes as has been observed when relaxed competition above barriers alters selective forces. The paucity of common-rearing studies can in part be addressed by building *in situ* pedigrees of wild populations using high-marker SNP panels, RAD-seq data, or multiplexed microsatellites, to estimate pairwise relatedness of individuals in the wild and therefore calculate trait heritability without the need to common-rear individuals (Gienapp et al. 2017, Gervais et al. 2019). In the future, copy-number variant and microhaplotype studies could outperform unphased SNP studies in detecting neutral and adaptive genomic changes (Baetscher et al. 2018, Dorant et al. 2020). High-marker panels and increasing computational power can also be used to detect when and why hybridization between populations or species occurs following impoundment; we found only 14 studies addressing this question. Genomic approaches can also be used in tandem with developments in graph theory to calculate effective distances through riverscapes of varying resistance pathways (Landguth et al. 2012). Recent developments in population genetics can also be leveraged to calculate standardized indices of barrier permeability (Prunier et al. 2020). Finally, few studies to date have robustly examined behavioral selection (figure 1d), although advances in transcriptomics may provide alternatives to challenging field assays.

The accelerated rate of dam removals in the United States and Europe provides an exciting opportunity to track evolutionary restoration, and evolutionary recovery following relaxation of anthropogenic selection is a burgeoning field (Isanta-Navarro et al. 2021). Do allelic diversity and heterozygosity return to preimpounded levels, or is a new equilibrium reached? Similarly, are dam-adapted traits such as altered migration, body shape, or life-history strategies maladaptive when the lotic environment is restored? If so, do they disappear from the population or persist in low frequency? Strong impoundment-induced selection has the potential to constrain plasticity and inhibit recovery following impoundment, although this has not been explicitly examined. Limited evidence indicates that high densities of culverts in headwaters negatively affect resident species; do we expect to see rapid recovery following removal, which is less expensive and time consuming than dam removal? Finally, demonstrated reduction in trait variation following impoundment suggests that dams shift selection patterns from balancing selection on several migratory trait values to directional or stabilizing selection on a single trait value (Franssen 2011, Sturrock et al. 2020), but it is unknown whether this pattern extends to other traits and whether balancing selection can restore a suite of migratory phenotypes following barrier removal.

Rapid evolutionary changes following impoundment can have ecological ramifications, but many key questions remain. Dams have been demonstrated to catalyze ecoevolutionary feedbacks in well-studied resident and anadromous alewife (box 2; Palkovacs and Post 2008), but it is unknown whether ecoevolutionary feedbacks are widespread phenomena as a consequence of impoundment. Numerous studies have examined phenotypic adaptation following impoundment ($n = 64$), but not enough work has focused on behavioral adaptations or physiological adaptations to modified temperatures in reservoirs. Stocking has been a staple of population management but can erode genetic diversity, and well-designed programs may counteract inbreeding and genetic drift above barriers by translocating individuals. Another approach to reconnect populations is fishway installation, but fishways have demonstrated selection differentials and must be engineered to avoid selection on body size and morphological traits. Finally, research on the evolutionary consequences of ubiquitous culverts and small dams is underexplored and critically important. In conclusion, the installation and removal of dams are ongoing experiments in a global laboratory, and the genomic revolution provides tools to learn about the scale and ecological significance of rapid evolution in nature.

Acknowledgments

We thank Tommy Detmer, Ethan Duvall, Kimberly Fitzpatrick, Nelson Hairston, Sebastian Heilpern, Meredith Holgerson, Greg Jacobs, Pete McIntyre, Carl Saint John, Suresh Sethi, Amelia Weiss, three anonymous reviewers, and the BioScience editorial staff for helpful comments on earlier versions of the manuscript. Simone des Roches, Megan Sabal, and Christopher Zobek assisted with the systematic review screening methods. Patrick Rooney (www.rooneydesign.com) generously provided artistic assistance with figure 2. DMP was funded by National Science Foundation DEB grant no. 1556848 and no. 2046474. EPP was funded by National Science Foundation DEB grant no. 2102763 and by the NOAA Cooperative Institute for Marine, Earth, and Atmospheric Systems. LJZ was funded by the Northeast Climate Adaptation Science Center and conducted the research for this review at Cornell University, located on the traditional territory of the Gayogohó:nǫ', members of the Haudenosaunee Confederacy, an alliance of six sovereign Nations with an ongoing presence on this land.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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