

Climate-Driven Range Expansions in Freshwater Fishes: Taxonomic Consequences, Cryptic Invasions, and Phylogeographic Shifts

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Abstract

Climate-driven redistribution of freshwater fishes is increasingly apparent, yet its taxonomic and evolutionary implications remain inadequately integrated into distributional assessments. This critical review connects thermal and hydrological niche change with river-network dispersal, taxonomic uncertainty, cryptic invasions and phylogeographic reorganization. Long-term records reveal asymmetric population responses near cooler and warmer range margins and frequent lags between changing climate and realized geographic movement. DNA barcodes and population genomics show why species-level maps can obscure independently structured lineages or genetically foreign introductions. The spread of rainbow trout ancestry into native cutthroat trout populations illustrates how climatic trends may accelerate introgressive hybridization against a background of historical stocking. We distinguish natural climate tracking, human-mediated introductions, previously overlooked occurrence and taxonomic reassignment, and propose an integrated evidence sequence combining repeated detection-corrected surveys, voucher-based taxonomy, eDNA, genomic source assignment, historical collections and network-aware models. Climate suitability must not be conflated with colonization, molecular detection with establishment, or hybridization with demonstrated adaptive benefit. A shift toward lineage-aware, temporally explicit assessments is necessary to conserve both species persistence and evolutionary diversity under rapid environmental change.

Keywords: Climate Change; Freshwater Fishes; Cryptic Invasions; Integrative Taxonomy; Phylogeography; Population Genomics; Introgression; River Connectivity; Environmental DNA

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Introduction

Freshwater biodiversity must be interpreted in the context of interacting pressures rather than climate change in isolation. Major syntheses identify habitat transformation, altered flows, pollution, overexploitation and introduced species as mutually reinforcing threats; their effects can coincide with temperature trends and create misleading attribution if they are omitted from the analysis (Dudgeon et al., 2006; Strayer and Dudgeon, 2010; Reid et al., 2019). Globally mapped river stressors show why the surrounding catchment and upstream drainage are integral to biodiversity assessment, not incidental background variables (Vörösmarty et al., 2010).

General biogeographic syntheses provide context but should not be substituted for direct fish evidence. Broad multispecies analyses reported geographically coherent climate-related biological responses and poleward distribution shifts, whereas dendritic river networks impose different accessibility constraints from the landscapes represented in those studies (Parmesan and Yohe, 2003; Hickling et al., 2006; Fagan, 2002). Accordingly, freshwater range attribution should be framed as an explicit comparison of competing climate, habitat and introduction hypotheses.

Freshwater fish redistribution under contemporary climate change is not a simple matter of moving northward or upstream. The direction and rate of spread reflect thermal physiology, flow variability, dispersal constraints, historical drainage structure and interactions with native and introduced fishes. Because freshwater habitats are networked rather than continuously accessible, climatic opportunity can greatly exceed realized colonization (Comte and Grenouillet, 2013; Isaak et al., 2015).

Global exposure projections underscore the stakes. Barbarossa et al. (2021) assessed approximately 11,500 riverine fish species and estimated that 4%, 9% and 36% would experience climatic extremes across more than half their present range at global warming levels of 1.5, 2.0 and 3.2°C, respectively, under a no-dispersal assumption. These figures measure exposure, not extinction probabilities or observed range contraction. Their divergence across scenarios illustrates how changes in thermal and hydrological extremes can radically alter prospective habitats.

Existing research nevertheless tends to separate ecological range changes from molecular taxonomy and population history. That

separation matters: a population newly recorded in a watershed could reflect natural expansion, unrecognized historic occurrence, deliberate stocking, a cryptic non-native lineage, or hybrid descendants. Morphologically indistinguishable populations can carry very different ancestry and conservation significance (Hubert et al., 2008; Morais and Reichard, 2018). This review integrates climatic attribution, cryptic invasion and phylogeographic restructuring into a common inferential framework.

Review scope and approach

Literature eligibility for this revised manuscript is restricted to works published on or before 31 March 2025. This temporal boundary concerns sources reviewed; it does not imply or assert an earlier date of manuscript preparation, submission, acceptance, or publication. Citations are incorporated according to the specific inferential role of each source; general terrestrial or methodological studies are identified as conceptual comparators rather than direct evidence of fish redistribution.

This is a critical narrative synthesis of published empirical studies and established methods rather than a PRISMA systematic review or quantitative meta-analysis. Studies are considered most persuasive when they include repeated sampling through time, explicit detection models, geographically representative reference material, documented introduction histories, or multilocus genomic evidence. Modelled suitability, observed expansion, abundance changes and genome-wide ancestry shifts are treated as distinct response variables.

Quantitative displays reproduce clearly identified values from published research; no pooled mean, confidence interval, cross-study synthesis estimate or new experimental finding is presented. The emphasis is on causal contrasts and methodological limitations that can guide future hypothesis-driven work.

Climatic and hydrological mechanisms of expansion

Biological reorganization also occurs at the assemblage level. Buisson et al. (2008) projected accelerated stream-fish assemblage turnover under climate change; such turnover is not equivalent to the uniform arrival of species across all river segments. Daufresne et al. (2009) documented warming-related size-structure changes in aquatic systems, illustrating that population and community responses may be detectable even where geographic range boundaries are stable. Comte et al. (2014) demonstrated that phylogenetic history and species traits influence the direction and magnitude of fish range responses, while Comte et al. (2016) showed that climatic and human drivers jointly influence local extirpation dynamics.

The spatial geometry of rivers changes the expected dispersal process. Fagan (2002) demonstrated how dendritic fragmentation can alter metapopulation extinction risk, and Radinger and Wolter (2014) synthesized empirical evidence for strongly heterogeneous fish movements across species and ecological contexts. These findings argue against converting projected shifts in thermal suitability directly into assumed rates of colonization: reachability, propagule supply and establishment must be modelled separately.

Water temperature regulates growth, activity, respiration, recruitment and the timing of reproduction, but its effects depend on dissolved oxygen, discharge, habitat complexity and biotic interactions. Warming can benefit populations close to cooler distribution margins while increasing physiological stress at warm margins. Brown et al. (2024) coupled multicontinental abundance time series from 1958–2019 with thermal conditions, reporting an increase in the annual maximum of monthly water temperature of 0.21°C per decade. Abundances tended to rise at cooler poleward margins and decline toward warmer equatorward margins; responses varied with altitude and species characteristics.

Changes in abundance must not be misreported as colonization of new sites. Boundary expansion, shifting range centres and demographic trends are different measures that respond at different timescales. In France, Comte and Grenouillet (2013) evaluated 32 stream fish species and identified upstream and elevational distribution shifts that frequently lagged behind contemporaneous climatic velocities. Comte and Grenouillet (2015) likewise demonstrated the significance of distinguishing climatic, bioclimatic and biotic velocities.

Hydrological connectivity constrains movement and reshapes the response to climatic extremes. Flood pulses may temporarily permit crossings or upstream dispersal, while drought can isolate reaches and increase population mortality. Reservoirs, culverts, dams and fish passages alter these dynamics asymmetrically across species and life stages. Hence, a purely climatic envelope is insufficient for inferring establishment, especially in heavily engineered drainages.

Cold-water refugia can interrupt regional warming trends. Groundwater-fed channels, shaded tributaries and topographically protected streams can maintain viable coldwater populations even when neighbouring reaches deteriorate. The climate-shield framework for salmonids illustrates why spatially explicit thermal heterogeneity should inform management rather than reliance on regional average air temperatures (Isaak et al., 2015).

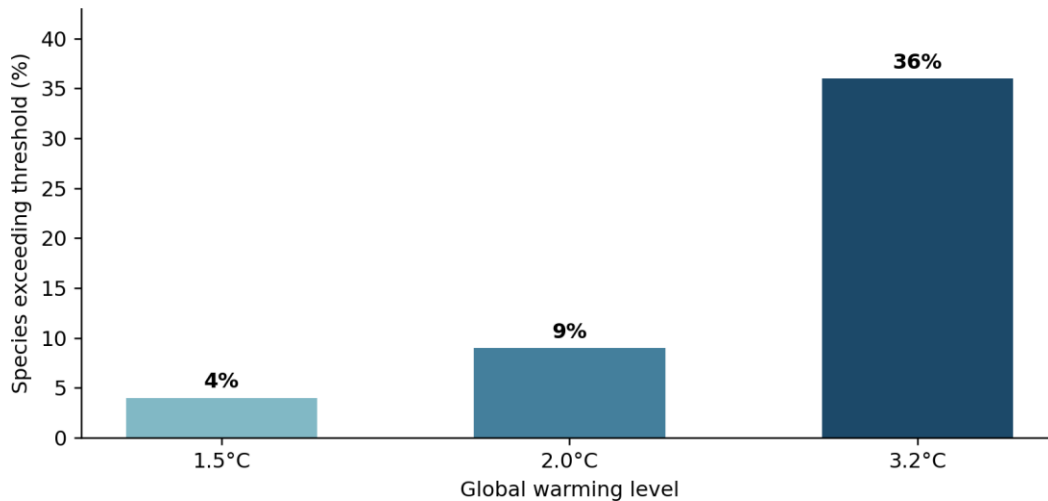


Figure 1. Published projected percentage of approximately 11,500 riverine fish species exposed to novel temperature or flow extremes across >50% of their current range under three warming levels (no-dispersal assumption). Replotted from reported values in Barbarossa et al. (2021); these are exposure projections, not extinction estimates.

Taxonomic consequences: beyond names on distribution maps

The logic of barcode-based identification rests on the use of reference-linked sequence variation, first formalized as a scalable approach by Hebert et al. (2003). However, sequence clustering and species delimitation are conceptually different exercises. Pons et al. (2006), in an insect-system methods study, illustrated how sequence-based delimitation can identify candidate independently evolving groups, but transfer of such approaches to freshwater fishes requires testing species-specific processes including hybridization, incomplete lineage sorting and geographically structured intraspecific variation. Thus, molecular operational taxonomic units must not automatically become formal taxa or new range-expansion records.

Range-change inference presupposes stable and correctly identified taxonomic units. In freshwater fishes this assumption is frequently weak because morphological convergence, plasticity, incomplete lineage sorting, introgression and geographically structured divergence complicate identification. A newly sampled lineage may be a distinct species, an intraspecific conservation unit, an introduced lineage of the same species, or a result of changed taxonomy rather than recent arrival.

Hubert et al. (2008) analysed Canadian freshwater fish DNA barcodes and documented both substantial discriminatory power and cases of deeper-than-expected intraspecific divergence or limited separation among close relatives. Similarly, the FISH-BOL programme established the utility of barcode reference libraries without eliminating problems posed by hybridization and recent divergence (Ward et al., 2009). Therefore, COI matches should be reported as provisional identification evidence when lineage identity or hybrid status is the main research question.

Cryptic species are independently evolving entities whose diagnoses may require evidence beyond gross morphology. Cryptic lineages may instead be differentiated populations within a named species; a large mitochondrial distance is not itself proof of reproductive or evolutionary independence. Appropriate taxonomic reassessment requires archived voucher specimens, nuclear evidence, sampling across range-wide variation, and where relevant examination of type material and diagnostic morphology.

Temporal comparisons add another hazard: first detection is not synonymous with first arrival. Intensive recent surveys and improved assays can reveal long-established populations previously missed by earlier monitoring. Historical name changes, inconsistent synonymies, locality errors and misidentified museum records can create apparent range shifts without biological movement. Studies in Java and Bali demonstrate that DNA-assisted inventories can materially change knowledge of regional fish identities and distributions (Dahrudin et al., 2017). Their taxonomic findings should not be misrepresented as demonstrating climate-driven movement.

Source of apparent expansion	Diagnostic evidence	Main analytical risk
New cryptic species	Voucher morphology plus multilocus delimitation	Mistaking taxonomic discovery for new colonization
Foreign intraspecific lineage	Range-wide SNP ancestry with stocking records	Unseen genetic invasion under stable species names
Historical name change	Re-examined museum vouchers and synonymy audit	Artificial shift in mapped occurrence
eDNA-only occurrence	Independent assays and repeated direct survey	Mistaking transported DNA for establishment

Table 1. Alternative explanations for a newly detected freshwater fish taxon or lineage (synthesis).

Cryptic invasions and anthropogenic dispersal

At the landscape scale, the spread of commonly introduced fishes can increase faunal similarity among drainages while eliminating distinctive regional assemblages. This process was demonstrated for United States fish faunas by Rahel (2000) and developed in a broader freshwater synthesis by Rahel (2002). Olden and Poff (2004) used fish faunas to test mechanisms of biotic homogenization, while Olden et al. (2004) emphasized its ecological and evolutionary consequences. Their combined implication is that regional species counts may remain unchanged, or increase, even as biogeographic distinctiveness is eroded.

Climate change may transform the invasion process at several stages without removing human introduction as its initiating mechanism. Rahel and Olden (2008) reviewed pathways by which temperature, hydrology and human responses could affect invasive species; García-Berthou (2007) cautioned against simplistic identification of universal traits that predict fish invasiveness. The appropriate unit of analysis is consequently the introduction–establishment–spread sequence, incorporating propagule pressure, recipient community and dispersal opportunity rather than attributing all new occurrences to climatic facilitation.

Biogeographic range expansion and biological invasion are not interchangeable concepts. Climate tracking may result from natural dispersal within accessible networks, whereas invasion usually entails human-mediated translocation beyond historic dispersal barriers followed by survival, reproduction and spread. Climate can amplify the latter without causing the original introduction. Morais and Reichard (2018) identify cryptic introductions both between morphologically similar species and among distinguishable genetic lineages within a nominal species.

Human release and transfer routes include fishery stocking, aquaculture escape, ornamental-fish disposal and interbasin movement. A propagule may persist at low abundance until environmental conditions become favourable, generating a substantial time lag between introduction and an observable range expansion (Gozlan et al., 2010; Bernery et al., 2022). Thus, climatic attribution must adjust for historical propagule pressure rather than treating recently detected populations as spontaneous responses to warming.

Intraspecific invasions can be especially consequential because routine visual surveys classify both introduced and resident lineages under the same species name. Mixing of formerly isolated stocks may erase local ancestry through introgression or replacement even if species richness is unchanged. Hybridization outcomes are context dependent; neither genetic admixture nor the persistence of a familiar species name alone establishes conservation benefit or harm (Funk et al., 2012).

Ecological impacts require independent evidence. The establishment of a predatory non-native fish may affect prey recruitment, behavioural ecology, food webs or competitive hierarchies, but temporal association alone cannot distinguish invasion impacts from co-occurring drought, pollution or warming. Inference should connect an explicit mechanism to monitored outcomes and ideally employ comparators or before–after designs (Britton, 2023).

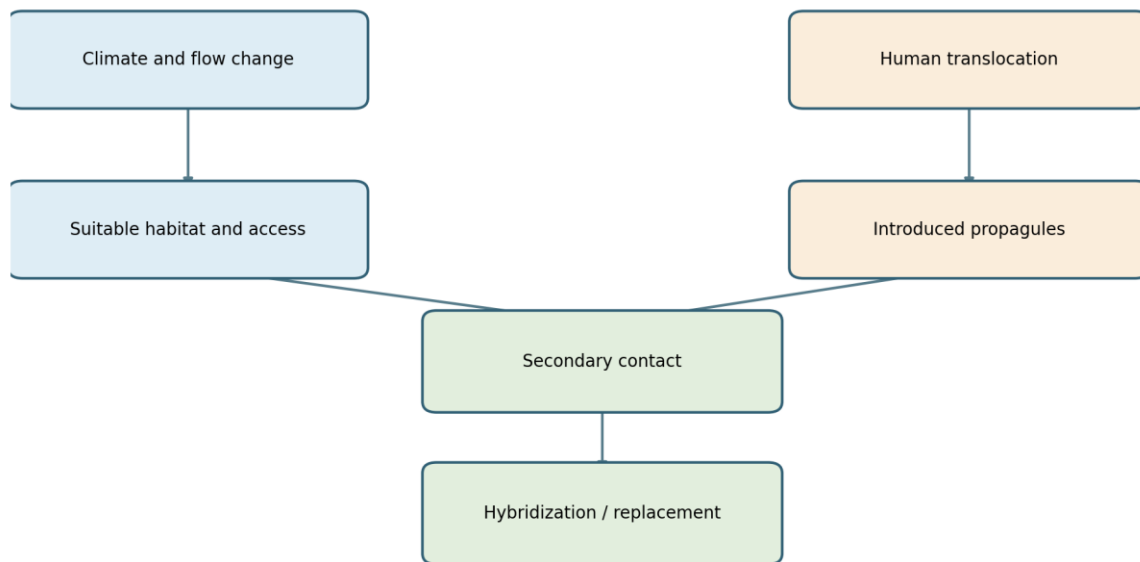


Figure 2. Original conceptual figure showing interacting climatic and introduction pathways to secondary contact and genomic change. Arrows signify hypotheses and plausible mechanisms, not universally established causal effects.

Phylogeographic shifts and genomic reorganization

Contemporary phylogeographic adjacency is not a reliable substitute for demographic history. Waters et al. (2023), analysing New Zealand *Galaxias* lineages with genome-wide data, detected substantial introgression signatures even among presently disjunct taxa, consistent with historical shifts in contact and drainage structure. This offers a direct warning against dating hybridization from current range overlap alone. In another freshwater fish context, Brauer et al. (2023) reported reduced modelled genomic vulnerability in naturally hybridizing Australian rainbowfish populations and genomic patterns consistent with possible adaptive introgression. These findings motivate fitness-based follow-up rather than the assumption that introgression is intrinsically adaptive or deleterious.

Phylogeography supplies the historical baseline against which apparent modern redistribution must be interpreted. Quaternary refugia, drainage capture and postglacial expansion created regional differences in mitochondrial haplotypes, nuclear allele frequencies and adaptive characteristics (Provan and Bennett, 2008; Gavin et al., 2014). The topology of freshwater drainage systems often preserves such differentiation longer than straight-line distance would suggest.

At colonization fronts, repeated founder events and genetic drift can lower allelic richness while strengthening population differentiation. Yet multiple-source colonization and recurrent migration can raise local diversity and produce mixed ancestry. Low diversity is therefore not unique evidence for recent expansion; bottlenecks and historical isolation are alternative explanations. Coalescent or explicit demographic comparison should distinguish these competing histories.

Climate-driven or climate-enabled secondary contact can destabilize formerly isolated ancestry. Invasive rainbow trout hybridizing with native westslope cutthroat trout present a particularly informative example. Muhlfeld et al. (2014) used genetic and environmental observations to show the expansion of hybridization associated with warmer summer stream temperatures and changed climatic conditions, against a background of historical introductions. The analysis supports climate-mediated acceleration of introgression rather than a claim that climate initiated all introductions.

Genetic change may precede conspicuous shifts in community composition. A drainage may retain individuals assignable to a nominal native taxon while the distribution of characteristic native alleles progressively contracts. Conversely, some introgression may introduce potentially advantageous alleles; adaptive benefit must be established through selection, phenotype and fitness evidence rather than by labeling introgression adaptive on the basis of environmental association alone.

Conservation units should therefore capture population history and both neutral and potentially adaptive genetic variation. Genome-wide SNP panels, local ancestry estimates and temporal tissue archives can quantify replacement. However, ancestry software may misassign individuals when the true source is missing from the reference data; analyses should include sensitivity tests to unsampled

or closely related sources (Funk et al., 2012).

Process	Possible genomic signature	Important alternative
Founder expansion	Reduced diversity at leading edge	Older bottlenecks
Secondary contact	Ancestry admixture and clines	Ancient admixture
Introgression	Cytosuclear discordance and mixed nuclear ancestry	Incomplete lineage sorting
Source mixing	Elevated local diversity	Long-standing structured populations
Lineage replacement	Declining native ancestry through time	Biased reference sampling

Table 2. Phylogeographic hypotheses and alternative interpretations (synthesis).

Methodological framework for causal attribution

Imperfect detection is a statistical problem rather than a minor survey inconvenience. MacKenzie et al. (2002) developed an approach for estimating occupancy when species may be present but not observed; MacKenzie et al. (2003) extended such inference to colonization and local extinction. For fish surveys, replicated visits, explicit observation models and comparable spatial frames are necessary before claiming changes in occupancy. Uncertainty in historical monitoring cannot be repaired by treating nondetections as confirmed absences.

Environmental DNA should be interpreted as a complementary detection tool with its own uncertainty structure. Thomsen and Willerslev (2015) reviewed the potential of eDNA for biodiversity monitoring, while Goldberg et al. (2016) specified essential design, contamination-control and reporting considerations. Deiner et al. (2017) documented how eDNA metabarcoding broadens community surveillance, but assay bias, incomplete reference databases, DNA transport and heterogeneous shedding can distort inferred distributions. Species identification, lineage assignment, occurrence and establishment therefore require separate validation steps. A rigorous assessment begins by defining the estimand. Is the study concerned with changed occupancy, abundance, northern boundary, river-network position, detection of a non-native lineage, or decline in native genomic ancestry? Combining these into a single expansion response can conceal contradictory results. A paired design should preserve spatial location, seasonal context, fishing gears, and site-level effort where possible (Kirk, 2023).

Detection-corrected multiseason occupancy models provide a means of estimating site-specific colonization and local extinction while accommodating imperfect surveys. In notation, $\Pr(z[i,t+1]=1 \mid z[i,t]) = z[i,t](1-\epsilon[i,t]) + (1-z[i,t])\gamma[i,t]$, where ϵ is local extinction probability and γ is colonization probability. Both can be functions of water temperature, flow, barriers, land use and propagule pressure. Without repeated surveys, an apparent increase in records can instead be an increase in detection effort.

Network-aware distribution models should separate climatically suitable habitat from habitat reachable through actual dispersal pathways. Stream order, flow direction, dams, fish passages and drainage divides should define the movement graph. Modelling air temperature without local water-temperature measurements also obscures thermal buffering by groundwater or canopy cover.

An identification module should combine morphological vouchers, validated mitochondrial assays and appropriate nuclear markers. Environmental DNA can provide sensitive evidence of possible occupancy: Jerde et al. (2011) demonstrated its value for detecting rare aquatic fishes, but DNA detection does not by itself verify a living, breeding population. Transport through the watershed, assay specificity, field contamination and transient source organisms demand controls and confirmation.

Finally, source attribution should reconstruct introduction histories from stocking registers, archived specimens and range-wide genomic references. The strongest climate-causation tests compare locations with similar introduction pressures but different temperature trajectories, or exploit longitudinal designs in which climatic change precedes repeated, detection-corrected changes in fish occupancy and ancestry.

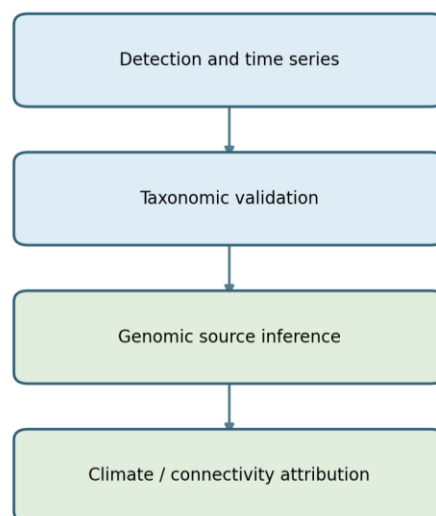


Figure 3. Proposed sequential evidence workflow for evaluating climate-linked fish range expansion. Original synthesis.

Evidence layer	Question answered	Minimum control	quality
Repeat surveys	Has occupancy truly changed?	Detection probability and stable effort	
Historical vouchers	Was the taxon previously present?	Documented dates and georeferencing	
COI and morphology	What fish was detected?	Voucher and curated references	
Genome-wide ancestry	Where did the population originate?	Diverse source populations	
Network climate model	Was new habitat both suitable and accessible?	Barriers, water temperatures and flows	
Reproductive observations	Has the population established?	Age classes or repeated reproductive evidence	

Table 3. Recommended triangulation of ecological, taxonomic and genomic evidence.

Geographic contrasts and conservation trade-offs

A wider conservation-biogeographic perspective calls for forecasts that include non-climatic threats, spatial heterogeneity and altered community composition. Olden et al. (2010) identified the need to integrate fish traits, invasion dynamics, extinction risk and emerging assemblages into future freshwater conservation research. Region-specific interpretation should likewise consider the vulnerability of basins exposed to multiple interacting stressors (Reid et al., 2019), rather than generalizing a northern-temperate pattern of upstream movement to all river systems.

French stream-fish data reveal uphill and upstream adjustment combined with incomplete climate tracking (Comte and Grenouillet, 2013, 2015). At a wider European scale, the emergence of novel climates within river sub-basins raises concern that even connected populations may fail to encounter suitable future conditions (Tsavdaridou et al., 2022). Conservation interventions must therefore evaluate both accessibility and persistence.

North American lakes and rivers highlight a different interaction: opportunities for warmwater fish expansion coexist with a long legacy of fish introductions. Historic stocking makes it particularly difficult to attribute an invading trout or centrarchid population solely to contemporary warming. Yet genomic observations can directly expose processes, such as introgression, that occurrence maps cannot detect (Muhlfeld et al., 2014).

Tropical Asian basins contain high fish diversity but often lack temporally standardized population surveys and robust species-level references. Barcoding can resolve identification problems and expose cryptic diversity (Dahrudin et al., 2017), yet it cannot replace demographic or historical evidence needed to conclude that climate change induced colonization.

Connectivity must be managed as a conditional asset. Barrier removal can restore movement to thermal refugia and facilitate native recovery, but can also transmit introduced predators or foreign genetic ancestry. Cold-water habitat that protects native salmonids thermally may remain threatened genetically if invasive or stocked lineages reach it. Strategic restoration therefore requires drainage-specific evaluation of ecological and evolutionary outcomes (Isaak et al., 2015; Funk et al., 2012).

Setting	Main signal	Interpretive problem
European streams	Elevational and longitudinal displacement	Failure to track climatic velocity
North American trout drainages	Climate-associated spread of introduced ancestry	Historical stocking confounds attribution
Asian tropical catchments	High diversity and reference gaps	New identification vs new colonization
Coldwater headwaters	Refugial persistence	Thermal security does not ensure genomic security

Table 4. Regional contrasts motivating lineage-aware management.

Research priorities

In addition to tracking species occurrence, longitudinal designs should quantify whether the same genetic lineages persist through time, because faunal homogenization and introgression can proceed without conspicuous species turnover (Olden et al., 2004; Waters et al., 2023). A high-priority validation experiment would pair environmental DNA and conventional surveys with genome-wide ancestry assignment and repeated observations of age structure; each evidence type resolves a different ambiguity (Goldberg et al., 2016; MacKenzie et al., 2003; Brauer et al., 2023).

Five research priorities emerge. First, create long-term paired ecological and genomic monitoring in regions with detectable warming gradients. Second, archive voucher specimens and tissues to permit retrospective identifications. Third, construct reference panels that represent both natural and introduced source populations. Fourth, replace unconstrained geographic envelopes with hydrologically explicit dispersal and demography models. Fifth, evaluate fitness and reproductive consequences of introgression rather than equating admixture automatically with loss or adaptation.

Testable hypotheses include the expectation that connectivity moderates rates of realized climatic niche tracking, that introduction history predicts the establishment of foreign ancestry, and that genetically differentiated lineages show divergent thermal-response functions even where they share a species name. Such hypotheses should be analysed with preregistered spatial and temporal contrasts and sensitivity analyses for imperfect detection and missing genomic source populations.

Limitations

This synthesis does not constitute a systematic evidence census or a novel meta-analysis. Included studies vary in temporal coverage, geographic focus, taxonomic resolution and outcome metrics, preventing direct pooling. Climate exposure projections must not be presented as realized local extinctions; genomic hybridization does not prove contemporaneous climate causation; and apparent new occurrences may reflect increased sampling or taxonomic change. The conceptual pathways and assessment workflow are proposals for testing, not experimentally established universal rules.

Conclusions

Freshwater fish range shifts should be interpreted as interacting changes in suitability, accessibility, demography and ancestry. Warming can facilitate expansion at cool margins and contraction at warm margins, but river topology, hydrological extremes and human-mediated introductions produce striking departures from simple geographic expectations. Species-level occurrence data alone cannot distinguish cryptic invasion from natural climate tracking or identify genomic replacement of historically differentiated populations.

The most defensible future assessments will couple repeated detection-corrected monitoring with integrative taxonomy, verified introduction histories, landscape connectivity, historical collections and time-series population genomics. Such integration reframes

freshwater biodiversity conservation from preserving species names on maps to preserving viable populations, authentic evolutionary history and adaptive capacity under rapid environmental change.

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