Title: Genetics and the Question of Purity in Cutthroat Trout Restoration

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Abstract: As molecular techniques become more advanced, scientists and practitioners are calling for restoration to leverage genetic and genomic approaches. We address the role of genetics in the restoration and conservation of cutthroat trout in the western U.S., where new genetic insights have upended previous assumptions about trout diversity and distribution. Drawing on a series of examples, we examine how *genetically pure* trout populations are identified, protected, and produced through restoration practices. In landscapes that have been profoundly impacted by human activities, genetics can offer seemingly objective metrics for restoration projects. Our case studies, however, indicate that (1) genetic purity is fragile and contingent, with notions of what genetics are "pure" for a given species or subspecies continually changing, and (2) restoration focused on achieving "genetically pure" native populations can deliberately or inadvertently obscure the socio-ecological histories of particular sites and species, even as (3) many "genetically pure" trout populations have endured on the landscape as a result of human modifications such as roads and dams. In addition to raising conceptual questions, designations of genetic purity influence policy. These include tensions between restoring connectivity and restoring genetic purity, influencing Wild and Scenic River Act designations, and the securing of water rights. Cutthroat trout restoration would benefit from adopting a broader, more holistic framework rather than fixating exclusively or primarily on genetic purity and hybridization threats.

Key words: genetics, trout, fisheries management, restoration, biodiversity, conservation

Conceptual Implications:

- Genetic and genomic data are reshaping how ecosystems are prioritized for restoration or conservation and how environmental policies are applied.
- Many trout populations with genetics that are considered "pure" are the products of socio-ecological histories involving human landscape modifications and fish translocation.
- Dedicating conservation and restoration decisions to genetic purity can offer false assurances of certainty, objectivity, and ecological integrity, which may ultimately undermine restoration's capacity to work with future ecosystems.
- Native species restoration should be guided by a framework that accommodates not only molecular insights, but also a variety of social, ecological, and ethical values.

Introduction

As molecular techniques become cheaper, faster, and more refined, many scientists and practitioners are calling for ecological restoration to leverage genetic and genomic approaches (Breed et al. 2019; Williams et al. 2014). Molecular technologies can be used to monitor restored ecosystems for invasive species (Larson et al. 2020), to reconstruct historical baselines to serve as reference points (Proft et al. 2018), and to inform plant and animal breeding for resilience to rapid environmental change (Prober et al. 2015). These applications are part of a broader “molecular turn” toward conservation genetics in restoration and conservation science and practice, where attention is increasingly oriented toward the molecular scale, enabled by new DNA sequencing technologies (Hennessy 2015; Holderegger et al. 2019).

Here we address the role of genetics in trout restoration in the U.S. West, where fisheries managers and restoration practitioners are implementing long-term restoration projects for cutthroat trout (*Oncorhynchus clarkii*). We suggest that a fixation on trout genetic composition, guided by an ideal of genetic purity, may inadvertently undermine restoration and conservation efforts, for example by de-valuing established and reproducing cutthroat trout populations, undermining habitat connectivity, and reducing the number of streams eligible for legal protection. Moreover, measuring the value of populations and organisms against an ideal of genetic purity echoes unethical logics of eugenics and nativism, and unnecessarily narrows the knowledge and evidence base available to guide management actions. We raise these points to help foster a restoration ecology informed by genetics and genomics, yet keenly aware of the limitations, contingencies, and broader impacts of molecular information. Trout restoration should be guided by a more holistic framework that places genetic identities in fuller contexts of human-environment interaction, accommodating not only molecular insights, but also a variety of social, ecological, and ethical values. In our conclusion, we offer a series of questions designed to broaden approaches to trout management, restoration, and conservation. These include considerations of indigeneity, relational ethics, ecological resiliency, and connectivity.

Our arguments are based upon analysis of documents and policy related to cutthroat trout restoration and conversation in the U.S. West and 16 semi-structured telephone or videocall interviews with fisheries managers, aquatic scientists, and conservation and restoration professionals, conducted between July 2020 and May 2021. Interviews were recorded and transcribed, then analyzed by theme and key concepts (King and Horrocks 2010; Hay and Cope 2021).

Restoring "Native" Trout

Many state and federal fisheries agencies and environmental groups now embrace restoration and conservation of native fish as a central management goal, especially for cutthroat trout, a species of salmonid native to the inland western U.S. ("Native," in the context of fisheries management, signifies a population evolved in a particular watershed without being stocked.) These restoration efforts follow, and in some cases coincide with, more than a century of hatchery production and stocking of non-native fish, including rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and brook trout (*Salvelinus fontinalis*). As a result of stocking, along with habitat loss and fragmentation, populations of cutthroat trout declined across the inland West over the twentieth century. During this time, introduced species established self-sustaining populations – what managers typically call "wild trout" - in many locations. In watersheds with both introduced rainbow trout and cutthroat trout, interbreeding has produced self-sustaining populations with various levels of genetic admixture.

To better grasp the complex geography of trout, fisheries scientists have increasingly turned to genetic analysis (e.g. Allendorf and Leary 1988). By analyzing DNA of individual fish, scientists can identify and quantify hybridization and conceptualize evolutionary relationships between different populations and lineages (or subspecies) of trout. In addition, environmental DNA (eDNA) is now used to monitor watersheds for hybrid, non-native trout using water samples (Carim et al. 2020). These techniques have yielded surprising findings about the genetic composition of some trout populations. In Colorado, greenback cutthroat trout (*O. c. stomias*) that were protected under the Endangered Species Act and restored to the South Platte and Arkansas River watersheds from the 1970s through the 2000s were found to be variants of an entirely different subspecies: Colorado River cutthroat trout (*O. c.*

pleuriticus) (Metcalf et al. 2007, 2012). For westslope cutthroat trout (*O. c. lewisi*) in the Northern Rockies, genetic analysis has revealed that not only are most populations hybridized (Shepard et al. 2005), but hybridization appears to be increasing over time, despite Montana ceasing stocking streams with rainbow trout in 1974 (Muhlfeld et al. 2017).

Genetic analysis has also led to the identification of cutthroat trout populations with what are classified as “pure” genetics (i.e. no genes from introduced species or other cutthroat lineages). In Yellowstone National Park, where hybridization is considered the greatest threat to the remaining native fish populations in many parts of the park (Koel et al. 2017: 7-8), managers found “pure” populations of westslope cutthroat trout in Last Chance Creek and Geode Creek, prompting efforts to establish isolated refugia for unhybridized populations and to reintroduce these to watersheds previously occupied by hybridized or non-native fish (Koel et al. 2007). Similarly, a Colorado study analyzed DNA from nineteenth century museum specimens (Metcalf et al. 2012), which later led to the identification and discovery of the San Juan lineage of cutthroat trout.

In short, the genetic composition of fish (and other taxa) has taken on significant importance in management, buoyed by the proliferation of molecular data. Exemplifying this shift, a federal fisheries manager explained, “The purity of native cutthroat trout, or the purity of cutthroat trout in populations across the landscape, is what we feel is the highest priority.” Terms such as “purity,” “genetic purity” or “genetically pure” are often used to refer to an unhybridized organism or population, but this condition is rarely explicitly defined and brings with it the problem of reference condition: which point in time – or which population in which habitat – should be used to evaluate this state of purity? (Higgs et al. 2014). While molecular techniques can assist in unravelling evolutionary history and biogeographic patterns of cutthroat trout, ideas about which genetics are “pure” for a given species or lineage are far from resolved. Questions remain about the distribution of cutthroat trout lineages across western North America, how these dispersed, and their relationship to one another (Trotter et al. 2015). Knowledge of genetic structure and phylogeny continues to change as DNA sequencing technologies evolve. In order to negotiate ecological and social contexts successfully, restoration efforts will likely also need to need to be able to adapt to these changing genetic and taxonomic distinctions, rather than fixating on achieving a genetically pure state.

Nonetheless, organisms' molecular pedigree has emerged as a guiding concept that now shapes life-or-death management decisions. In Yellowstone National Park's 2010 Native Fish Conservation Plan, for example, genetic analyses and designations are crucial factors. Projects follow a process of (1) isolating restoration areas (to prevent fish movement and gene flow); (2) chemically or mechanically removing hybridized or non-native fish, followed by eDNA testing to ensure complete eradication; and (3) restocking "genetically unaltered native fish" (Koel et al. 2010: 45-46). Yellowstone National Park is not alone in this pursuit: projects following similar processes have been implemented across the U.S. West, as fisheries managers embrace restoration and conservation of genetically pure native trout. As we discuss below, these genetics-directed actions have important ecological and social impacts.

Genetic Purity, Nativeness, and Naturalness

In the context of restoration and conservation, genetic purity is often conflated with nativeness, or by extension, "naturalness" (i.e. historical independence from human activities (Siipi 2004)). Molecular analysis that documents an organism's genetic purity might suggest that it is *of this place*, emerging from a deep history of natural selection and evolution, and thus uniquely adapted to the conditions of its watershed. In short, the genetic signature is presented – explicitly or by implication – as verification of historic nativeness and belonging. Streams or lakes that are home to populations deemed "pure" through genetic analysis are often viewed as closer to a pre-European conquest reference condition and thus prioritized for protection; conversely, "impure" populations may lead managers to treat a water body with toxicants to eradicate its hybridized residents. Such efforts rest upon making a distinction between a “natural” reference ecosystem (or, in this case, a “natural” reference genetic composition) and the degraded ecosystem’s “impure” population that warrants restoration. A federal fisheries biologist we interviewed explained how this distinction shapes legal obligations under the Endangered Species Act: “Usually when I get asked that question – ‘Why are you removing this cutthroat trout to put in another?’ – I just say, ‘Well, my short answer is we’re legally obligated to do that, and that hybrid population of cutthroat trout is not a *pure* greenback cutthroat trout.’”

Given restoration ecology’s persistent attention to the threat posed by invasive species, the impulse to “bring back the natives” comes as little surprise, but this managerial response may reflect increasingly outdated ideals of returning an ecosystem to a prior, “original” condition (Davis et al. 2011), and fail to acknowledge or accommodate the dynamic character of most ecosystems. For many watersheds, creating strict boundaries between what is native or natural and what is not disregards what has actually occurred in these places. For example, interpreting genetic purity as evidence of nativeness or naturalness may misrepresent or obscure the human actions that have shaped the character of an ecosystem over time. Many of the most prized conservation populations of “pure” trout (e.g. greenback cutthroat trout in Bear Creek, Colorado; westslope cutthroat trout in Last Chance and Geode Creeks, Yellowstone National Park) exist not in watersheds that have avoided human intervention, but rather in those that have been modified in particular ways. Whether this comes in the form of translocating trout into historically fishless waters, as restoration efforts have done with San Juan cutthroat trout in Colorado, or native trout benefiting from downstream habitat modifications (e.g. road culverts or dams) that ensured their genetic isolation, the resulting ecosystems and the populations inhabiting them might more aptly be considered the products of interwoven histories of human activity and natural selection, rather than exemplars of historical independence from human activities.

If we fail to account for the processes by which “pure” fish arrived in a particular watershed, or remain genetically isolated and thus protected, we may inappropriately attribute their origins. This can establish a false understanding of how certain organisms, places, or processes actually exist – the ecosystem’s ontology – and also reinforce dualisms of nature and culture, thereby contributing to a problematic epistemology, or how we come to understand these relationships and processes. Rather than prioritizing the restoration of “pure” populations as a means to repair the mistakes of earlier generations of fisheries managers, trout restoration and recovery efforts might instead think of genetic knowledge as one piece of a broader management framework that allows for multiple perspectives and forms of evidence, without recourse to a hierarchy of knowledge that gives precedence to genetic data. In our conclusion, we explore what questions might arise from such a framework, but first we discuss some of the practical challenges of managing fisheries with an emphasis on genetics and genetic purity.

The Fragility of Genetic Purity

Operating under an either-or framework that disregards the meaningful hybrid processes influencing watersheds or ecosystems is not just a conceptual problem, but also may substantially de-value populations that are deemed “impure.” If only populations meeting a certain genetic threshold are granted moral or biological standing in ecological restoration, then we find ourselves needing to write off or eradicate populations even in places where they may be functionally productive or benign. As genetic tests come with increasingly refined capabilities to detect signs of introgression, populations that just a few years ago were considered valuable for conservation – or in some cases, were actively stocked because of their apparent genetic integrity – now face relocation or eradication (Fendt 2019; Perkins 2020).

Native fish restoration must contend with a genetic landscape that is continually shifting underfoot due to advances in molecular methods and fish movement and interbreeding. Molecular analyses of trout have expanded from studies of allozymes in the 1970s and 1980s, to mitochondrial DNA and microsatellites in the 1990s, to single nucleotide polymorphisms in the 2000s (Allendorf 2017). With rapidly evolving techniques, the genetics considered “pure” for a given species or lineage have changed over time, as have estimates of the level of purity of populations (notwithstanding changes in populations themselves). For example, trout in Whites Creek, Montana, were subject to seven rounds of genetic analysis between 2005 and 2014, using three different molecular techniques. Each of these analyses indicated that the fish were genetically pure westslope cutthroat trout (Leary et al. 2014). The fish were subsequently used as a donor source for a large westslope cutthroat trout restoration project, which restored these trout to nearly 100 km of Cherry Creek in southwestern Montana (Clancey et al. 2019). In 2014, an eighth round of analysis of Whites Creek trout found alleles characteristic of a different subspecies, Yellowstone cutthroat trout (*O. c. bouvieri*) in three samples, indicating possible hybridization. Geneticists could not determine if these alleles arose from hybridization with translocated fish or if they simply represented “natural” genetic variation within westslope cutthroat trout. Still, they advised Montana Fish, Wildlife, and Parks to stop using Whites Creek fish in native trout restoration projects, to avoid introducing tainted organisms (Leary et al. 2014).

These findings can be inconvenient and confounding for managers, as better techniques and a clearer picture of a population’s genetics loom just ahead, but still out of reach. As one federal fisheries manager explained to us, “Every year methods are improving and getting more high resolution, and that’s awesome, but it almost can get to be frustrating from a management perspective… I mean, that kind of thing can paralyze you.”

In addition to the evolving nature of genetic science, there is a second form of fragility related to the materiality of fish themselves: the genetic and evolutionary precariousness of fish that have lived in small, isolated populations for extended periods of time. Many of these fish exhibit deformities or limited viability associated with genetic bottlenecking, as is the case for the sole remaining genetically pure population of greenback cutthroat trout in Colorado (Fendt 2019). Such problems tend to be especially pronounced when individuals from isolated populations are captured and bred in hatcheries.

The Impacts of Pursuing Genetic Purity

Designations of genetic purity also interact with existing environmental practices and policies, reshaping how resources are allocated and ecosystems are prioritized for restoration or conservation. We illustrate this through three examples.

First, the drive to protect and restore genetically pure trout has led to a tension between restoring *ecological connectivity* through the removal of dams and other barriers to fish passage versus restoring *genetic purity* through the construction of artificial barriers to prevent fish passage and hybridization. Different restoration values – connectivity and purity – come into conflict with each other and cannot be easily resolved based on genetic data alone. As one conservationist reflected, "It's funny, because we went from, in the '90s, opening up fish passage everywhere, to the 2000s where we started closing fish passage and locking out the non-natives. I'm tempted to think the pendulum has swung too far." In addition, a focus on purity over connectivity often translates into the protection of small, isolated populations which are vulnerable to both genetic bottlenecks and disturbances such as wildfire, flooding, and drought. Fish barriers and infrastructure constructed to maintain genetic isolation are also vulnerable to disturbances. In 2007, for example, the Owl Fire burned through Yellowstone National Park's East Fork Specimen Creek westslope cutthroat trout restoration site, destroying a fish barrier and water diversion structure that had been built a year earlier to maintain isolation of a "pure" population (Koel et al. 2007).

Second, both genetic purity and isolation of fish populations are now crucial factors in streams' eligibility for protection under the 1968 National Wild and Scenic Rivers Act. Agencies such as the U.S. Forest Service determine eligibility using criteria that increasingly include genetic thresholds and isolation requirements. In New Mexico's Carson National Forest, for example, streams with Rio Grande cutthroat trout (*O. c. virginalis*) meet eligibility criteria when the population's genetics are "unaltered" (no more than 10% introgression), a full barrier is in place, and non-native species are absent (U.S. Forest Service 2019). As a result, several streams that were previously eligible for Wild and Scenic designation are no longer, while others have become eligible following genetic analyses or stocking of genetically "pure" fish. A conservation professional discussed how this process played out similarly in Montana's Custer-Gallatin National Forest:

> *"We thought that the Taylor Fork of the Gallatin River should have been a Wild and Scenic eligible stream because it has native cutthroat trout, and the Forest Service came back and said, 'Actually we don't include that as a fish value because those fish are less than 95% pure.' They are probably like 90% pure. It raised the issue… at what point on the purity scale does a native fish population have value as a native fish population?"*

Here, value is ascribed to an entire ecosystem based largely on a single population's presumed level of genetic purity.

Water rights represent a third management domain in which genetic purity is operationalized. In southwestern Colorado, fisheries managers pursued an instream flow water right for a small stream, home to one of only eight populations of San Juan cutthroat trout. Following testing to confirm the genetic composition and purity of the fish, the Colorado Water Conservation Board approved instream flow protection for the stream in 2019. According to fisheries managers, the water right would not likely have been granted without genetic testing. This may be interpreted as a victory for environmental protection, as it sets a precedent for demonstrating the importance of instream flow using genetic evidence, but at the same time, if genetic purity is as fragile a designation as we have suggested, it may be risky and short-sighted to base stream protection and water rights disproportionately on designations of purity.

Conclusion

To develop and maintain fisheries that support ecological processes, biodiversity, and human well-being in the present and future, we ought to avoid mobilizing genetic information in ways that (a) swing between care and neglect for ecosystems, (b) narrow the field of view to exclusively focus on fish genetic composition rather than multiple ecological or social parameters, or (c) view restoration as a means to an outcome – e.g. genetically pure native trout – rather than an iterative and dynamic process of relationship-building and care for ecosystems and living beings (including people). Rather than pursuing a strict dualism of native versus non-native, or pure organism versus hybrid (which typically maps onto loaded values of good and bad), one possible alternative might be to orient around questions of indigeneity that avoid binaries. Conceived this way, indigeneity foregrounds "systems among humans and nonhumans operative in particular places over many generations" (Whyte 2016, 2). This challenges us to understand how and why organisms exist as they do in relation to ecological and human processes. Such an approach need not render genetic identities meaningless, but instead places them in fuller contexts of human-environment interaction. In other words, the attribution of value for organisms and populations is not solely in their genetic makeup or even their historical origins, but rather in the relationships that have developed over time in these adoptive rivers, including with the people who interact with them. This framework also has implications for how we generate the knowledge that guides species restoration and recovery projects. Instead of relying on genetics to objectively validate life-or-death management decisions, a relational approach to knowledge generation (e.g. Reid et al. 2021) would seek out multiple perspectives and forms of evidence to improve our understanding of cutthroat trout fisheries in the western U.S.

We recognize that some fisheries scientists, ecologists, or restoration practitioners may not embrace a relational approach to conservation and management, and that ideals of indigeneity may be challenging to implement. The benefits of moving beyond a strictly genetic approach to wildlife management might also be brought to the fore by considering some or all of the following questions when evaluating restoration and conservation strategies: Is the population as it currently exists able to respond to changes in the watershed associated with climate change and ecological disturbance? How does the existing population interact with other organisms within the ecosystem, and what socioecological benefits does it provide? Are the population size and genetic diversity sufficient to prevent genetic bottlenecking or issues associated with limited viability? Are there ways to manage conservation populations that do not require long-term isolation of a population? If an existing population is eradicated using a chemical piscicide, what impacts can be expected on aquatic invertebrates, amphibians, and other taxa?

We provide these questions not as a comprehensive decision-making guide, but as examples of types of questions that can help avoid reductionist management strategies by placing genetics in a fuller context of human-environment interactions. Restoration ecology will surely want to leverage molecular techniques and genetic information as valuable tools to reveal the complex histories of organisms across socio-ecological landscapes, but we caution against an exclusive emphasis on genetic purity. This remains a far more fragile and fluid concept than strict interpretations of DNA might suggest, and jeopardizes the diverse, multi-faceted approaches that stand out as some of ecological restoration's significant strengths.

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