

Ecological segregation moderates a climactic conclusion to trout hybridization

Invasive hybridization, in which an introduced species may introgressively hybridize with a native taxon and threaten its persistence, is prominently featured in the conservation literature. One of the most frequently cited examples of this phenomenon involves interactions between native westslope cutthroat trout *Oncorhynchus clarkii lewisi* and introduced rainbow trout *Oncorhynchus mykiss* in a portion of the U.S. Northern Rocky Mountains (Allendorf & Leary, 1988). A recent paper by Muhlfeld et al. (2017) revisited this issue and concluded that introgressive hybridization between these taxa is ubiquitous and related primarily to climatic factors and propagule pressure from rainbow trout, findings which corroborate an earlier study (Young et al., 2016) that accurately quantified how broad riverscape gradients—not thresholds—in temperature, zoogeographic characteristics, and propagule pressure were related to levels of introgression. Yet, Muhlfeld et al. (2017) argued that there were deficiencies in that analysis and discounted that these same gradients can result in resistance of westslope cutthroat trout populations to invasive hybridization. Instead, based on extrapolation of decadal trends at nonrandom monitoring sites, they asserted that genomic extinction—the loss of all unhybridized parental forms—is inevitable for most

populations of westslope cutthroat trout in the absence of physical obstacles to upstream dispersal by rainbow trout or human intervention to remove them. We question this assertion based on our field observations and critical review of the subject (McKelvey et al., 2016; Young et al., 2016), the emerging recognition of environmental constraints on introgression (Wang & Bradburd, 2014), and the ecophysiological differences between these taxa and their hybrids (Rasmussen, Robinson, Hontela, & Heath, 2012). Resolving this issue is crucial, because resources to effect conservation are limited and poorly informed efforts can be costly and have unintended consequences (Fausch, Rieman, Dunham, Young, & Peterson, 2009).

Our uncertainty about the inevitability of genomic extinction stems from our own observations and a meta-analysis of 29 other studies involving hybridization between these species (McKelvey et al., 2016). Collectively, these studies revealed that apparently nonintrogressed cutthroat trout were common in most locations that also harbored rainbow trout or hybrids between the two. Moreover, the alleles of both taxa were strikingly nonrandomly distributed among samples of individuals (Figures 1 and 2) despite over a century of potential hybridization and the subsidy of rainbow trout

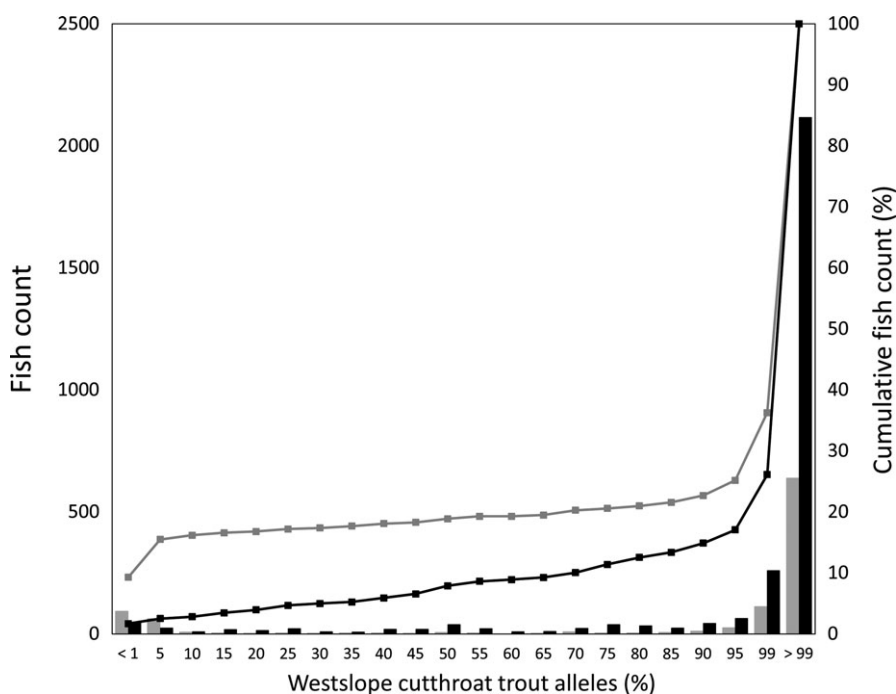


FIGURE 1 The count (bars) and cumulative percentage (lines) of fish ($n = 3,865$) with varying levels of westslope cutthroat trout alleles inside (gray) and outside (black) the historical range of rainbow trout drawn from a representatively structured sample of sites on public lands in northern Idaho and western Montana. We regard specimens with >99% westslope cutthroat trout alleles as nonintrogressed. Redrawn from McKelvey et al. (2016)

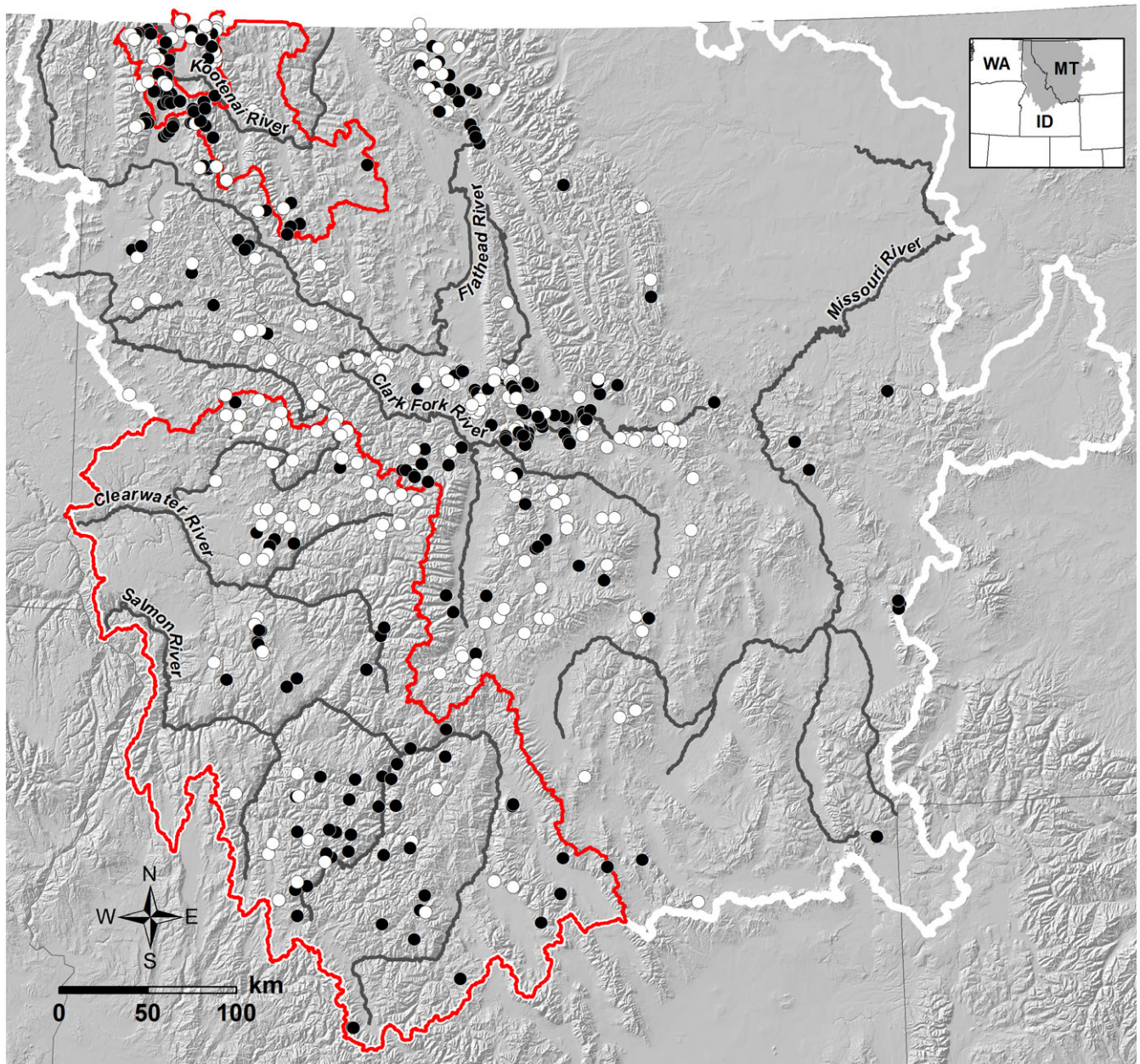


FIGURE 2 Locations ($n = 501$) represented by essentially nonintrogressed westslope cutthroat trout ($<1\%$ rainbow trout alleles in a sample; white circles) or hybridized fish ($>1\%$ rainbow trout alleles; black circles) in the Northern Rocky Mountains of Idaho and Montana. Basins encircled in red are in the historical range of rainbow trout. Redrawn from Young et al. (2016)

propagules from the stocking of hundreds of millions of fish for anglers.

That nonrandomness implies substantial resistance to introgression and likely reflects the ecological segregation of these taxa. Cutthroat trout tend to be found in smaller, colder, and less productive streams, whereas rainbow trout occupancy peaks in larger, warmer environments, preferences that probably arise from differences in their physiological traits (Rasmussen et al., 2012). Consequently, longitudinal gradients in hybridization between these species in streams are the norm and appear to represent environmentally mediated hybrid zones, a pattern observed between countless taxa in many

environments, including historically sympatric species (Jiggins & Mallet, 2000). Also instructive, although not considered by Muhlfeld et al. (2017), is that rainbow trout have naturally co-occurred with westslope cutthroat trout elsewhere in the Northwest since the last glacial maximum or longer. There, these species also readily hybridize and patterns in allele distributions and hybrid zone structure along environmental gradients are nearly indistinguishable from those where rainbow trout are non-native, with one exception: levels of introgression are markedly higher within the native range of rainbow trout (Young et al., 2016). Yet this region remains a stronghold for effectively genetically intact populations of westslope cutthroat

trout, despite thousands of generations for hybridization to spread (Figure 2).

We are not blithely sanguine about the threats posed by invasive hybridization to populations of westslope cutthroat trout in this era of rapid environmental change and non-native species invasions (Isaak, Young, Nagel, Horan, & Groce, 2015). Instead, our emphasis is on critically weighing conservation risks to guide timely, strategic decision making. Examining hybridization risks between taxa in the spatial context of entire river networks or landscapes and the broad environmental gradients therein can greatly contribute to the realism and geographic generality of models and the inferences they provide. In the case of hybridization between rainbow trout and westslope cutthroat trout, we coupled those types of models (Young et al., 2016) with our understanding of the climate inertia of cold water mountain streams (Isaak et al., 2016) to make spatially explicit predictions about the current and future positions and characteristics of hybrid zones under a variety of climate and invasion scenarios. Those analyses suggested that nonintrogressed populations of westslope cutthroat trout will remain, albeit in fewer locations and smaller populations (in which they are relatively persistent; Isaak et al., 2015), because of their ecological differences and the geomorphological diversity inherent to mountainous terrain. Those predictions—and our dataset—are publicly available online (<https://www.fs.fed.us/rm/boise/AWAE/projects/CutthroatRainbowTrout.html>) to permit fellow researchers to replicate, test, or expand on our results in the collective effort to develop a more nuanced and comprehensive understanding of environmental change and the eventual outcomes of species interactions.

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REFERENCES

- Allendorf, F. W., & Leary, R. F. (1988). Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. *Conservation Biology*, 2, 170–184.
- Fausch, K. D., Rieman, B. E., Dunham, J. B., Young, M. K., & Peterson, D. P. (2009). Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology*, 23, 859–870.
- Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., ... Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, 113, 4374–4379.
- Isaak, D. J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, 21, 2540–2553.
- Jiggins, C. D., & Mallet, J. (2000). Bimodal hybrid zones and speciation. *Trends in Ecology & Evolution*, 15, 250–255.
- McKelvey, K. S., Young, M. K., Wilcox, T. M., Bingham, D. M., Pilgrim, K. L., & Schwartz, M. K. (2016). Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams. *Ecology and Evolution*, 6, 688–706.
- Muhlfeld, C. C., Kovach, R. P., Al-Chokhachy, R., Amish, S. J., Kershner, J. L., Leary, R. F., ... Allendorf, F. W. (2017). Legacy introductions and climatic variation explain spatiotemporal patterns of invasive hybridization in a native trout. *Global Change Biology*, <https://doi.org/10.1111/gcb.13681>
- Rasmussen, J. B., Robinson, M. D., Hontela, A., & Heath, D. D. (2012). Metabolic traits of westslope cutthroat trout, introduced rainbow trout and their hybrids in an ecotonal hybrid zone along an elevation gradient. *Biological Journal of the Linnean Society*, 105, 56–72.
- Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, 23, 5649–5662.
- Young, M. K., Isaak, D. J., McKelvey, K. S., Wilcox, T. M., Pilgrim, K. L., Carim, K. J., ... Schwartz, M. K. (2016). Climate, demography, and zoogeography predict introgression thresholds in salmonid hybrid zones in Rocky Mountain streams. *PLoS ONE*, 11, e0167711.

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