Received: 3 June 2017 | Accepted: 12 June 2017
DOI: 10.1111/gcb.13825

RESPONSE TO EDITOR

WILEY Global Change Biology

No evidence for ecological segregation protecting native trout from invasive hybridization

We appreciate the comments of Young et al. (2017) on our recent paper (Muhlfeld et al., 2017) concerning spatiotemporal dynamics of hybridization between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; WCT) and introduced coastal rainbow trout (*Oncorhynchus mykiss irideus*; RBT). Nevertheless, we believe there is no evidence for "ecological segregation" protecting WCT from hybridization with invasive RBT. Here we consider their three major arguments for ecological segregation and find their conclusions invalid.

First, Young et al. (2017) argue that the current distribution of WCT in cold, headwater streams and RBT in larger, warmer environments reflects physiological differences between species. This argument is incorrect based on historical and contemporary data. WCT were historically abundant throughout watersheds, including downstream habitats (Behnke, 1992; Shepard, May, & Urie, 2005). WCT populations are currently restricted to headwater streams as a result of the ongoing spread of introduced RBT from the legacy of stocking in lower elevation lakes and rivers and habitat loss. Although climatic conditions affect habitat choice, there is no evidence that natural selection favors RBT in warmer environments (Kovach et al., 2015, 2016), and RBT admixture was evident across the range of thermal variation found in our study area (Muhlfeld et al., 2017). These patterns corroborate data showing that RBT and WCT have similar optimum temperatures (Bear, McMahon, & Zale, 2007), and that minor physiological differences between the species are often intermediate in hybrids (Yau & Taylor, 2014).

Second, Young et al. (2017) contend that the nonrandom distribution of RBT alleles in hybridized samples and the presence of nonhybridized individuals provides further evidence for "ecological segregation" and "resistance to introgression". However, the most likely explanation for the nonrandom distribution of RBT alleles is that many of these samples are recently hybridized, include highly admixed migrants (immigrants) from lower elevation areas, or nonhybridized WCT from above barriers (e.g., Boyer, Muhlfeld, & Allendorf, 2008; Kovach et al., 2015). Further, some of the genotyped loci are linked so that nonrandom distribution of genotypes (i.e., linkage disequilibrium, LD) will persist for many generations (Forbes & Allendorf, 1991).

For example, McKelvey et al. (2016) reported that Grouse Creek had 10.8% RBT alleles at diagnostic loci, and that these alleles were nonrandomly distributed among individuals. However, there is substantial LD among all pairs of diagnostic loci in this sample. Moreover, there are three fish that appear to be nonhybridized WCT, several fish that appear to be F2 backcrosses with nonhybridized WCT, and all of the loci in this sample are in Hardy–Weinberg proportions—indicating random mating. Together, these facts suggest that the immigration of RBT alleles into the WCT population is recent, not that the population is resistant to introgression. Recent hybridization and hybrid immigration is particularly likely given that samples genotyped in McKelvey et al. (2016) and used in Young et al. (2016) were primarily from higher elevation streams where hybrid dispersal and subsequent admixture are expected to be more recent than in lower-elevation reaches near historical stocking locations.

McKelvey et al. (2016) used 68 diagnostic loci between WCT and RBT, and there are 30 chromosome pairs in the coastal RBT karyotype (Thorgaard, 1983). Thus, many pairs of diagnostic loci must be on the same chromosome. Linkage between loci will reduce the rate of decay of LD from one-half per generation to (1-r), where r is the rate of recombination between loci. We have not reanalyzed data from McKelvey et al. (2016) for LD between all pairs of diagnostic loci, but two diagnostic loci (*OclWD_P53_307Kal* and *OclRD_P53T7R2_Har*) appear to be closely linked because strong LD is present in all samples. WCT and RBT alleles at these loci will remain nonrandomly distributed for many generations.

Finally, the natural sympatry of WCT with the Columbia River redband (i.e., native) rainbow trout (rRBT; *Oncorhynchus mykiss gairdneri*) does not imply ecological segregation between WCT and introduced hatchery coastal RBT. Data presented in Young et al. (2016) and (2017) do not distinguish between hybridization with native (rRBT) and introduced RBT. Nonnative coastal rainbow trout were widely stocked in Idaho, USA. Weigel, Peterson, and Spruell (2003) concluded that hybrids in the Clearwater Basin of Idaho resulted from hybridization between native WCT and introduced RBT, not WCT and rRBT. Similarly, Allendorf, Espeland, Scow, and Phelps (1980) detected both rRBT and introduced coastal RBT in the Kootenai Basin, Montana, USA. Hybridization between naturally sympatric populations of WCT and rRBT appears rare when introduced coastal RBT are absent, while the presence of coastal RBT acts as a genetic threat to both WCT (Shepard et al., 2005) and rRBT (Muhlfeld et al., 2015). This pattern is consistent with observations from other salmonids indicating maintenance of reproductive barriers between species in areas of natural sympatry and erosion of barriers following the introduction of hatchery fish (e.g., Castillo et al., 2008).

Our 40-year genetic monitoring data clearly demonstrate that hybridization has increased over time (Muhlfeld et al., 2017), further reducing the limited range of nonhybridized WCT (10%–20% of their historical range; Shepard et al., 2005). Further, most remaining WCT populations are not viable in the long-term because they are small and isolated. To prevent genomic extinction of additional populations of native WCT, conservation strategies must mitigate human stressors that interact with climate to promote the expansion of invasive RBT. We applaud the extraordinary efforts of fisheries managers to restore and protect WCT populations, and we emphasize the need to continue these conservation efforts in an era of rapid environmental change.

Ryan P. Kovach[1]
Clint C. Muhlfeld[1,2]
Robert Al-Chokhachy[3]
Stephen J. Amish[2]
Jeffrey L. Kershner[3]
Robb F. Leary[4]
Winsor H. Lowe[5]
Gordon Luikart[2]
Phil Matson[2]
David A. Schmetterling[4]
Bradley B. Shepard[6]
Peter A. H. Westley[7]
Diane Whited[2]
Andrew Whiteley[8]
Fred W. Allendorf[5]

[1]*Northern Rocky Mountain Science Center, U.S. Geological Survey, West Glacier, MT, USA*
[2]*Flathead Lake Biological Station, Division of Biological Sciences, University of Montana, Polson, MT, USA*
[3]*Northern Rocky Mountain Science Center, U.S. Geological Survey, Bozeman, MT, USA*
[4]*Montana, Fish, Wildlife and Parks, Missoula, MT, USA*
[5]*Division of Biological Sciences, University of Montana, Missoula, MT, USA*
[6]*B.B. Shepard & Associates, Livingston, MT, USA*
[7]*College of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AK, USA*
[8]*Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, Missoula, MT, USA*

Correspondence
Clint C. Muhlfeld, U.S. Geological Survey, West Glacier, MT, USA.
Email: cmuhlfeld@usgs.gov

REFERENCES

Allendorf, F. W., Espeland, D. M., Scow, D. T., & Phelps, S. (1980). Coexistence of native and introduced rainbow trout in the Kootenai River Drainage. *Proceedings Montana Academy of Sciences*, *39*, 28–36.

Bear, E. A., McMahon, T. E., & Zale, A. V. (2007). Comparative thermal requirements of westslope cutthroat trout and rainbow trout: Implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society*, *136*, 1113–1121.

Behnke, R. J. (1992). *Native trout of western North America*. Bethesda, MD: American Fisheries Society Monograph, vol. 6.

Boyer, M. C., Muhlfeld, C. C., & Allendorf, F. W. (2008). Rainbow trout (*Oncorhynchus mykiss*) invasion and the spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*, 658–669.

Castillo, A. G. F., Ayllon, F., Moran, P., Izquierdo, J. I., Martinez, J. L., Beall, E., . . . Garcia-Vazquez, E. (2008). Interspecific hybridization and introgression are associated with stock transfers in salmonids. *Aquaculture*, *278*, 31–36.

Forbes, S. H., & Allendorf, F. W. (1991). Associations between mitochondrial and nuclear genotypes in cutthroat trout hybrid swarms. *Evolution*, *45*, 1332–1349.

Kovach, R. P., Hand, B. K., Hohenlohe, P. A., Cosart, T. F., Boyer, M. C., Neville, H. H., . . . Luikart, G. (2016). Vive la résistance: Genome-wide selection against introduced alleles in invasive hybrid zones. *Proceedings of the Royal Society B*, *283*, 20161380.

Kovach, R. P., Muhlfeld, C. C., Boyer, M. C., Lowe, W. H., Allendorf, F. W., & Luikart, G. (2015). Dispersal and selection mediate hybridization between a native and invasive species. *Proceedings of the Royal Society B*, *282*, 20142454.

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., Albeke, S. E., Gunckel, S. L., Writer, B. J., Shepard, B. B., & May, B. E. (2015). Status and conservation of interior redband trout in the Western United States. *North American Journal of Fisheries Management*, *35*, 31–53.

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

Shepard, B. B., May, B. E., & Urie, W. (2005). Status and conservation of westslope cutthroat trout within the western United States. *North American Journal of Fisheries Management*, *25*, 1426–1440.

Thorgaard, G. (1983). Chromosomal differences among rainbow trout populations. *Copeia*, *1983*, 650–662.

Weigel, D. E., Peterson, J. T., & Spruell, P. (2003). Introgressive hybridization between native cutthroat trout and introduced rainbow trout. *Ecological Applications*, *13*, 38–50.

Yau, M. M., & Taylor, E. B. (2014). Cold tolerance performance of westslope cutthroat trout (Oncorhynchus clarki lewisi) and rainbow trout (Oncorhynchus mykiss) and its potential role in influencing interspecific hybridization. *Canadian Journal of Zoology*, *92*, 777–784.

Young, M. K., Isaak, D. J., McKelvey, K. S., Wilcox, T. M., Campbell, M., & Corsi, M., . . . Schwartz, M. K. (2017). Ecological segregation moderates a climactic conclusion to trout hybridization. *Global Change Biology*, https://doi.org/10.1111/gcb.13828.

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*, e0163563.