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ARTICLE

Spreading the Risk: Native Trout Management in a Warmer and Less-Certain Future

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Abstract

Management strategies that increase biological diversity and promote varied approaches to population protection are more likely to succeed during a future in which global warming drives rapid environmental change and increases uncertainty of future conditions. We describe how the concept of a diverse management portfolio can be applied to native trout conservation by increasing *representation* (protecting and restoring diversity), *resilience* (having sufficiently large populations and intact habitats to facilitate recovery from rapid environmental change), and *redundancy* (saving a sufficient number of populations so that some can be lost without jeopardizing the species). Saving diversity for native trout requires the conservation of genetically pure populations, the protection and restoration of life history diversity, and the protection of populations across the historical range. Protecting larger stronghold populations is important because such populations will have a better chance of surviving future disturbances, including those associated with climate change. The long-term persistence of populations is likely to require management for larger population sizes and larger habitat patches than currently exist for many native trout populations. Redundancy among these elements is important given that many populations are small and occupy reduced habitat in fragmented stream systems and therefore are increasingly vulnerable to extirpation. Application of the concept is further described in case studies of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* and Rio Grande cutthroat trout *O. clarkii virginalis*, two subspecies that illustrate many of the challenges that are common to management of western native trout.

One of the basic tenets of conservation biology is that biological diversity provides stability to communities (Primack 2002). Biologically rich systems can more easily withstand disturbances and swings in environmental conditions that would destabilize communities that are dominated by few species or destabilize species that are represented by only a few small populations (Tilman and Downing 1994). The ability of diverse natural systems to maintain their function and productivity in the face of rapid environmental change has been termed the “portfolio effect,” a concept that is analogous to the desire among financial managers to maintain a diverse economic portfolio as a hedge against uncertain futures (Figge 2004). In fisheries, the concept has been applied to the biocomplexity inherent in the Bristol Bay sockeye salmon *Oncorhynchus*

nerka fishery, which is supported by several-hundred discrete populations that maintain a much higher level of productivity than would be possible from a fishery that is supported by only a few populations (Hilborn et al. 2003; Schindler et al. 2010). Over the long term, this diversity has allowed the Bristol Bay sockeye salmon fishery to maintain a high level of production despite substantial variability in environmental conditions. On the other hand, a weak portfolio of stocks within the fall-run Chinook salmon *O. tshawytscha* complex in California’s Central Valley appears to have contributed to the 2008 collapse of the California and southern Oregon Chinook salmon fishery, which was largely supported by a single Sacramento River stock (Carlson and Satterthwaite 2011).

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Among the factors that have made western trout so numerous and persistent are their diverse life histories and wide range of occupied habitats. Migratory life histories facilitate access to more habitats and to habitats of varying size and location. Such migratory lifestyles allow fish to avoid streams that are degraded by disturbances and to subsequently reoccupy streams once the habitats recover (Rieman and Clayton 1997). Many native trout historically occupied habitats of various sizes, elevations, and water quality characteristics. Even lake habitats varied greatly in size, depth, and productivity. For example, Bonneville cutthroat trout *O. clarkii utah* once ranged from small, low-elevation streams in the West Desert along the Nevada–Utah border to larger rivers draining the High Uinta Mountains in northern Utah. Various authors have described the importance of preserving life history diversity and habitat connectivity in efforts to sustain native trout (Rieman and Dunham 2000; Colyer et al. 2005; Neville et al. 2009).

Rapid global warming is likely to have significant negative impacts on most native salmonids (Haak et al. 2010a; Wenger et al. 2011), especially those that have lost substantial amounts of their historical biological diversity. Global warming will not only increase the temperatures of lakes and streams (Wenger et al. 2011) but also the frequency and intensity of disturbances such as flooding, drought, and wildfire (Poff 2002; Westerling et al. 2006). Already, in many parts of the western USA, stream runoff is peaking earlier in the year and flows are declining relative to conditions recorded in the early 20th century (Luce and Holden 2009; Clark 2010; Clow 2010; Fu et al. 2010). Because of their small population sizes and isolation, small headwater trout populations will be particularly vulnerable to an increased frequency, magnitude, or extent of disturbance (Brown et al. 2001; Williams et al. 2009). Fausch et al. (2006, 2009) recently summarized threats to persistence in isolated populations of trout, which included loss of genetic variability, loss of resilience, demographic stochasticity, and natural and human-caused catastrophes. Furthermore, Rahel and Olden (2008) described how climate change is likely to provide for new pathways of introduction for invasive aquatic species and to increase the incidence of whirling disease and other pathogens.

A variety of strategies has been proposed in response to threats from climate change, including recommendations for increasing connectivity, increasing the number of habitat reserves, protecting larger areas, increasing reserve size, and practicing intensive management to secure populations and remove outside stressors (Heller and Zavaleta 2009; Lawler 2009). Most of these strategies promote the concept of enhancing resistance and resilience of ecological systems as a way to assist their adaptation to climate change. Resistance represents the capacity of habitats or populations to absorb rapid change or disturbance with limited or negligible change in condition (West and Salm 2003; Rieman and Isaak 2010). Resilience refers to the ability of habitats or populations to recover from rapid change or disturbance (e.g., reductions in number or condition) and to eventually rebound to a previous level or new state (Holling 1973; Heller

and Zavaleta 2009). Increasing the size and connectivity of protected habitats and populations helps to increase resistance and resilience.

Numerous authors have called for immediate action to adapt habitats, populations, species, and broader ecological systems to climate change. In a review of recommendations over the past 22 years, Heller and Zavaleta (2009) classified various proposals from 112 peer-reviewed articles but concluded that the vast majority of recommendations lacked sufficient specificity for their implementation. Heller and Zavaleta (2009) argued that concrete examples and case studies demonstrating how broad concepts could be implemented on the ground were badly needed to link actual management with conceptual frameworks.

In this paper, we describe an approach to increase native trout resistance and resilience; this approach utilizes commonly available genetic, life history, and geographical diversity data across a suite of habitat types. Our presumption is that increases in these elements of diversity will help to spread the risk of loss in a future that is likely to provide increasing peril for coldwater fishes as well as increased uncertainty associated with these threats. The concept is similar to the financial manager's desire to diversify a financial portfolio (Figure 1). After describing the approach, we quantify case studies of two wide-ranging subspecies of cutthroat trout *O. clarkii* and describe opportunities for portfolio improvement. The Yellowstone cutthroat trout *O. clarkii bouvieri* is found in a more northern and wetter environment that is characterized by both lake and stream habitats, whereas the Rio Grande cutthroat trout *O. clarkii virginalis* inhabits smaller streams and a more xeric environment. Both subspecies are in decline, and the Rio Grande cutthroat trout is a candidate for listing pursuant to the U.S. Endangered Species Act.

METHODS

In comparison with other fishes, salmonids are relatively well studied and their conservation status is often tracked over time. For most native trout, there are interagency workgroups or recovery teams that track population status and periodically report on rangewide conditions, including the genetic purity and extent of populations, local life history attributes, and other important characteristics (e.g., May et al. 2007; Alves et al. 2008) that facilitate broad-scale comparisons of conservation status among multiple species (Williams et al. 2007; Haak et al. 2010b). As a result, we can quantify and map population status and genetic purity and infer other important elements of diversity across the entire range for many trout species and subspecies. For both the Yellowstone cutthroat trout and Rio Grande cutthroat trout, interagency work groups regularly collect and report population status data, which comprise the population numbers used herein.

The 3-R Framework

To provide a structure for describing existing and potential future levels of diversity, we adopt the 3-R framework of *representation* (protecting and restoring diversity), *resilience* (having

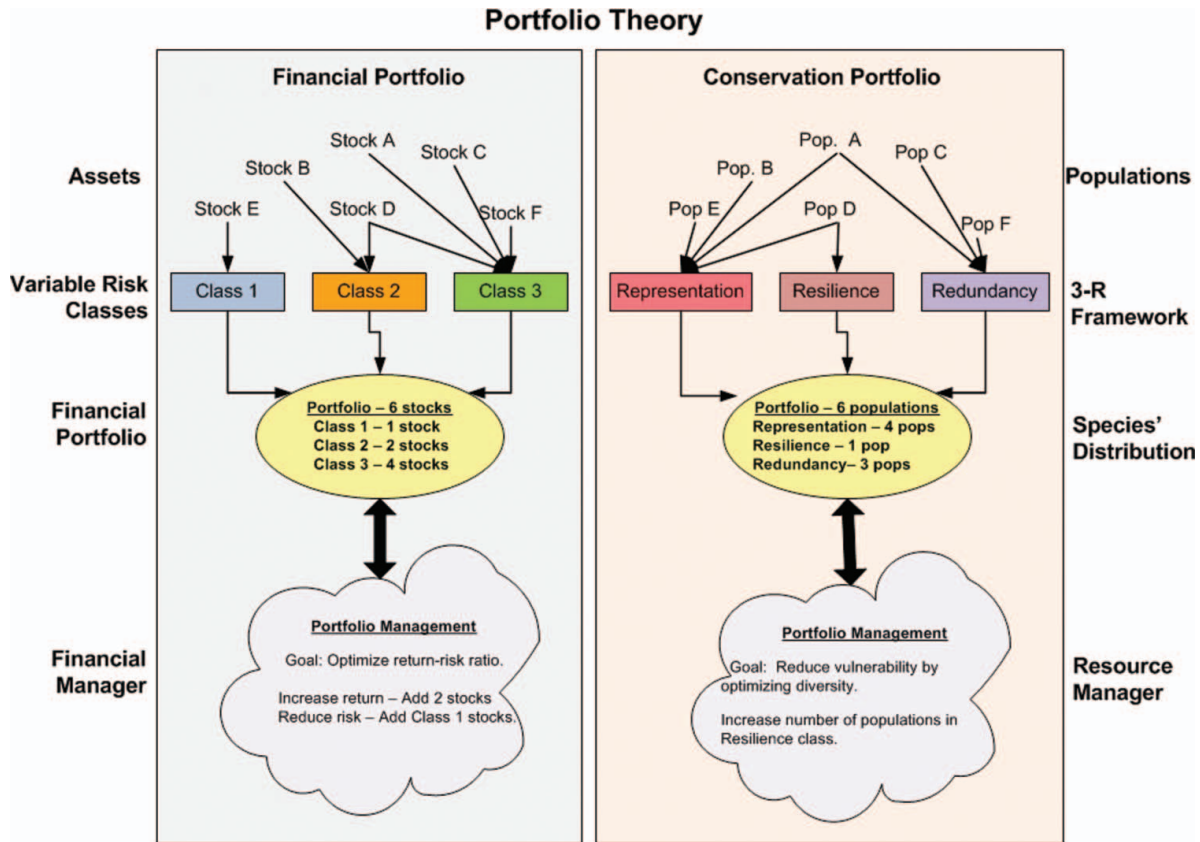


FIGURE 1. Comparison of portfolio theory in the financial and ecological realms. In this hypothetical comparison, populations (pops) are the assets to be managed in the portfolio. The 3-R framework is a way to categorize different assets that are valued within the conservation portfolio. According to portfolio theory, increasing the number of assets within each 3-R category will diversify and stabilize the portfolio. In the example shown, the conservation portfolio lacks assets in the resilience category, which should therefore become the focus for the resource manager.

sufficiently large populations and intact habitats to facilitate recovery from rapid environmental change), and *redundancy* (saving a sufficient number of populations so that some can be lost without jeopardizing the species; Table 1; Shaffer and Stein 2000). This framework incorporates basic principles in the science of conservation biology and has been adopted by the U.S. Fish and Wildlife Service in developing recovery plans for threatened and endangered species (Carroll et al. 2006). Therefore, evaluations using this framework have the added benefit of informing managers relative to the needs of listed or candidate species.

Application of the 3-R framework to native trout conservation relies on the most recent rangewide status assessments for spatial information on population distribution and associated tabular data on extent, density, genetic purity, and life history. May et al. (2007) and supplemental analyses (Anderson 2010) provided the most recent rangewide data available for Yellowstone cutthroat trout; a study by Alves et al. (2008) yielded the best rangewide data available for Rio Grande cutthroat trout. The Yellowstone cutthroat trout assessments included both the fine-spotted and large-spotted forms. Assessments for both subspecies defined discrete conservation populations based on the

potential for reproductive exchange within a grouping of occupied habitat segments. The populations must also be either genetically unaltered or have specific attributes of conservation significance (e.g., unique habitat or life history form). Data from the assessments on conservation populations are compiled and analyzed spatially in a geographical information systems environment and are then summarized within the 3-R framework.

Representation.—Representation encompasses three population attributes that are important to diversification of the subspecies’ portfolio: genetic purity, life history, and geography. Each of these elements is quantified based on the number of conservation populations that are genetically pure, exhibit a migratory life history form (fluvial or adfluvial), or occupy a unique geographic region as indicated by the presence of peripheral populations.

We do not measure genetic diversity directly; rather, we infer diversity by examining the genetic purity of populations across drainages and geographic management units (GMUs). Campbell et al. (2011) found substantial genetic structuring of Yellowstone cutthroat trout across occupied drainages, presumably as a result of long-term isolating mechanisms among different drainage basins. We presume, therefore, that maintaining

TABLE 1. Applying the 3-R framework to develop management goals, objectives, and indicators of success in the conservation of native trout. Thresholds for necessary stream habitat length and habitat patch size were derived from Hilderbrand and Kershner (2000) and Dunham et al. (2002).

Management goal	Objectives	Indicators of success
Representation	<ol style="list-style-type: none"> 1. Conservation of genetic diversity 2. Protection and restoration of life history diversity 3. Protection of geographic (ecological) diversity 	<ol style="list-style-type: none"> 1. Presence of genetically pure populations 2. Presence of all life histories that were present historically 3. Presence of peripheral populations
Resilience	<ol style="list-style-type: none"> 1. Protect or restore strongholds 2. Protect or restore metapopulations 	<ol style="list-style-type: none"> 1. Occupied stream habitat exceeds 27.8 km, and habitat patch size exceeds 10,000 ha 2. Occupied stream habitat supports migratory life history and exceeds 50 km, and habitat patch size exceeds 25,000 ha
Redundancy	<ol style="list-style-type: none"> 1. Protect multiple populations within each subbasin 	<ol style="list-style-type: none"> 1a. Five persistent populations within each subbasin; or 1b. Two or more larger strongholds within each subbasin; or 1c. One metapopulation within each subbasin 2. One metapopulation within each larger basin

genetically pure populations in each drainage basin within the historical range helps to sustain genetic diversity.

Determination of genetic purity is based on the reach-scale data associated with each conservation population as presented in the status assessments (May et al. 2007; Alves et al. 2008). This information represents a combination of (1) genetic sampling extrapolated to occupied stream segments and (2) expert opinion. The genetics data in the status assessments are broken down into seven discrete classes based on the degree of introgression and whether or not fish from the reach were tested. We reclassified the reach-scale data into four classes: unaltered (<1% introgressed), some hybridization (1–10% introgressed), hybridized (>10% introgressed), and mixed (co-occurrence of hybridized and unaltered individuals). We then calculated the proportion of the total occupied stream extent for each conservation population associated with each of the four categories. For the genetic purity component of representation, we counted only those populations that were classified as genetically unaltered in at least 80% of the occupied habitat.

Life history diversity is quantified based on the presence of migratory individuals within a conservation population as described in the status assessments (May et al. 2007; Alves et al. 2008). We do not distinguish between fluvial and adfluvial forms in our summation of populations that exhibit a migratory life history.

We rely on Haak et al. (2010b) for the identification of peripheral populations as an indicator of geographic diversity. Peripheral populations can be defined as those populations that exist at the geographic margins of a species' range (Bunnell et al. 2004). Peripheral populations are generally more isolated than populations at the core and consequently experience different selective pressures, resulting in unique genetic characteristics that contribute to within-species diversity (Lesica and Allendorf 1995; Nielsen et al. 2001). Haak et al. (2010b) distinguished between

peripheral populations that are continuous with the core populations and those that are disjunct from the core populations. Our quantification of geographic diversity does not make this distinction; instead, we summarize all peripheral populations as contributing equally to geographic diversity.

Resilience and redundancy.—The resilience and redundancy portions of the portfolio require classification of populations into five groups based on abundance, occupied stream extent, or both and on habitat patch size: metapopulation, stronghold, persistent, marginally persistent, and not persistent. Numerous studies have been conducted to determine the habitat requirements for the long-term viability of native trout populations (Hilderbrand and Kershner 2000; Dunham et al. 2002; Harig and Fausch 2002; Young et al. 2005; Rieman et al. 2007). The Harig and Fausch (2002) model incorporates detailed habitat metrics for factors (e.g., water temperature and deep pool counts) that are not available on a rangewide basis, whereas Hilderbrand and Kershner (2000) and Young et al. (2005) used the extent of occupied stream habitat to estimate population size as a surrogate for persistence. Hilderbrand and Kershner (2000) assumed a uniform density throughout the stream extent, while Young et al. (2005) found that abundance increased based on the square of stream length due to the increased habitat diversity, which allowed for higher densities. To classify populations for the resilience and redundancy analyses, we draw on the findings of Hilderbrand and Kershner (2000) and Young et al. (2005) as well as assumptions described by Dunham et al. (2002) with regard to habitat patch size.

In quantifying resilience for the portfolio, we distinguish between strongholds and metapopulations based on the extent of occupied stream habitat, the drainage area or patch size, and life history (Table 1). Hilderbrand and Kershner (2000) found that a mean stream length of 27.8 km was sufficient to provide for the long-term viability of a population, even at very low densities.

We combine this threshold with the assumption by Dunham et al. (2002) that the likelihood of withstanding environmental change is higher for populations that inhabit large patch sizes ($\geq 10,000$ ha) than for those that occupy smaller patches. By integrating a patch size component with stream length, we guard against the inclusion of populations that occupy high-density first-order streams in small drainage areas and thus are less likely to be resilient. Our classification of metapopulations is an approximate doubling of these two parameters, with the additional criterion that the population supports a migratory life history form. We recognize that due to a lack of data on population dynamics, this definition does not explicitly account for the functional attributes of a metapopulation. However, we believe that migratory populations occupying over 50 km of interconnected habitat throughout a large drainage area ($>25,000$ ha) are likely to function as metapopulations.

Redundancy in the portfolio provides a spatial hedge against losses by securing multiple populations within each subbasin of the historical range. In quantifying redundancy for the portfolio, we are primarily dealing with small populations within short sections of stream habitat rather than populations in larger patch sizes. For a population to count towards redundancy, it must satisfy criteria for both persistence and genetic purity.

Our assessment of population persistence integrates data on population abundance and occupied stream extent. To reduce demographic and stochastic extinction risks, an effective population size (N_e) of approximately 500 interbreeding adults is needed (Franklin 1980). Because N_e may be a small fraction of the actual population size, a greater population is typically required (Nelson and Soule 1987). Hilderbrand and Kershner (2000) recommended a census population size (N) of approximately 2,500 individuals of 75 mm total length or larger to achieve the N_e of 500 for stream fishes. Young et al. (2005) found that a stream length of 8.8 km could support a population of 2,500 individuals, assuming high-quality habitat functioning at maximum carrying capacity. However, degraded habitat or the presence of nonnative species may suppress population size. Therefore, we calculate population abundance based on population densities reported in the rangewide status assessments (e.g., May et al. 2007; Alves et al. 2008). The use of 2,500 for a target census population yields an N_e/N ratio of 0.2, but this ratio will vary greatly because of several factors, including annual fluctuation in population size and whether the estimate of N includes only adults or some combination of juveniles and adults (Frankham 1995).

Our calculation of population abundance is based on the population density determinations provided at the stream reach scale in the rangewide status assessments. This information relied on both expert opinion and empirical data and was compiled by following the standardized protocols developed by Bruce May and Shannon Albeke (see May et al. 2007; Alves et al. 2008) for rangewide status assessments of cutthroat trout. Both status assessments reported number of individuals per stream mile based on best available information. For Yellowstone cutthroat trout,

May et al. (2007) defined adults as individuals greater than 15 cm in small streams with resident populations and individuals greater than 30 cm in larger rivers. Alves et al. (2008) defined adult Rio Grande cutthroat trout as individuals at least 12 cm in length. Densities are reported as ranges (e.g., 0–50 or 51–150 fish/mi [0–31 or 32–93 fish/km]) for each stream segment occupied by a conservation population.

To calculate abundance, we multiplied the midpoint of the specified range (e.g., 25 fish/mi [16 fish/km] for segments with a density of 0–50 fish/mi [0–31 fish/km]) by the length of the associated reach. Reach-scale results are summarized for each conservation population to provide estimates of total abundance at the population level. Recognizing the importance of available habitat to long-term population viability, we apply the findings of Young et al. (2005) and establish a minimum threshold of 8.8 km for occupied stream length; Young et al. (2005) identified this stream length as having the potential to support a population of 2,500 individuals. To account for suboptimal habitat conditions, we also set an abundance threshold of 2,500 individuals of 75 mm total length or larger. Populations with an occupied stream extent of at least 8.8 km and a total abundance of 2,500 individuals were classified as persistent, whereas any population with fewer than 2,500 individuals was classified as not persistent. In some situations, a population may satisfy our criteria for abundance but occupies a stream extent of less than 8.8 km. We classified such populations as marginally persistent and applied them to the redundancy portion of the portfolio but with a reduced conservation value.

Our genetics standard for redundancy applies the same methodology used in determining genetic purity for the representation portion of the portfolio. However, for the redundancy component, we include all populations except those classified as hybridized (i.e., $>10\%$ introgressed) throughout 80% or more of the occupied stream habitat. This allows for the inclusion of populations that exhibit reduced levels of hybridization.

We apply the methods of Rieman et al. (2007) for the determination of subbasin (8-digit U.S. Geological Survey [USGS] hydrologic unit codes) goals for redundancy. Based on their assumption that vulnerability is related to the size and number of habitat patches, we make a distinction between small resident populations and larger strongholds. To satisfy the objectives for redundancy, each subbasin must contain one of the following: (1) five or more nonnetworked populations that meet our persistence criteria; (2) two or more stronghold populations; or (3) one metapopulation. All of these populations must also meet the genetics criteria for redundancy. An alternative goal for redundancy is the presence of at least one metapopulation within each major river basin (4-digit USGS hydrologic unit codes) of the historical range.

Diversity Measures

We apply the Shannon–Wiener diversity index (H') to the portfolios of different subspecies as the basis for making comparisons between the two cutthroat trout subspecies. This

TABLE 2. Current portfolio status (within the 3-R framework; Table 1) for Yellowstone cutthroat trout. For representation, we show the number of populations (N_p) within each basin that are genetically pure (genetic integrity), possess multiple life histories (life history diversity [LHD]), and are peripheral populations (geographic diversity). For geographic diversity, "NA" refers to basins that historically contained only core populations (i.e., no peripheral populations). Basins with a value of zero for geographic diversity historically contained peripheral populations, all of which were eliminated. For resilience, we present the number of stronghold populations and the number of metapopulations (metapop). For redundancy, the number of persistent populations (N_p) that are not more than 10% introgressed is presented.

Basin	Occupied habitat			Representation			Resilience		Redundancy: persistent and $\leq 10\%$ introgressed (N_p)
	Total N_p	Stream (km)	Lake (ha)	Genetic integrity (N_p)	LHD (N_p)	Geographic diversity (N_p)	Stronghold (N_p)	Metapop (N_p)	
Upper Snake River	102	4,217	20,465	93	56	NA	2	20	30
Yellowstone River	53	3,387	34,373	35	25	NA	9	6	27
Lower Snake River	84	2,740	9,310	51	29	23	9	7	27
Bighorn River	66	1,358	912	47	36	14	5	4	17
Tongue River	1	1	0	1	0	1	0	0	0
Total	306	11,703	65,060	227	146	38	25	37	101

diversity measure provides a metric for determining the order within a particular system as a function of the number of different elements within that system and the proportion of individuals associated with each element. The index increases as more elements are added and as individuals are more evenly distributed between elements.

We use the six portfolio elements (i.e., genetic purity, life history diversity, geographic diversity, stronghold, metapopulation, and redundancy) as the basis for the analysis. The rangewide population totals for each element are used to calculate H' using the equation $H' = -\sum(P_i \cdot \log_e P_i)$, where P_i represents the proportional abundance of each portfolio element (e.g., genetic purity or life history diversity) relative to the entire portfolio. The entire portfolio is defined as the sum of all of the populations associated with each of the six portfolio elements. Because many individual populations are frequently associated with two or more of the portfolio elements (e.g., genetic purity and redundancy), the sum of the portfolio elements is greater than the number of conservation populations. The proportional abundance is then calculated for each element by dividing the number of populations that satisfy the criteria for that element by the sum of all portfolio elements. The maximum value for H' is the natural logarithm of the number of elements being evaluated, which in this case is six, thus yielding a maximum value of 1.79 for our portfolios. Portfolios that are missing any of the six elements (e.g., no metapopulations) or that are heavily skewed to one type of element will have lower diversity measures.

Using H' , we also calculate an evenness index (E), which measures how evenly populations are distributed between the different portfolio elements. For this computation, we use the following equation: $E = H'/H_{max}$. Portfolios with similar proportions between all elements will have an E -value of 1, while portfolios with unbalanced representation within the different elements will have decreased E -values.

RESULTS

Yellowstone Cutthroat Trout

The most recent rangewide assessment for Yellowstone cutthroat trout included data for 306 conservation populations occupying 11,703 km of stream habitat (i.e., 65% of historical stream habitat) and 65,060 ha of lacustrine habitat (May et al. 2007; Anderson 2010). Population data from these assessments are used to quantify the representation, resilience, and redundancy categories within the 3-R framework for this case study.

The historical range for Yellowstone cutthroat trout is divided into five GMUs that approximate the boundaries of five major river basins: Yellowstone, upper Snake, lower Snake, Bighorn, and Tongue rivers (May et al. 2007). Results of the 3-R framework are summarized at the population level for each of the GMUs (Table 2). From a rangewide perspective, the portfolio appears to be well diversified, with numerous populations contributing to each of the three Rs. However, at the GMU scale, there is considerable variability. The upper Snake River is an important stronghold that contains 102 conservation populations, 90% of which are genetically pure and 55% of which support a migratory life history. In contrast, the lower Snake River supports 84 conservation populations, only 60% of which are genetically pure and only 35% of which support a migratory life history. The Tongue River historically supported interconnected peripheral populations in its headwaters, but currently there is only one remaining population and it occupies only 1 km of stream habitat.

Nearly 90% of the conservation populations contribute to one or more of the representation elements: 74% are genetically pure, 48% support a migratory life history, and 12% are located in peripheral areas (Figure 2). Overall, geographic representation has suffered the greatest loss, with remaining peripheral populations occupying less than 15% of the historical peripheral habitat (Haak et al. 2010b). Of particular concern is the

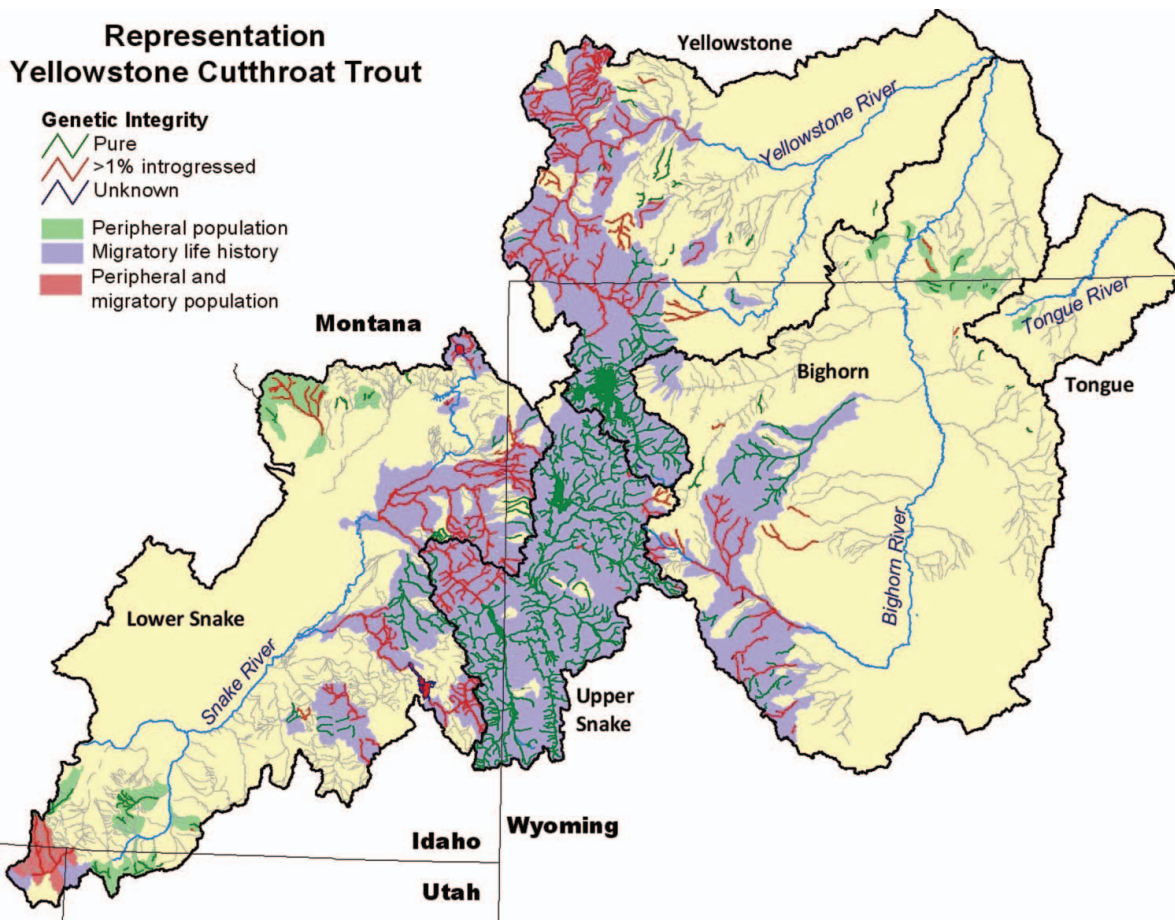


FIGURE 2. Rangewide distribution map for Yellowstone cutthroat trout, showing the representation component (i.e., genetically pure, migratory, and peripheral populations) of the 3-R framework in the context of historical and current distributions within the Yellowstone, upper Snake, lower Snake, Bighorn, and Tongue River basins.

fact that the two largest remaining peripheral populations in the lower Snake River (i.e., Goose and Medicine Lodge creeks) are hybridized. The number of genetically pure populations is relatively high, and 70 satisfy the criteria for long-term persistence. The core habitat in the upper Snake River and headwaters of the Yellowstone River contains the most extensive network of genetically pure populations, while populations that are more removed from the core have a higher degree of hybridization (May et al. 2007).

Twenty percent of the conservation populations are classified as resilient; among these resilient populations are 37 metapopulations, the majority of which are associated with the core habitat in the headwaters of the Snake, Yellowstone, and Bighorn rivers (Figure 3). Of the 146 populations identified by May et al. (2007) as supporting a migratory life history, 49 meet the resilience criteria. The remaining populations are associated with small lakes and tributary habitats that support resident and adfluvial life histories but provide little resistance or resilience to environmental change. Peripheral populations occupying small streams at the downstream extent of the Snake and Bighorn rivers as well as

the headwaters of the Tongue River tend to have limited habitat extents such that only 4 of these 38 peripheral populations are classified as resilient. Many of the genetically pure populations have been isolated above barriers to protect them from hybridization with other taxa. Because of the increasing isolation of the small populations, 31 of the 227 genetically pure populations are classified as resilient. The largest of these is the Yellowstone Lake population, which occupies nearly 800 km of stream habitat and over 34,000 ha of lacustrine habitat. Other genetically pure metapopulations are found in the upper Snake River above Palisades Reservoir and Jackson Lake.

Given the limited extent of many of the genetically pure populations and given the hybridization risk to large populations, it is not surprising that fewer than one-third of the conservation populations satisfy both the persistence and genetics criteria for redundancy and that only 19 of the 36 occupied subbasins meet the subbasin portfolio objectives. As shown in Figure 3, the majority of these are concentrated around the core populations at the center of the range, while the subbasins around the periphery contain many populations with more limited extents or higher

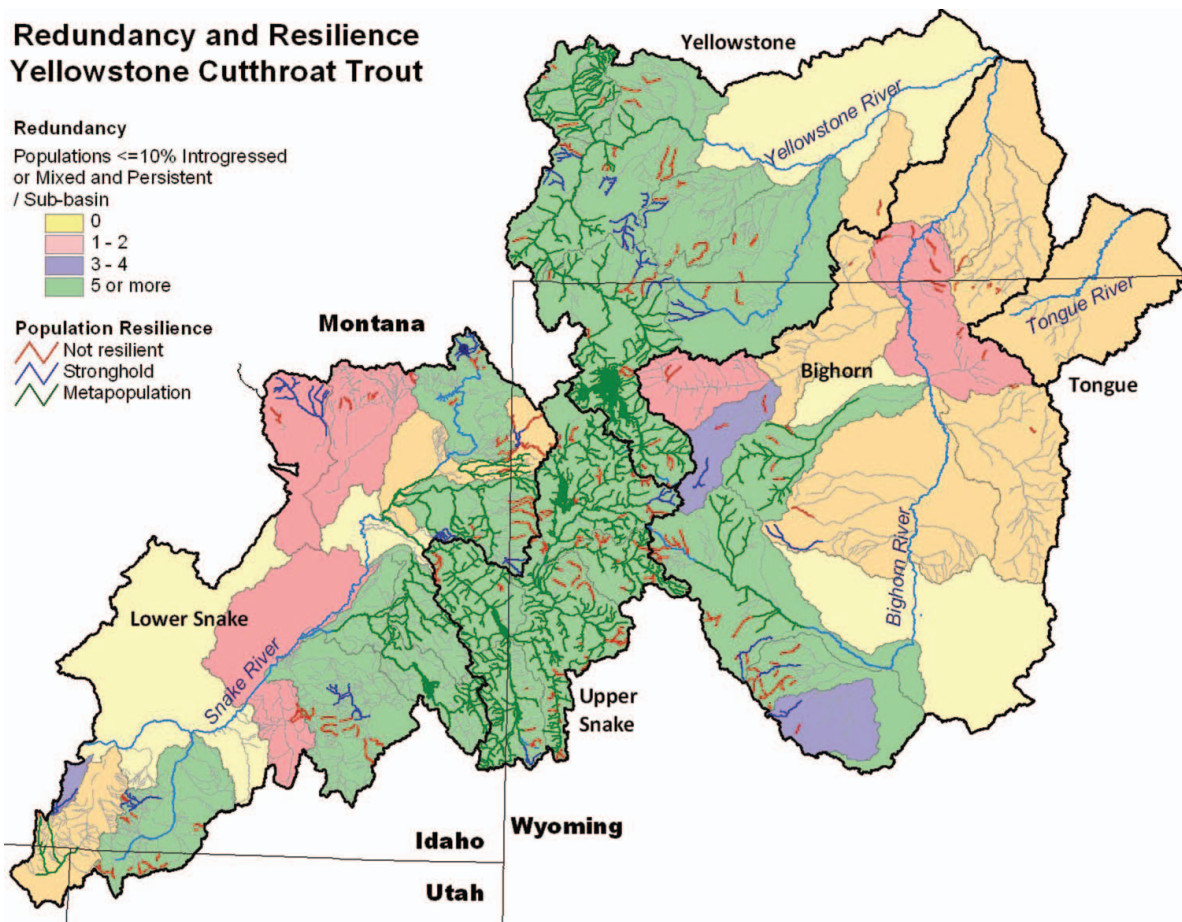


FIGURE 3. Rangewide distribution map for Yellowstone cutthroat trout, illustrating the resilience and redundancy components of the 3-R framework. Streams shown in dark green (metapopulations) and dark blue (strongholds) comprise the elements for resilience. Redundancy is shown by the subbasin colors (e.g., green indicates subbasins that meet the goal of containing five or more persistent populations).

degrees of hybridization. However, the basin-scale goal of one large, interconnected metapopulation within each major river basin has been met in all of the basins with the exception of the Tongue River, where there is limited historical habitat available for restoring larger populations (May et al. 2007).

The H' analysis for Yellowstone cutthroat trout indicates that the current portfolio for this subspecies is fairly well diversified, exhibiting a score of 1.51 out of a maximum potential score of 1.79. The E of 0.84 is also indicative of a portfolio that is well distributed among the different elements of diversity. Habitat loss and degradation have been more pronounced at the lower elevations and edges of the subspecies' range, whereas populations in the central core, which are located primarily on protected federal lands (e.g., national parks and wilderness areas), have remained relatively intact.

Rio Grande Cutthroat Trout

The most recent rangewide assessment for Rio Grande cutthroat trout included data for 121 remaining conservation populations that occupy 1,124 km of stream habitat in Colorado

and New Mexico, thus representing slightly more than 10% of the historical habitat (Alves et al. 2008). Population data from this assessment are used to quantify the representation, resilience, and redundancy categories in the 3-R framework. The subspecies has been eliminated from the Texas portion of its range (Garrett and Matlock 1991) as well as from the disjunct subbasins at the southern extents of the Rio Grande and Pecos River basins in New Mexico.

The current range of Rio Grande cutthroat trout is divided into four GMUs: Rio Grande headwaters, lower Rio Grande, upper Canadian River, and Pecos River (Alves et al. 2008). Genetic integrity is the strongest of the portfolio elements, with 73% of the populations classified as genetically pure (Table 3). However, in terms of genetic diversity as inferred from the geographic distribution of the 89 genetically pure populations, 73 such populations are located within the Rio Grande system, 9 are found in the upper Canadian River GMU, and 7 are found in the Pecos River GMU (Figure 4). The upper Canadian River and Pecos River GMUs do not contain any peripheral or migratory populations. All four of the populations that exhibit a migratory

TABLE 3. Current portfolio status (within the 3-R framework; Table 1) for Rio Grande cutthroat trout. For representation, we show the number of populations (N_p) within each basin that are genetically pure (genetic integrity), possess multiple life histories (life history diversity [LHD]), and are peripheral populations (geographic diversity). For geographic diversity, “NA” refers to basins that historically contained only core populations (i.e., no peripheral populations). Basins with a value of zero for geographic diversity historically contained peripheral populations, all of which were eliminated. For resilience, we present the number of stronghold populations and the number of metapopulations (metapop). For redundancy, the number of persistent populations (N_p) that are not more than 10% introgressed is presented.

Basin	Total N_p	Occupied stream habitat (km)	Representation			Resilience		Redundancy: persistent and $\leq 10\%$ introgressed (N_p)
			Genetic integrity (N_p)	LHD (N_p)	Geographic diversity (N_p)	Stronghold (N_p)	Metapop (N_p)	
Rio Grande headwaters	40	466	36	3	NA	1	0	15
Lower Rio Grande	58	489	37	1	8	0	0	14
Upper Canadian River	12	109	9	0	NA	0	0	1
Pecos River	11	60	7	0	0	0	0	2
Total	121	1,124	89	4	8	1	0	32

life history are associated with small lakes as the fluvial life history has been lost throughout the range (Alves et al. 2008). Only eight peripheral populations remain, occupying less than 10% of their historical habitat (Haak et al. 2010b); among these peripheral populations, only two populations meet persistence criteria and both populations are slightly introgressed.

Scores for resilience and redundancy are low and are the weakest elements of the portfolio for this subspecies. There is only one stronghold population, which is located in the Rio Grande headwaters, and there are no metapopulations (Table 3). Two subbasins meet the subbasin goals for redundancy, and both of these subbasins are in the Rio Grande system (Figure 5). Populations in five historically occupied subbasins have been extirpated, and another four subbasins do not contain any persistent populations that are less than 10% introgressed. The upper Canadian River and Pecos River GMUs only support one and two populations, respectively, that contribute to redundancy in the portfolio. The criterion of having one large metapopulation with a fluvial life history in each major river basin has also not been met.

The results of our H' analysis for Rio Grande cutthroat trout show a decreased level of both diversity and E in comparison with the results for Yellowstone cutthroat trout. Assuming a maximum H' of 1.79 based on the six elements of diversity, the low score of 0.92 for Rio Grande cutthroat trout is indicative of both a lower “richness” (only five of the six potential elements exist in the current portfolio) and a poor distribution for those elements that are present. The disproportionate number of genetically pure populations relative to the other portfolio elements is further evidenced by the low E -value of 0.51.

DISCUSSION

Portfolio theory in financial management was developed during the 1950s (Markowitz 1952) and has since become a common approach for spreading the risk of loss by diversifying

investments and assets. As Figge (2004) observed, it is surprising that portfolio theory has seldom been applied to biological systems because it is commonly recognized that diversity leads to stability in the natural world. The future for both financial and ecological systems is filled with risks and uncertainties, and our ability to diversify our assets—whether they are market stocks or fish stocks—as a hedge against future change seems prudent.

Our capacity to precisely estimate the risks associated with climate change, invasive species, and other factors is improving as additional studies are conducted and as models are perfected. Nonetheless, our knowledge remains far from perfect for these factors. Furthermore, some threats are likely to interact in complex and poorly understood ways. Rahel and Olden (2008), for example, described how future climate change may provide novel introduction pathways and modified environments that are likely to favor additional aquatic species invasions.

The genetic structure and gene flow within most wide-ranging fish taxa are poorly understood. For many species that occur in a diversity of habitats and regions, there are likely to be local adaptations to divergent habitats and considerable genetic diversity among and within drainages. Campbell et al. (2011) found significant genetic structuring among Yellowstone cutthroat trout populations both within and among drainages. This argues for caution in conserving local populations and for the need to provide replicates of populations within drainages when possible. Obviously, the task of managing wide-ranging populations to maintain genetic diversity will provide a major challenge in the future, especially if environmental conditions are likely to change as much as predicted (Haak et al. 2010a; Wenger et al. 2011).

A variety of criteria could be selected to analyze the portfolio approach. The 3-R framework provides one approach that has been widely accepted by the conservation community, but undoubtedly there are other frameworks that would be more useful in different situations. Similarly, we have chosen criteria

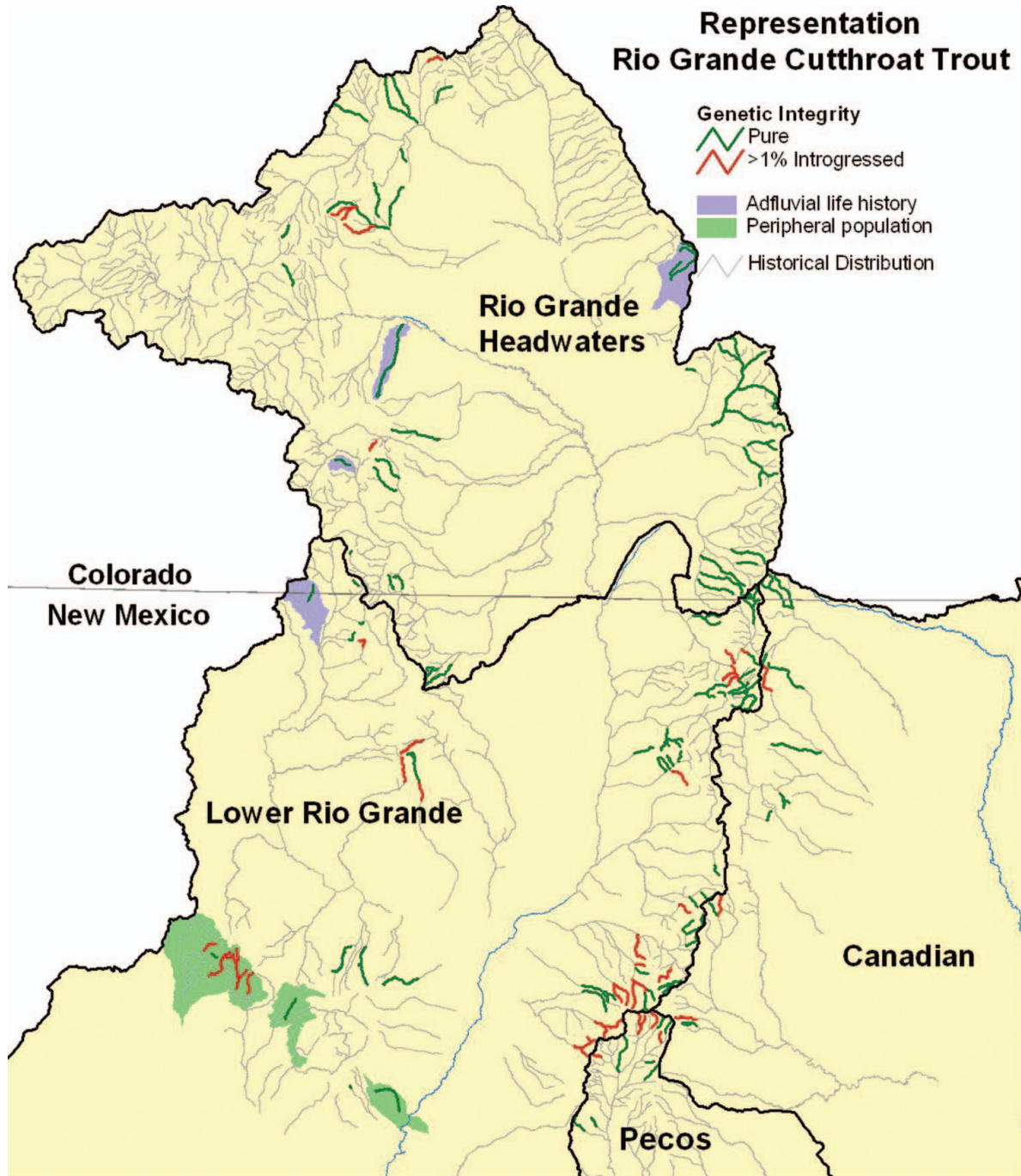


FIGURE 4. Distribution map for Rio Grande cutthroat trout, showing the representation component (i.e., genetically pure, adfluvial, and peripheral populations) of the 3-R framework in the context of historical and current distributions within the Rio Grande headwaters and lower Rio Grande, Pecos River, and Canadian River basins.

(e.g., peripheral populations and population persistence) that can be quantified for the 3-R framework and that are described in the scientific literature as being important for native trout, but these criteria may not be suitable for application to all taxa. For instance, the range of the Apache trout *O. gilae apache* (a subspecies of the Gila trout *O. gilae*) is so small that the

concept of peripheral populations may not be applicable for that subspecies. Our intent in this paper is not to focus attention on the specific criteria we have chosen but rather to encourage application of the portfolio concept and the 3-R framework as viable tools that can assist managers in assessing a species' or subspecies' ability to survive rapid environmental change.

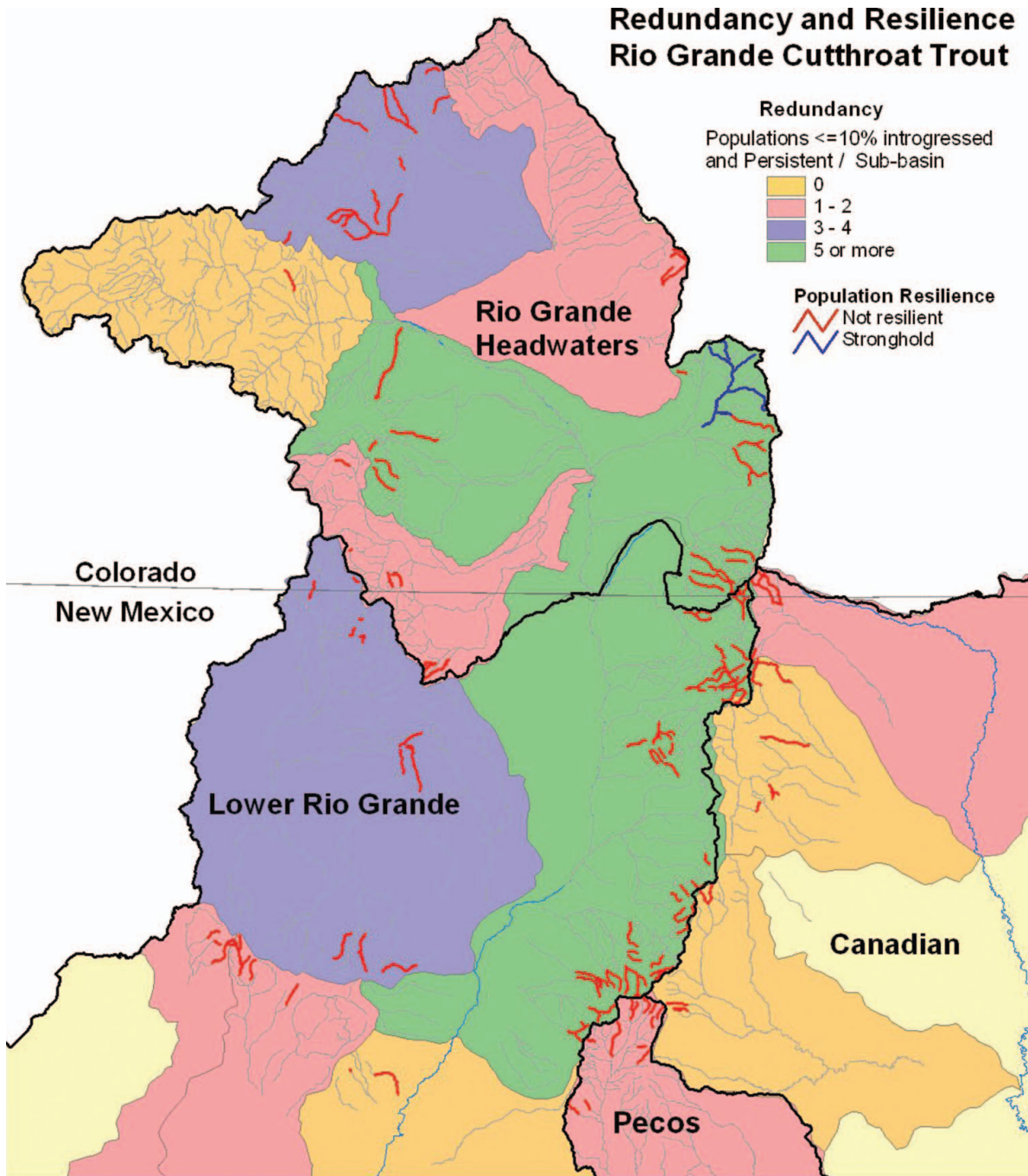


FIGURE 5. Distribution map for Rio Grande cutthroat trout, illustrating the resilience and redundancy components of the 3-R framework. Only one resilience element is present: a single stronghold (dark-blue stream system) in the Rio Grande headwaters. Redundancy is shown by the subbasin colors (e.g., green indicates subbasins that meet the goal of containing five or more persistent populations).

It is important to recognize the limitations in dealing with rangewide data on population size and genetic purity, as such limitations may have influenced the results of our 3-R analyses. First, data on population sizes and genetic integrity were collected by a variety of methods and agencies across various time periods. In particular, population size will vary as a function of

precipitation cycles (i.e., wet or dry periods), which influence the amount of habitat available to the population. In many areas, the genetic purity of native trout is declining more rapidly than monitoring efforts can keep up with invading nonnative trout species. Although agencies strive to maintain up-to-date population data, their task is daunting. As a result, data on individual

populations may be questionable even if they represent the best information available.

There is substantial evidence to suggest that risks to native trout from disturbances such as floods, drought, and wildfire are increasing as our climate changes (Brown et al. 2001; Williams and Meka Carter 2009; Haak et al. 2010a). In many western states, there is already evidence for winter snowpack reductions and streamflow alterations that appear to be caused by rapid climate change during the past four to five decades (Kapnick and Hall 2009; Luce and Holden 2009; Clark 2010; Fu et al. 2010). Fisheries managers have many tools, including various forms of restoration and reintroduction, to cope with these changes, and many agencies are actively engaged in such efforts. Herein, we offer an approach to climate change adaptation that decreases the likelihood of biodiversity loss by maintaining or increasing genetic, geographic, and life history diversity across the historical range. Such changes may be viewed as a “no-regrets approach” because the actions proposed cause no harm and increase future management options. Application of portfolio theory to native fish conservation should be helpful in recognizing existing conservation gaps and for prioritizing future management actions.

Management Implications

Nonnative salmonids threaten the persistence of Yellowstone cutthroat trout primarily through hybridization and predation (Gresswell 1995). Predation and competition are particularly problematic in Yellowstone Lake, where an illegal introduction of lake trout *Salvelinus namaycush* has caused a substantial decline in the abundance of native cutthroat trout in the lake and major tributaries (Koel et al. 2010). Rangelwide, about 65% of the occupied stream habitat supports genetically pure fish, with the lower Snake River drainage containing the highest levels of hybridization. An increased management emphasis on protecting genetic purity by isolating populations above barriers has occurred at the expense of migratory life histories, leaving resident populations more vulnerable to stochastic events (Fausch et al. 2006, 2009).

Although the rangelwide portfolio for Yellowstone cutthroat trout contains a wide range of desired elements, our analysis suggests that strategic additions could augment the present portfolio and thus protect this subspecies from existing and future threats. Small, isolated, genetically pure populations are relatively common and should be protected. Expansion and reconnection of populations to create larger, more resilient strongholds and metapopulations are suggested, particularly at the lower elevations and at range margins, where habitat fragmentation has already significantly reduced the geographic representation of this subspecies. For example, populations in the Goose Creek drainage in the southwestern edge of the historical range offer an opportunity to secure an interconnected metapopulation, but hybridization is a problem for the existing populations in that drainage. Efforts to control lake trout in Yellowstone Lake are vital to securing core habitat and restoring what was once the largest metapopulation of Yellowstone cutthroat trout. Only

one small population remains in the Tongue River basin, where reintroduction efforts could increase geographic diversity and redundancy. The Greybull River subbasin offers an opportunity to reestablish a larger, more resilient population by reconnecting the remaining genetically pure populations in the area. More specific recommendations will benefit from analysis of climate risk factors in these areas (e.g., Haak et al. 2010a) as well as more site-specific knowledge, which is beyond the scope of this analysis.

For Rio Grande cutthroat trout, much of the decline can be attributed to habitat degradation from livestock grazing, timber harvest, and water diversions and to competition from and hybridization with introduced rainbow trout *O. mykiss* and nonnative cutthroat trout (Rinne 1995). To protect them from nonnative trout, many populations have been isolated above in-stream barriers, resulting in the retention of genetic purity but also the loss of larger, more resilient populations.

Available stream habitat is a major limitation for this subspecies and greatly restricts management options. According to recent surveys, 67% of Rio Grande cutthroat trout populations occur in streams with streamflows less than 0.028 m³/s (1 ft³/s; A. Todd, USGS, unpublished data). Clearly, there are limited opportunities for establishing larger stronghold populations in this arid region, but given the high risk from drought, wildfire, and other climate-related disturbances (Haak et al. 2010a), all potential options should be closely analyzed. The Rio Costilla watershed restoration project represents a multiyear effort that is underway to restore populations and connectivity within the headwaters of the lower Rio Grande near the Colorado–New Mexico border (J. McGurrin, Trout Unlimited, personal communication). Completing this project and establishing one or two additional large-scale restoration efforts would greatly improve resilience.

The headwaters of the Pecos River above its confluence with the Rio Mora historically provided more than 170 km of stream habitat, yet less than one-third of this area is currently occupied by Rio Grande cutthroat trout (Alves et al. 2008). The higher elevation in this area provides some security from the drought conditions and higher temperatures that plague much of the subspecies' range (Haak et al. 2010a) and appears to be a good candidate for reintroduction efforts. High-elevation streams in the Rio Grande headwaters have similarly low climate change risk. Given the lack of resilience throughout the subspecies' portfolio and the inherent risk to isolated populations from stochastic events (e.g., wildfire, flood, and drought), it is particularly important to build redundancy.

Our case studies also highlight the importance of regularly collecting and reporting high-quality, population-specific data for these fishes. During recent years, state and federal agencies and their nongovernmental partner organizations have made significant progress in the collection of such information, yet many gaps remain. If the future will be characterized by as much environmental change as is anticipated by a growing number of scientists (e.g., Wenger et al. 2011), then the importance of

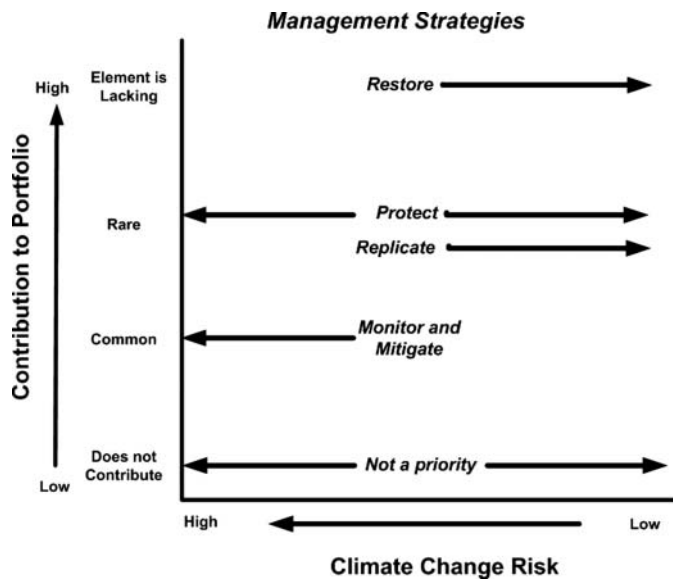


FIGURE 6. Conceptual model for prioritizing management actions based on a given population's conservation value to the portfolio versus the population's climate change risk. Highest management priorities are given to populations that are contributing a rare element in the portfolio and that occur in areas with a predicted low risk of being affected by climate change. Low management priorities are given to populations that (1) do not contribute to the portfolio or are very common in the portfolio and (2) occur in areas of high climate change risk. Haak et al. (2010a) provide general climate change risk maps for most inland trout species in the western USA.

building consistent, long-term monitoring data sets cannot be overemphasized. Better data and long-term monitoring would be beneficial to any future application of the portfolio theory.

Figure 6 provides a conceptual model for prioritizing management strategies for a given trout species or subspecies based on the conservation portfolio and risk from climate change. At the lowest level, hybridized resident populations do not contribute to the portfolio and therefore do not warrant any focused management efforts regardless of the climate change risk. Isolated, genetically pure populations, which are the most common portfolio element for both subspecies analyzed herein, should be monitored in high-risk areas and, where necessary, habitat improvements should be implemented to mitigate some of the adverse impacts from climate change. The rare elements are those with limited occurrence in the portfolio from either the rangewide or GMU perspective. This may include genetically pure populations that are otherwise common rangewide but scarce in one GMU. When assessing the uniqueness of a particular population, it is important to keep in mind the intended conservation value of that population. For example, a peripheral population is unique within the portfolio, but if it is highly introgressed it may have lost its value as an important element of genetic diversity. Management efforts should focus on protecting these rare elements of diversity and replicating them where suitable habitat exists, especially in areas with a reduced threat from climate change impacts. Reduced threat from

climate change would be indicated, for example, if a watershed is sufficiently high in elevation to maintain a winter snow precipitation regime or if it is sufficiently low in fuel loading to reduce risk from high-intensity wildfire (see Haak et al. 2010a for other examples).

The 3-R framework may be most useful when interpreting diversity at the GMU or subbasin scale. When used at these scales, it can provide guidance on where to prioritize different management strategies within the context of what is feasible given local constraints. Due to current as well as historical conditions, diversity will never be equally distributed among GMUs. However, GMUs with a large number of genetically pure populations but little resilience may present opportunities to restore a stronghold if several isolated populations are located in a common drainage. In situations involving populations that are widely dispersed, building redundancy through replications and reintroductions may be the more appropriate strategy. The final decision on any management action will require weighing the conservation value of the population against the action's cost and feasibility as influenced by current conditions and future risks.

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