

Where might freshwater species persist in an arid state? Assessing aquatic refugia in New Mexico, U.S.A.

D. Max Smith^{*}, Megan M. Friggens, Karen C. Chaudhry

USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM 87102, USA

ARTICLE INFO

Keywords:

Aquatic refugia
Aquatic ecosystems
New Mexico
Precipitation
Temperature

ABSTRACT

Climate change is impacting freshwater ecosystems, which contain many species already threatened by anthropogenic activities. To help managers protect imperiled species, we developed a framework for assessing the potential for aquatic refugia within the state of New Mexico, U.S.A. We used literature review and state-generated lists of sensitive species and habitats to develop five taxa-specific habitat groups as targets for assessment (cold-water fish habitat, perennial streams, perennial water amphibian and reptile habitat, ephemeral catchments, and springs). We then selected sets of indicators representing macrorefugia (areas of relative climate stability) and hydrorefugia (local features that protect aquatic ecosystems from changes in temperature and precipitation) for each habitat group. Refugia scores, generated from standardized indicator values, showed considerable variation in refugia potential among habitat groups and geographic locations. In most cases, areas with greatest potential for hydrorefugia were separate from those with greatest potential for macrorefugia. Mountainous regions typically scored highest for potential refugia, highlighting the importance of these areas to a variety of aquatic species. Our results can be used to identify additional areas for conservation and to inform species-specific management plans.

1. Introduction

The aquatic fauna of the southwestern U.S. is characterized by species with unique adaptations to spatial and temporal variation in the availability of surface water. Examples include amphibians and invertebrates that emerge following years-long dormancy to reproduce in ephemeral lakes and ponds filled by rain (MacKay et al., 1990), fishes and invertebrates that tolerate high temperature and mineral concentrations in springs (Shuster, 1981; Williams et al., 1985), and fishes that retreat to perennial reaches when stream networks are fragmented by drought (Van Horn et al., 2022). Throughout the Southwest, the natural dynamics of waterbodies have been modified by dams, diversions, and pumps to meet growing water demands (Abdelmohsen et al., 2025; Sabo et al., 2010). Aquatic ecosystems have also been disrupted by introductions of nonnative species (Rinne, 1994). As a result of these changes, dozens of aquatic species are federally threatened or endangered, and several have been extirpated (Hoagstrom et al., 2010; Platania et al., 1991). These include fully aquatic taxa such as fishes, arthropods, and mollusks, as well as amphibians and reptiles that depend on freshwaters (NMGF, 2016).

By further altering the availability and quality of surface water, climate change poses an additional threat to aquatic species. Hydrological impacts of climate change are expected to be greatest at mid latitudes in areas where freshwater ecosystems have already been heavily modified, such as the southwestern U.S. (Strayer, 2006). Documented impacts include increases in stream temperatures (Isaak et al., 2018; Sadayappan and Li, 2025), reduction in snowpack (Elias et al., 2021; Harpold et al., 2012; Mote et al., 2005; Stewart, 2009), reduction in runoff efficiency (Chavarria and Gutzler, 2018; Lehner et al., 2018; Woodhouse et al., 2016), and seasonal reductions in precipitation (Rumsey et al., 2020; Woodhouse and Udall, 2022). Increases in air temperature have been observed throughout the southwestern U.S., but the region's complex topography and vegetation create heterogeneity in the response of hydrological characteristics such as stream volume, stream temperature, and peak flow timing (Lehner et al., 2018; Zeigler et al., 2012). Areas that are less hydrologically impacted could therefore protect aquatic species in a warming climate. Additionally, features such as aquifers and springs can maintain persistence and quality of surface water during periods of drought (Walters et al., 2024). These observations suggest that certain watersheds have the capacity to buffer

^{*} Corresponding author.

E-mail addresses: david.smith3@usda.gov (D.M. Smith), megan.friggens@usda.gov (M.M. Friggens), karen.cooperchaudhry@usda.gov (K.C. Chaudhry).

<https://doi.org/10.1016/j.ecolind.2026.115391>

Received 16 January 2026; Received in revised form 3 August 2026; Accepted 24 August 2026

Available online 31 August 2026

1470-160X/Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

River Basins and Conservation Opportunity Areas

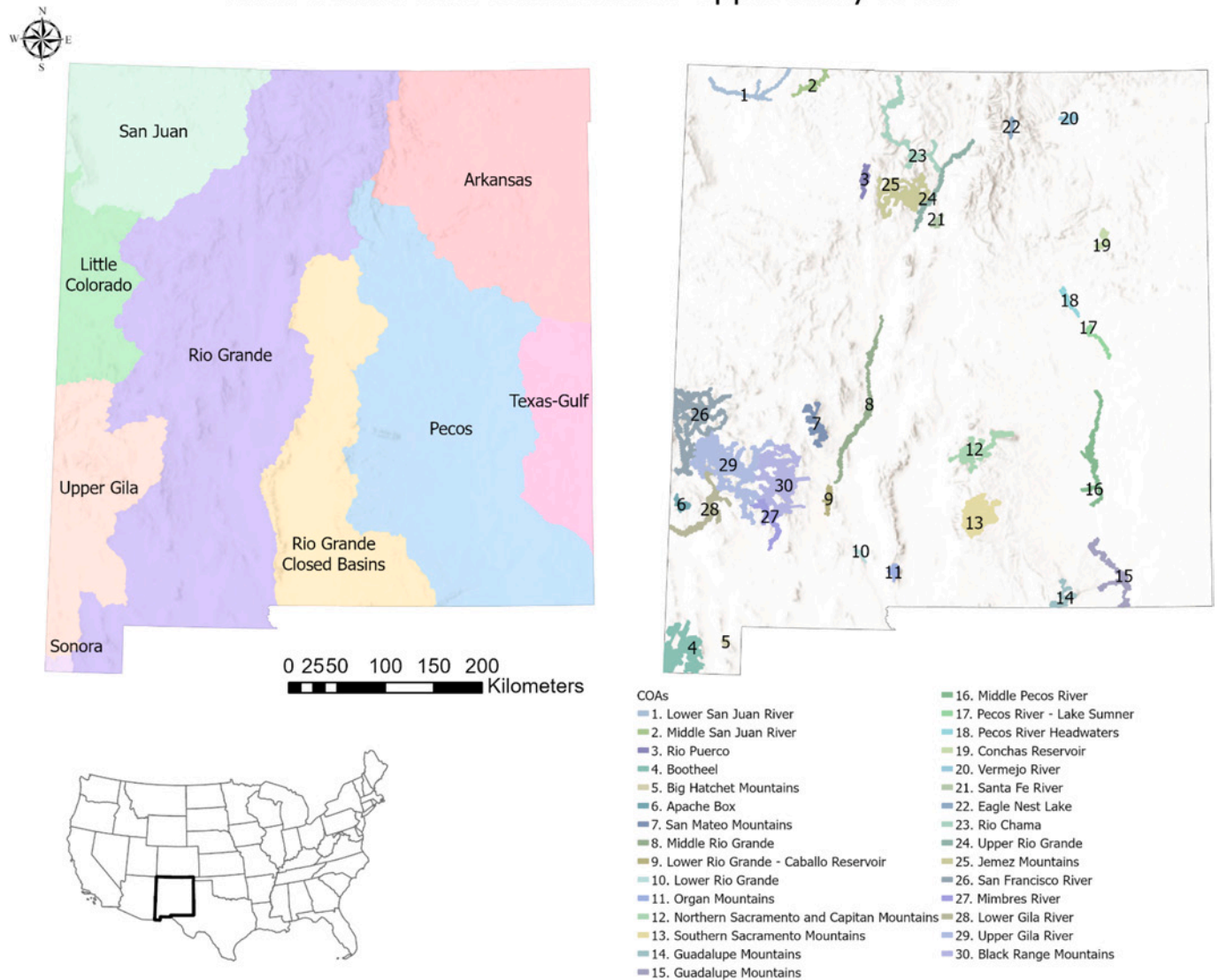


Fig. 1. Major river basins (left) and Conservation Opportunity Areas (right) within New Mexico.

aquatic ecosystems from impacts of climate change.

Climate refugia are locations that remain suitable for species persistence as the climate changes (Ashcroft, 2010). For aquatic animals, such as salmonid fishes, refugia have been identified at various spatial and temporal scales, from macrorefugia that buffer populations against future climate changes across landscapes, to localized hydrological features that protect individuals or populations from disturbance (Isaak and Young, 2023; Sedell et al., 1990). Local features are defined as hydrological or thermal *refuges* if individuals move to them for temporary relief. Alternatively, hydrological features are considered *refugia* if entire populations are buffered from unfavorable conditions long enough to allow persistence (Sullivan et al., 2021). Examples of aquatic refuges and refugia include stream reaches that remain watered or cool during hot and dry periods (Cushway and Schwalb, 2024; Ebersole et al., 2003; Magoulick and Kobza, 2003), springs that continue to flow during droughts (Cartwright and Johnson, 2018), and ephemeral pools that are decoupled from changes in precipitation and temperature (Cartwright et al., 2022).

Methods to assess climate vulnerability or refugia potential include analyses of biodiversity or physical habitat features. For example, studies have examined influences of topography (Cartwright and

Johnson, 2018), geomorphology (Ebersole et al., 2003; Gombert et al., 2023) lithology (Ishiyama et al., 2023), soils (Cartwright et al., 2020), and vegetation (Ebersole et al., 2003) on aquatic refugia potential, as well as their influence on freshwater biodiversity (Craig et al., 2016; Hollien et al., 2023). Aquatic refugia have been specifically evaluated for stream-dwelling fishes, species dependent upon springs, and amphibians that breed in ephemeral pools (Cartwright and Johnson, 2018; Cartwright et al., 2022; Isaak et al., 2015). However, a joint assessment across these and other taxa is needed for managers to prioritize large-scale conservation efforts in response to climate change. Managers can use this information to prioritize restoration or protection of aquatic habitats to protect imperiled species (Zeigler et al., 2012).

We developed a spatial climate refugia analysis, with results applied to current conservation planning efforts in the state of New Mexico, U.S. A. Our objectives were to 1) identify different types of aquatic refugia within the state; 2) select potential indicators of refugia for aquatic taxa; and 3) evaluate the potential for existing Conservation Opportunity Areas to provide climate refugia. New Mexico's unique assemblage of surface water and groundwater networks support highly specialized aquatic ecosystems, including cold-water mountain streams, karstic springs, and desert playas (Eastoe and Rodney, 2014; Haukos and Smith,

A.

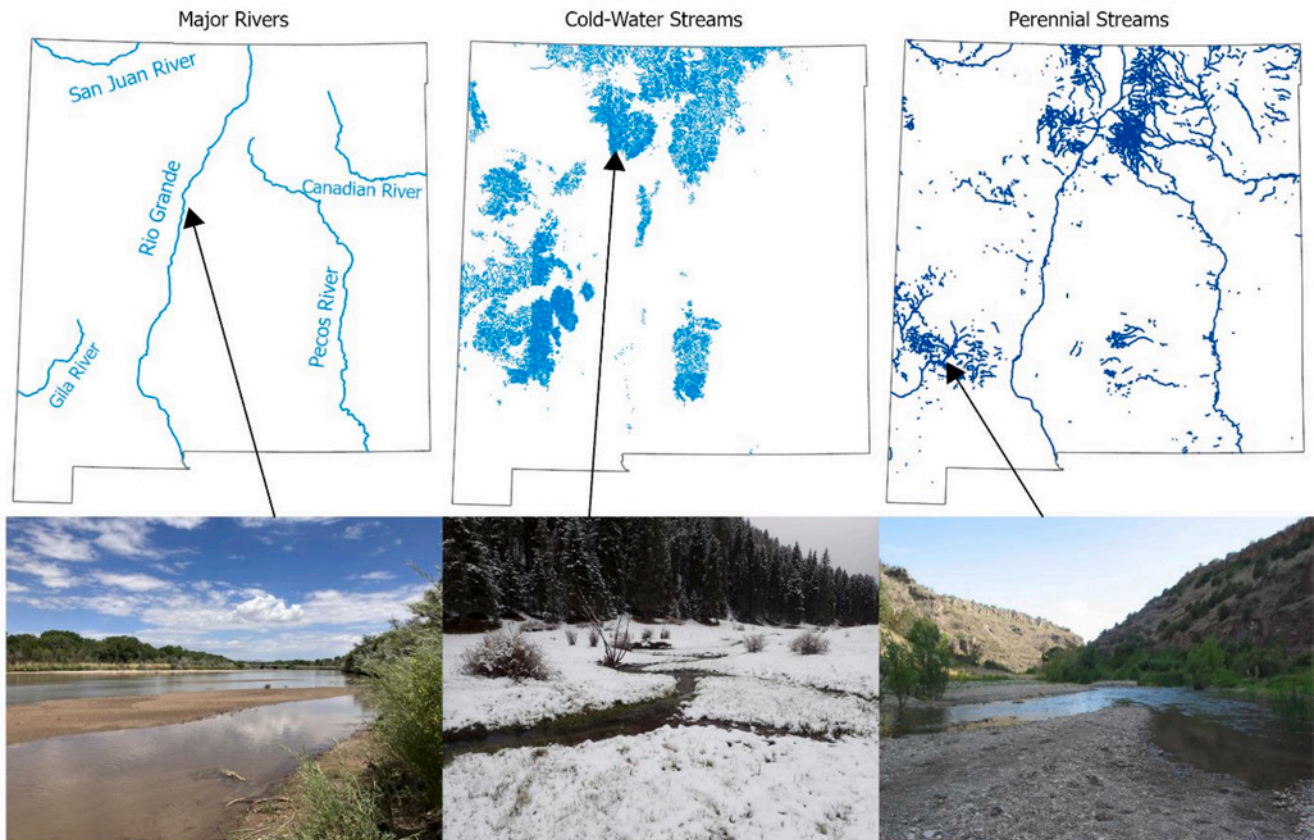


Fig. 2. Distribution and examples of (A) stream-based aquatic habitats and (B) lakes, ponds, reservoirs, playas, and springs in New Mexico. Photos by D. max Smith.

1994; Zeigler et al., 2012). These features provided an ideal opportunity to develop an aquatic refugia analysis critical to the protection of biodiversity in the southwestern U.S.A,

2. Methods

2.1. Study area

Our analysis is focused within the state of New Mexico, encompassing an area of 315,194 km², ranging in elevations from 867 to 4013 m. Within New Mexico's boundaries are several major rivers, including the Rio Grande, which flows north to south, bisecting the state. Other rivers include the Canadian River of the Arkansas River Basin, the Gila River of the Lower Colorado Basin, the San Juan River of the Upper Colorado Basin, and the Pecos River of the Rio Grande Basin (Fig. 1). Within the state are 19 Pueblos, Navajo and Apache Reservations, and the traditional territories of other Indigenous groups. Although much of New Mexico is considered arid, the state contains a variety of aquatic ecosystems including 11,058 km of cold-water streams; 9474 km of perennial warm-water streams; thousands of lakes, reservoirs, and ponds (Fig. 2); and many specialized organisms dependent on surface water and groundwater (NMDGF, 2016).

A variety of aquifer systems affect the movement and storage of groundwater, which in turn influences the distribution and dynamics of springs and perennial streams throughout the state. Major aquifer systems include carbonate aquifers in the Sacramento Mountains and Roswell Basin in the southeastern part of the state (Eastoe and Rodney,

2014), the Rio Grande Basin-fill Aquifer system that runs through the central part of the state (Bexfield, 2010), and the High Plains Aquifer in the eastern part of the state (Rawling and Rinehart, 2017). There are also smaller, locally important sources of groundwater such as the volcanic and carbonate aquifers of the Jemez Mountains (Trainer, 1974). Playa lakes and other catchments are important sources of recharge for the High Plains Aquifer and other groundwater systems (McKenna and Sala, 2017; Smith et al., 2011).

This project was designed to facilitate the efforts of the New Mexico Department of Game and Fish (NMDGF) to identify areas to implement climate-smart conservation actions as part of their 2025 comprehensive review and revision of the State Wildlife Action Plan (SWAP; NMGE, 2016, <https://nmswap.org/>). As part of their statewide effort to sustainably manage non-game wildlife within New Mexico, the NMDGF has identified Conservation Opportunity Areas (COAs; Fig. 1) that contain an exceptionally high level of Species of Greatest Conservation Need (SGCN), diversity, and higher-value habitats for wildlife. Implementing conservation actions within these COAs may be especially beneficial for a variety of SGCN and their habitats (NMDGF, 2016).

2.2. Literature review

We searched for government documents and scientific literature to identify targets for our assessment and generate a list of aquatic refugia indicators. We began by using information from the SWAP (NMDGF, 2016) to inform our selection of focal habitats and taxa. The SWAP describes eight aquatic habitats: perennial cold-water streams; perennial

B.

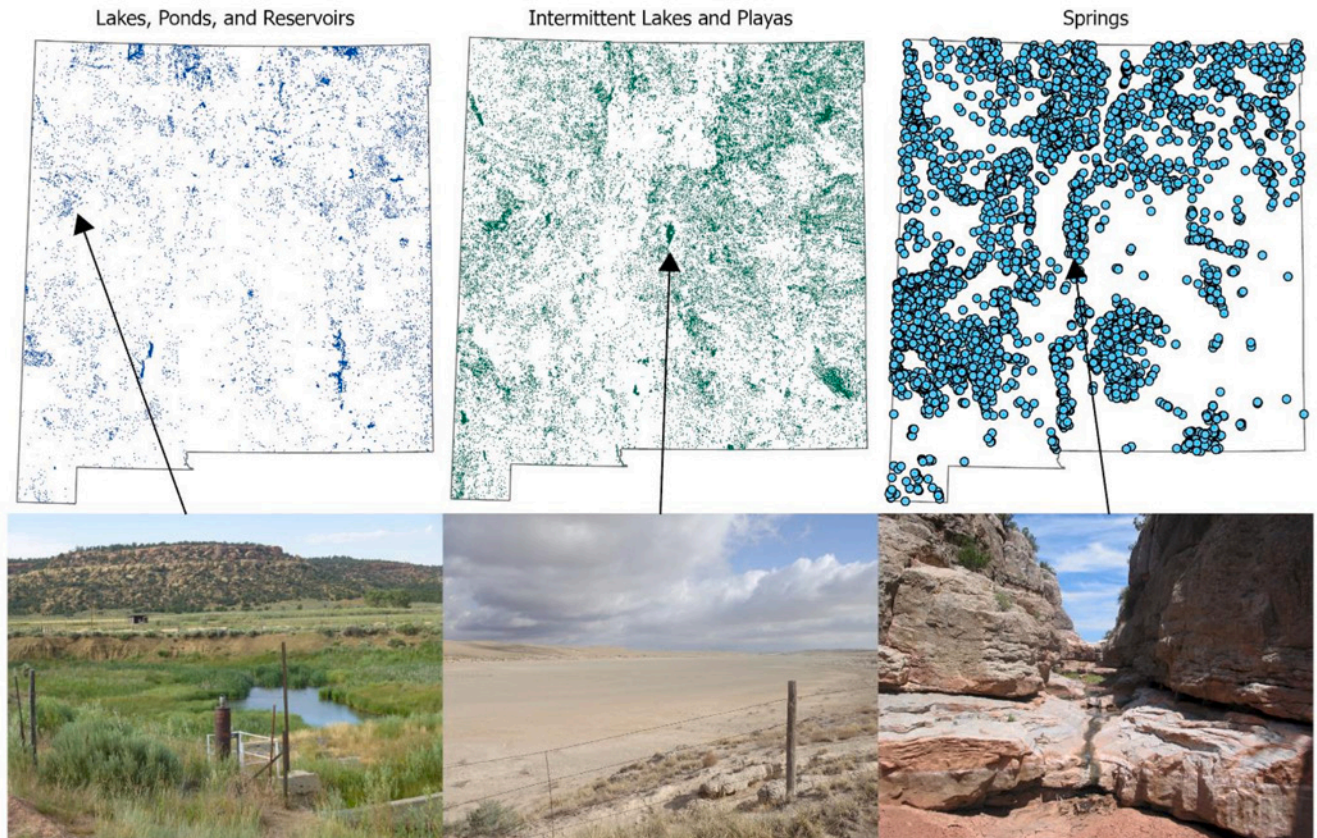


Fig. 2. (continued).

warm-water streams; perennial lakes, cirques, and ponds; perennial marshes, cienegas, springs, and seeps; perennial cold-water reservoirs; perennial warm-water reservoirs; ephemeral marshes, cienegas, and springs; and ephemeral catchments. The SWAP also lists SGCN. We selected taxa from this list that are entirely aquatic or are dependent on aquatic ecosystems for a considerable portion of their lives. These taxa are fishes, amphibians, reptiles (garter snakes, water snakes, and turtles), and invertebrates. We reviewed the scientific literature and species profiles in the Biota Information System of New Mexico (BISON-M database; bison-m.org) for species within these groups to identify their aquatic habitat needs in the southwestern U.S. By identifying areas of overlap between aquatic SGCN habitat needs and the aquatic habitats in the SWAP, we developed five habitat groups for assessment: (1) cold-water fish habitat, (2) perennial streams, (3) perennial water amphibian and reptile habitat, (4) ephemeral catchments, and (5) springs. We describe the habitat groups in greater detail in Appendix A, Section S1.

We also searched for literature that described climate impacts from direct changes in precipitation, temperature, and related changes in water volume and water quality. We limited papers and documents to those that discussed responses of aquatic species and ecosystems to climate impacts. We searched online databases (e.g., Google Scholar [<https://scholar.google.com/>]; TreeSearch [<https://research.fs.usda.gov/treesearch>]) for papers that included the terms “climate change + aquatic + refugia.” We also included the five habitat groups into the search (e.g., “climate change + refugia + cold-water fish habitat”).

2.3. Spatial data preparation

2.3.1. Base layers

To measure potential refugia across the entire state of NM, we analyzed indicators and created composite indices for 12th-digit hydrologic unit code boundaries, referred to hereafter as HUC12s. We downloaded boundary shapefiles for HUC12s from the U.S. Geological Survey (USGS) National Record Clearinghouse (now National Map at <https://apps.nationalmap.gov/downloader/>). In 2025, we obtained a newly revised shapefile representing 30 COAs from NMDGF (Fig. 1). We projected spatial data into the NAD 1983 UTM Zone 13 N coordinate system and clipped all layers to the state of New Mexico. Preparation and analysis of data were completed using ArcGIS Pro 3.3.6 (Esri Inc., 2024) and R 3.4.4 (R Core Team, 2021) statistical software.

We determined the statewide extent of analysis for each habitat group by selecting HUC12s that were likely to contain key features. As a result, the number of HUC12s and COAs assessed varied among the five habitat groups. The extent of cold-water fish habitat and perennial streams is limited in New Mexico; these habitat groups therefore had the smallest number of HUC12s included for analysis. For cold-water fish habitat, we selected stream reaches from the NORWEST database with modeled current summer stream temperatures of 17 °C or less (Wahlberg et al., 2023). HUC12s containing any of these stream segments were included in the analysis for cold-water fish habitat. When examining overlap with COAs, we excluded HUC12s from cold-water fish habitat analysis if the cold-water stream segments did not overlap the COA boundaries. For perennial streams, we merged National Hydrography Dataset (<https://www.usgs.gov/national-hydrography/>)

[national-hydrography-dataset](#)) reaches with flowline fcode 46,006 (which represents perennial stream reaches) with an ArcGIS Online Major Rivers of the U.S. shapefile. HUC12s containing these merged stream segments were included in the analysis for perennial streams. We initially included all New Mexico HUC12s for analysis of perennial water amphibian and reptile habitat, but we later excluded HUC12s that lacked indicator data (described below) that were specific to the habitat needs of these taxa. Ephemeral catchments and springs are widespread in the state (Fig. 2) and therefore we included all the state's HUC12s in those analyses, apart from those lacking indicator data.

2.3.2. Value metrics

For each habitat group, we calculated two metrics of conservation value. These metrics were used to evaluate refugia variables and to test for alignment of refugia potential with existing resources. For each habitat group, we calculated one metric based on physical habitat features and another on species richness, a measure of biotic value. Data sources and methods are listed in Appendix A, Section S2.

We summarized hydrologic spatial data to create metrics of value based on availability of specific habitat features. For cold-water fish habitat, we calculated the percentage of stream reaches in each HUC12 that were currently colder than ideal temperatures for salmonids ($\leq 10^\circ\text{C}$) but are assumed to have suitable temperatures in a future climate when currently suitable reaches are too warm (Appendix A, Section S2). For perennial streams, we calculated the percentage of stream reaches currently classified as perennial in each HUC12. For perennial water amphibian and reptile habitat, we obtained total waterbody area (lakes, ponds, reservoirs, estuaries, playas, swamps, and marshes) for each HUC12. For ephemeral catchments, we calculated the percent coverage of waterbodies classified as playas or intermittent lakes for each HUC12. Finally, for springs, we calculated the density of springs mapped in each HUC12.

We used spatial data to estimate species richness of four taxa groups: fishes (for cold-water fish habitat and perennial streams), ephemeral catchment-dependent amphibians (for ephemeral catchments), perennial water-dependent amphibians and reptiles (for perennial water amphibian and reptile habitat), and native aquatic species (for springs). For fishes, ephemeral catchment-dependent amphibians, and perennial water-dependent amphibians and reptiles, we downloaded shapefiles of species distributions and then calculated the number of native species with ranges that overlap each HUC12 (species listed in Appendix A, Tables S1–S3). We used lists compiled by NMDGF to differentiate between native and introduced species and excluded introduced species (most of which are fishes) from our estimates. We used a preprocessed shapefile to calculate total native aquatic species richness for each HUC12.

2.3.3. Refugia indicators

2.3.3.1. Approach and terminology. We selected indicators of refugia separately for each habitat group because we expected considerable variation in the dynamics of different aquatic habitats and in the responses of associated species to changes in temperature and precipitation. For each group, we selected indicators for two types of refugia: hydrefugia and macrorefugia. *Macrorefugia* represent areas with sustained climatic suitability across broad spatial and temporal gradients (Isaak and Young, 2023; Stralberg et al., 2018). *Macrorefugia* indicators were measures of projected changes in precipitation, temperature, and variables derived from precipitation and temperature. We used these indicators to identify watersheds that are expected to have smaller changes relative to regional climate projections (in terms of air temperature, precipitation, streamflow volume, and water temperature). We define *hydrefugia* as local features that, by maintaining the stability of water volume and/or quality, have the potential to influence persistence of species during climate change. Areas with high potential for

Table 1

List of variables selected as indicators to identify climate refugia. *Macrorefugia* represents expected changes in climatic conditions. *Hydrefugia* are associated with soil properties, lithology, topography, vegetation, and landscape heterogeneity. Climate datasets are derived from future climate projections for mid-century time periods (~2050) under a Coupled Model Intercomparison Project 5 (CMIP5), Representative Concentration Pathway 4.5 greenhouse gas emission scenario. Backwards Velocity is a multidimensional (consider both precipitation and temperature) measure of climate. Variables were compared and selected through an iterative process using Random Forest and Linear Regression Methods. Group abbreviations: All = all habitat groups, AmpRep = Perennial Water Amphibian and Reptile Habitat, ColWat = Cold-Water Fish Habitat, EphCat = Ephemeral Catchments, PerStr = Perennial Streams, Spr = Springs. Variable abbreviations: Change = Change from current to future conditions, Diff = Difference, Max = Maximum, Pct = Percent, Precip = Precipitation, SDI = Shannon Diversity Index, and Temp = Temperature.

Macrorefugia indicator	Group(s)	Expected relationship with value metrics and refugia
Backwards Climate Velocity	AmpRep, ColWat, EphCat	Negative
Change Soil Moisture Content (SMC)	EphCat	Positive
Change Snow Water Equivalent (SWE)	AmpRep, ColWat, PerStr, Spr	Positive
Change Evapotranspiration (ET)	AmpRep, EphCat	Negative
Change Potential Evapotranspiration of Natural Vegetation (PNV)	ColWat, PerStr, Spr	Negative
Diff Max Temp Warmest Month (Bio5)	AmpRep, ColWat, EphCat, PerStr	Negative
Diff Mean Temp Wettest Quarter (Bio8)	AmpRep, ColWat, PerStr, Spr	Negative
Diff Mean Temp Driest Quarter (Bio9)	All	Negative
Pct Change Precip Driest Month (Bio14)	EphCat	Positive
Pct Change Precip Wettest Month (Bio13)	PerStr	Positive
Pct Change Precip Warmest Quarter (Bio18)	AmpRep, ColWat, EphCat	Positive
Pct Change Precip Coldest Quarter (Bio19)	AmpRep, ColWat, PerStr, Spr	Positive
Pct Change June Streamflow Volume	AmpRep, ColWat, PerStr	Positive
Pct Change August Stream Temp	ColWat	Negative
Hydrefugia indicator		
Topography		
Mean Compound Topographic Index	AmpRep, EphCat	Positive
Mean Elevation	AmpRep, ColWat, PerStr	Positive
Mean Heat Load Index	AmpRep, ColWat, EphCat, Spr	Negative
Mean SDI for Aspect	AmpRep, ColWat, EphCat	Positive
Mean SDI for Geomorphology	AmpRep, ColWat, EphCat	Positive
Mean Vector Ruggedness	Spr	Positive
Lithology		
Aquifer Richness	PerStr, Spr	Positive
Pct Carbonate Karst	AmpRep, ColWat, PerStr, Spr	Positive
Pct Volcanic Karst	ColWat, PerStr, Spr	Positive
Pct Unconsolidated Aquifers	PerStr	Positive
Soils		
Mean Soil Bulk Density	AmpRep, ColWat, PerStr, Spr	Negative

(continued on next page)

Table 1 (continued)

Macrorefugia indicator	Group(s)	Expected relationship with value metrics and refugia
Mean Soil Water Storage	AmpRep	Positive
Pct Slow-Infiltrating Soils	EphCat	Positive
Vegetation		
Mean Riparian Canopy Height	AmpRep, ColWat	Positive
Pct Marsh/Wet Meadow	AmpRep,	Positive
Vegetation	ColWat, PerStr	
Pct Riparian Woodland/Shrubland	ColWat	Positive
Pct Stream Buffer with Tree Canopy	AmpRep, ColWat	Positive

hydrorefugia may contain cold-water stream segments (Isaak and Young, 2023), springs (Cartwright et al., 2020; Davis et al., 2013), and frequently inundated pools (Cartwright et al., 2022). We consider these features to be types of refugia because of their potential to influence range dynamics of aquatic species (Keppel et al., 2012). Hydrorefugia indicators were characteristics of lithology, soils, topography, and vegetation likely to influence the volume and/or temperature of water available for aquatic organisms (described in Appendix A, Section S2 and listed in Table S4). These variables represent potential buffers against extreme conditions such as loss of surface water and increased stream temperature. We later selected a subset of these variables to be indicators.

We identified areas of potentially greater stability (macrorefugia) based on the calculated change between current and future climate variables as well as climate indices representing relative conditions across the landscape. We obtained pre-processed climate output from multiple research platforms (Appendix A, Section S2), which vary in projection periods, number of climate models considered, and emission scenarios. These differences likely influence comparability among the selected macrorefugia variables (Table 1), but for this analysis we were focused on spatial variability with each variable.

We summarized indicator values and calculated composite refugia scores for HUC12 watersheds, which are components of larger watersheds. For habitats that are influenced by the movement of surface water and/or groundwater (e.g., streams and springs), habitat dynamics within a HUC12 may be influenced by dynamics occurring at scales larger than the HUC12 (Strayer, 2006; Yang et al., 2025). We therefore summarized indicators involving movement of surface water or groundwater at the larger HUC8 scale for cold-water fish habitat, perennial streams, perennial water amphibian and reptile habitat, and springs. We then applied indicator values summarized at the HUC8 scale to the HUC12s within each HUC8.

2.4. Indicator selection

We established separate workflows to analyze A) macrorefugia variables representing climate data; and B) hydrorefugia variables representing topography, lithology, soils, and vegetation (Appendix A, Fig. S1). We conducted a series of preliminary analyses to reduce variables processed at the HUC12 scale and identify which variables provide the most meaningful information for each habitat group. The steps were: 1) Select initial value sets for each habitat group based on literature review. 2) Use our professional judgement to determine which variables are most applicable to each habitat group. 3) Use Forest-based and Boosted Classification and Regression for an initial reduction of variables. 4) Test the remaining variables for intercorrelations, outliers, or unexpected relationships with value metrics. Together, these processes led to a final set of indicators (Table 1) that contributed unique knowledge to our final composite score.

We used the Forest-based algorithm of the Forest-based and Boosted Classification and Regression Tool (Random Forest; RF) in ArcGIS Pro to test the relationship between certain hydrorefugia variables (lithology,

soils, and topography) and value metrics for each habitat group. We applied this analysis only to these variables because, prior to testing, we expected many of them to be redundant and to have the strongest influence, as a group, on value metrics (species richness and density of habitat features). Also, the relatively large number of potential variables in this group necessitated a quantitative approach for reduction. We did not apply RF to the vegetation variables, which were smaller in number. Random Forest builds multiple decision trees based on random subsets of data and predictor variables and averages resulting predictions to improve prediction accuracy and reduce overfitting (Breiman, 2001). We used RF models to identify variables that were most important for predicting value metrics while accounting for complex non-linear relationships and interactions (Cutler et al., 2007; Evans et al., 2011). We tested model performance using a split sample validation approach where 15% of observations were withheld from each model run and used for an independent test of model accuracy. We tested prediction stability by running each model 3 times with different random splits. For each habitat group, we ranked the examined hydrorefugia variables based on RF importance scores for species richness and habitat features (Appendix A, Table S5). For habitat groups with greater than 10 of these variables, we dropped variables if they ranked in the bottom 20% for both species richness and habitat features.

We evaluated the remaining variables using Pearson correlations and the Exploratory Regression (Ordinary Least Squares [OLS]) Tool in ArcGIS Pro. We conducted separate analyses for each set of macrorefugia and hydrorefugia indicators and used an iterative process based on correlations and OLS to identify redundancies, biases, and performance among each set of variables. Our goal was to reduce our indicator set by removing those that held redundant information, which at this stage was determined by the presence of strong linear correlations in raw values. We implemented OLS using default parameters, including a correlation coefficient cutoff of 0.7 and a maximum Variance Inflation Factor (VIF) of 7.5. Where multicollinearity was found ($VIF > 7.5$), we removed variables with the highest VIF scores and reran the tool on the remaining subset. We repeated this process until no variables had a $VIF > 7.41$. Where variables had similar VIFs, we considered the summary of variable significance to identify “good” (significant [i.e., higher percent significance] and consistent relationship) indicators for retention and “poor” (less significant or more varied relationship) indicators for exclusion. We used results indicating the significance and sign of variable coefficients, as well as results from literature review, to evaluate potential relationships between refugia indicators and value metrics for each habitat group. Where we found significant ($p < 0.05$) and strong ($r > 0.70$) Pearson correlations within variable groups, we used the criteria described above to determine which variables to drop, and which to include in the analysis.

2.5. Optimization and calculation of refugia scores

After obtaining final sets of indicators to represent macrorefugia and hydrorefugia (Table 1), we transformed their raw values in HUC12s using Z scores to reduce potential biases arising from variation in the distributions of different metrics (Becker et al., 2017). Prior to standardization, we identified variables with theoretically expected negative relationships with multiplied variables with species richness, habitat features, or refugia. We multiplied the raw values of these variables by -1 . Resulting Z scores, which typically fall between -4 and $+4$, were then used in optimization routines and to calculate final refugia scores, where higher scores indicated greater refugia potential. Standardizing variables often led to new correlations among variables, which were noted during weight optimization runs. Where found, we dropped additional variables until no two in the same category had a strong Pearson correlation coefficient ($r > 0.70$).

We used a constrained linear optimization routine to define indicator weights to ensure that each standardized indicator contributed equally to the final composite scores for hydrorefugia and macrorefugia

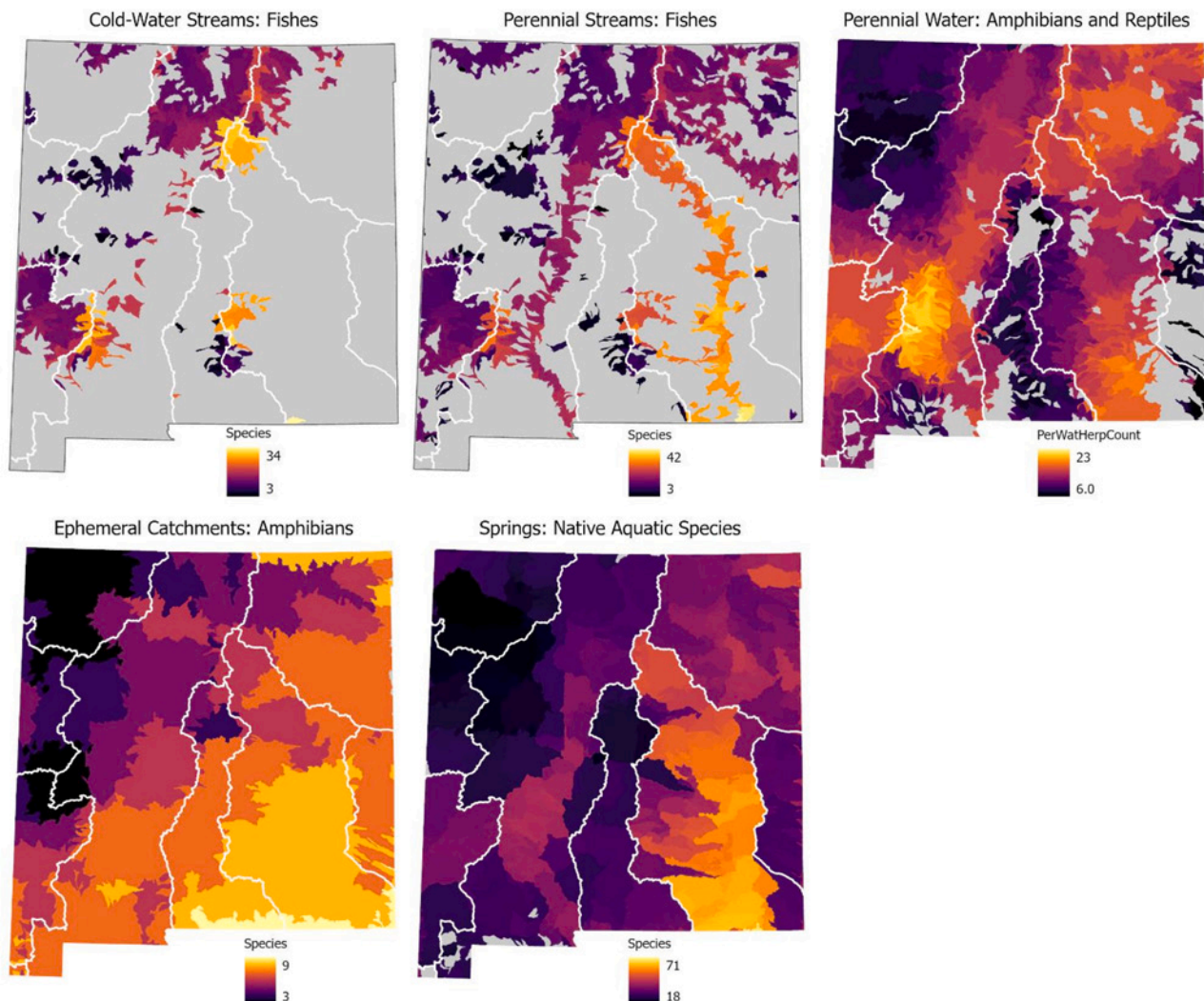


Fig. 3. Biotic value metrics (species richness) for animals associated with the five aquatic habitat groups assessed for climate refugia.

(Paruolo et al., 2013; Becker et al., 2017). This approach addresses scale differences among indicators and prevents any single variable from disproportionately influencing refugia classification due to its statistical structure rather than ecological relevance. Weights were optimized using the COBYLA (Constrained by Linear Approximation) optimization algorithm implemented in SciPy (<https://docs.scipy.org/doc/scipy/>) through the NLOpt function (non-linear optimization routines) in R 4.4.1 (see Appendix A, Section S3 and Tables S6 and S7 for descriptions and results). The COBYLA algorithm is a derivative-free method that searches for optimal weights without assuming the solution landscape is smooth (i.e. it can handle non-linear constraints). We included a minimum constrained weight of 0.05, maximum weight of 0.3, and required all weights to sum to 1. We included entropy and variance penalties to encourage spread of values and discourage uniform and extreme-weight distributions.

We calculated composite scores for macrorefugia and hydrefugia (for each habitat group) within each HUC12 as:

$$\text{Refugia composite score} = \sum_i^n a_i * x_i$$

where a is the optimized weight for group i and x is the indicator variable. Final refugia scores were standardized to a value between 0 and 1. Higher values represent greater potential for refugia to be present.

2.6. Conservation opportunity areas

To evaluate alignment of aquatic refugia potential with existing conservation planning efforts, we calculated mean refugia scores for each COA, from the HUC12s it overlapped. For each habitat group, we identified COAs with the highest mean refugia scores (top 20%) and compared scores with statewide means. We also calculated the percentage of each COA overlapping HUC12s with high levels of species richness and high densities of important habitat features. These HUC12s were in the 5th quantile (top 20%) of values calculated for each habitat group.

2.7. Sensitivity analysis and correlation comparison

We assessed the robustness of our refugia composite index through a sensitivity analysis that tested the influence of different weighting schemes on composite score performance. We compared our optimized equal-contribution weighting approach against two alternative methods: (1) equal arithmetic weights (weight = $1/n$), and (2) weights derived from the first principal component of a PCA (Appendix A, Table S6). For each scheme, we calculated composite indices and compared them to our baseline optimized index using Pearson correlation coefficients and spatial agreement (percentage of watersheds consistently ranked in top 20% of refugia scores across comparisons).

To determine whether Pearson correlations were the appropriate

Table 2

River basins in New Mexico with the highest mean value metric or mean refugia scores for each habitat group assessed. Means and standard deviation, calculated across 12th-digit hydrologic unit code watersheds (HUC12s), are shown. The top two greatest mean scores are in bold. Full summary statistics for all basins examined are included in Appendix A, Table S8. Macrorefugia are areas with sustained climatic suitability across broad spatial and temporal gradients. Hydrorefugia are areas where local features maintain the stability of water volume and/or quality.

Habitat group	Area	Biotic value mean (sd)	Habitat value mean (sd)	Hydrorefugia mean (sd)	Macrorefugia mean (sd)
Cold-water fish habitat	Arkansas River Basin	17.6 (4.1)	0.8 (2.0)	0.19 (0.11)	0.65 (0.09)
	Pecos River Basin	25.1 (7.7)	1.9 (5.0)	0.16 (0.10)	0.64 (0.10)
	Rio Grande Basin	14.7 (5.8)	1.3 (3.0)	0.21 (0.13)	0.63 (0.14)
	Gila River Basin	14.6 (4.3)	0.08 (0.3)	0.10 (0.06)	0.79 (0.07)
	Little Colorado River Basin	9.7 (3.6)	0	0.17 (0.10)	0.77 (0.13)
	Pecos River Basin	29.8 (6.1)	9.1 (7.5)	0.20 (0.07)	0.30 (0.13)
Perennial streams	Arkansas River Basin	16.6 (3.7)	13.1 (11.1)	0.24 (0.11)	0.50 (0.14)
	Little Colorado River Basin	8.5 (3.3)	6.6 (7.0)	0.25 (12)	0.62 (0.23)
	Rio Grande Closed Basins	9.2 (8.4)	3.6 (3.9)	0.25 (0.04)	0.17 (0.10)
	Rio Grande Basin	15.0 (5.7)	8.2 (9.6)	0.35 (0.17)	0.50 (0.20)
	Gila River Basin	14.4 (4.1)	7.7 (7.3)	0.16 (0.04)	0.68 (0.15)
	Gila River Basin	15.2 (2.0)	0.32 (2.40)	0.18 (0.05)	0.55 (0.10)
Perennial water amphibian and reptile habitat	Arkansas River Basin	14.8 (1.9)	0.37 (0.9)	0.20 (0.06)	0.32 (0.10)
	Texas Gulf Basin	8.1 (2.2)	0.69 (1.6)	0.12 (0.04)	0.29 (0.07)
	San Juan River Basin	8.4 (1.0)	0.40 (1.5)	0.18 (0.05)	0.49 (0.09)
	Rio Grande Closed Basins	9.6 (2.4)	0.26 (1.7)	0.21 (0.04)	0.22 (0.11)
	Rio Grande Basin	13.4 (3.2)	0.27 (1.3)	0.21 (0.08)	0.43 (0.13)
	Little Colorado River Basin	10.3 (2.9)	0.29 (0.4)	0.18 (0.03)	0.57 (0.16)
Ephemeral catchments	Pecos River Basin	7.5 (0.9)	0.20 (0.3)	0.38 (0.07)	0.32 (0.07)
	Texas Gulf Basin	7.2 (0.5)	0.30 (0.8)	0.34 (0.10)	0.33 (0.03)
	Gila River Basin	5.4 (1.4)	0.31 (3.1)	0.31 (0.08)	0.46 (0.05)
	Rio Grande Closed Basins	7.0 (1.3)	0.26 (1.3)	0.41 (0.12)	0.32 (0.10)
	Little Colorado River Basin	3.9 (0.7)	0.20 (0.4)	0.37 (0.05)	0.41 (0.07)
	Arkansas River Basin	38.3 (4.2)	0.02 (0.04)	0.29 (0.14)	0.57 (0.11)
Springs	Pecos River Basin	48.8 (10.6)	0.01 (0.01)	0.39 (0.19)	0.49 (0.11)
	Gila River Basin	32.3 (4.1)	0.04 (0.05)	0.29 (0.12)	0.68 (0.23)
	Rio Grande Closed Basins	28.0 (3.6)	0.02 (0.05)	0.50 (0.12)	0.38 (0.07)
	Rio Grande Basin	29.5 (6.4)	0.02 (0.04)	0.45 (0.02)	0.44 (0.14)

method for selecting indicators, we replicated pairwise correlations among variables using Spearman correlations. We applied the Spearman test to raw summaries of variables and to values that were standardized using Z scores. We compared results from the two methods to identify indicators that would not have been selected had Spearman correlation been used.

3. Results

3.1. Indicator selection

Our literature review yielded information on aquatic species and habitats in New Mexico, as well as variables impacting climate refugia (Appendix A, Section S1). We used this information to select conservation value metrics and refugia variables from which we developed our final refugia indicators. We selected 15 climate indicators to estimate macrorefugia (Table 1). Of these, seven were bioclimate indicators and eight were derived climate indicators. We selected 17 indicators for hydrorefugia. Six of the hydrorefugia indicators were measures of topography, four were measures of lithology, three were soil variables, and four were vegetation variables. The results from literature review and modeling produced different combinations of indicators for each habitat group.

3.2. Value metrics

Patterns in species richness, our indicator of biotic value, varied among taxa (Fig. 3). For several taxa groups mean species richness was greatest in the Arkansas River and Pecos River Basins (Table 2). In addition, species richness of perennial water-dependent amphibians and reptiles was high in the Gila River Basin and ephemeral catchment

species richness was high in the Texas Gulf Basin (see Appendix A, Table S8 for full summary statistics).

In terms of physical value indicators, the areas of New Mexico with the greatest importance also varied among habitat groups (Fig. 4). Mean percentage of stream segments with mean August stream temperatures of 10 degrees or less was greatest in the Pecos River and Rio Grande Basins (Table 2). The HUC12s with the greatest percentages of cold reaches were in the headwaters of these basins in northern New Mexico (Fig. 4). Mean percentage of stream segments that were perennial was greatest in the Arkansas River and Pecos River Basins. Waterbody area was greatest in the San Juan River and Texas Gulf Basins. Percent coverage of intermittent lake and playa was greatest in the Gila River and Texas Gulf Basins.

3.3. Refugia scores

For the most part, there was little overlap among parts of the state with high scores for value metrics, hydrorefugia, and macrorefugia. Across habitat groups, mean hydrorefugia scores were highest in the Rio Grande Basin, and the Rio Grande Closed Basins, while mean macrorefugia scores were highest in the Gila River and Little Colorado Basins (Table 2). Areas with the greatest mean value metrics, such as the Pecos River Basin and the Texas Gulf Basin, typically had relatively low mean refugia scores.

Our application of refugia scores to Conservation Opportunity Areas shows mixed results in terms of their expected efficacy of protecting aquatic refugia. Mean refugia scores were lower for COAs than for HUC12s, apart from perennial water amphibian and reptile habitat hydrorefugia, springs hydrorefugia, and ephemeral catchments macrorefugia (Table 3). The COAs with the greatest mean hydrorefugia scores were often in different areas of New Mexico than COAs with the highest

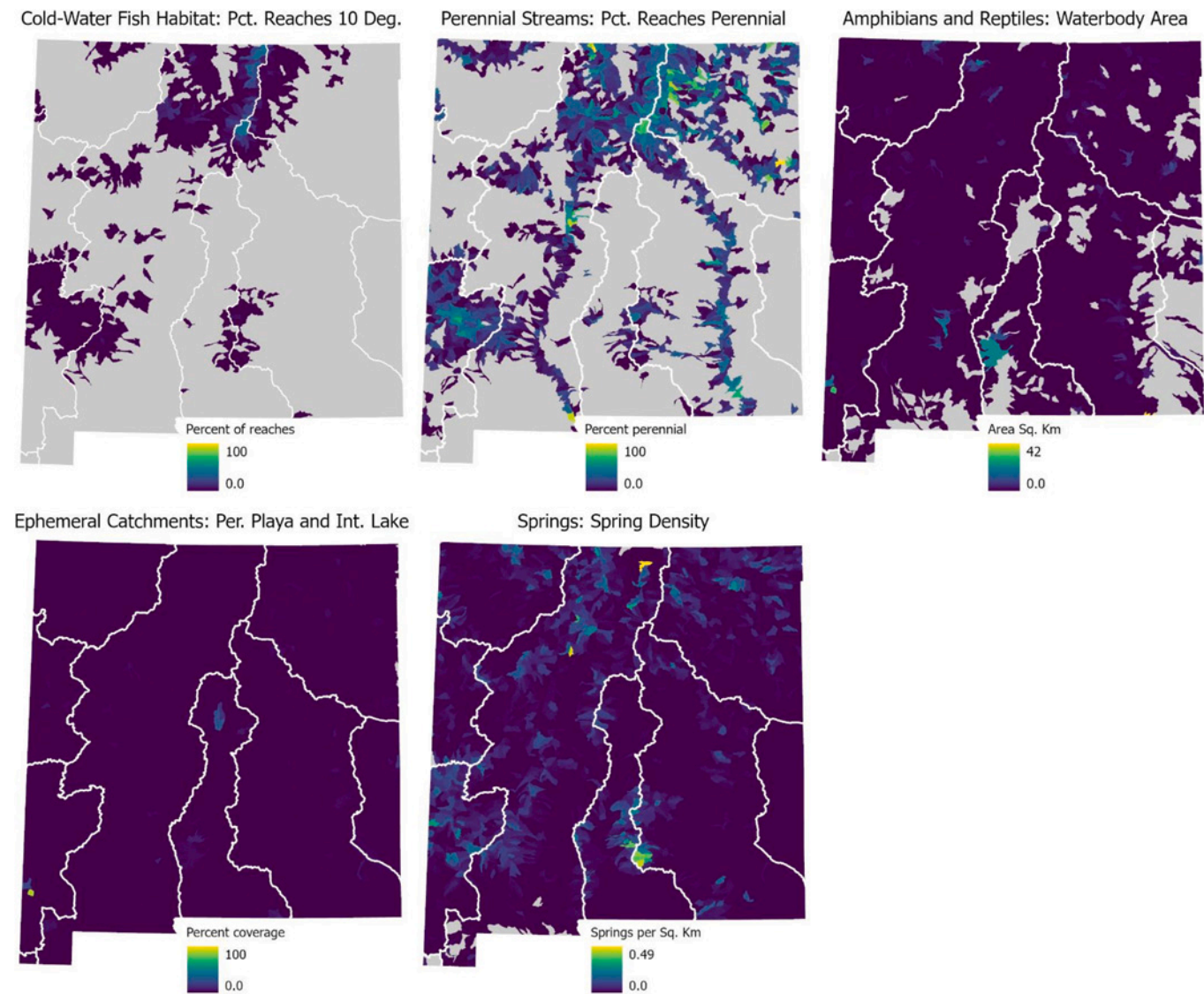


Fig. 4. Physical value metrics (habitat features) for the five aquatic habitat groups assessed for climate refugia.

Table 3
Mean refugia scores for 12th-digit hydrologic unit code watersheds (HUC12s) and Conservation Opportunity Areas (COAs) assessed for aquatic refugia habitat groups in New Mexico, U.S.A.

	Hydrefugia scores*		Macrorefugia scores	
	HUC12s (sd)	COAs (sd)	HUC12s (sd)	COAs (sd)
Cold-Water Fish Habitat	0.18 (0.11)	0.16 (0.10)	0.65 (0.15)	0.57 (0.14)
Perennial Streams	0.26 (0.15)	0.22 (0.11)	0.47 (0.20)	0.40 (0.19)
Perennial Water Amphibian and Reptile Habitat	0.19 (0.06)	0.22 (0.07)	0.38 (0.15)	0.36 (0.13)
Ephemeral Catchments	0.36 (0.08)	0.33 (0.07)	0.37 (0.10)	0.37 (0.12)
Springs	0.36 (0.20)	0.41 (0.16)	0.49 (0.14)	0.48 (0.17)

* Higher values indicate greater potential for hydrefugia (areas where local features maintain the stability of water volume and/or quality) or macrorefugia (areas with sustained climatic suitability across broad spatial and temporal gradients).

mean macrorefugia scores (Figs. 5–9; Appendix A, Table S9). Several

COAs, however, overlapped HUC12s with high refugia scores and high conservation value metrics (Appendix A, Table S10). These include Eagle Nest Lake, Jemez Mountains, and Southern Sacramento Mountains for hydrefugia and San Francisco River and Rio Puerco for macrorefugia (Table 4).

3.4. Sensitivity analysis and correlation comparison

Sensitivity to weighting method was low for all groups with relatively consistent spatial overlap among different methodologies (Pearson $r = 0.64$ to 0.94 ; Spatial agreement = 57% to 90%, Table 5). Cold-water fish habitat showed the greatest sensitivity to weighting method where approximately 26% to 43% of high-ranking watersheds change depending on weighting scheme (Table 5). In general, trends for high (>80%) Pearson r paired with lower spatial agreement values indicates that weighting schemes lead to similar results regarding value and rank of watershed scores but does result in some shifts in where those watersheds are located. We observed this pattern in all habitat groups except for cold-water fish habitat, which is the most spatially limited. In absence of empirically derived information on population response to spatial data used in this analysis; we argue that optimized weighting methods provide a viable means to generate composite representation of

Cold-Water Fish Habitat

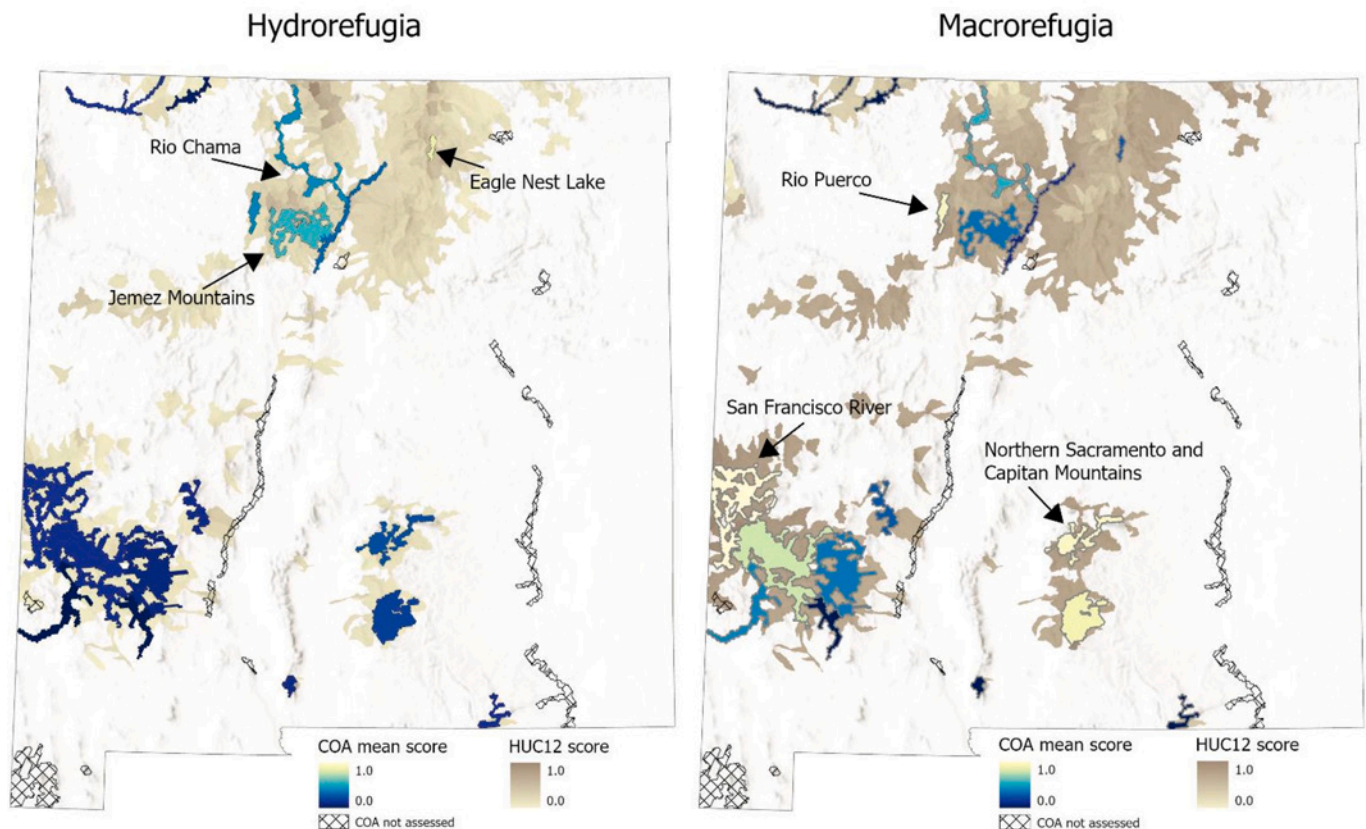


Fig. 5. Mean refugia scores for cold-water fish habitat hydrorefugia and macrorefugia for conservation opportunity areas (COAs, yellow to blue polygons) and HUC12 watersheds (brown polygons) in New Mexico, with COAs with mean refugia scores in the top quantile labeled by name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diverse data.

For both macrorefugia and hydrorefugia variables, Pearson and Spearman correlations yielded similar results (Appendix A, Table S11). The use of Spearman correlations would only have affected the inclusion of two variables for cold-water fish habitat: Mean Difference in Maximum Temperature of the Warmest Month and Mean Difference in Temperature of Wettest Quarter.

4. Discussion

4.1. Utility of assessment

The application of climate refugia to aquatic ecosystem management is a relatively new practice and has only been applied to a select group of taxa. Methods for assessing the presence or potential of aquatic refugia have typically focused on identification of discrete features within a watershed based on use by, or suitability for, a taxon of interest, such as freshwater fishes (Isaak and Young, 2023) or aquatic invertebrates (Cushway and Schwalb, 2024; Nadeau et al., 2022). Our framework for a multi-taxon, large-scale assessment of aquatic refugia can help managers use limited resources to preserve a variety of freshwater ecosystems during periods of water scarcity. We identified high-value watersheds (i. e., those containing higher-value refugia scores) by describing aquatic habitat groups, quantifying value metrics, and evaluating a suite of aquatic refugia indicators. We then applied our results to current conservation planning efforts by calculating mean refugia scores for COAs.

Our methods for assessing aquatic refugia differed from those developed for terrestrial refugia in several ways. First, we used lists of imperiled species and their habitats to develop habitat groups as targets

of the assessment. Second, we compiled sets of macrorefugia indicators that were specific to each of the five habitat groups. Third, we developed the concept of hydrorefugia, to reflect the importance of physical and biotic features in maintaining the volume and quality of surface water required by each habitat group. This approach allowed us to incorporate the variation inherent in New Mexico's aquatic ecosystems, which include small, spring-fed creeks; large, turbid rivers; and rain-fed playa lakes. Our methods are easily transmitted to other arid regions if climate data are available for calculating macrorefugia scores. In addition, different types of hydrorefugia can be conceptualized and modeled to reflect the geological and biotic characteristics of other regions.

4.2. Implications for conservation

Most COAs overlapped HUC12s with high-scoring macrorefugia or hydrorefugia for at least one habitat group. A small percentage of COAs, however, contained high-scoring watersheds for multiple groups. These include the Rio Puerco, Santa Fe River, and Upper Rio Grande, all of which are mountainous areas in the northern part of the state. Considering the amount of overlap with high-scoring watersheds, the San Francisco River COA, in the Gila River watershed, appeared to be a particularly important area for macrorefugia. On the other hand, Eagle Nest Lake and the Jemez Mountains, in the northern part of the state, appeared to be important for hydrorefugia. Collectively, these results indicate that the COAs associated with mountainous areas cover a range of habitats with moderate to high potential for aquatic refugia. These COAs may be critical to the persistence of native amphibians, fishes, reptiles, and spring-dependent species. The Pecos River – Lake Sumner COA and other lowland areas are the most likely to provide refugia for

Perennial Streams

Hydrefugia

Macrorefugia

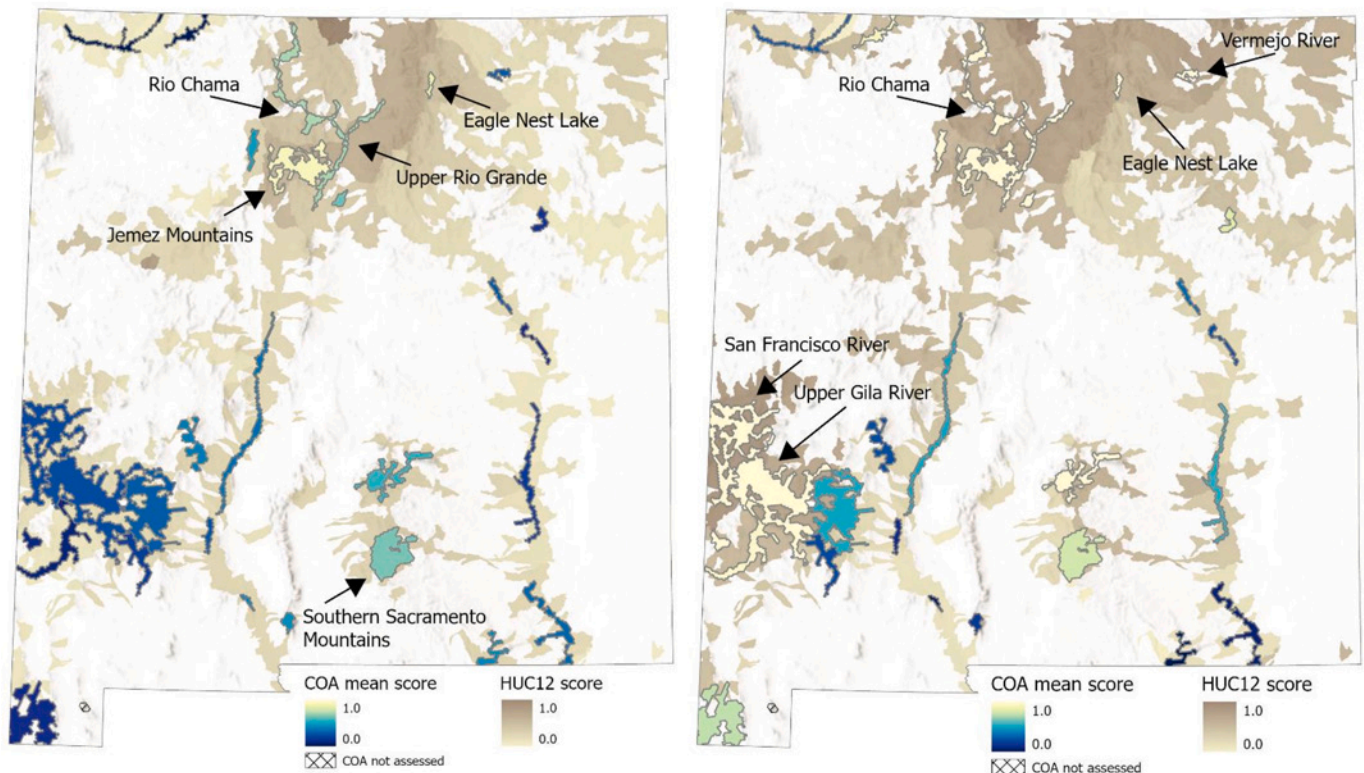


Fig. 6. Mean refugia scores for perennial streams hydrefugia and macrorefugia for conservation opportunity areas (COAs, yellow to blue polygons) and HUC12 watersheds (brown polygons) in New Mexico, with COAs with mean refugia scores in the top quantile labeled by name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species dependent on ephemeral catchments. By establishing additional COAs in locations such as the Pecos River Basin and the Texas Gulf Basin, managers could increase refugia potential for these highly specialized communities.

To prioritize areas for protection of aquatic ecosystems, information is needed on the distributional patterns of native species, and the aquatic habitat features necessary for survival in a warming and drying climate (Costelloe and Russell, 2014; Dudgeon et al., 2006). For our assessment of aquatic refugia, we calculated richness of native species, and the density of important features specific to each aquatic habitat group. Our results indicate that areas such as the Pecos River Basin support high species richness of several taxa, whereas the distribution of important habitat features varies among the groups examined. In general, stream reaches with cold water temperatures and perennial flows are most abundant at higher elevations in the northern part of the state. In contrast, watersheds with high density of springs and/or ephemeral catchments are distributed throughout the state. These results indicate that strategies addressing the greatest variety of taxa and geographical locations would be the most successful for ensuring persistence of New Mexico's aquatic ecosystems.

We found considerable spatial variation in values of refugia indicators and composite scores, both across the state and among habitat groups. Our results highlight some of the challenges that managers face when attempting to protect aquatic species. Areas with high potential for macrorefugia are often in different locations than areas with high potential for hydrefugia. As a result, there may be few opportunities for managers to protect both types of aquatic refugia within a single watershed or protected area. We also found that some of the most

important areas for freshwater species have low potential for at least one type of refugia. Examples include the ecologically important playa lakes of the Texas Gulf Basin (Haukos and Smith, 1994), where many watersheds have low macrorefugia scores for ephemeral catchments. Likewise, many species-rich watersheds in the Pecos River Basin have low hydrefugia scores for perennial streams. Also, there were few areas with high potential for both refugia types for cold-water fish habitat in the northern and southwestern portions of the state where the coldest streams occur. There was, however, high refugia potential for springs in the Jemez, Mogollon, and Sacramento Mountains where springs are relatively abundant, highlighting the conservation value of these areas.

Identification of watersheds or COAs with high refugia potential may be used to establish protected areas based on refugia or refugia networks that protect species from climate change and direct impacts of human activity (Ebersole et al., 2020). For example, our results highlight potential areas for protection such as the Jemez Mountains in the northern part of the state and the Sacramento Mountains in the south. These areas have physical features such as high elevations and water-permeable bedrock units that promote hydrefugia and macrorefugia for cold-water fish, spring-dependent species, and other taxa (Rawling and Newton, 2016; Trainer, 1974). Results can also be used to identify locations where hydrefugia can be created or enhanced. For example, managers could improve hydrefugia for cold-water fish by reestablishing shading vegetation or restoring springs that discharge to streams (Baker and Bonar, 2019; Ebersole et al., 2003). Management of existing or potential hydrefugia can also be used to promote adaptive capacity. Examples include vegetation and soil management to enhance seasonal inundation and limit sedimentation in ephemeral catchments in

Amphibians and Reptiles

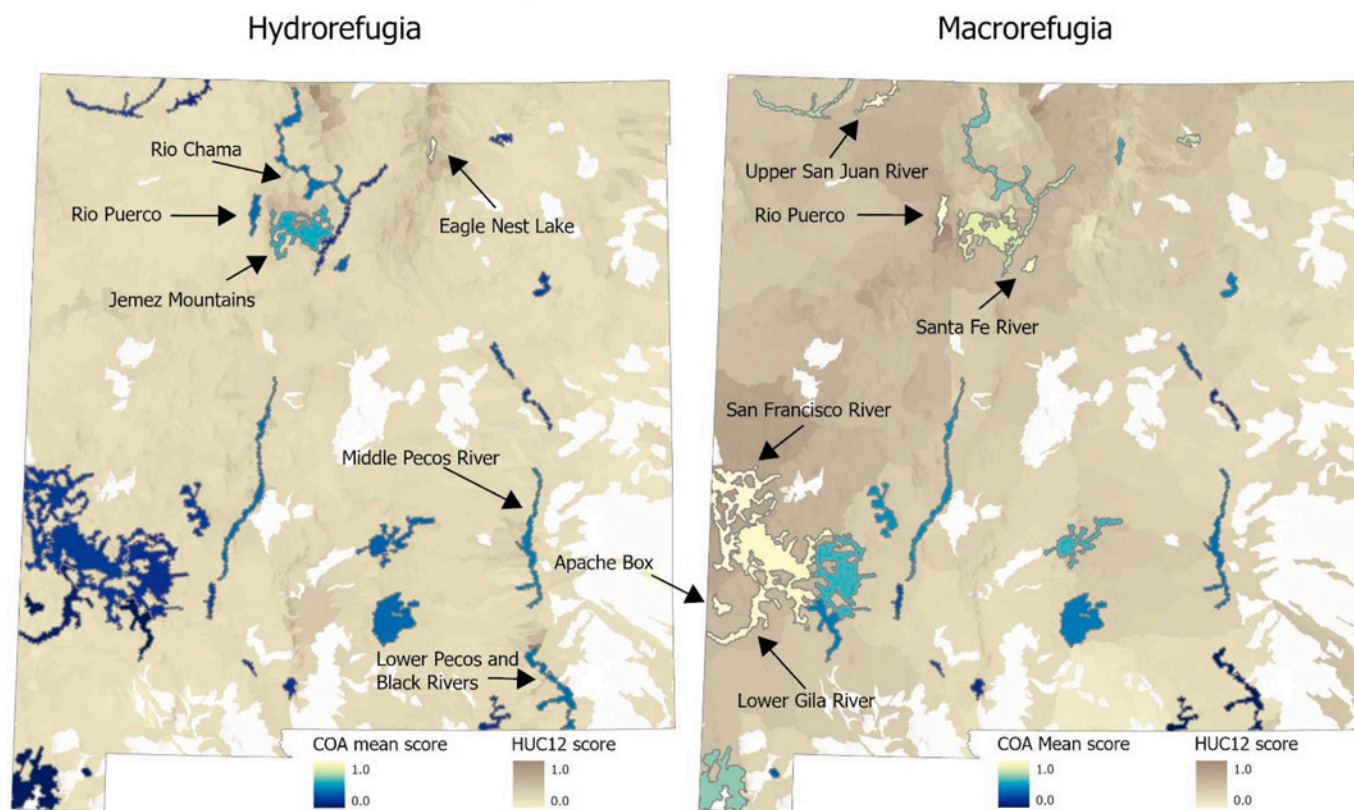


Fig. 7. Mean refugia scores for perennial water amphibian and reptile habitat hydrorefugia and macrorefugia for conservation opportunity areas (COAs, yellow to blue polygons) and HUC12 watersheds (brown polygons) in New Mexico, with COAs with mean refugia scores in the top quantile labeled by name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ephemeral Catchments

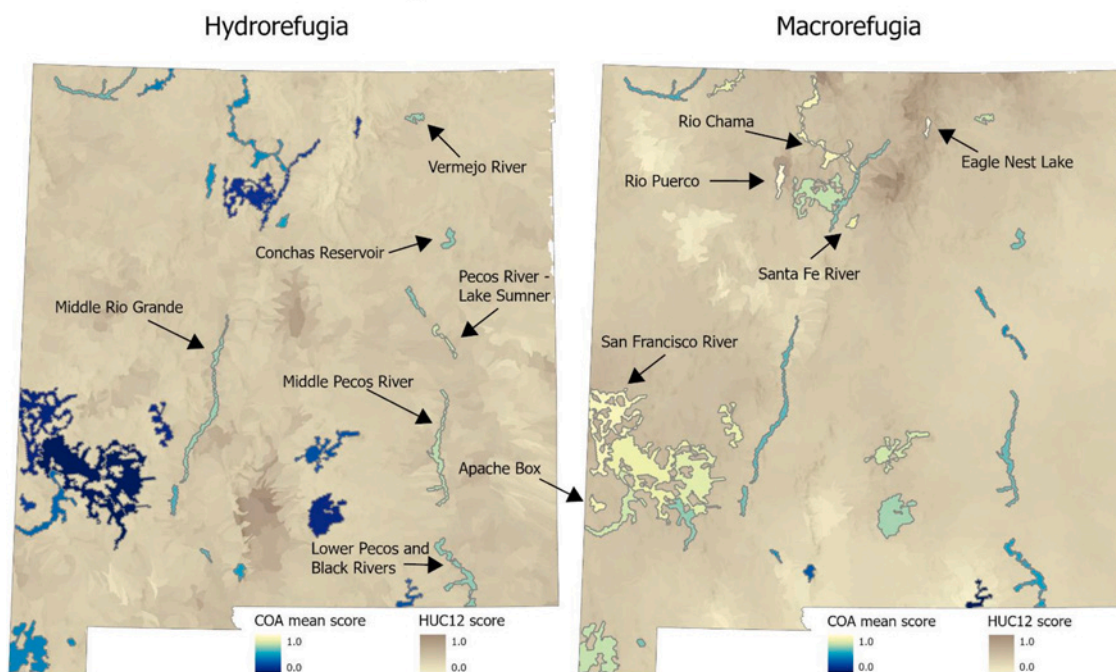


Fig. 8. Mean refugia scores for ephemeral catchments hydrorefugia and macrorefugia for conservation opportunity areas (COAs, yellow to blue polygons) and HUC12 watersheds (brown polygons) in New Mexico, with COAs with mean refugia scores in the top quantile labeled by name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Springs

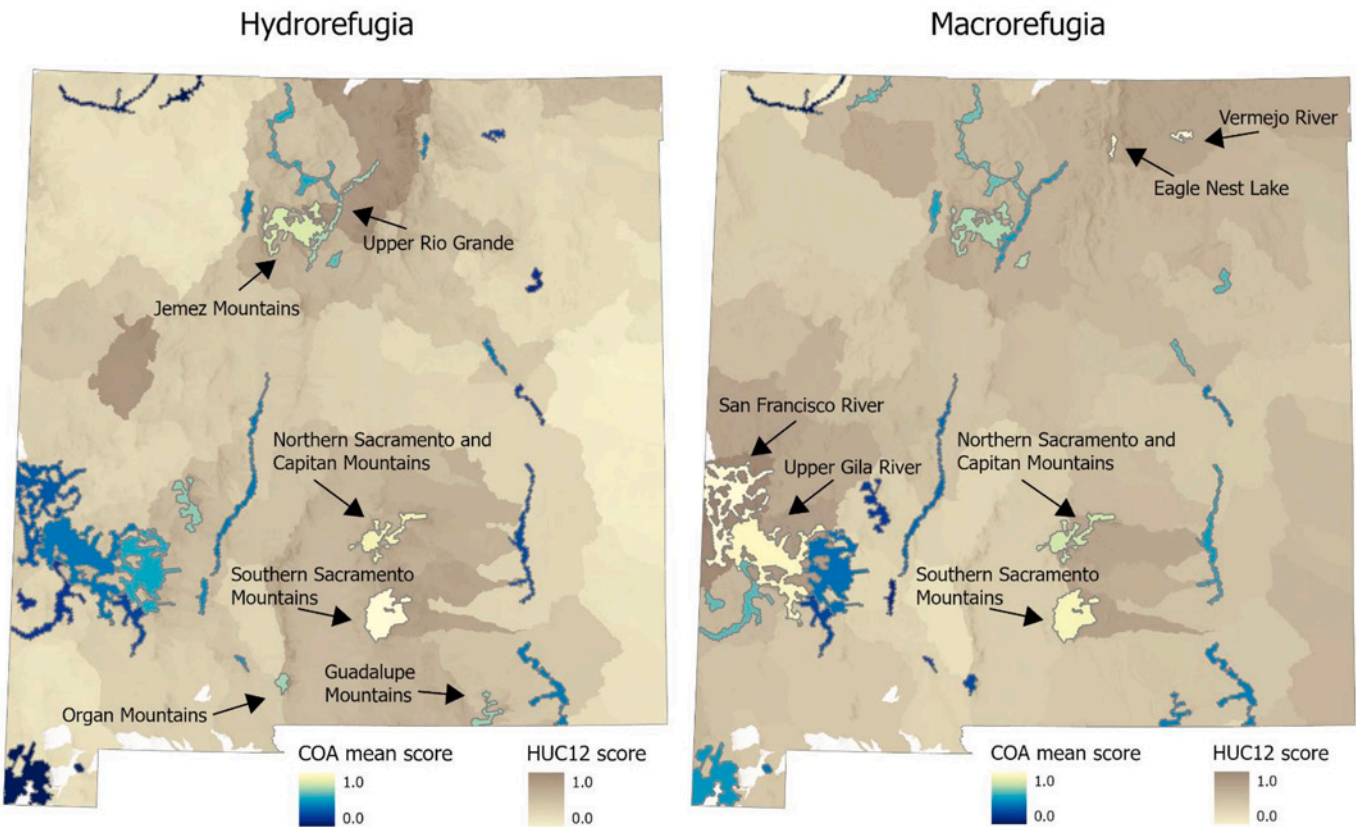


Fig. 9. Mean refugia scores for springs hydrorefugia and macrorefugia for conservation opportunity areas (COAs, yellow to blue polygons) and HUC12 watersheds (brown polygons) in New Mexico, with COAs with mean refugia scores in the top quantile labeled by name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Conservation Opportunity Areas in New Mexico with the highest mean hydrorefugia and macrorefugia scores for each habitat group assessed. The value in parentheses represents the percent difference between the average refugia score for 12th-digit hydrologic unit code watersheds (HUC12s) within each COA and the average refugia score for all HUC12s. Macrorefugia are areas with sustained climatic suitability across broad spatial and temporal gradients. Hydrorefugia are areas where local features maintain the stability of water volume and/or quality. The top refugia are in bold. For each of the habitat groups assessed, measurements of species richness and habitat features were calculated for HUC12s throughout the state. Percent high values indicate percentage of COAs that overlap HUC12s with the high measures (top 20%) of species richness (biotic values) and physical habitat features (habitat values: percent of reaches with August stream temperatures $\leq 10^{\circ}\text{C}$ [cold-water fish habitat], percent of streams perennial [Perennial streams], total waterbody area [perennial water amphibian and reptile habitat], percent coverage of playa/intermittent lake [ephemeral catchments], and spring density [springs]) Results for all COAs examined are included in Appendix A, Tables S9 and S10.

Habitat group	COA	Mean hydrorefugia score (%diff)	Mean macrorefugia score (%diff)	Percent high biotic value	Percent high habitat value
Cold-water fish habitat	Eagle Nest Lake	0.43 (59)	0.57 (–15)	100	47.4
	San Francisco River	0.11 (–57)	0.75 (13)	0	3.5
Perennial streams	Jemez Mountains	0.46 (44)	0.51 (7)	0	23.5
	San Francisco River	0.16 (–59)	0.77 (39)	0	10.3
Perennial water amphibian and reptile habitat	Eagle Nest Lake	0.48 (58)	0.34 (–13)	100	75.1
	Rio Puerco	0.26 (24)	0.69 (45)	0	6.9
Ephemeral catchments	Pecos River - Lake Sumner	0.44 (18)	0.24 (–52)	24.1	3.2
	Rio Puerco	0.35 (–4)	0.69 (46)	0	8.8
Springs	Southern Sacramento Mountains	0.78 (54)	0.71 (31)	0	90.1
	San Francisco River	0.34 (–5)	0.92 (47)	0	89.5

response to precipitation changes (Alvarez et al., 2024; Skagen et al., 2008). In addition, the removal of dispersal barriers allows fishes and other stream species to access upper elevation and spring-fed reaches that are protected from high temperatures and desiccation (Baker and Bonar, 2019; Williams et al., 2015).

4.3. Limitations and future directions

We identified areas of high refugia potential for certain taxa and their habitats, but these results were influenced by our selection of refugia indicators and habitat groups and the scale of analysis. Species-specific management plans would require information regarding habitat requirements and current habitat conditions at a finer resolution.

Table 5

Results of sensitivity analysis evaluating weighting methodology on final refugia scores. We compared refugia scores and watershed ranks using three different weighting methods: the optimized weight method presented in this paper, un-weighted equal-contribution method, and first principal component analysis (PCA). Macrorefugia are areas with sustained climatic suitability across broad spatial and temporal gradients. Hydrefugia are areas where local features maintain the stability of water volume and/or quality. Equal weighting is calculated as $1/n$ and makes no assumptions about relative importance of indicators. PCA calculates a correlation matrix from indicators and weights are derived from loadings of the 1st principal component such that indicators that load on PC1 are those that are strongly associated with dominant pattern of covariation and are given the greatest weight (see **Appendix A, Section S3** for additional description).

	No. indicators	Weighting methods (Optimized vs Equal, PCA)	
		Pearson r	Spatial agreement
		Equal, PCA	Equal, PCA
Cold-water fish habitat hydrefugia	11	0.72, 0.64	60.6%, 56.9%
Cold-water fish habitat macrorefugia	10	0.76, 0.68	71.6% 74.3%
Perennial streams hydrefugia	7	0.91, 0.93	73.7%, 89.8%
Perennial streams macrorefugia	6	0.92, 0.94	65.9%, 76.1%
Perennial water amphibian and reptile habitat hydrefugia	11	0.74, 0.70	60.5%, 56.9%
Perennial water amphibian and reptile habitat macrorefugia	9	0.89, 0.87	74.7%, 75.3%
Ephemeral catchments hydrefugia	5	0.86, 0.87	66.7%, 65.6%
Ephemeral catchments macrorefugia	7	0.90, 0.85	80.0%, 81.4%
Springs hydrefugia	6	0.93, 0.88	79.2%, 82.0%
Springs macrorefugia	5	0.93, 0.91	83.5%, 81.7%

Our assessment used macrorefugia indicators based on temperature, precipitation, and related variables. Climate change is also affecting habitats by interacting with disturbances such as wildfire, post-fire flooding, and invasive species (Dunham et al., 2007; Isaak et al., 2010; Leonard et al., 2017; Touma et al., 2022). Future assessments could benefit from the inclusion of these impacts. In addition to climate change, surface water and groundwater use has modified freshwater ecosystems throughout New Mexico and will likely continue to do so into the future (Dunbar et al., 2022). Data reflecting current and projected rates of water use and watershed development could also help to determine the suitability of watersheds and COAs for management as refugia.

4.4. Conclusions

In conducting this assessment, we identified areas of New Mexico that are important for the conservation of aquatic species. We also ranked areas based on potential to provide climate refugia. For some habitat groups, we found considerable differences between watersheds with high refugia potential, and areas previously prioritized for conservation. If aridification continues in New Mexico as projected, COAs may fail to protect aquatic ecosystems, creating a need to identify new areas to prioritize. In this scenario, assessments like ours will serve as important tools for protecting biodiversity and imperiled species.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used Claude by Anthropic for methodological guidance on optimization code. The authors reviewed and edited the output as needed and take full responsibility for the content of the published article.

Statement on inclusion

Our study is conducted by scientists based in the country where the study was carried out. Efforts were made to incorporate the diverse interests of the Pueblos, Tribal Reservations, and state of New Mexico when selecting resources for assessment and interpreting results.

CRediT authorship contribution statement

D. Max Smith: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Megan M. Friggins:** Writing – review & editing, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation. **Karen C. Chaudhry:** Visualization, Formal analysis, Data curation.

Funding

This work was supported by the U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS) and through a grant awarded to RMRS by New Mexico Department of Game and Fish to support this Share with Wildlife Project (State Wildlife Grant T-80-R-1).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This analysis is part of a New Mexico Department of Game and Fish Share with Wildlife Project. We would like to thank several people that provided us with expertise and feedback during this process including Virginia Seamster, Karen H. Gaines, and Chelcy Miniati. This project was funded by the U.S. Department of Agriculture (USDA), Forest Service, Rocky Mountain Research Station (RMRS) and through a grant awarded to RMRS by the New Mexico Department of Game and Fish to support this Share with Wildlife Project (State Wildlife Grant T-80-R-1). The findings and conclusions in this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.115391>.

Data availability

Data and code are currently available in this repository: <https://github.com/dmaxsmith/AquaticRefugia> and will be publicly available in the Forest Service Research Data Archive.

References

- Abdelmohsen, K., Famiglietti, J.S., Ao, Y.Z., Mohajer, B., Chandanpurkar, H.A., 2025. Declining freshwater availability in the Colorado River basin threatens sustainability of its critical groundwater supplies. *Geophys. Res. Lett.* 52 (10), e2025GL115593.
- Alvarez, J.A., Rogers, C., Shea, M.A., 2024. Restoration of bedrock vernal pools for the threatened vernal Pool fairy shrimp in Central California. *Ecol. Restor.* 42 (3), 169–174.
- Ashcroft, M.B., 2010. Identifying refugia from climate change. *J. Biogeogr.* 37 (8), 1407–1413. <https://doi.org/10.1111/j.1365-2699.2010.02300.x>.
- Baker, J.P., Bonar, S.A., 2019. Using a mechanistic model to develop management strategies to cool apache trout streams under the threat of climate change. *N. Am. J. Fish Manag.* 39 (5), 849–867.
- Becker, W., Saisana, M., Paruolo, P., Vandecasteele, I., 2017. Weights and importance in composite indicators: closing the gap. *Ecol. Indic.* 80, 12–22. <https://doi.org/10.1016/j.ecolind.2017.03.056>.
- Bexfield, L.M., 2010. Conceptual understanding and groundwater quality of the basin-fill aquifer in the Middle Rio Grande Basin, New Mexico. In: Section 11 In Conceptual Understanding and Groundwater Quality of Selected Basin-fill Aquifers in the Southwestern United States, 1781. US Geological Survey Professional Paper, pp. 189–218.
- Breiman, L., 2001. Random Forests. *Machine Learning* 45, 5–32 <https://doi.org/10.1023/A:1010933404324>.
- Cartwright, J., Johnson, H.M., 2018. Springs as hydrologic refugia in a changing climate? A remote-sensing approach. *Ecosphere* 9 (3), e02155.
- Cartwright, J., Morelli, T.L., Grant, E.H.C., 2022. Identifying climate-resistant vernal pools: hydrologic refugia for amphibian reproduction under droughts and climate change. *Ecohydrology* 15 (5), e2354.
- Cartwright, J.M., Dwire, K.A., Freed, Z., Hammer, S.J., McLaughlin, B., Misztal, L.W., Schenk, E.R., Spence, J.R., Springer, A.E., Stevens, L.E., 2020. Oases of the future? Springs as potential hydrologic refugia in drying climates. *Front. Ecol. Environ.* 18 (5), 245–253.
- Chavarria, S.B., Gutzler, D.S., 2018. Observed changes in climate and streamflow in the upper Rio Grande Basin. *JAWRA J. Am. Water Resour. Assoc.* 54 (3), 644–659. <https://doi.org/10.1111/1752-1688.12640>.
- Costelloe, J.F., Russell, K.L., 2014. Identifying conservation priorities for aquatic refugia in an arid zone, ephemeral catchment: a hydrological approach. *Ecohydrology* 7 (6), 1534–1544.
- Craig, C.A., Kollaus, K.A., Behen, K.P., Bonner, T.H., 2016. Relationships among spring flow, habitats, and fishes within evolutionary refugia of the Edwards plateau. *Ecosphere* 7 (2), e01205.
- Cushway, K.C., Schwalb, A.N., 2024. When rivers run dry: perennial pools as ecological refuges for freshwater mussels during drought. *Freshw. Biol.* 69 (2), 226–239.
- Cutler, D.R., Edwards Jr., T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random Forests for Classification in Ecology. *Ecology* 88, 2783–2792. <https://doi.org/10.1890/07-0539.1>.
- Davis, J., Pavlova, A., Thompson, R., Sunnucks, P., 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Glob. Chang. Biol.* 19 (7), 1970–1984.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L., Sullivan, C. A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81 (2), 163–182.
- Dunbar, N.W., Gutzler, D.S., Phillips, F.M., Pearthree, K.S., Allen, C.D., Dubois, D.W., King, J.P., McFadden, L.D., Thomson, B.M., Tillery, A.C., 2022. Climate Change in New Mexico over the Next 50 Years: Impacts on Water Resources. New Mexico Bureau of Geology and Mineral Resources, Socorro, NM, USA, pp. vii–26.
- Dunham, J.B., Rosenberger, A.E., Luce, C.H., Rieman, B.E., 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10 (2), 335–346.
- Eastoe, C.J., Rodney, R., 2014. Isotopes as tracers of water origin in and near a regional carbonate aquifer: the southern Sacramento Mountains, New Mexico. *Water* 6 (2), 301–323.
- Ebersole, J.L., Liss, W.J., Frissell, C.A., 2003. Cold water patches in warm streams: physicochemical characteristics and the influence of shading 1. *JAWRA J. Am. Water Resour. Assoc.* 39 (2), 355–368.
- Ebersole, J.L., Quinones, R.M., Clements, S., Letcher, B.H., 2020. Managing climate refugia for freshwater fishes under an expanding human footprint. *Front. Ecol. Environ.* 18 (5), 271–280.
- Elias, E., James, D., Heimel, S., Steele, C., Steltzer, H., Dott, C., 2021. Implications of observed changes in high mountain snow water storage, snowmelt timing and melt window. *J. Hydrol. Reg. Stud.* 35, 100799. <https://doi.org/10.1016/j.ejrh.2021.100799>.
- Esri Inc., 2024. *ArcGIS pro* (version 3.3.6) [software]. <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>.
- Evans, J.S., Murphy, M.A., Holden, Z.A., Cushman, S.A., 2011. Modeling species distribution and change using random forest. In: Drew, C.A., Wiersma, Y.F., Huettmann, F. (Eds.), Predictive species and habitat modeling in landscape ecology: Concepts and applications. Springer, pp. 139–159. https://doi.org/10.1007/978-1-4419-7390-0_8.
- Gombert, C.E., Lancaster, S.T., Grant, G.E., Flitcroft, R.L., 2023. Novel dimensionless index for physically based assessment of thermal refugia characterizes off-channel habitat on gravel bed river. *JAWRA J. Am. Water Resour. Assoc.* 59 (4), 615–634.
- Harpold, A., Brooks, P., Rajagopal, S., Heidbuchel, I., Jardine, A., Stielstra, C., 2012. Changes in snowpack accumulation and ablation in the intermountain west. *Water Resour. Res.* 48 (11), 1–11. <https://doi.org/10.1029/2012WR011949>.
- Haukos, D.A., Smith, L.M., 1994. The importance of playa wetlands to biodiversity of the southern High Plains. *Landsc. Urban Plan.* 28 (1), 83–98.
- Hoagstrom, C.W., Remshardt, W.J., Smith, J.R., Brooks, J.E., 2010. Changing fish faunas in two reaches of the Rio Grande in the Albuquerque Basin. *Southwest. Nat.* 55 (1), 78–88.
- Hollien, K.D., Gill, B.A., Eppehimer, D.E., Bogan, M.T., 2023. Effects of stream drying, season, and distance to refuge on macroinvertebrate community structure in an arid intermittent stream basin. *Ecohydrology* 16 (8), e2598.
- Isaak, D.J., Young, M.K., 2023. Cold-water habitats, climate refugia, and their utility for conserving salmonid fishes. *Can. J. Fish. Aquat. Sci.* 80 (7), 1187–1206.
- Isaak, D.J., Luce, C.H., Rieman, B.E., Nagel, D.E., Peterson, E.E., Horan, D.L., Parkes, S., Chandler, G.L., 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecol. Appl.* 20 (5), 1350–1371. <https://doi.org/10.1890/09-0822.1>.
- 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. *Glob. Chang. Biol.* 21 (7), 2540–2553.
- Isaak, D.J., Luce, C.H., Chandler, G.L., Horan, D.L., Wollrab, S.P., 2018. Principal components of thermal regimes in mountain river networks. *Hydrol. Earth Syst. Sci.* 22 (12), 6225–6240.
- Ishiyama, N., Sueyoshi, M., García Molinos, J., Iwasaki, K., Negishi, J.N., Koizumi, I., Nagayama, S., Nagasaka, A., Nagasaka, Y., Nakamura, F., 2023. Underlying geology and climate interactively shape climate change refugia in mountain streams. *Ecol. Monogr.* 93 (2), e1566.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.* 21 (4), 393–404.
- Lehner, F., Wahl, E.R., Wood, A.W., Blatchford, D.B., Llewellyn, D., 2017. Assessing recent declines in upper Rio Grande runoff efficiency from a paleoclimate perspective. *Geophys. Res. Lett.* 44 (9), 4124–4133.
- Leonard, J.M., Magaña, H.A., Bangert, R.K., Neary, D.G., Montgomery, W.L., 2017. Fire and floods: the recovery of headwater stream systems following high-severity wildfire. *Fire Ecol.* 13, 62–84.
- MacKay, W.P., Loring, S.J., Frost, T.M., Whitford, W.G., 1990. Population dynamics of a playa community in the Chihuahuan Desert. *Southwest. Nat.* 35 (4), 393–402.
- Magoulick, D.D., Kobza, R.M., 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshw. Biol.* 48 (7), 1186–1198.
- McKenna, O.P., Sala, O.E., 2017. Groundwater recharge in desert playas: current rates and future effects of climate change. *Environ. Res. Lett.* 13 (1), 014025.
- Mote, P.W., Hamlet, A.F., Clark, M.P., Lettenmaier, D.P., 2005. Declining mountain snowpack in western North America. *Bull. Am. Meteorol. Soc.* 86 (1), 39–50. <https://doi.org/10.1175/BAMS-86-1-39>.
- Nadeau, C.P., Giacomazzo, A., Urban, M.C., 2022. Cool microrefugia accumulate and conserve biodiversity under climate change. *Glob. Chang. Biol.* 28 (10), 3222–3235.
- New Mexico Department of Game and Fish, 2016. State Wildlife Action Plan for New Mexico. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.
- Paruolo, P., Saisana, M., Saltelli, A., 2013. Ratings and rankings: voodoo or science? *J. R. Stat. Soc. Ser. A* 176, 609–634.
- Platanía, S.P., Bestgen, K.R., Moretti, M.A., Propst, D.L., Brooks, J.E., 1991. Status of Colorado squawfish and razorback sucker in the San Juan River, Colorado, New Mexico, and Utah. *Southwest. Nat.* 36, 147–150.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rawling, G.C., Newton, B.T., 2016. Quantity and location of groundwater recharge in the Sacramento Mountains, south-Central New Mexico (USA), and their relation to the adjacent Roswell Artesian Basin. *Hydrogeol. J.* 24 (4), 757–786.
- Rawling, G.C., Rinehart, A.J., 2017. Lifetime Projections for the High Plains Aquifer in East-Central New Mexico. New Mexico Bureau of Geology and Mineral Resources, Socorro, NM, USA, pp. 500–599.
- Rinne, J.N., 1994. Declining southwestern aquatic habitats and fishes: are they sustainable? In: US Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report, 247, pp. 256–265.
- Rumsey, C.A., Miller, M.P., Sexton, G.A., 2020. Relating hydroclimatic change to streamflow, baseflow, and hydrologic partitioning in the upper Rio Grande Basin, 1980 to 2015. *J. Hydrol.* 584, 124715.
- Sabo, J.L., Sinha, T., Bowling, L.C., Schoups, G.H., Wallender, W.W., Campana, M.E., Cherkauer, K.A., Fuller, P.L., Graf, W.L., Hopmans, J.W., Kominoski, J.S., 2010. Reclaiming freshwater sustainability in the Cadillac Desert. *Proc. Natl. Acad. Sci.* 107 (50), 21263–21269.
- Sadayappan, K., Li, L., 2025. Riverine heat waves on the rise, outpacing air heat waves. *Proc. Natl. Acad. Sci.* 122 (39), e2503160122.
- Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., Hawkins, C.P., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environ. Manag.* 14, 711–724.
- Shuster, S.M., 1981. Life history characteristics of *Thermosphaeroma thermophilum*, the Socorro isopod (Crustacea: Peracarida). *Biol. Bull.* 161 (2), 291–302.
- Skagen, S.K., Melcher, C.P., Haukos, D.A., 2008. Reducing sedimentation of depressional wetlands in agricultural landscapes. *Wetlands* 28 (3), 594–604.
- Smith, L.M., Haukos, D.A., McMurtry, S.T., LaGrange, T., Willis, D., 2011. Ecosystem services provided by playas in the High Plains: potential influences of USDA conservation programs. *Ecol. Appl.* 21 (sp1), S82–S92.
- Stewart, I.T., 2009. Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrol. Processes* 23 (1), 78–94.
- Stralberg, D., Carroll, C., Pedlar, J.H., Wilsey, C.B., McKenney, D.W., Nielsen, S.E., 2018. Macrorefugia for north American trees and songbirds: climatic limiting factors and

- multi-scale topographic influences. *Glob. Ecol. Biogeogr.* 27 (6), 690–703. <https://doi.org/10.1111/geb.12731>.
- Strayer, D.L., 2006. Challenges for freshwater invertebrate conservation. *J. N. Am. Benthol. Soc.* 25 (2), 271–287.
- Sullivan, C.J., Vokoun, J.C., Helton, A.M., Briggs, M.A., Kurylyk, B.L., 2021. An ecohydrological typology for thermal refuges in streams and rivers. *Ecohydrology* 14 (5), e2295.
- Touma, D., Stevenson, S., Swain, D.L., Singh, D., Kalashnikov, D.A., Huang, X., 2022. Climate change increases risk of extreme rainfall following wildfire in the western United States. *Sci. Adv.* 8 (13), eabm0320. <https://doi.org/10.1126/sciadv.abm0320>.
- Trainer, F.W., 1974. Field Conference Guidebook. 25th Annual Field Conference. New Mexico Geological Society, Ghost Ranch, North-Central NM, USA, pp. 337–345. Ground water in the southwestern part of the Jemez Mountains volcanic region, New Mexico.
- Van Horn, D.J., Reale, J.K., Archdeacon, T.P., 2022. Water quality in three potential drought refuges in an arid-land river: assessing habitat suitability for at-risk fish species. *Knowl. Manag. Aquat. Ecosyst.* 423, 7.
- Wahlberg, M.M., Triepke, F.J., Rose, A.K. and Ryerson, D.E. 2023. “Aquatic-Riparian Climate Change Vulnerability Assessment – Executive Report. USDA Forest Service resource report available online <https://www.fs.usda.gov/main/r3/landmanagement/gis> Southwestern Region, Regional Office, Albuquerque, NM, 24p.
- Walters, A.W., Clancy, N.G., Archdeacon, T.P., Yu, S., Rogosch, J.S., Rieger, E.A., 2024. Refuge identification as a climate adaptation strategy to promote fish persistence during drought. *Fish. Fish.* 25 (6), 997–1008.
- Williams, J.E., Bowman, D.B., Brooks, J.E., Echelle, A.A., Edwards, R.J., Hendrickson, D. A., Landye, J.J., 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. *J. Ariz. Nev. Acad. Sci.* 1–61.
- Williams, J.E., Neville, H.M., Haak, A.L., Colyer, W.T., Wenger, S.J., Bradshaw, S., 2015. Climate change adaptation and restoration of western trout streams: opportunities and strategies. *Fisheries* 40 (7), 304–317.
- Woodhouse, C.A., Udall, B., 2022. Upper Gila, salt, and Verde Rivers: arid land rivers in a changing climate. *Earth Interact.* 26 (1), 1–14.
- Woodhouse, C.A., Pederson, G.T., Morino, K., McAfee, S.A., McCabe, G.J., 2016. Increasing influence of air temperature on upper Colorado River streamflow. *Geophys. Res. Lett.* 43 (5), 2174–2181. <https://doi.org/10.1002/2015GL067613>.
- Yang, C., Condon, L.E., Maxwell, R.M., 2025. Unravelling groundwater–stream connections over the continental United States. *Nat. Water* 3, 70–79.
- Zeigler, M.P., Todd, A.S., Caldwell, C.A., 2012. Evidence of recent climate change within the historic range of Rio Grande cutthroat trout: implications for management and future persistence. *Trans. Am. Fish. Soc.* 141 (4), 1045–1059.