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ARTICLE

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# Declining ecological resilience and invasion resistance under climate change in the sagebrush region, United States

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**Abstract**

In water-limited dryland ecosystems of the Western United States, climate change is intensifying the impacts of heat, drought, and wildfire. Disturbances often lead to increased abundance of invasive species, in part, because dryland restoration and rehabilitation are inhibited by limited moisture and infrequent plant recruitment events. Information on ecological resilience to disturbance (recovery potential) and resistance to invasive species can aid in addressing these challenges by informing long-term restoration and conservation planning. Here, we quantified the impacts of projected future climate on ecological resilience and invasion resistance (R&R) in the sagebrush region using novel algorithms based on ecologically relevant and climate-sensitive predictors of climate and ecological drought. We used a process-based ecohydrological model to project these predictor variables and resulting R&R indicators for two future climate scenarios and 20 climate models. Results suggested widespread future R&R decreases (24%–34% of the 1.16 million km$^2$ study area) that are generally consistent among climate models. Variables related to rising temperatures were most strongly linked to decreases in R&R indicators. New continuous R&R indices quantified responses to climate change; particularly useful for areas without projected change in the R&R category but where R&R still may decrease, for example, some of the areas with a historically low R&R category. Additionally, we found that areas currently characterized as having high sagebrush ecological integrity had the largest areal percentage with expected declines in R&R in the future, suggesting continuing declines in sagebrush ecosystems. One limitation of these R&R projections was relatively novel future climatic conditions in particularly hot and dry areas that were underrepresented in the training data. Including more data from these areas in future updates could further improve the reliability of the projections. Overall, these projected future declines in R&R highlight a growing challenge for natural resource managers in the region, and the resulting spatially explicit datasets provide information that can improve long-term risk assessments, prioritizations, and climate adaptation efforts.

**KEYWORDS**
climate adaptation, dryland, land management planning, long-term prioritization, restoration, sagebrush ecological integrity, wildfire

## INTRODUCTION

Anticipating climate impacts is a recognized challenge for natural resource managers and policymakers working to sustain ecosystem services. Climate change and associated altered disturbance regimes are expected to restructure ecosystems across the globe (Nolan et al., 2018). Changing climate in combination with anthropogenic and ecosystem disturbances are transforming ecosystems, particularly in drylands of the Western United States (Doherty, Theobald, Bradford, et al., 2022; Herrick et al., 2012). These trends motivated the emergence of climate adaptation frameworks to support decision-making for natural resource management, for example, the resist-accept-direct (RAD) framework (Lynch et al., 2021; Schuurman et al., 2022). Slowing, reversing, or directing these transformations through strategic planning and prioritization of conservation and restoration actions is a pressing ecological challenge in the 21st century (Svejcar et al., 2023), and the United Nations declared 2021–2030 the "Decade on Ecosystem Restoration" (United Nations Environment Agency, 2019).

Understanding climate impacts is especially urgent in dryland regions, defined by high climatic aridity, and which cover ~40%–45% of the global land surface (Prăvălie, 2016; UNEP et al., 1997). Rising temperatures and extreme conditions are among the most consistent projected aspects of climate change, and as higher temperatures exacerbate aridity, dryland regions may be especially impacted by climate change (Huang et al., 2017). In addition to climate change, drylands are being transformed by altered disturbance regimes, biological invasions, and growing land use pressures, often impeding efforts to sustain or restore these ecosystems (Kildisheva et al., 2016). Persistent land degradation due to combinations of these factors has emerged as one of the most pressing contemporary management challenges in dryland regions (Herrick et al., 2012).

Understanding climate impacts in dryland ecosystems is complex because ecological drought (i.e., a deficit in moisture available to plants, Munson et al., 2021) is not easily estimated. The strong dependence of dryland ecosystems on moisture may make them especially vulnerable to future changes in precipitation and patterns of water cycling (Huang et al., 2017; Huxman et al., 2004). However, accurately assessing climate impacts in drylands requires an understanding of how soil moisture changes, in addition to climatic variables, because dryland plants respond to soil moisture, not precipitation (Noy-Meir, 1973). Ecological dynamics in drylands, including responses to disturbance, are driven primarily by the availability of soil moisture in critical periods within the growing season (Gremer et al., 2015; Renne et al., 2019; Schlaepfer et al., 2012; Shriver et al., 2018; Thoma et al., 2019; Witwicki et al., 2016). Because climatic conditions, edaphic properties, and vegetation feedbacks interact to influence soil moisture availability, dryland vulnerability to climate change, invasive species, and disturbances is highly heterogeneous in space and time, representing a substantial challenge to informed management of natural resources in dry environments. Consequently, long-term climatic aridity or other meteorologically defined drought metrics do not directly capture ecologically relevant measures of soil moisture limitation (Barnard et al., 2021; McColl et al., 2022; Silvertown et al., 2015). Examples of limitations in metrics that do not account for soil moisture and plant water use include O'Connor et al. (2020) for the Standardized Precipitation-Evapotranspiration Index (SPEI) and Swann et al. (2016) for the Palmer Drought Severity Index (PDSI). Thus, the impact of climate change on dryland vegetation is difficult to infer from climate alone.

Drylands in the Western United States comprise a large portion of public and tribal lands (Carter et al., 2020; Huenneke et al., 2002), making the need to understand and adapt to climate change especially important for public land management. In the Western United States, the size and cost of restoration treatments by federal agencies are steadily growing (Copeland et al., 2018). However, restoration in drylands is notoriously difficult, particularly for warmer and drier ecosystems because variable and prevailing dry conditions impede seedling establishment when seeds are sowed (Shackelford et al., 2021).

Among the most important applied information needs are a reliable understanding of geographic patterns in ecosystem vulnerability to climate change and subsequent impacts on ecological resilience to disturbance and other stressors (Briske et al., 2015). Because disturbances and degradation are common in dryland environments, understanding ecological resilience (i.e., the capacity of ecosystems to recover from stresses and disturbances) and resistance to invasion (hereafter, resistance; i.e., the ability of ecosystems to limit the population growth of invasive species, which is related to the concept also known as "invasibility" elsewhere in the literature) is critical for developing informed management strategies (Chambers et al., 2014, 2023b; Chambers, Allen, & Cushman, 2019), particularly in the context of climate change. Quantitative evaluation of climate vulnerability and ecological resilience and invasion resistance (R&R) at broad spatial scales requires providing consistent, reliable information about environmental conditions that influence ecosystem response to stressors. Because ecological dynamics in drylands are determined by access to available moisture, which is defined by complex interactions among climate, soils, and vegetation that can emerge within days (Barnard et al., 2021; McColl et al., 2022; Silvertown et al., 2015), approaches to quantify R&R need to include these detailed ecohydrological processes in order to capture the important controls under changing climatic conditions (Bradford et al., 2019). Ultimately, drought and disturbances may, in coming decades, promote large-scale transformations in dryland vegetation structure and composition (Breshears et al., 2005; Martínez-Vilalta & Lloret, 2016; Renne et al., 2019; Yuan et al., 2023).

Ecological R&R concepts have become widely utilized in drylands of the Western United States (Chambers et al., 2014; Chambers, Allen, & Cushman, 2019; Chambers, Brooks, et al., 2019; Chambers, Maestas, et al., 2017). Decision-makers need a quantitative, systematic way to recognize how locations differ in their expected responses to disturbances and management activities. The most widely utilized existing effort to provide this information in western North America is the R&R framework (Chambers et al., 2014, 2023b; Chambers, Allen, & Cushman, 2019), which has been applied to prioritize conservation investments and land management strategies (Chambers, Beck, et al., 2017; Chambers, Brooks, et al., 2019; Chambers, Maestas, et al., 2017; Crist et al., 2019; Maestas et al., 2016; Williams & Friggens, 2017). The R&R framework has been operationalized using an indicator system with categories ranging from low to high which are estimated from environmental conditions such as climate, topography, and soils and which can be mapped across the region at small and large scales (Chambers et al., 2014, 2023b; Chambers, Allen, & Cushman, 2019). This information enables efficient prioritization and resource allocation by identifying areas where management activities can increase the adaptive capacity of ecosystems and minimize adverse impacts. Incorporating climate change in the R&R framework can identify areas where important changes in climate are expected and can allow managers to evaluate all options for responding to transitioning ecological conditions, for example, directing ecosystems to new conditions (Millar et al., 2007; Schuurman et al., 2022; Snyder et al., 2018).

Recognizing the need for ecologically informed dryland perspectives on R&R, recent work has updated and improved the climate and drought metrics that define indicators of the R&R framework. Specifically, new studies addressed several important limitations to utilizing the soil moisture regimes and soil temperature regimes based on soil surveys and soil taxonomic concepts for ecological assessments of climate change vulnerability and ecological R&R (Bradford et al., 2019). The new R&R indicators are based on predictive models that were built with >24,000 field sites (Chambers et al., 2023b). Predictor variables describing climate and ecological drought conditions were specifically developed to quantify spatial and temporal dynamics in dryland ecosystems (Chenoweth et al., 2023). In addition to being an important improvement over previous versions (Chambers et al., 2023b), these new R&R indicators represent an opportunity to assess the potential impact of climate change on dryland R&R. These new R&R indicators are appropriate for assessing climate change impacts because they are built upon metrics from a mechanistic water balance model that includes the key processes that drive R&R (i.e., daily, multi-depth site-specific soil profiles, below- and aboveground plant influences) and the key processes that will change with climate (i.e., atmospheric $CO_2$ concentration and daily weather).

Here, our overall goal is to understand where and why climate change will alter the distribution of R&R indicators in the sagebrush region of the Western United States throughout the 21st century. Identifying the areas that are likely to transition under climate change will provide necessary information for prioritizing areas for management and determining the appropriate actions. To accomplish this goal, we pursued five specific objectives: Objective 1 was to estimate R&R categories under future climatic conditions and quantify changes from historical reference distributions of R&R using novel, recently published R&R models (Chambers et al., 2023b). We expected that R&R would generally decline under warmer future temperature conditions because of the R&R models' sensitivity to temperature and moisture (Chambers et al., 2023b). These new R&R indicators involved integrating long-term climate projections into an ecosystem water balance model to estimate the climate and ecological drought metrics that are used as predictors in the R&R models (Chambers et al., 2023b; Chenoweth et al., 2023). Objective 2 was to develop continuous R&R indices that integrate information from the predicted class probabilities of the categorical R&R models. We expected that continuous R&R indices would provide additional insights for land management decision-makers across the large areas that are in low R&R categories even under recent climatic conditions (Chambers et al., 2023b). Objective 3 was to assess the robustness of projected changes in R&R to (3a) uncertainty in future climatic conditions, (3b) uncertainty of the predictions of R&R categories, and (3c) novelty among predictor variables (i.e., combinations among variables not available in the training data). We expected higher levels of robustness in areas where the consistent signal of warming temperature most strongly influences future R&R projections and lower levels of robustness in areas where moisture, which is associated with higher levels of uncertainty among climate models (Bradford et al., 2020), most strongly influence the R&R projections. Objective 4 was to attribute the causes of projected changes in R&R to predictor variable changes due to climate change. We determined which climate and ecological drought metrics were most strongly associated with shifts in R&R indicators. We expected that changes in R&R would be most clearly attributable to changes in temperature, because rising temperatures generally have a larger magnitude of change relative to historical variability than projected changes in precipitation or drought patterns (Bradford et al., 2020). Objective 5 was to examine how future projected R&R indicators relate to recently defined geographic patterns of ecological integrity across the sagebrush region (Doherty, Theobald, Bradford, et al., 2022). We expected that projections of decreasing R&R would be less prevalent in areas that currently have high ecological integrity than in other areas because areas with high ecological integrity tend to occur in relatively cooler and wetter conditions (Doherty, Theobald, Bradford, et al., 2022).

# METHODS

## Study area

We investigated areas supporting rangelands and woodlands within the sagebrush region, also known as the sagebrush biome (Jeffries & Finn, 2019), encompassing 1.16 million km$^2$ in the Western United States. This large area includes a variety of dryland ecosystems (Appendix S1: Figure S1) that are dominated by limited and variable moisture. Big sagebrush, *Artemisia tridentata* Nutt., is the characteristic species over large areas providing habitats for a range of wildlife species and species of conservation concern (Manier et al., 2013) and other ecosystem services including forage for livestock grazing (Davies et al., 2018). The distribution and ecological quality of these habitats have declined over the last decades, and climate change is expected to further alter these systems (Doherty, Theobald, Bradford, et al., 2022). Large-scale geology and topography vary, and the area includes the cold deserts such as the Great Basin, Colorado Plateau, and Wyoming Basins, the lower slopes of several mountainous areas including the Southern and Middle Rocky Mountains, and semiarid prairies in the northeast (Appendix S1: Figure S1). Similarly, overall climatic conditions vary and include mean annual temperature ranging from 3.9 to 12.4°C with a median of 7.9°C, mean annual precipitation ranging from 190 to 596 mm with a median of 327 mm, and seasonal timing of precipitation regimes ranging from cool-season dominated in the west to warm-season in the semiarid prairies and in the southeast.

## Objective 1: Resilience and resistance under projected future climatic conditions

We applied the recently updated and published R&R indicator models (Chambers et al., 2023b) that used random forests (RFs), a machine learning algorithm, to classify indicators of both resilience (RSL) and resistance (RST). The two models used 19 ecologically relevant predictor variables (Appendix S2: Table S1) that represented dryland-focused perspectives on climate, ecological drought, and soil moisture availability and developed for their suitability in ecological assessments under climate change conditions (Chenoweth et al., 2023). Chambers et al. (2023b) developed these R&R indicator models using field plots that represented sagebrush, salt desert, and pinyon-juniper woodland ecosystems across seven Level III Environmental Protection Agency (EPA) ecoregions (US Environmental Protection Agency [US EPA], 2023) within the sagebrush biome in the Western United States (Jeffries & Finn, 2019). The resistance model was created to represent resistance to invasion by *Bromus tectorum* (cheatgrass) because cheatgrass is the most widespread and problematic non-native invasive annual grass across the biome (Chambers et al., 2023b). Additional details on model development, validation, and performance can be found in Chambers et al. (2023b). Here, we used the published models to make spatial predictions of R&R across all rangelands and woodlands within the sagebrush biome using a spatial mask developed by Chambers et al. (2023b). The study region included some ecoregions that were outside the training data (1.16 million $km^2$; Appendix S1: Figure S1; Appendix S2: Table S2).

For this study, we developed a simulation experiment to quantify responses of R&R, as predicted by the published R&R indicator models, under climate change throughout the 21st century. We created a database with the 19 predictors (Appendix S2: Table S1) under ambient observed conditions and 100 projected climatic conditions ($n = 101$). Ambient conditions for years 1980–2020 were the same as those used by Chambers et al. (2023b) and were derived from the daily, 4-km gridded meteorological product gridMET (also known as METDATA, Abatzoglou, 2013). The 100 projected climatic conditions were derived from the daily, 4-km downscaled climate projection product MACAv2-METDATA (Abatzoglou & Brown, 2012) that contains the output of 20 global climate models (GCMs; Appendix S2: Table S3) for coupled model intercomparison project phase 5 (CMIP5; Taylor et al., 2012) under historical conditions and two future emission scenarios (representative concentration pathway 4.5 [RCP4.5]; RCP8.5). Historical projected climatic conditions for 1950–2005 are constructed using MACAv2-METDATA; however, they represent the statistical behavior of 1979–2009 gridMET and serve as a reference to calculate change values for future projected conditions (https://www.climatologylab.org/maca.html). We represented the future emission scenarios with two time periods for years 2029–2064 and 2064–2099.

We calculated the 19 predictors for each of the 101 climatic conditions from daily simulated soil moisture and water balance using the SOILWAT2 ecohydrological model (SOILWAT2 v6.3.0; Schlaepfer, 2022). SOILWAT2 represents daily ecosystem water balance pools and fluxes with a focus on the dynamics of soil moisture and ecological drought across multiple soil layers and on multiple, $CO_2$-responsive vegetation types that can participate in hydraulic redistribution. SOILWAT2 has been used and validated across North America and globally for historical conditions and used for projections under future climate conditions (e.g., Bradford et al., 2014, 2020; Chenoweth et al., 2023; Schlaepfer et al., 2012, 2017, 2021). The simulation runs were set up identically to those described in detail in Chambers et al. (2023b); however, we updated soil specifications using the USDA Natural Resources Conservation Service [USDA NRCS] October 2021 release of gNATSGO (Soil Survey Staff, 2021) resulting in 97,468 simulation units across the study area. The simulation units were based on soil map unit polygons underlying gNATSGO (utilizing the dominant soil component), and for large polygons, their intersections with gridMET grid cells. We then mapped our results across simulation units back onto the 30-m gNATSGO grid (Appendix S1: Figure S2; Appendix S2: Table S4).

We next obtained projected R&R values for each of the 101 climatic conditions by applying the R&R prediction models to our predictor database. The prediction models were implemented in R (R Core Team, 2023) with the package "randomForest" (Liaw & Wiener, 2002). The output of categorical RF models were vote counts for each of the four modeled R&R categories; Chambers et al. (2023b) developed the four categories Low ("L"), Moderately-Low ("ML"), Moderate ("M"), and High/Moderately-High ("H + MH") as resilience and resistance indicators. We converted the vote counts into probabilities (i.e., the probabilities across the four categories sum to 1), $p$, and calculated the most likely category as the category with the highest probability, that is, max $\{p(\mathrm{L}), p(\mathrm{ML}), p(\mathrm{M}), p(\mathrm{H+MH})\}$.

We summarized results across sets of 20 outcomes derived from the 20 individual model projections for each climate scenario and time period. For the groups of related variables associated with each R&R (four probabilities, most likely category, and a continuous index which is described below), we first calculated a low (10%-percentile), median, and high (90%-percentile) value across the 20 model projections of the associated continuous resilience or resistance index. Then, we identified the model projections that were closest to these low, median, and high values. Finally, we used the four probabilities and most likely category from those three identified model projections as the low, median, and high summaries. This guaranteed that each prediction group, including the four probabilities, most likely R&R category, and continuous index, remained congruent. For all other variables, for example, the 19 predictors, we utilized the low (10%-percentile), median, and high (90%-percentile) values of the variables.

We calculated change from historical conditions as the difference between a projected future outcome and the projected historical (not observed ambient) outcome following the recommended approach by MACAv2-METDATA (see section "Analysis Tips" at https://climate.northwestknowledge.net/MACA/MACAanalysis.php). For categorical outcomes, we defined change through a convolution matrix, that is, change in categorical R&R was described with 16 categories where the four categories under future conditions could be originating from any of the four categories under historical conditions (e.g., future L from historical L, future L from historical ML, and future M from historical H + MH).

## Objective 2: Continuous indices of ecological resilience and resistance

We developed new continuous R&R indices that combine information from all four probability values. Specifically, we defined the continuous index (Equation 1) of resilience or resistance as a linear combination:

$$\text{Continuous index} = -1 \times p(\mathrm{L}) - 1/3 \times p(\mathrm{ML}) + 1/3 \times p(\mathrm{M}) + 1 \times p(\mathrm{H+MH}) \tag{1}$$

The continuous index varied from −1 to +1 (Appendix S1: Figure S3), and the value of the continuous index is −1 exactly if the probability of the Low category is equal to 1, that is, $p(\mathrm{L}) = 1$, and +1 exactly if the probability of the High/Moderately-High (H + MH) category is equal to 1, that is, $p(\mathrm{H+MH}) = 1$. However, values between −1 and +1 do not map uniquely to distinct sets of the four underlying probabilities. An important caveat is that Equation (1) assumes the four categories to be equidistant even though the R&R indicators were developed on an ordinal scale without defined and fixed distances among categories.

## Objective 3: Uncertainty in predicted R&R

We determined the degree of consistency in the climate change signal for each spatial unit and for each variable as the number of model projections (of the 20 individual model projections per future emission scenario and time period) for which the sign of change from historical conditions agreed with the sign of the median change summary of that variable. We defined the sign of change for R&R categories as positive if the future category was higher than the historical category (e.g., future M from historical ML), as zero if the future and historical categories were identical (e.g., future L from historical L), and as negative if the future category was lower than the historical category (e.g., future ML from historical M). We then used the robust climate signal terminology developed by Bradford et al. (2020) and classified a change as robust if 19 or 20 out of the 20 model projections (>90%) were consistent.

Additionally, we quantified how the certainty of categorical RF model prediction changes under projected climatic conditions. Specifically, we defined RF-certainty as excess probability (Equation 2), that is, the difference between the probabilities of the most likely ($l$) and second most likely category:

Let $l(r, n)$ be the $n$-th largest element of the set of $r = \{p(\mathrm{L}), p(\mathrm{ML}), p(\mathrm{M}), p(\mathrm{H+MH})\}$, then

$$\text{RF certainty} = l(r,1) - l(r,2) \tag{2}$$

RF-certainty varies from 0 to +1 (Appendix S1: Figure S4). If the model prediction is completely certain about the most likely category, then one category is predicted with a probability of 1 and the three others each have a probability of 0, and the RF-certainty becomes 1; if the prediction is increasingly uncertain about the most likely category, then the probabilities of the two most likely categories become increasingly similar, and the RF-certainty approaches 0. RF-certainty reaches 0 when the two most likely categories are predicted with the same probability (that is, equal to or larger than the predicted probabilities of the remaining categories).

Finally, we quantified predictor novelty to assess how much predictor values under projected climatic conditions differed from the model training data under ambient climatic conditions. We investigated two aspects of predictor novelty: (1) a univariate (box) perspective that measures the distance to the range of individual predictors and (2) a multivariate perspective that identifies novel combinations of predictors. We calculated novelty as "NT1" which we based on the univariate "NT1(original)" metric developed by Mesgaran et al. (2014) and as "DI-ratio" which we based on the multivariate "AOA" metric developed by Meyer and Pebesma (2021). To make these two metrics directly comparable, we put them on the same scale by slightly adjusting the original metrics (Equations 3 and 4):

$$\mathrm{NT1} = 1 - \mathrm{NT1(original)} \tag{3}$$

$$\text{DI ratio} = {}^{\mathrm{DI}_k(\mathrm{AOA})}\!/_{\text{threshold}} \tag{4}$$

where $\mathrm{DI}_k(\mathrm{AOA})$ refers to the original, standardized weighted distances "$\mathrm{DI}_k$" and the threshold is the original, outlier-removed maximum distance of the training data (calculated as the 75th-percentile plus 1.5 times the interquartile range) as implemented in the R package "CAST" v0.8.1 (Meyer et al., 2023). We calculated DI-ratio without cross-validation folds or variable importance weights as they only had a small impact (not shown). Thus, both NT1 and DI-ratio range from 0 to plus infinity where values from 0 to 1 identify predictor values similar to the training data and where values larger than 1 identify novel predictor values.

## Objective 4: Attribution of projected changes in R&R to model predictors

We identified the most impactful variables of the projected R&R changes with a local sensitivity analysis. Specifically, we quantified which single modified predictor variable led to the largest deviations from a prediction under a future model projection, that is, this analysis estimates the impact of variables by combining exposure to climate change and importance/sensitivity in the RF models (Appendix S1: Figure S5). First, we created 19 modified predictor sets, one for each of the 19 predictors. Each modified predictor set contained the values under the future climatic condition except for one predictor for which the value was reset to its historical value. Second, we applied the R&R RF models to the 19 modified predictor sets and generated 19 modified predictions where each prediction consists of a set with four probabilities $\{p(\mathrm{L}), p(\mathrm{ML}), p(\mathrm{M}), p(\mathrm{H+MH})\}$. Third, we calculated the Euclidean distances between the (original) prediction under the future climatic condition and each of the 19 modified predictions. Fourth, the largest of the 19 distances identified the most impactful variable that, when modified, caused the largest deviations. We resolved ties at random. We carried out this procedure for every simulation unit and for all future climatic conditions.

## Objective 5: Relationships between sagebrush ecological integrity and projected changes in resilience and resistance

We combined projected changes in R&R indicators with the threat-based sagebrush ecological integrity (SEI) index (SEI version 1, Doherty, Theobald, Bradford, et al., 2022), building on recent work by Chambers et al. (2023c), which utilizes this combination for prioritizing management actions in sagebrush ecosystems. We spatially intersected the SEI categories “other rangelands” (ORA), “growth opportunity areas” (GOA), and “core sagebrush areas” (CSA) using current (2017–2020) values and tabulated areas with increases, decreases, or no changes in projected R&R categories, and we further separated these into areas with a robust change signal and other areas.

# RESULTS

## Objective 1: Resilience and resistance under projected future climatic conditions

Our results suggest greater extents of lower R&R categories under future climate. We evaluated R&R separately and report summarized results for both where appropriate. We focus here on results for the moderate emission RCP4.5 scenario at the end of the century for brevity and because results are analogous (Figures 1–3), that is, declines in R&R were stronger and included more widespread robust signals later in the century than mid-century and under the higher emission RCP8.5 scenario than the RCP4.5 scenario (Appendix S1: Figures S6–S13; Appendix S2: Tables S5 and S6). Across the study area, decreasing R&R was estimated for 24% (21%–30% among model projections) of the area for resilience and 34% (28%–41% among models) for resistance. In most remaining areas, R&R was not projected to decline and remained in the same categories as under historical conditions (Figure 2).

Nearly all historically Low R&R areas remained low under future climate, and much of those areas are robust across climate models (75% robust for resilience and 64% for resistance; Figure 3). Areas that transitioned to Low R&R from a higher category primarily infilled ecoregions in the western part of the study area and expanded across the Colorado Plateau and Wyoming Basin, especially for resilience (Figure 1). Overall, Low R&R areas increase by 135,000 (58,000–214,000) km$^2$ for resilience and by 159,000 (86,000–222,000) km$^2$ for resistance from historical conditions (Appendix S2: Table S6).

Substantial portions of areas with Moderately-Low, Moderate, and High/Moderately-High categories decreased to lower categories under future climate (Figure 3). Areas that decreased to Low R&R included 42% (24%–66%) of the historically Moderately-Low resilience areas and 34% (20%–51%) of historically Moderately-Low resistance areas; however, robust consistency among climate models occurred across only 19% and 13% of the areas that decreased to Low R&R from historically Moderately-Low resilience and resilience, respectively. Overall, transitions from the Moderate or High/Moderately-High categories resulted in an uncertain, small net increase of the area with Moderately-Low category by 6000 (−40,000 to +60,000) km$^2$ for resilience and a net increase by 58,000 (54,000–75,000) km$^2$ for resistance (Appendix S2: Table S6). Moderate R&R areas were projected to experience the largest loss in area under future climate, with declines of 37% (33%–49%) for resilience and 56% (48%–71%) for resistance, with a considerable area of robust change (Figure 3). These areas represented a net loss of 87,000 (56,000–124,000) km$^2$ for moderate resilience and 134,000 (57,000–219,000) km$^2$ for moderate resistance (Appendix S2: Table S6). Areas converting away from Moderate R&R were almost entirely converted to Low R&R (e.g., Northern Basin and Range) or to Moderately-Low R&R, as shown for resistance in the Wyoming Basin and Semiarid Prairies (Figures 1 and 2). Of the historically Moderate R&R areas that remained Moderate in the future, 41% were robust for resilience and 15% for

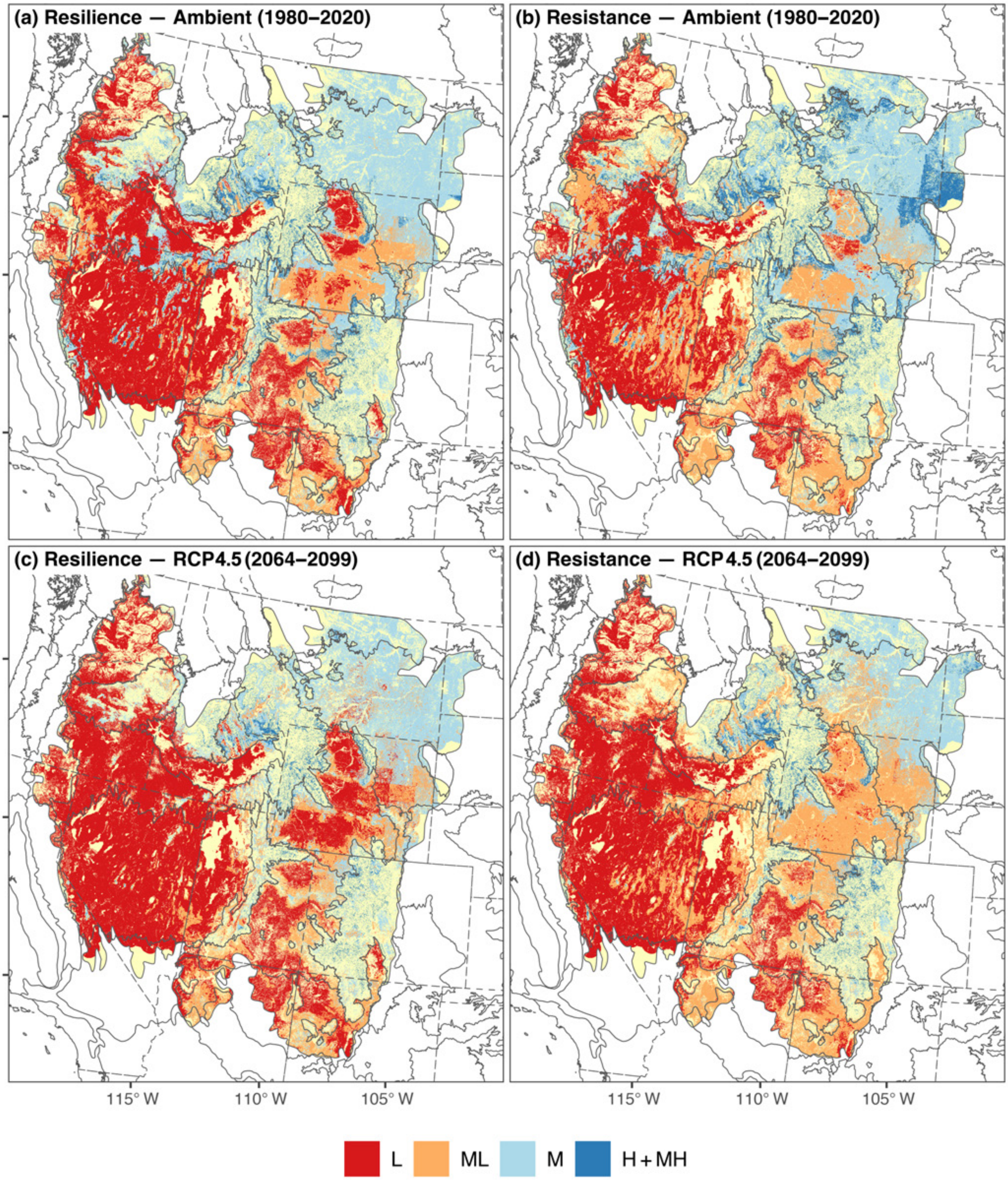


**FIGURE 1** Maps of predicted resilience (a, c) and resistance (b, d) categories (H + MH, High or Moderately-High; L, Low; M, Moderate; ML, Moderately-Low) under ambient (1980–2020; a, b) and future climatic conditions (representative concentration pathway [RCP] 4.5 2064–2099; c, d). Level III Environmental Protection Agency (EPA) ecoregions and administrative boundaries (states, provinces) are delineated. Areas that do not support the study ecosystems are shown in light yellow.

resistance (Figure 3). High/Moderately-High areas experienced the largest proportional decline under future climate with decreases of 59% (51%–69%) for resilience and 61% (51%–63%) for resistance, although only small fraction of these areas displayed robust changes (Figure 3). Overall, the net loss of High/Moderately-High areas represented a

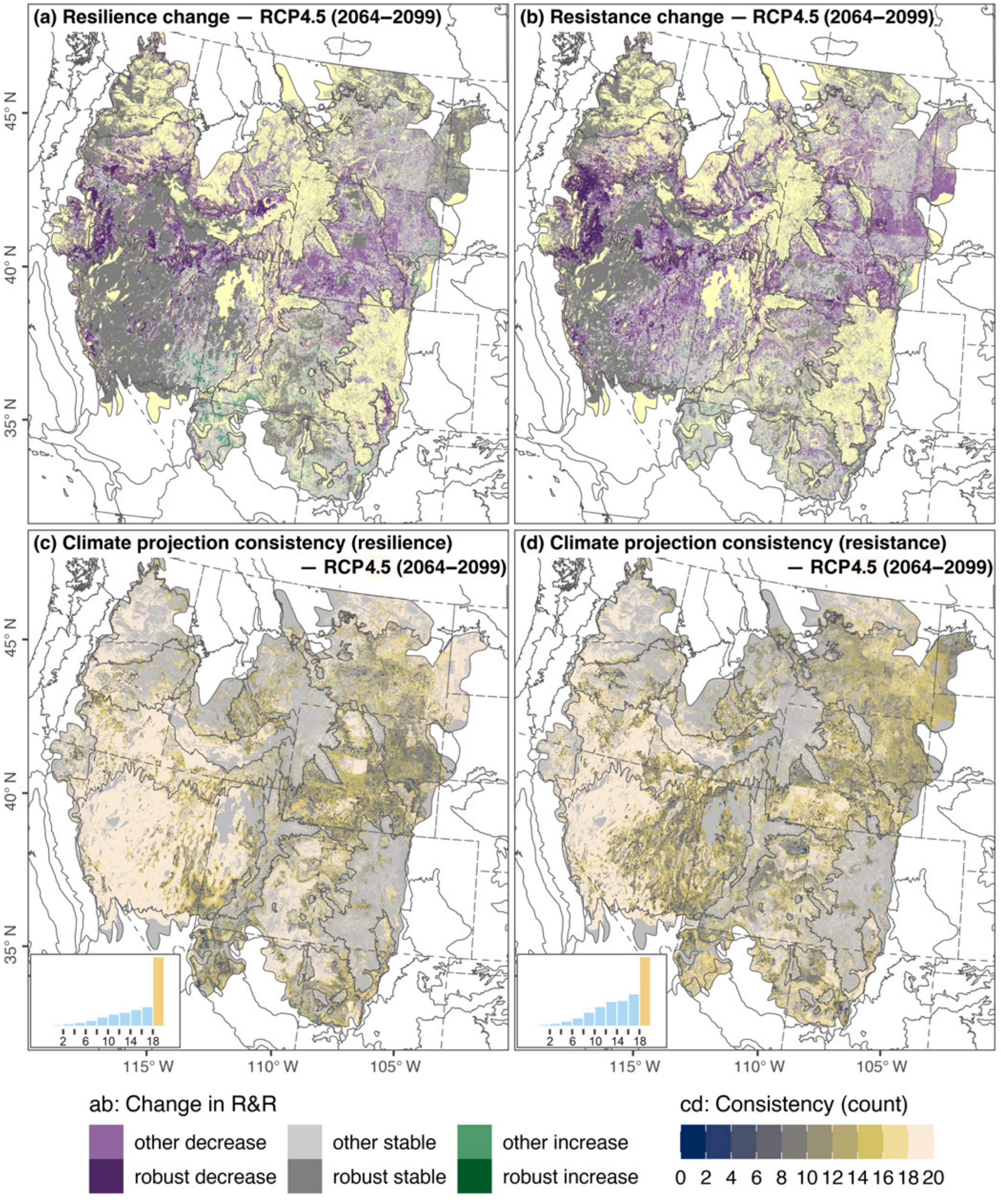


**FIGURE 2** Maps of projected median change (a, b) and associated consistency (c, d) in predicted resilience (a, c) and resistance (b, d) (R&R) categories as change between simulations under future (representative concentration pathway [RCP] 4.5 2064–2099) and historical (1950–2005) climatic conditions. Maps of consistency among the 20 model projections as number of projections that agree in the direction of change (c, d). Robust change is defined where >18 out of 20 of model projections are consistent (tan color in c, d). Insets show proportion of area in each consistency bin. Level III Environmental Protection Agency (EPA) ecoregions and administrative boundaries (states, provinces) are delineated. Areas that do not support the study ecosystems are shown in light yellow (a, b) or gray (c, d).

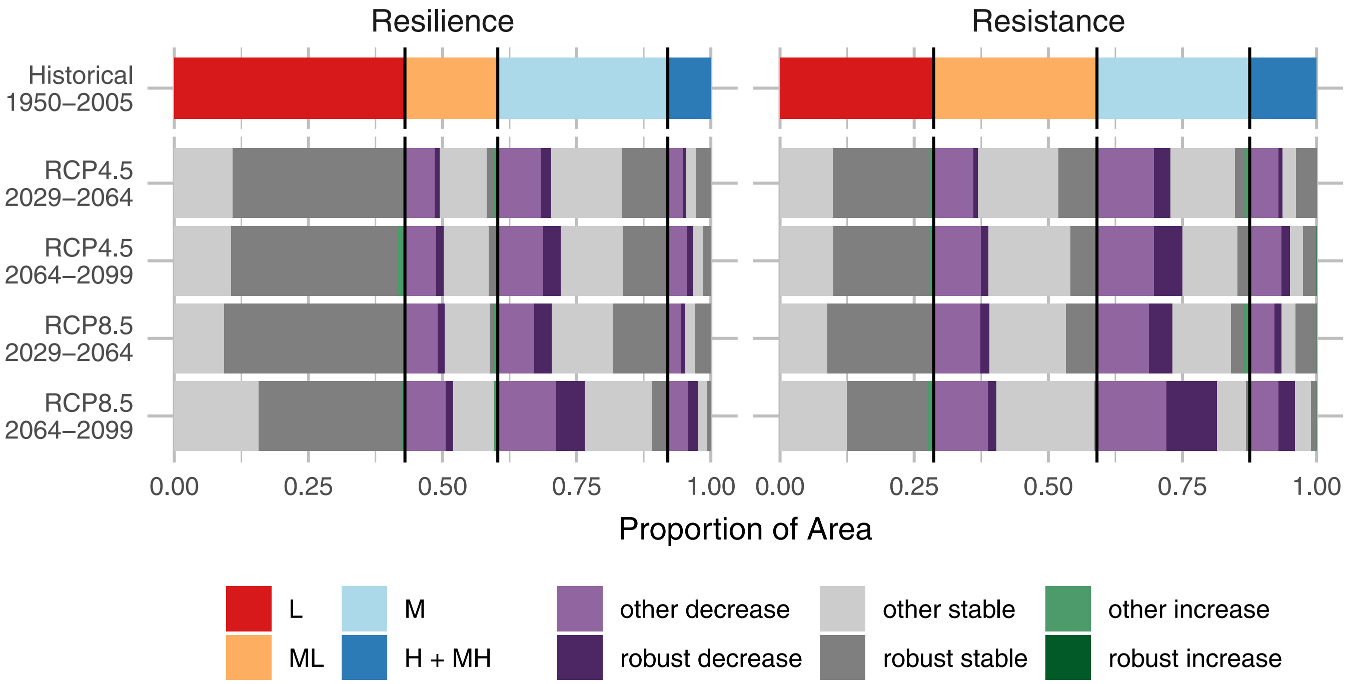


**FIGURE 3** Proportion of study area by resilience and resistance (R&R) categories under historical (1950–2005) and future climatic conditions as robust median change between projected and historical R&R predictions where >18 out of 20 of model projections are consistent in the direction of change. Black vertical lines highlight historical values of resilience and resistance categories. H + MH, High or Moderately-High; L, Low; M, Moderate; ML, Moderately-Low; RCP, representative concentration pathway.

decrease of 54,000 (50,000–62,000) $km^2$ for resilience and 83,000 (57,000–105,000) $km^2$ for resistance (Appendix S2: Table S6). High/Moderately-High areas decreased most strongly in the Semiarid Prairies and to a lesser extent at high elevations (Figures 1 and 2).

## Objective 2: Continuous indices of ecological resilience and resistance

The continuous R&R indices reflected the spatial patterns of the corresponding R&R categories (Figure 4; Appendix S1: Figure S14; Appendix S2: Table S7). The density of values under ambient conditions showed peaks at low values and at intermediate high values that matched the widespread Low and Moderate categories. The peak at intermediate high values disappeared or was strongly reduced under future climatic conditions (Appendix S1: Figure S14) that matched with the large losses in the Moderate categories. Comparable to the changes of the R&R probabilities under future climate, the continuous indices decreased robustly across the Northern Basin and Range, some areas of the Central Basin and Range, Blue Mountains, some areas between the Snake River Plain, Idaho Batholith, and Middle Rockies, as well as Wyoming Basin and the Northwestern Great Plains (see Appendix S1: Figure S1 for a map of ecoregions). Small increases in indices values occurred mostly across southern areas yet none of those showed a robust signal (Figure 4).

## Objective 3: Uncertainty in predicted R&R

Robust signals occurred across the study area for resilience (48% for initial categories and 43% for the continuous index) and for resistance (35% for initial categories and 53% for the continuous index; Figures 2–4; Appendix S2: Tables S5–S7). The geographic distribution of areas with robust signals for the categorical indicators differed from those for the continuous indices (Figures 2 and 4). Robust signals for the categorical indicators occurred mostly in the western parts of Central and Northern Basin and Range, Snake River Plain, Columbia Plateau, portions of the Colorado Plateaus, small pockets in the Wyoming Basin, and portions of the Semiarid Plains (Figure 2). These spatial patterns were dominated by areas where the Low categories remained Low under future climate projections (Figure 3). Robust signals for the continuous indices occurred across the Northern Basin and Range, some areas of the Central Basin and Range, Blue Mountains, some areas between the Snake River Plain, Idaho Batholith, and Middle Rockies, and Wyoming Basin and the Northwestern

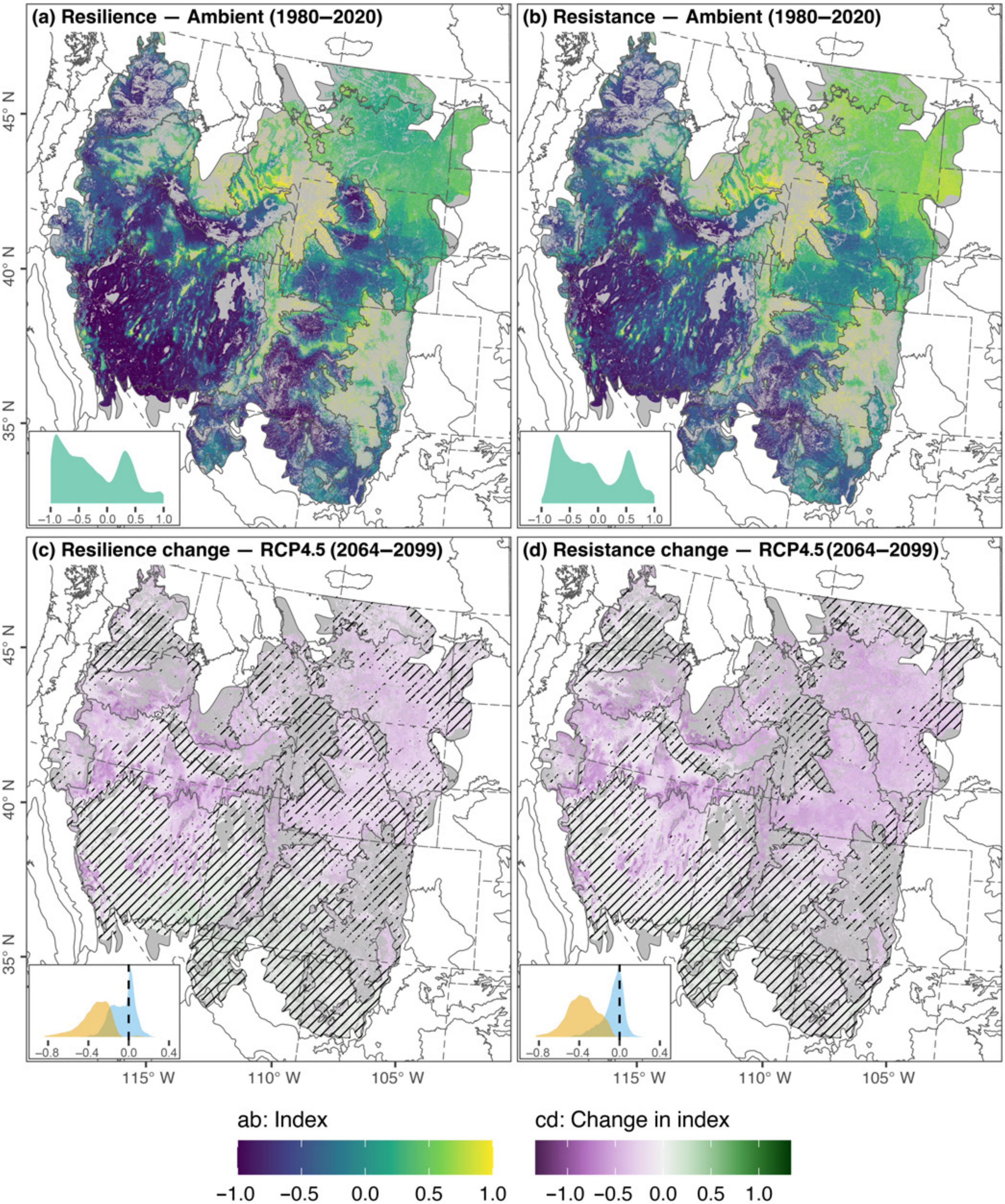


**FIGURE 4** Maps of predicted continuous resilience (a, c) and resistance (b, d) indices under ambient conditions (1980–2020; a, b) and maps of median change in predicted indices (c, d) between simulations under future (representative concentration pathway [RCP] 4.5 2064–2099) and historical (1950–2005) climatic condition. Cross-hatching marks areas where ≤18 out of 20 of model projections are consistent in the direction of change. Insets show area-weighted density distributions (separated by robust [orange] and other [blue] areas in c, d). Level III Environmental Protection Agency (EPA) ecoregions and administrative boundaries (states, provinces) are delineated. Areas that do not support the study ecosystems are shown in gray.

Great Plains (Figure 4). These spatial patterns were dominated by areas where probabilities of Low robustly increased and where probabilities of higher categories robustly decreased under future climate projections (Appendix S1: Figures S6–S9).

The ability of the underlying RF to identify the most likely R&R categories with certainty varied spatially under ambient conditions (Appendix S1: Figure S15; Appendix S2: Table S8). Areas with high certainty occurred, particularly for resilience indicators, for the Low categories in the western parts of the Central Basin and Range and for the High/Moderately-High categories in the Middle Rockies. This type of certainty did not change much under future climate projections where areas with a robust signal were small and mostly occurred in the western parts of the Northern Basin and Range.

The univariate novelty metric NT1 identified few areas with novelty in predictor values across the study area under ambient conditions (11%), whereas the multivariate metric DI-ratio identified novelty in some southern and northern parts (46%; Figure 5; Appendix S1: Figure S16; Appendix S2: Table S9). Novelty based on DI-ratio occurred mostly across the southernmost areas, the Arizona und New Mexico Mountains and Plateaus, and, to a lesser degree, across the northwestern parts of the study area, including the Blue Mountains and the Columbia Plateau. Future climate projections increased novelty as quantified by NT1 by a moderate amount, 17% (6%–75%), whereas DI-ratio identified all areas as having novel predictor combinations, with the southernmost areas exhibiting the greatest degree of novelty (Figure 5).

## Objective 4: Attribution of projected changes in R&R to model predictors

Declines in R&R were most strongly linked to variables related to rising temperatures (Figure 6). Annual temperature was projected to increase by 3.25°C (2.0–4.1°C) under RCP4.5 for 2064–2099 throughout the study area (Appendix S1: Figure S2; Appendix S2: Table S4), and this variable was the most impactful variable for explaining resilience changes across 52% (38%–59%) and resistance changes across 53% (41%–61%) of the areas (Figure 6; Appendix S1: Figure S17). The second most impactful variable was the temperature of the coldest month, which was projected to increase by 3.06°C (2.3–3.9°C) throughout the study area (Appendix S1: Figure S2; Appendix S2: Table S4). Increasing temperature of the coldest month was the most impactful variable over larger areas of resistance, 24% (22%–25%), than resilience, 12% (8%–17%), and across much of the Semiarid Plains, along the edges of the Snake River Plain, and some low elevations of the Central and Northern Basin and Range (Appendix S1: Figure S17). The third most impactful explainer of resilience change was climatic water deficit across 9% (7%–9%) of the area, which was projected to increase by 59 mm (33–83 mm) throughout the study area (Appendix S1: Figure S2; Appendix S2: Table S4). The third most impactful explainer of resistance change was June–September total precipitation, which was projected to change by +3.4 mm (−7.5 to +16.6 mm) averaged across the study area (although changes are largely not robust; Appendix S1: Figure S2; Appendix S2: Table S4). June–September precipitation was important for 6% (3%–9%) of the area mostly in the southern parts of the Central Basin and Range and Colorado Plateau (Appendix S1: Figure S17).

## Objective 5: Relationships between SEI and projected changes in resilience and resistance

R&R indicators were consistent with the SEI index at a large-scale under ambient conditions (Figure 7). Specifically, CSA coincided the least with Low R&R categories and the most with Moderate categories. ORA coincided the most with the Low categories and the least with High/Moderately-High categories, and GOA were in the middle (Figure 7; Appendix S2: Table S10). Under projected future climate, CSA experienced the largest proportional declines in resilience, 40% (32%–49%), and resistance, 52% (44%–60%). These declines were stronger for the high than medium emission scenario and late than middle century. By contrast, future declines in resilience, 15% (14%–20%), and in resistance, 23% (20%–27%), are projected over only small proportions of ORA and R&R declines in GOA were intermediate.

# DISCUSSION

Understanding climate change impacts on dryland R&R is essential for developing management strategies that will be durable for multiple decades. Decisions about where to invest conservation and restoration resources require information about the long-term viability of the species and plant communities that are prioritized for conservation or restoration management. The new R&R indicators provide an opportunity to incorporate climate change impacts into assessments of the recovery potential of dryland ecosystems following disturbances and management actions. Here, we conducted a comprehensive

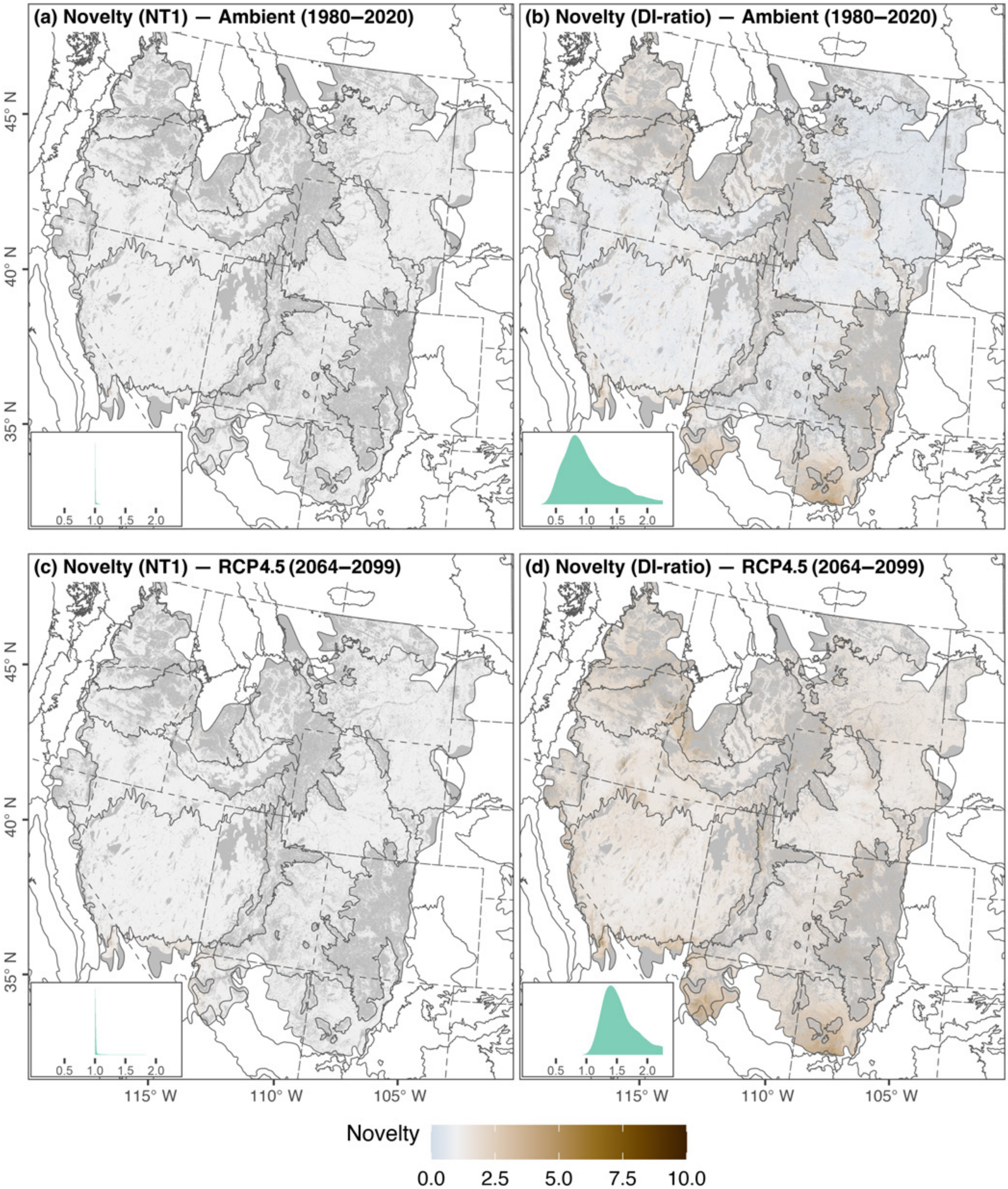


**FIGURE 5** Maps of univariate (NT1: a, c) and multivariate (DI-ratio: b, d) novelty in predictor space beyond model training conditions under ambient (1980–2020; a, b) and median future climatic conditions (representative concentration pathway [RCP] 4.5 2064–2099; c, d). Values between 0 and 1 (blue hues) indicate no novelty; values larger than 1 (brown hues) represent increasing novelty. Insets show area-weighted density distributions. Level III Environmental Protection Agency (EPA) ecoregions and administrative boundaries (states, provinces) are delineated. Areas that do not support the study ecosystems are shown in gray.

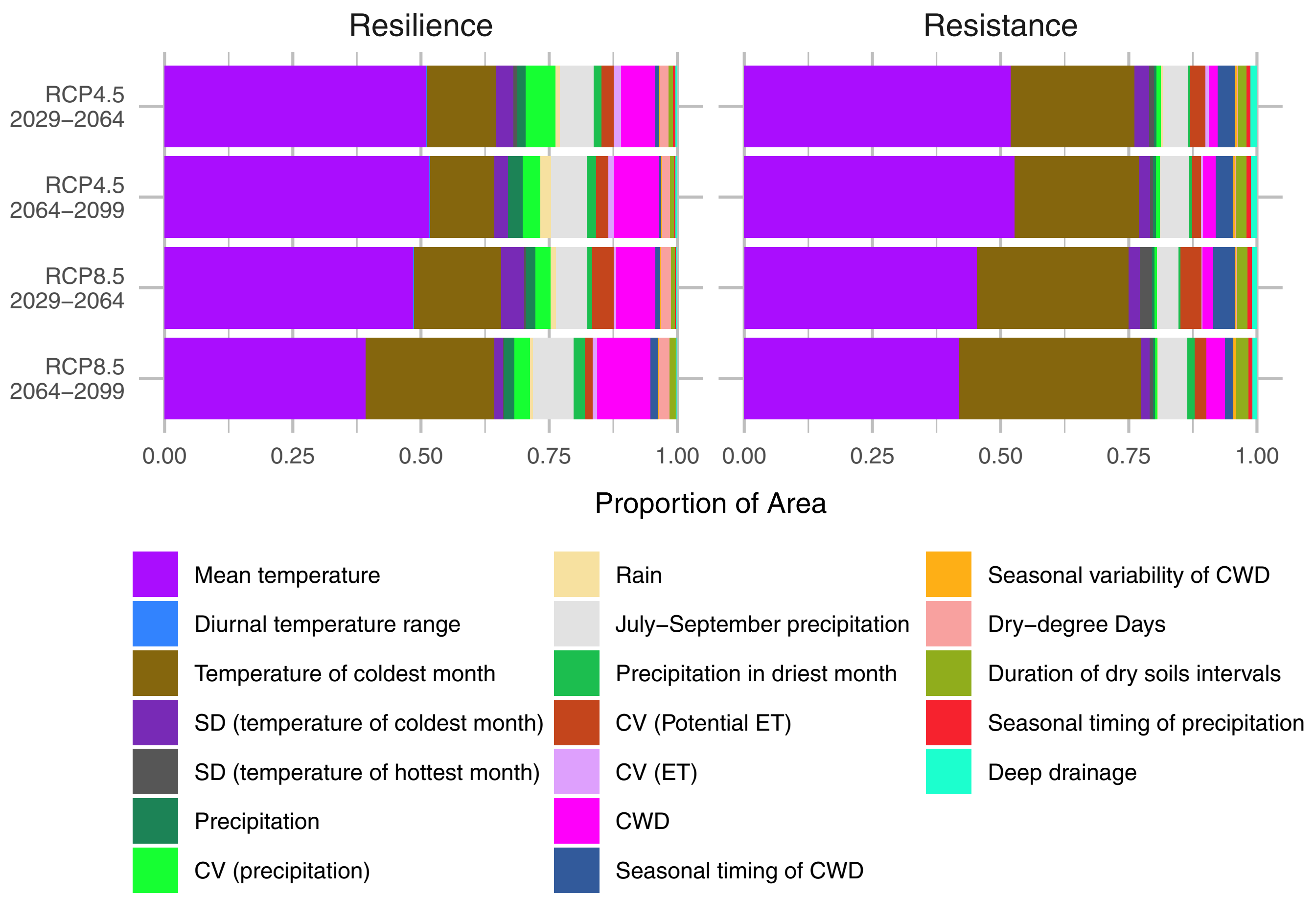


**FIGURE 6** Proportion of the study area by median most impactful predictor variable for the change in resilience and resistance between future (representative concentration pathways [RCPs]) and historical (1950–2005) climatic conditions. See Appendix S2: Table S1 for full definition including units of predictor variables; all variables represent long-term means unless noted otherwise. Maps depicting the spatial distribution of the most impactful predictor variables are available in Appendix S1: Figure S17. CWD, climatic water deficit; ET, evapotranspiration.

evaluation of climate change effects on the new R&R indicators, and we identify several important findings.

## Resilience and resistance under projected future climatic conditions

Twenty-first-century climate change is likely to promote decreases in dryland R&R (Figures 1–4), which highlights a substantial concern for natural resource managers. Most historically Low R&R places remained low, while many areas of historically Moderately-Low, Moderate, and High/Moderately-High categories decreased to lower categories. Areas of historically High/Moderately-High R&R experienced the largest proportional declines, and historically Moderate R&R experienced the largest total areal loss. These projections for R&R declines are more severe and more widespread under climatic conditions expected at the end of the century and under the high-emissions RCP8.5 scenario (Figure 3). The projected changes are important because ecosystems in many parts of the study area are already being transformed by the combination of non-native invasive annual grasses, more frequent and extensive wildfires, and warming conditions (Abatzoglou & Kolden, 2013; Bradley et al., 2018). Historically, these transformations were most likely in low R&R areas, and future decreases in R&R indicate that an increasingly large proportion of these drylands will be vulnerable. As a result, avoiding transformations is likely to require increasingly effective mitigation of wildfire risk and restoration techniques that minimize the risk of post-wildfire conversion to non-native invasive annual grasses in Low to Moderate resistance areas (Chambers et al., 2023c; Chambers, Brooks, et al., 2019). Mitigating fire risk and restoring native plants are common management objectives but are particularly challenging in warmer and drier ecosystems (Boyd, 2022; Davies et al., 2020; Svejcar et al., 2017). As climate changes, and

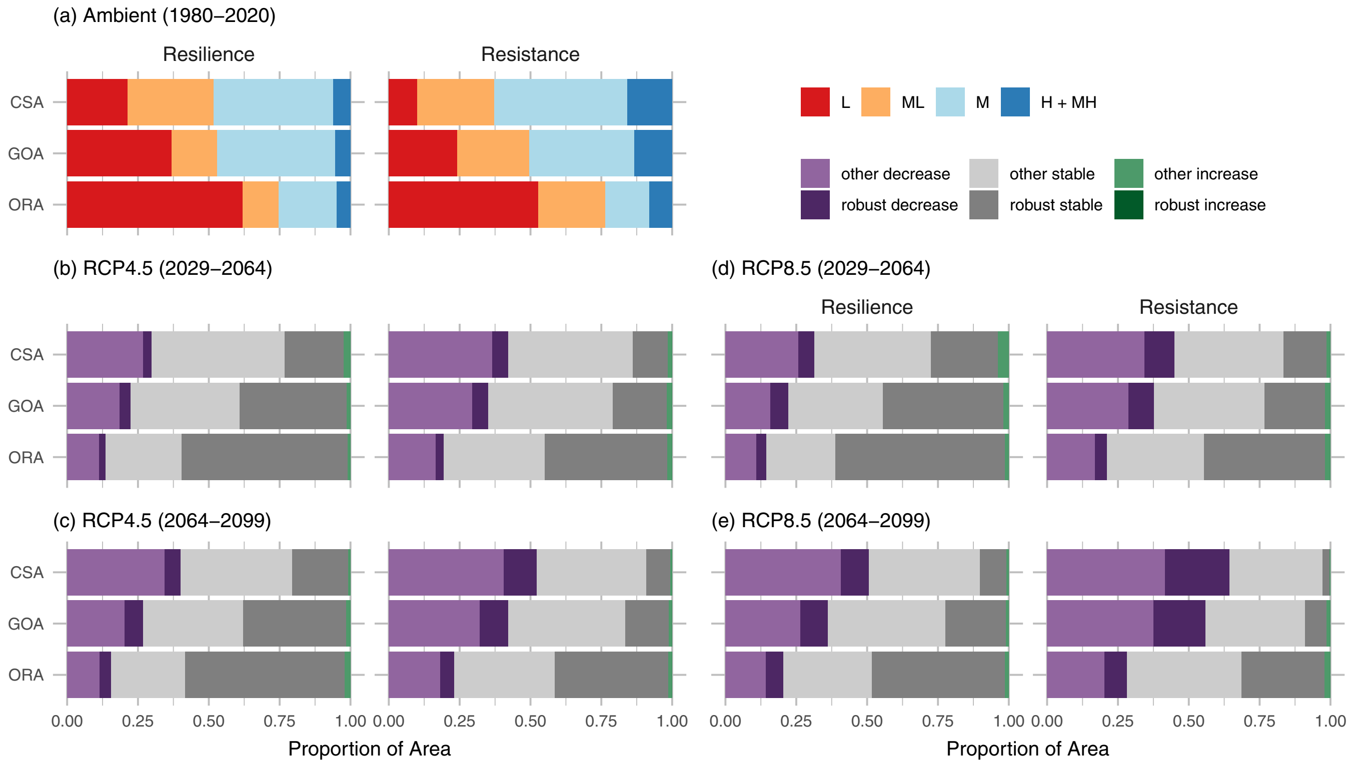


**FIGURE 7** Proportion of the study area of the spatial intersection of changes in resilience and resistance categories with current sagebrush ecological integrity (SEI) categories under ambient (1980–2020) and future (representative concentration pathways [RCPs]) climatic conditions as robust median change between projected future and historical predictions where >18 out of 20 model projections agree in the direction of change. CSA, core sagebrush area; GOA, growth opportunity areas; ORA, other rangelands.

the area characterized by lower R&R increases, minimizing wildfires and maximizing restoration success are likely to become both more difficult and more important to sustain native plant communities in drylands (Schlaepfer et al., 2021).

## Uncertainty in predicted R&R

Future decreases in R&R are largely consistent among climate models. Uncertainty about long-term climatic conditions and ecological impacts is a pervasive complication for 21st-century natural resource management (Schuurman et al., 2022). In this context, our projections of R&R declines are robust across simulations driven by different climate models (here, ≥90% of simulations agree) for 35%–53% of the study area (Figures 2c,d and 4c,d), showing a clear signal that can be useful for guiding forward-looking restoration and conservation decisions. The robust evidence for future declines in R&R emerged because rising temperature is among the most reliable characteristic of climate projections (IPCC et al., 2021), and because temperature-related variables are important for determining R&R (Chambers et al., 2023b). Changes in most moisture-related aspects of climate change, including precipitation, aridity, and some soil moisture conditions, were not consistent among climate models, but temperature increases were consistent and substantial relative to historical variability (Bradford et al., 2020). The combination of importance for R&R estimation and substantial increases helps explain why metrics closely related to temperature (especially mean annual temperature and mean temperature of the coldest month) emerged as dominant drivers of changing R&R. Our metric of robustness requires agreement among model projections both in space and in the direction of the signal. Even where projections may disagree in space, they often agree considerably in the signal when summarized across space (e.g., low-high results that do not include 0). Besides identifying agreement among R&R projections, we comprehensively evaluated uncertainty in R&R projections by mapping predictor novelty and predictive model uncertainty, by covering multiple emission scenarios (e.g., see Figure 3), and by quantifying spread among model projections (e.g., see Appendix S2: Tables S4–S10).

More widespread robust signals in projected R&R, however, were constrained by remaining uncertainty of long-term climate projections. Important factors in dryland water balance included, among others, amount and seasonal timing of available moisture (Noy-Meir, 1973);

however, related climate variables are among the most difficult to physically represent in climate models, and consequently, future projections varied considerably (Lehner et al., 2020). Among such variables were timing, amount, and geographic occurrence of summer monsoon or summer convective storms that have large impacts on seasonal ecosystem function in our study region. Additional sources of uncertainty existed via the choice of a downscaled dataset of climate projections and the provenance of the climate projections utilized for the downscaling (here, MACA downscaling method based on CMIP5-era projections).

## Continuous indices of ecological resilience and resistance

Our development of new, quantitatively continuous indices for R&R may be helpful for understanding both historical and future R&R patterns. Because the continuous R&R indices were derived from the categorical probabilities (Appendix S1: Figures S6–S9), the continuous R&R indices captured the spatial patterns across the corresponding R&R categories. The continuous indices also help provide more perspective on areas with expected future shifts in R&R that do not create a change in R&R category. For instance, the continuous indices allow for a decreased value even in areas with a historically Low R&R category that remained low in the future even though the underlying probabilities decreased (e.g., compare Figure 2c,d with Figure 4c,d). In addition, these continuous R&R indices can be integrated into other analyses that may not be able to utilize probabilities for each of the four R&R categories. One insight from the continuous R&R indices is that while areas with robust signals for decreasing continuous R&R were widespread, we found no areas with robust signals for increasing resistance or resilience (Figure 4c,d).

## Relationships between SEI and projected changes in resilience and resistance

Our results have implications for SEI areas currently categorized as core and growth areas. Our analysis added the perspective of long-term climate projections to a recently developed framework to prioritize sagebrush ecosystems for appropriate management actions (Chambers et al., 2023c) by combining the recently developed SEI index categories (SEI; Doherty, Theobald, Bradford, et al., 2022) with the new R&R indicators. Similar to Chambers et al. (2023c), we found that SEI and R&R were both consistent and complementary to each other under ambient climatic conditions. However, our results suggested that areas with the currently highest SEI, that is, CSA, are expected to experience the largest proportional declines in R&R under future climate. Declining R&R in CSA is consistent with our results showing robust R&R declines in areas with historically higher R&R (Figure 3). This suggests that areas with historically higher R&R (which tend to coincide with high SEI) will behave more like lower R&R areas in the future. For instance, the prioritization framework suggests good restoration potential for areas with high SEI and Moderate R&R under ambient climatic conditions (e.g., areas in the Wyoming Basins) with some preventative management intervention to maintain function and minimize risk of invasion (Chambers et al., 2023c). However, our future projections indicated that substantial areas of CSA will experience decreasing R&R (40% or 54,000 $km^2$ for resilience and 52% or 71,000 $km^2$ for resistance, respectively; Appendix S2: Table S10). Therefore, the potential for restoration success may decrease, and the intensity of interventions required to maintain high SEI may increase substantially. These projections for substantial R&R declines in high-quality habitats warrant further investigation, potentially by intersecting future continuous R&R with future projections for SEI (instead of values under recent climate) to fully assess climate impacts on conservation and restoration prioritization in the sagebrush biome.

## Future improvements

Opportunities for further improvement include addressing limitations and caveats related to input data, predictive R&R models, and representation of future conditions. Issues with input data included incomplete or inconsistent soil surveys across the study area (e.g., efforts are ongoing to complete the soils data in SSURGO; Soil Survey Staff, 2021), and inconsistent development of ecological site descriptions (ESDs) among US states (Maynard et al., 2019). Another challenge is adequately representing climate variables and ecological drought metrics at the desired spatial resolution, and a further refinement could include using consistent spatial resolution, which currently is a combination of polygons of the soil map units, 4-km gridded climate, and the underlying 30-m gNATSGO raster. Intermediate approaches may be followed to evaluate the utility of spatially downscaling the predicted R&R values based on high-resolution datasets such as topographic information. Alternatively, it may be possible to downscale the predictor climate and water availability variables in the R&R models until the soil survey is complete. Future iterations of this work will utilize updated climate model projections and new downscaled datasets for the study region as they become available. For instance, this work was based on CMIP5-era projections, and the work is in progress to downscale CMIP6-era climate model projections for the study region.

Opportunities also exist for improving predictive R&R models, particularly for areas with low R&R values. The development of the current predictive R&R models was based on four categories only and biased toward sagebrush-dominated areas. This resulted in limited differentiation across large areas where a Low R&R category was predicted, for example, most of the Central Basin and Range, so future projections were not capable of predicting decreases in those Low (warm and dry) areas that became warmer and drier. Consequently, our current results include model projection artifacts that manifested as small, non-robust increases in a few hot and dry areas. To address these issues related to predictive R&R models, future studies intended to apply to extensive landscapes could consider including areas for model training that exhibit very low R&R conditions (i.e., lower than even what we considered "Low," for example, by including more arid and hotter ecosystems such as salt deserts); develop models that directly predict continuous R&R metrics (instead of constructing a continuous index after the fact); and train such models on continuous R&R metrics that represent the entire landscape and are developed by relating observed vegetation dynamics to climate, ecological drought, and soil characteristics. Including additional areas with more extreme conditions in model training could also reduce novelty in predictor space. We detected small amounts of novelty in the southern areas of the sagebrush biome when mapping R&R, and this was because these hot and dry areas occurred outside the ecoregions originally utilized to train these predictive R&R models (see, Chambers et al., 2023b).

## Implications for climate adaptation and land management prioritization approaches

These long-term projections for changing R&R can be useful for informing climate adaptation and prioritization approaches across the broad extent of sagebrush ecosystems. Our results are region-wide and spatially explicit, which allows systematic and consistent evaluations of future impacts of climate on ecological R&R and are supported by a reasonably comprehensive representation of climate uncertainty. Conservation and restoration frameworks based on R&R concepts for prioritizing areas for management and determining effective management strategies are well-developed for sagebrush ecosystems within the sagebrush biome (Chambers, Beck, et al., 2017; Crist et al., 2019; Remington et al., 2021) and have been successfully applied in assessments of risks for high-value ecosystems, including sage-grouse seasonal habitats, National Parks, and other conservation areas (e.g., Chambers, Allen, & Cushman, 2019; Chambers, Brooks, et al., 2019; Ricca et al., 2018; Ricca & Coates, 2020; Rodhouse et al., 2021). The new threat-based SEI index helps identify relatively intact core sagebrush and GOAs (Doherty, Theobald, Bradford, et al., 2022) that can be used to identify risks further and prioritize areas for management (Chambers et al., 2023c). Our comprehensive evaluation of climate change effects on the new R&R indicators provides necessary information for adapting management prioritization strategies as the climate changes.

Our projections for declining R&R over broad (~24%–34% of the region), but not all, areas are a concern that reinforces the need to embrace climate adaptation while highlighting areas with potential to support high-quality sagebrush ecosystems. Critically, areas with low R&R and a robust signal for declining R&R are places where ecological transformation is likely over the long term. Our results can help inform long-term management objectives in areas with high SEI and potential decreasing R&R. For instance, effective monitoring of the changes occurring and continually updating our tools and frameworks can help prioritize areas for management and determine effective strategies. As climate changes and R&R decreases, strategies developed for lower R&R areas will be relevant for a growing portion of the sagebrush biome. For example, invasion of a non-native annual grass into areas that are becoming warmer and drier and thus more climatically suitable for the invader (Bradley et al., 2016; Smith et al., 2022) can be addressed through early detection and rapid response approaches (Garner & Lakes, 2019). Widespread declines in R&R suggest that ecological transformation is possible for many areas, but not everywhere within the sagebrush region. Resource management may benefit from a structured approach identifying both near-term and long-term goals for adapting to these changes and for managing for high-quality habitats, for example, the Sagebrush Conservation Design (Doherty, Theobald, Bradford, et al., 2022) and the RAD (*resist*, *accept*, or *direct*) framework (e.g., Lynch et al., 2021). Understanding how and where R&R are likely to change provides important insights into where transitions are most likely to occur and where efforts to *resist*, *accept*, or *direct* these changes should be focused. For areas with low R&R and/or a robust signal for declining R&R, ecological transformation is increasingly likely, and *accept* or *direct* may eventually be necessary. For areas where *resist* is the goal, declining or stable R&R reinforces the need to develop restoration strategies that are effective despite increasingly hot and dry conditions.


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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Datasets utilized for this research are as follows: USDA Natural Resources Conservation Service October 2021 release of gNATSGO (Soil Survey Staff, 2021), https://nrcs.app.box.com/v/soils; gridMET (Abatzoglou, 2013), https://www.climatologylab.org/gridmet.html; MACAv2-METDATA (Abatzoglou and Brown, 2012), https://www.climatologylab.org/maca.html; indicators of ecological resilience and invasion resistance (Chambers et al., 2023a) in Dryad at https://doi.org/10.5061/DRYAD.H18931ZPB; sagebrush ecological integrity (Doherty, Theobald, Holdrege, et al., 2022) in the USGS ScienceBase-Catalog at https://doi.org/10.5066/P94Y5CDV. R code (Schlaepfer, 2023a, 2023b) used for data processing, figures, and tables presented in this article (using R version 4.2.3, R Core Team, 2023) is available from Zenodo at https://doi.org/10.5281/zenodo.8310207 and https://doi.org/10.5281/zenodo.8310209. Data (Schlaepfer & Bradford, 2024) are available from the USGS ScienceBase-Catalog at https://doi.org/10.5066/P928Y2GF.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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