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Indicators of ecological resilience and invasion resistance – accounting for precipitation seasonality and climate change in southwestern U.S. drylands

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ABSTRACT

Spatially explicit and climate sensitive information on the responses of ecosystems to global change processes is required for strategic planning and prioritization of conservation and restoration. Indicators of ecological resilience and invasion resistance (R&R) are used increasingly to understand the influence of climate on ecosystem responses to these change processes and determine effective management strategies. We developed landscape-scale indicators of R&R based on climate regimes for southwest U.S. drylands that accounted for precipitation seasonality and climate change using 1 km Daymet climate data (1980–2019). We used temperature, precipitation, and monsoon index data to construct climate sensitive and ecologically meaningful climate regimes mirroring the soil temperature and moisture regimes in the U.S. National Cooperative Soil Survey data and Ecological Site Descriptions that are widely used by managers in the western U.S. We evaluated relationships of the climate regimes and R&R indicators to the dominant ecological types, plant species, including the widespread exotic annual, cheatgrass (*Bromus tectorum*), plant functional groups, and annual burn probabilities. The climate regimes were associated with the dominant ecological types and plant functional groups. Particularly important was identification of a monsoon index value (0.30) to delineate areas with a summer moist (ustic) precipitation regime as indicated by the frequency of C4 vs. C3 grass species. Cover of cheatgrass, a C3 species, was highest in warm (mesic) and very warm (hypermesic) areas with a winter moist (xeric) or dry (aridic) precipitation regime and corresponded well to the resistance indicator. Annual burn probabilities were highest in areas with a winter moist precipitation regime and high precipitation (productivity) and did not correspond directly to cheatgrass cover. Changes in climate regimes from 1980 to 1999 to 2000–2019 resulted in decreases in both R&R by about 10 %. Climate-sensitive R&R indicators can be used in conservation and restoration planning to determine effective strategies and locate management activities to maximize ecological benefits and returns on investment. Recent changes in climate indicate the need to assess the direction and rate of climate change within the focal area and consider the likely effects on R&R when developing management strategies.

1. Introduction

Global change processes, including altered disturbance regimes, biological invasions, and long-term climatic shifts, are altering ecosystems and causing transitions to novel ecological states (Díaz et al., 2019). Strategic planning and prioritization of conservation and restoration actions are essential for ensuring the persistence and recovery of both species and ecosystems (Tolvanen and Aronson, 2016; Brondizio et al., 2019). Ecological resilience concepts and indicators are increasingly used to understand the influence of climate and other abiotic variables on the responses of ecosystems to disturbances and stressors and develop effective prioritization schemes for large landscapes (Chambers et al., 2014a, b, 2017, 2019, 2023b; Ricca et al. 2018; Ricca and Coates, 2020; Rodhouse et al., 2021). Ecological resilience

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(resilience) is the capacity of ecosystems to reorganize and regain their fundamental structure, processes, and functioning (i.e., recover) when altered by stresses, like longer and more severe drought, and by disturbances, such as wildfire (Holling, 1973). Resistance to invasion (resistance) is a function of the abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen, 2004). In contrast to measures of ecological integrity or the current ecological conditions, indicators of resilience and resistance provide information on an area's potential to recover and ability to resist plant invasions (Chambers et al. 2023b). Resistance to invasive plant species is increasingly important in drylands because of the potential of these invaders to transform ecosystems into less desirable ecological states. Indicators of resilience and resistance (R&R) can be coupled with assessments of regional threats, such as invasive annual grasses and wildfire risk, to prioritize areas on the landscape for conservation and restoration where they are likely to have the greatest returns on investment and ecological benefits (Chambers et al., 2017; 2019; 2023b).

Temperature and moisture regimes are closely associated with R&R and the likelihood of change in dryland ecosystems of the western U.S. (Chambers et al., 2014a; Bestelmeyer et al., 2015). These regimes are major determinants of the potential vegetation, environmental suitability for invasive species, wildfire probabilities, and the likelihood of transitions to alternative states (Chambers et al., 2019; Holdrege et al., 2024; McMahon et al., 2021). Precipitation seasonality is a component of temperature and moisture regimes shown to influence R&R at local scales due largely to its effects on plant functional group dominance and site recovery potential (Prevéy and Seastedt, 2014; Larson et al., 2017), but its effects on R&R at landscape scales are not well understood.

Based on our previous conceptual model, we expected that precipitation seasonality affects R&R primarily via its effects on soil water storage and life form dominance (Chambers et al., 2016; fig. S-1). The different components of the model are well-supported in the literature. The amount of precipitation received during the period when temperature, and thus potential evapotranspiration, is low influences the amount of water stored in deep soil layers (fig. S-1A; Sala et al., 1997). Areas receiving more winter/spring precipitation typically have greater deep soil water storage and are dominated by woody species, which are more effective at using deep soil water (fig. S-1B). In contrast, areas receiving mostly summer precipitation are dominated primarily by grasses. High soil water availability during the period when temperatures are favorable for plant growth influences the balance between C3 and C4 species with C3 species dominating in areas with cool, wet springs and C4 species dominating in areas with warm, wet summers (Paruelo and Lauenroth, 1996; Sala et al., 1997; Lauenroth et al., 2014). Resilience to disturbances like wildfires is generally higher in more productive, cool and moist areas than warm and dry areas and in areas receiving predominantly summer precipitation as greater abundance of grasses facilitates recovery (fig. S-1C; Condon et al., 2011; Davies et al., 2012; Chambers et al., 2014a; Prevéy and Seastadt, 2014; Larson et al., 2017; Wainwright et al., 2020). Resistance to the widespread exotic annual grass, cheatgrass (*Bromus tectorum*) is higher in cool and moist areas due lower climate suitability and greater competition from herbaceous species (fig. S-1D; Chambers et al., 2007; Bansal and Sheley, 2016; Urza et al., 2017). Resistance generally increases with increasing summer precipitation due to strong competition from the grass species that dominate under this precipitation regime (Bradford and Lauenroth, 2006; Prevéy and Seastadt, 2014; Larson et al., 2017). Recent climate change projections indicate that these concepts are equally applicable to historic and future climate regimes (Palmquist et al., 2021).

An increasing concern in developing R&R indicators is the rate at which climate change is occurring and its effects on ecosystem recovery following disturbance. Climate change projections for the southwest U.S. from 1980 to 2010 to 2070–2100 suggest that mean annual temperature will increase about 4 to 6 °C (Bradford et al., 2020). Although mean annual precipitation also may increase in several areas, mean precipitation will be lower relative to potential evapotranspiration indicating drier conditions (Bradford et al., 2020). Species responses are expected to vary geographically and depend on the direction and magnitude of climate change. Longer or more severe droughts may negatively affect tree growth and forest stability of mountainous areas (Anderegg and HilleRisLambers, 2016; Ganey and Vojta, 2011) and result in acute water stress and die-offs in woodlands and shrublands of upland and desert areas (Breshears et al., 2005; Kannenberg et al., 2021). Perennial C3 grass and perennial forb biomass is projected to decline while perennial C4 grass biomass increases (Palmquist et al., 2021). Increases in extreme fire weather (Westerling, 2016) and higher severity wildfires are already causing vegetation type change in warmer and drier areas with low recovery potential (Coop et al., 2020; Guiterman et al., 2022). Indicators of R&R provide information on the likelihood of these conversions occurring and are most effective if the influence of a warming climate is considered.

The use of R&R indicators based on our conceptual model (fig. S-1) for landscape-scale assessment and prioritization has been well-established (). Our previous indicators of R&R used soil temperature and moisture regimes mapped as part of the U.S. National Cooperative Soil Survey (USDA NRCS, 2022a) (Maestas et al., 2016) or climate and water availability indicators derived from ecohydrological process models (Chambers et al., 2023a). Indicators of R&R based on soil temperature and moisture regimes were used successfully to develop prioritization strategies for fire prevention and management, invasive species management, conservation of species habitat, and restoration (Chambers et al., 2014b, 2017, 2019; Ricca et al., 2018; Rodhouse et al., 2021; Crist et al., 2019). An empirical test of these R&R indicators indicated that they were a useful tool for predicting the general outcomes of management actions at more local scales when site conditions were considered (Riginos et al., 2023). Separate indicators of resilience and resistance based on climate and soil water availability were used to develop treatment response groups for fire risk management (Chambers et al., 2023c) and management strategies for areas with varying ecological integrity in the sagebrush biome (Chambers et al., 2023b). These indicators were used successfully to show how R&R is likely to change with climate warming (Schlaepfer et al., 2024).

In this study, we developed landscape scale, multiclass indicators of R&R based on temperature and precipitation regimes for an area of the southwest U.S. with transitions from primarily winter to summer dominated precipitation regimes. The study area extends beyond the sagebrush biome and was inadequately represented in prior R&R classifications (Maestas et al., 2016; Chambers et al., 2023a). A strength of using soil temperature and moisture regimes to develop indicators of resilience and resistance is that they can be linked directly to a widely used land classification system based on USDA Natural Resources Conservation Service Soil Survey Information (Soil Survey; USDA NRCS, 2022a) and Ecological Site Descriptions (ESDs; USDA NRCS, 2022b) and can be scaled from project areas to large landscapes. However, R&R indicators based on atmospheric climate variables are likely preferrable to those based on soil climate because (1) soil temperature and moisture regimes from the Soil Survey are static and challenges exist in evaluating climate change effects based on these indicators (Bradford et al., 2019), (2) discontinuities exist in soil map units across state boundaries (Chambers et al., 2023a), and (3) many areas, notably some U.S. National Forests, do not yet have published soil surveys.

We developed climate-sensitive proxies for the soil temperature and moisture regimes in the Soil Survey based on temperature, precipitation, and precipitation seasonality. We used information from ESDs, the literature, and expert knowledge to categorize the proxy soil temperature and moisture regimes (climate regimes) according to R&R. We evaluated relationships of our climate regimes and R&R indicators to plant species identities and functional group cover, emphasizing exotic annual forbs and grasses, and annual burn probabilities. We evaluated recent changes in the climate regimes to illustrate how R&R are likely to change in the future. We asked: (1) How are the climate regimes, including precipitation seasonality, related to life form cover and relative abundance of C3 vs C4 species? (2) How are the climate regimes and R&R indicators related to the cover of invasive annual forbs and grasses and to annual burn probabilities? (3) How have the climate regimes and thus R&R changed in recent decades? We discuss the use of the R&R indicators for current and future management of these transitional systems in a warming environment. Because we used widely available and highly reliable climate spatial data layers to develop climate regimes and evaluate R&R, our approach is applicable to any areas where information exists for the focal ecosystems on the response to disturbances like wildfire and the susceptibility to plant invaders.

2. Materials and methods

2.1. Study area

We focused on an area of the southwest U.S. that exhibits a strong monsoonal gradient and that varies widely in relative abundance of invasive annual grasses and annual burn probabilities (Fig. 1). The range in mean annual temperature is −0.25 to 21.7 °C (mean 10.0 °C) and in mean annual precipitation is 140 to 937 mm (mean 340 mm) with cooler and moister conditions at higher elevations and warmer and drier conditions at lower elevations. The monsoon index (proportion of mean annual precipitation occurring in July, Aug, and Sept) ranges from 0.15 to 0.61 (mean 0.32) with higher summer precipitation generally in the south. The ecological types include forests, woodlands, shrublands, and grasslands with forests occurring in the coolest and wettest environments and shrublands and grasslands dominating the warmest and driest environments.

2.2. Generalized ecological types

To construct our R&R indicators, we first identified the dominant ecological types and their soil temperature and moisture regimes for the study area. Ecological types are groups of ecological sites with similar climate, geology, geomorphology, soils, and potential natural vegetation (Winthers et al., 2005). We used ecological site data from the USDA Natural Resources Conservation Service Soil Survey (USDA NRCS, 2022a) and Ecological Site Descriptions (USDA NRCS, 2022b), including ecological site ID and name, Major Land Resource Area, and select climate, soils, landform, vegetation composition, and productivity data. We grouped the ecological sites into generalized ecological types based on similarities in soil temperature and moisture regimes and moisture subclasses as well as soils and vegetation characteristics (see Chambers et al., 2023a). We used the soil temperature and moisture regimes and moisture subclasses of the generalized ecological types to assign each type to one of the proxy soil temperature and moisture regimes (climate regimes) that we subsequently developed (Table 1).

2.3. Proxy soil temperature and moisture regimes

We developed climate regimes that related directly to the dominant ecological types. We focused on mean annual air temperature, mean annual precipitation, and the monsoon index (Fig. 2), which in the sagebrush biome were closely related to the dominant ecological types and were associated with varying levels of R&R (Chambers et al., 2023a) and likely changes in R&R in a warming climate (Schlaepfer et al., 2024). We used Daymet annual and monthly climate summaries at a scale of 1 km for the time period from 1980 to 2019 to develop the climate regimes (Thornton et al., 2022; https://daymet.ornl.gov). We used the 40 yr dataset because this time period likely shaped the potential vegetation of the area. Daymet provides long-term, continuous, gridded estimates of daily weather and climatology variables by interpolating and extrapolating ground-based observations through statistical modeling techniques. The mean absolute error (MAE) for the North American dataset in comparison to weather station data for daily minimum temperatures (Tmin) was approximately 1.78 °C and for daily maximum temperature (Tmax) was 1.52 °C (Thornton et al., 2022). The MAE of daily precipitation decreased over time from around 1.8 mm/day to 1.4 mm/day. Errors are smaller in our study (particularly for

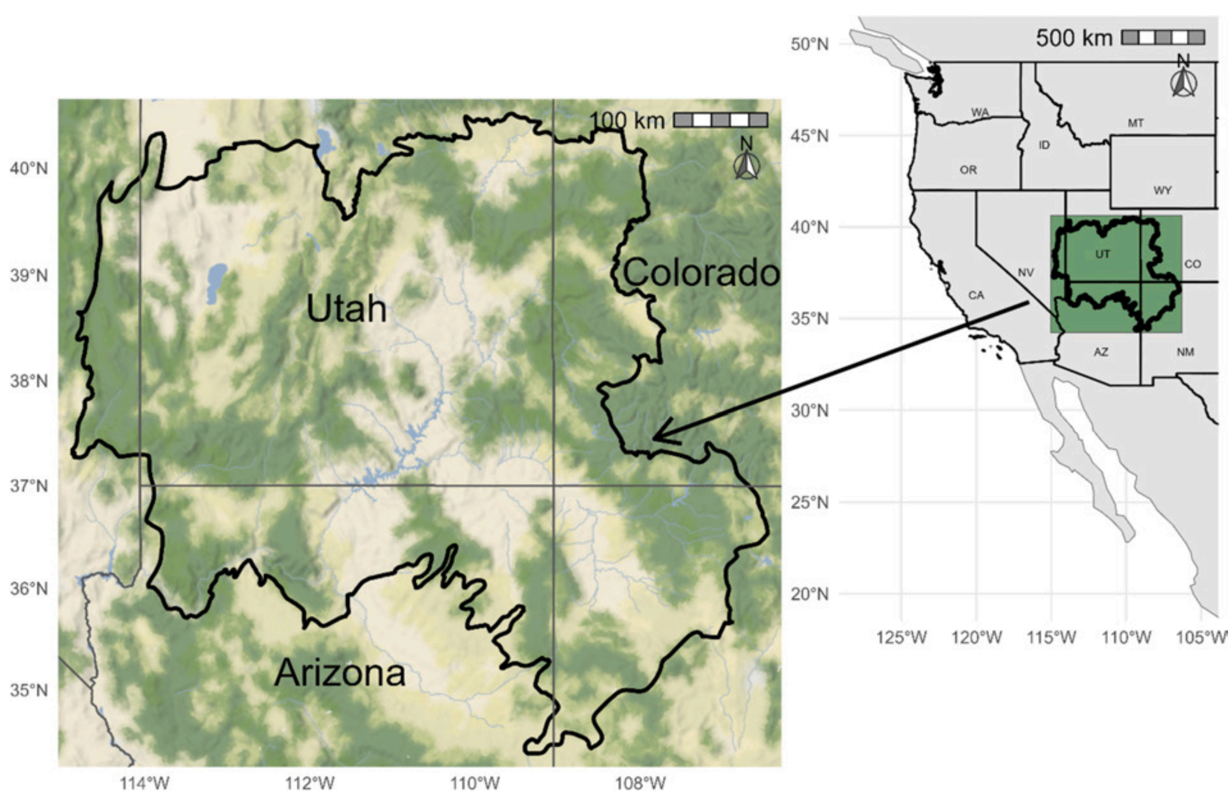

Fig. 1. Map of the study area and its location in the western U.S.

Table 1
A crosswalk showing the soil temperature and moisture regimes within the study area, the climate variables used to assign the proxy soil temperature and moisture regimes, the generalized ecological type and percent of landscape associated with each regime, and the resilience (RSL) and resistance (RST) classes assigned to each regime. Soil terms: cryic = cold; frigid = cool; mesic = warm; hypermesic = very warm. Udic = moist; ustic = summer moist; xeric = winter moist (>305 mm precipitation); aridic = winter moist (<305 mm precipitation).

RSL	RST	Soil Temperature and Moisture Regime		Proxy Soil Temperature and Moisture Regime			Generalized Ecological Type	% Landscape
		Soil temperature	Soil moisture	Temperature °C	Monsoon index	Precipitation mm		
10	10	Cryic	Udic	<6.5	> 0.30	559+	High mountain	0.9
10	10	Cryic	Udic	<6.5	> 0.30	406–559	Mountain	1.6
10	10	Cryic	Udic	<6.5	> 0.30	305–406	Mountain	0.9
10	10	Cryic	Xeric	<6.5	<0.30	660+	High mountain	1.3
9	10	Cryic	Xeric	<6.5	<0.30	508–660	High mountain	2.8
9	9	Cryic	Xeric	<6.5	<0.30	356–508	Mountain	1.6
9	9	Frigid	Ustic	6.5–8.5	> 0.30	547+	Mountain	1.6
8	9	Frigid	Ustic	6.5–8.5	> 0.30	356–547	Mountain	2.7
7	7	Frigid	Ustic	6.5–8.5	> 0.30	279–356	Upland	1.6
8	8	Frigid	Xeric	6.5–8.5	<0.30	547+	Mountain	3.7
7	7	Frigid	Xeric	6.5–8.5	<0.30	356–547	Mountain	3.1
6	6	Frigid	Xeric/aridic	6.5–8.5	<0.30	254–356	Upland	1.0
6	7	Mesic	Ustic	8.5–11.5	> 0.30	356+	Upland	6.6
4	6	Mesic	Ustic	8.5–11.5	> 0.30	279–356	Semidesert	10.7
2	4	Mesic	Ustic	8.5–11.5	> 0.30	178–279	Semidesert and Desert	10.8
6	4	Mesic	Xeric	8.5–11.5	<0.30	381+	Upland	5.0
4	2	Mesic	Xeric/aridic	8.5–11.5	<0.30	279–381	Upland and Semidesert	9.3
1	1	Mesic	Aridic	8.5–11.5	<0.30	178–279	Semidesert and Desert	6.5
4	3	Hypermesic	Ustic	11.5–14.5	> 0.30	279+	Semidesert	3.8
2	4	Hypermesic	Ustic	11.5–14.5	> 0.30	203–279	Semidesert	11.5
1	5	Hypermesic	Ustic	11.5–14.5	> 0.30	127–203	Desert	6.1
5	4	Hypermesic	Xeric	11.5–14.5	<0.30	381+	Upland	1.0
3	3	Hypermesic	Xeric/aridic	11.5–14.5	<0.30	279–381	Semidesert	2.5
1	2	Hypermesic	Aridic	11.5–14.5	<0.30	178–279	Desert	1.5

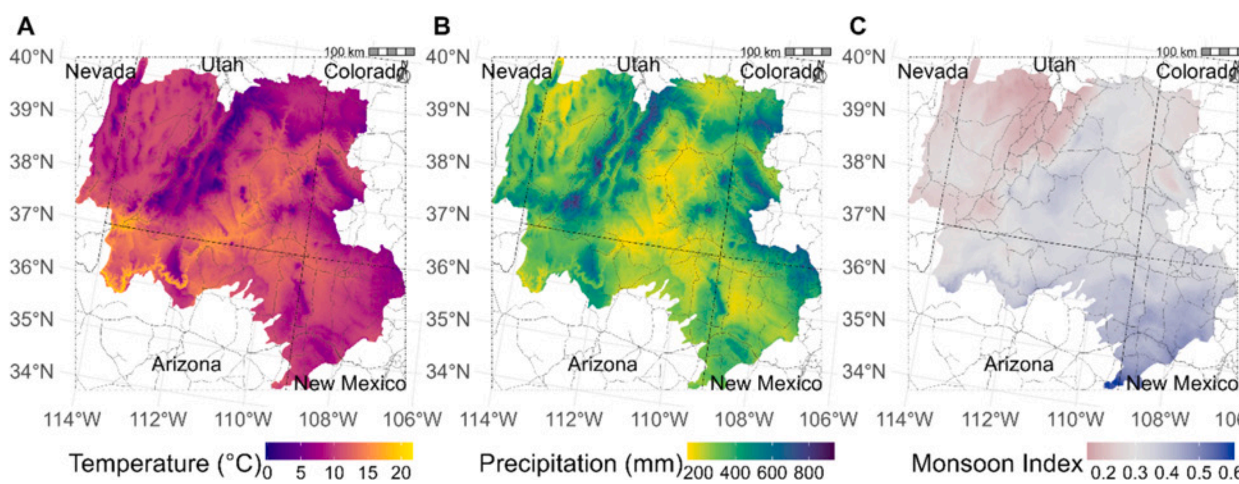

Fig. 2. Maps of mean annual temperature (A), mean annual precipitation (B), and the monsoon index (C; proportion of mean annual precipitation received in July, Aug, and Sept) in the study area. Climate values were calculated from Daymet monthly data at a 1 km scale for 1980–2019 (Thornton et al.,2022).

precipitation) than the reported errors across all of North America because of a higher density of weather stations (see Fig. 6 in Thornton et al. 2022).

We evaluated the soil temperature and moisture regimes of the dominant ecological types using a large, existing database of vegetation sample plots compiled from the USDOI Bureau of Land Management Assessment, Inventory, and Monitoring Program (AIM; USDOI BLM, 2022a; USDOI BLM, 2022b) (see Chambers et al., 2023a). Each plot in the database had information on (1) the soil temperature and moisture regimes and moisture subclasses, (2) the dominant ecological types, and (3) climate and soil water availability (Chenoweth et al., 2023; Chambers et al., 2023a). We used these data to evaluate the relationships of the soil temperature and moisture regimes and moisture subclasses to the climate variables for the dominant ecological types (Table S-2). We used this information to help determine the temperature ranges within each soil temperature regime and the associated moisture regimes.

To ensure the temperature values reflected the temperature regimes within the study area, we used k-means clustering (Hartigan and Wong, 1979) to find natural breaks in the distribution of the mean temperature values (Fig. S-3). Because of the broad span of temperatures and large area in the mesic (warm) category, we split it into mesic and hypermesic (very warm) (Fig. S-3). To separate summer moist (ustic) from the combination of winter moist (xeric) and dry (aridic), we used a monsoon index value of 0.30. Moist (udic) also had high summer precipitation (monsoon index > 0.30). These divisions were evident in the descriptions of the ESDs that comprised the ecological types, as well as the species composition of the ecological types.

To split out soil moisture subclasses, we evaluated the distribution of the mean annual precipitation within the climate regimes and derived three to four divisions of each regime that generally equated to moisture subclasses in the ecological types (Fig. S-4). This process resulted in a ruleset for assigning climate regimes based on temperature, the monsoon index, and precipitation values that were closely associated with the generalized ecological types (Table 1).

2.4. Resilience and resistance indicators

We assigned R&R indicator classes (1 through 10) to the climate regimes based on literature review, expert knowledge, and information in the ESDs using a process like that in Chambers et al. (2023a) (Table 1). The resilience classes were based on how quickly and to what degree an ecological type could recover after disturbances like inappropriate livestock grazing or wildfire (Chambers et al., 2014, 2023a). The resistance classes focused on the widespread exotic annual, cheatgrass, to obtain consistent ratings among ecological types. Climate suitability and soils were considered the primary determinants of resistance, but resource availability and competition from perennial herbaceous species were also considered (Chambers et al., 2014a, 2023a). The climate regime ruleset and R&R indicator crosswalk were used to generate spatial data layers for the climate regimes and R&R classes utilizing the appropriate gridded climate data.

2.5. Dominant plant functional groups, exotic annual grass cover, and burn probabilities

Plant species with the C3 photosynthetic pathway typically indicate a winter moist or dry precipitation regime, whereas those with the C4 pathway indicate a summer moist regime (Paruelo and Lauenroth, 1996; Sala et al., 1997; Lauenroth et al., 2014). To evaluate the photosynthetic pathways of the dominant grass species within each temperature and moisture regime, we used our existing database of vegetation sample plots from AIM and calculated the number and percentage of occurrences of the five most frequently sampled grass species within each climate regime.

We calculated the proportional cover of the dominant plant functional groups for the climate regimes and R&R indicator classes using Rangeland Analysis Platform (RAP; Allred et al., 2021; https://rangelands.app/) data from 2016 to 2022 at a spatial scale of 30 m. Estimated cover error for RAP data relative to a validation set of 7,500 field plots was +/- 7.0 % MAE for annual forb and grass pixels, 10 % MAE for perennial forbs and grasses, 6.2 % MAE for shrubs, and 2.6 % MAE for trees. We used data from the US Geological Survey Rangeland Exotic Plant Monitoring System (2023) to map and calculate proportional cover of cheatgrass within each of the temperature and moisture regimes and R&R indicator classes. Median absolute error (MdAE) for cheatgrass cover was 6.05 %. We also mapped and calculated the annual burn probabilities for each climate regime and R&R category using data from Dillon et al. (2023) at a 270 m resolution. Burn probability depicts the annual probability of wildfire occurrence at each specific pixel and is derived from simulation modeling of fuelscape data, contemporary weather and ignition patterns, as well as contemporary fire management policies (including fire prevention and suppression efforts) (Dillon et al., 2023).

2.6. Recent changes in the R&R categories

We evaluated changes in the R&R categories in recent decades by subsetting the 40 yr Daymet climate data into two periods: 1980–1999 and 2000–2019. We applied the ruleset for assigning climate regimes based on temperature, the monsoon index, and precipitation to each period. We then assigned R&R indicator classes (1 through 10) to the climate regimes as for the entire 40 yr dataset and mapped and compared the indicators for each period. All geospatial and database operations were performed in R 4.2.3 (R Core Team, 2023).

3. Results

3.1. Proxy soil temperature and moisture regimes

The proxy soil temperature and moisture regimes (climate regimes; Table 1; Fig. 3) provided clear separation of the dominant ecological types and their associated species (Table S-5).

Cryic areas with high precipitation were associated with high mountain types characterized by mixed conifers and aspen (*Populus tremuloides*) and transitioned to mountain types with mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and snowberry (*Symphoricarpos oreophilus*) as precipitation decreased (Table S-5). Frigid areas with higher precipitation were associated with mountain types characterized by tree and shrub species like ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*) and transitioned to upland types with pinyon (*Pinus edulis*, *P. monophylla*), juniper (*Juniperus osteosperma*), and sagebrush (*Artemisia* sp.) species as precipitation decreased. Mesic areas with higher precipitation were characterized by upland types with pinyon, juniper and sagebrush species and transitioned into semidesert to desert types with *Atriplex* and other salt desert species with decreasing precipitation. Hypermesic areas were characterized by semidesert and desert types with drought-adapted pinyon and juniper, sagebrush, blackbrush (*Coleogyne ramosissma*) and *Atriplex* species.

The climate regimes (Table 1; Fig. 3) separated summer (ustic) vs winter and dry (xeric and aridic) moisture regimes well as indicated by the photosynthetic pathways of the most frequently occurring graminoid species in the monitoring plots (Table S-6). The C4 grass blue grama (*Bouteloua gracilis*) was more common than the C3 grass species in frigid and mesic summer moist than winter moist monitoring plots receiving > 280 mm precipitation (Table S-6). Another C4 grass, James' galleta (*Pleuraphis jamesii*), was more common than the C3 grasses in mesic summer moist plots receiving < 280 mm precipitation and in hypermesic summer moist plots, although the C3 grass, Indian ricegrass (*Achnatherum hymenoides*), had high presence in these plots. In contrast, cheatgrass, a C3 exotic annual grass, was the most common species in winter moist and dry plots, except for those with a cryic temperature regime and those with a hypermesic aridic temperature and moisture regime where James' galleta and Indian ricegrass were equally common.

The diverse topography resulted in strong climatic gradients which influenced functional group composition. Total cover, an indicator of productivity, generally decreased as precipitation decreased regardless of temperature and moisture regime (Fig. 4).

Tree cover was highest in areas with > 380 mm precipitation. Shrub cover was generally greater in cryic areas with high precipitation but was relatively consistent across the other climate regimes. Perennial forb and grass cover was also higher in cryic areas and tended to be greater in summer moist than winter moist and dry areas, especially in warmer temperature regimes. In contrast, cover of annual forbs and grasses was lower in cryic and frigid areas and in summer moist than in winter moist and dry regimes (Fig. 4).

3.2. Resilience and resistance indicators

The R&R indicators calculated from the 40 yr dataset showed distinct patterns across the climatic regimes in the study area (Fig. S-7; Table 1, Table S-5). Resilience showed relatively consistent decreases as cover of the different life forms decreased along the productivity gradient (Fig. S-8). Resistance was determined by the suitability of the climate regimes to support the establishment and expansion of annual grasses and forbs and followed a less consistent pattern (Fig. S-8). In general, high mountain and mountain types with cryic to frigid temperatures and relatively high precipitation had the highest R&R (classes 9, 10; Table 1, Table S-5). Mountain and upland types with frigid temperatures that were winter moist transitioned to moderately high R&R (classes 7, 8) at higher precipitation values than those that were summer moist.

Upland and semidesert types with frigid temperatures and relatively

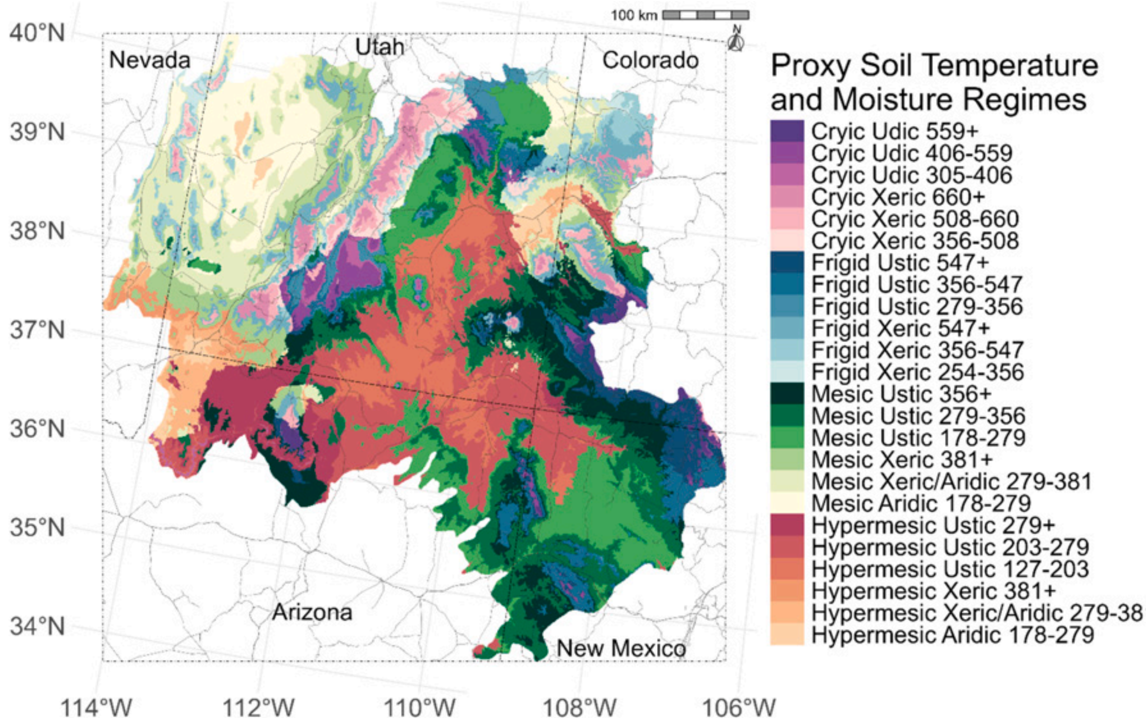

Fig. 3. Map of proxy soil temperature and moisture regimes developed for the study area. The proxy soil temperature and moisture regimes were derived from mean annual temperature and precipitation and the monsoon index using Daymet monthly data at a 1 km scale for 1980–2019 (Thornton et al., 2022). Soil term definitions: cryic = cold; frigid = cool; mesic = warm; hypermesic = very warm; udic = moist; ustic = summer moist; xeric = winter moist (>305 mm precipitation); aridic = dry (<305 mm precipitation).

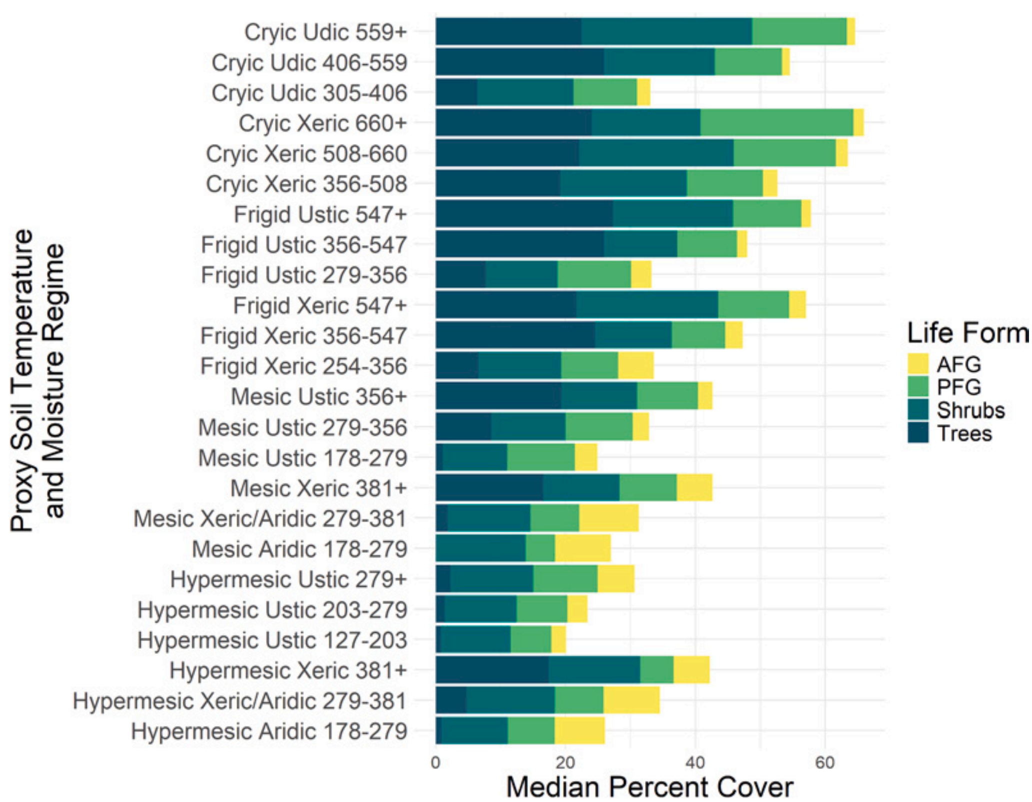

Fig. 4. Median percentage cover of trees, shrubs, perennial forbs and grasses (PFG), and annual forbs and grasses (AFG) within each proxy soil temperature and moisture regime. Vegetation cover was estimated from Rangeland Analysis Platform (RAP) data for 2018–2022 at a scale of 30 m (Allred et al., 2022). Soil term definitions: cryic = cold; frigid = cool; mesic = warm; hypermesic = very warm; udic = moist; ustic = summer moist; xeric = winter moist (>305 mm precipitation); aridic = dry (<305 mm precipitation).

low precipitation (<356 mm) or mesic and hypermesic temperatures and relatively high precipitation (>356 mm) had moderate resilience (classes 5, 6; Table 1, Table S-5). Semidesert types with intermediate precipitation (279 to 381 mm) had moderately low resilience (classes 3, 4), and semidesert to desert types with low precipitation (<279 mm), had low resilience (classes 1, 2) regardless of temperature and moisture regime. In upland, semidesert, and desert types, resilience was typically one class higher in summer moist than winter moist areas.

In contrast, upland and semidesert types that were frigid and winter moist or mesic and summer moist with intermediate precipitation

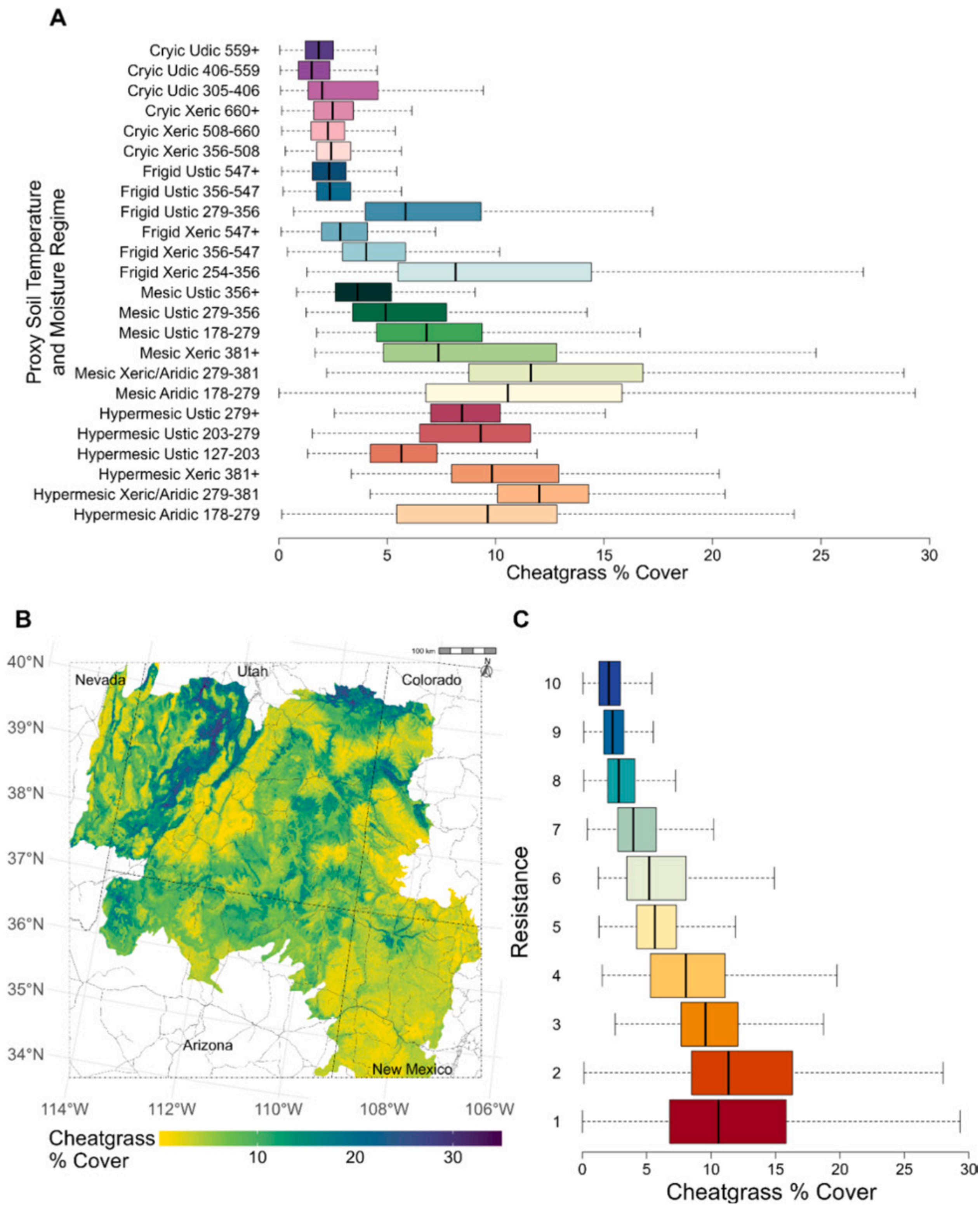

Fig. 5. Map shows the mean cover of cheatgrass for 2016–2022 from the USGS Rangeland Exotic Plant Monitoring Systems (B; 2023). The box plots show cheatgrass cover for each proxy soil temperature and moisture regime (A) and for the resistance classes (C), with the central mark showing the median, hinges showing the 1st and 3rd quartiles, and whiskers extending to 1.5 times the length of the hinges. Higher resistance class numbers indicate greater resistance.

(254–356 mm) had moderate resistance (classes 5, 6; Table 1, Table S-5). Mesic and hypermesic upland and semidesert types that were winter moist with relatively high precipitation (>381 mm) or summer moist with intermediate precipitation had moderately low resistance (classes 3, 4). Mesic and hypermesic semidesert and desert types that were winter moist and had low precipitation (<279 mm) had the lowest resistance (classes 1, 2). An exception was summer moist, hypermesic desert types with very low precipitation which had moderate resistance

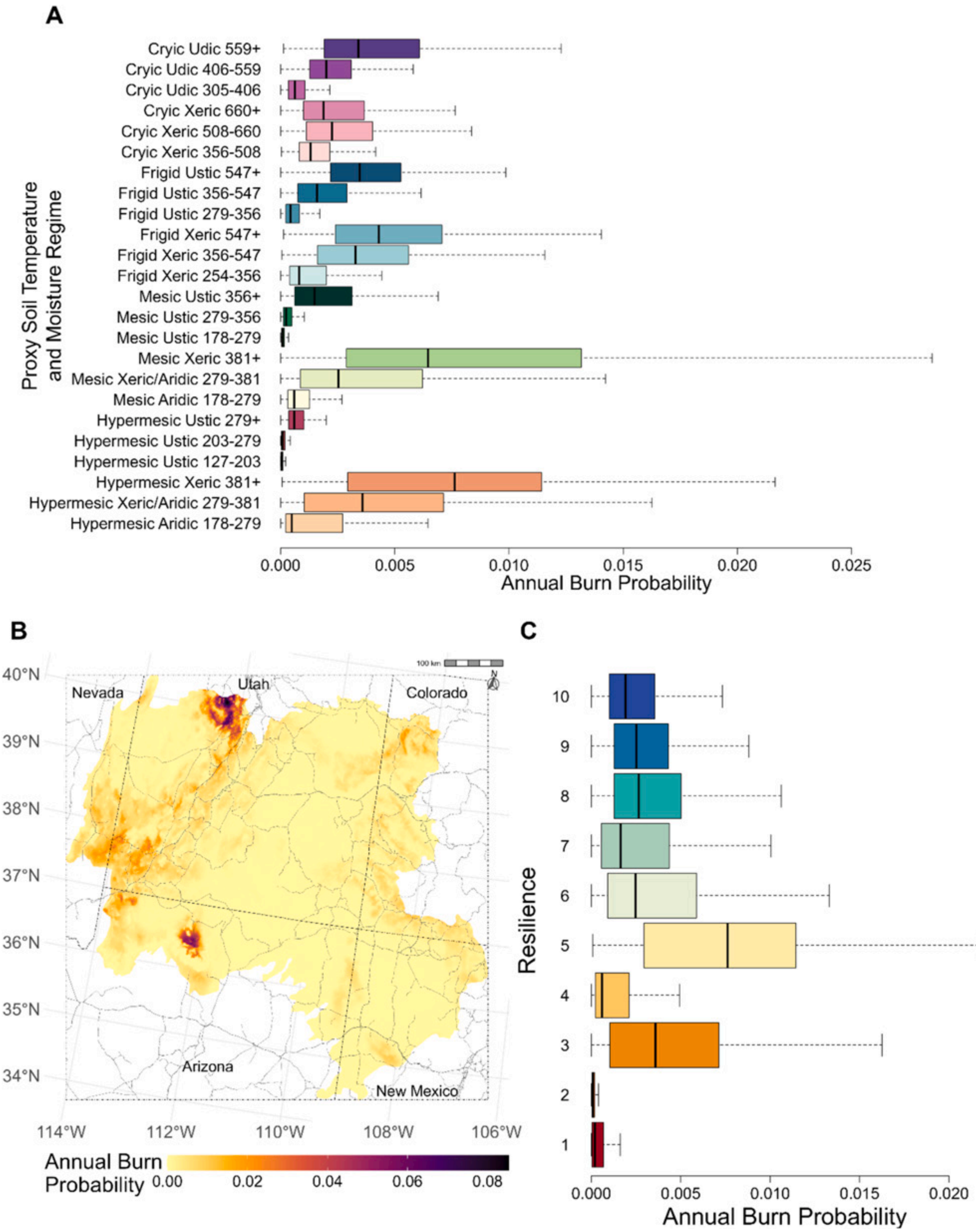

Fig. 6. Map shows the annual burn probabilities for the study area from Dillon et al. (B; 2023). The box plots show the annual burn probabilities for each proxy soil temperature and moisture regime (A) and for the resilience classes (C), with central mark showing the median, hinges showing the 1st and 3rd quartiles, and whiskers extending to 1.5 times the length of the hinges. Higher resilience class numbers indicate greater resilience.

(class 5).

3.3. Cheatgrass cover and burn probabilities

The cover of cheatgrass corresponded to the climate regimes and was mirrored in the resistance classes with cheatgrass cover showing progressive increases from resistance class 10 to classes 1 and 2 (Fig. 5). As expected, cheatgrass cover showed largely the same patterns as resistance across the climate regimes and productivity gradient. The box plots illustrate that the variability in cheatgrass cover increased as temperatures became warmer and was higher for winter moist and dry regimes than summer moist regimes.

The burn probabilities showed distinct patterns across the study area that were reflected in the climate regimes. Burn probabilities were consistently lower in summer than winter moist areas and increased as precipitation increased within a climate regime (Fig. 6). The highest burn probabilities were in mesic and hypermesic uplands and semideserts that were winter moist, received > 381 mm precipitation, and had moderate to moderately low resilience (classes 4, 5). Frigid and winter moist mountain types with > 457 mm precipitation and moderately high resilience (class 8) as well as hypermesic and winter moist semidesert types with 279–381 mm precipitation and moderately low resilience (class 4) also had relatively high burn probabilities. Notably, the mesic and hypermesic ecological types with high burn probabilities also had relatively high cheatgrass cover (Figs. 5, 6).

3.4. Recent changes in the resilience and resistance classes

Large changes in climate regimes and thus resilience and resistance classes occurred between 1980–1999 and 2000–2019. Most cryic and frigid climate regimes as well as the mesic and winter moist climate regime experienced decreases in area (Table S-9) caused largely by transitions to warmer temperature regimes (Fig. 7). In addition, 14 % of the study area shifted from winter moist or dry to moist or summer moist, whereas 4 % of the area shifted from moist or summer moist to winter moist (Fig. S-10). Consistently moist or summer moist comprised 52 %; winter moist or dry consistently comprised 32 %. The changes over time generally resulted in decreases in the areas of high mountain, mountain, and upland types with the largest losses occurring in frigid or mesic and winter moist mountain and upland types, and especially cryic and winter moist high mountain and mountain types. An exception was frigid mountain types that were winter moist and had relatively high precipitation (>457 mm), which increased in area as the cryic high mountain and mountain types decreased.

The changes in climate regimes resulted in losses to the moderate to high resilience classes 6–10 and large gains to the lowest resilience classes (1 and 2; Fig. 8; Fig. S-11, Table S-12). These decreases in resilience classes occurred across > 10 % of the study area with the largest losses generally occurring in high mountain, mountain, and upland types and the greatest gains occurring in semidesert types with summer moist precipitation regimes.

Similar trends existed for resistance with losses in resistance classes 6–9 and especially class 10 (Fig. 8; Fig. S-11, Table S-12). These losses translated to gains in the lower resistance classes 5, 4, 3, and 1. An exception was class 2 where the climate regimes that comprised the class both decreased in area (mesic and hypermesic, winter moist and dry). Overall, decreases in resistance class occurred across about 11 % of the study area.

4. Discussion

The climate variables that we used, mean annual temperature, precipitation, and monsoon index, allowed us to construct climate sensitive and ecologically meaningful climate regimes. These regimes mirrored the soil temperature and moisture regimes in the U.S. National Cooperative Soil Survey (USDA NRCS, 2022a) data and Ecological Site Descriptions (USDA NRCS, 2022b) that are widely used by managers in the western U.S. to evaluate the current ecological state of an ecological type and determine its recovery potential. The climate regimes reflected the dominant ecological types and plant functional groups in the study area and allowed us to develop meaningful, multiclass indicators of R&R. Identification of a monsoon index value (0.30) allowed

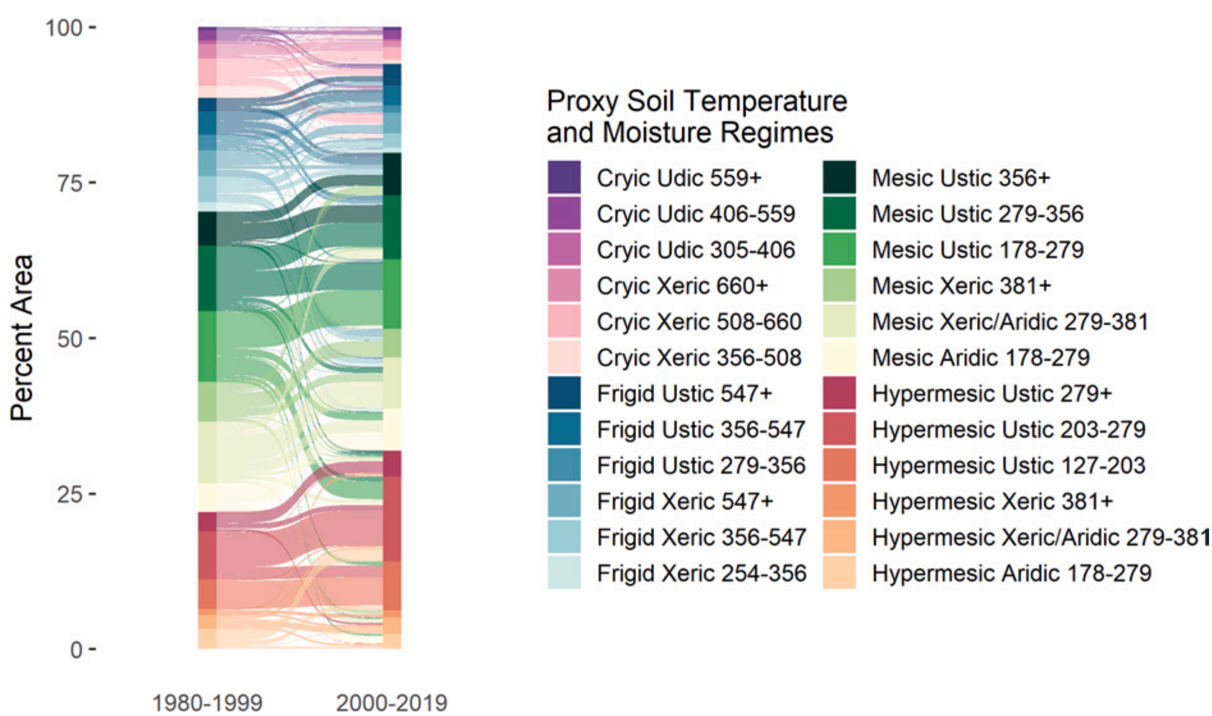

Fig. 7. Alluvial plot showing changes in area of proxy soil temperature and moisture regimes based on Daymet 1-km climate means from 1980 to 1999 and 2000–2019 (Thornton et al., 2022). Soil term definitions: cryic = cold; frigid = cool; mesic = warm; hypermesic = very warm; udic = moist; ustic = summer moist; xeric = winter moist (>305 mm precipitation); aridic = dry (<305 mm precipitation).

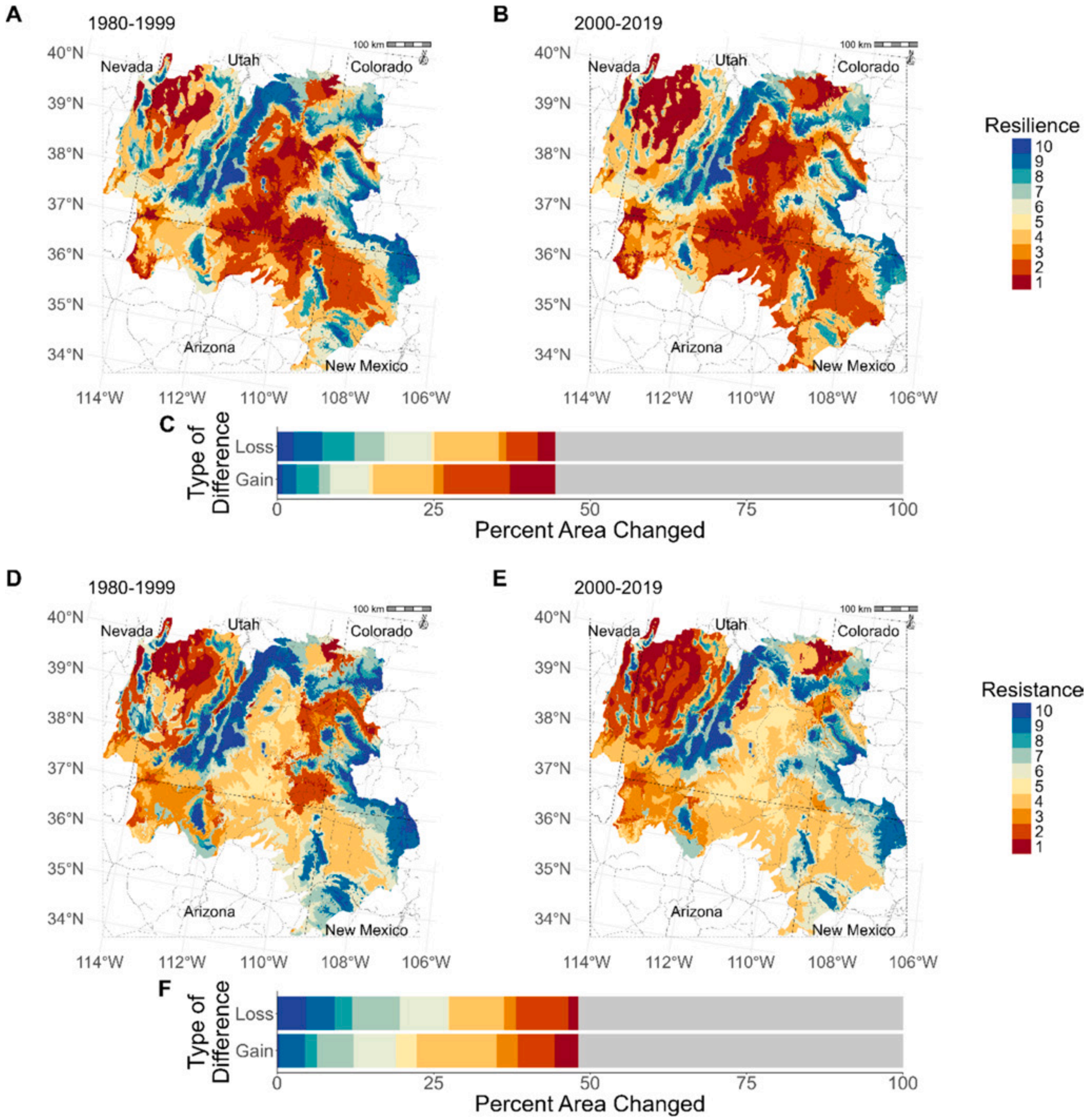

Fig. 8. Maps showing the classes of ecological resilience for 1980–1999 (A) and 2000–2019 (B) and for resistance to invasion of cheatgrass for 1980–1999 (D) and 2000–2019 (E). Changes between time periods, both gain and loss, are shown in stacked bar plots under the maps for resilience (C) and resistance (F), with the gray color representing the area with no change. The resilience and resistance classes were based on proxy soil temperature and moisture regimes calculated from 1-km Daymet climate data means (Thornton et al., 2022) and their associated Ecological Site Descriptions. Higher class numbers indicate greater resilience or resistance.

delineation of areas with an ustic (summer moist) precipitation regime as indicated by the frequency of C4 vs. C3 grass species. Patterns of cheatgrass cover across the landscape corresponded well to the climate regimes and resistance indicator. Areas with a winter moist precipitation regime and high precipitation (productivity) generally had the highest burn probabilities and in these areas, resilience varied from moderately high to moderately low. Empirical tests of the R&R indicators will be needed to evaluate their usefulness for predicting the outcomes of management actions at more local scales (e.g., Rignos et al., 2023). The 40-year climate record we used was intended to reflect the potential vegetation of the area, but our analyses of the changes in climate regimes and R&R from 1980 to 1999 to 2000–2019 indicated that climate warming was already having large effects. The climate regimes and multi-class R&R indicators allowed us to better detect the magnitude of these changes. Future studies will need to assess how well the mapped R&R indicators predict both current R&R and the ongoing changes related to life forms, C4 vs. C3 grass species, and wildfire probabilities.

4.1. Climate regimes and resilience and resistance indicators

Higher levels of resilience have generally been associated with greater resource availability and more favorable environmental conditions for plant growth and reproduction (Condon et al., 2011; Davies et al., 2012; Wainwright et al., 2020; Roundy and Chambers, 2021). We found that resilience generally followed productivity gradients increasing as temperature decreased and the amount of precipitation increased. In drylands, the timing and amount of water availability is the primary determinant of both abiotic and biotic processes (Noy-Meir, 1973; Wang et al., 2012) and thus the rate and magnitude of recovery following disturbance and management activities (Chambers et al., 2014a, 2016). As predicted in our conceptual model, resilience was typically higher for summer moist than winter moist regimes when precipitation was limiting. This has been attributed to the dominance of grasses, such as the rhizomatous C4 species, which promote recovery following disturbances, such as wildfire, via regrowth and reproduction (Bradford and Lauenroth, 2006; Prevéy and Seastadt, 2014; Larson et al., 2017).

Resistance was a function of the suitability of the climate regimes to support the establishment and proliferation of the widespread exotic annual, cheatgrass. The patterns of cheatgrass cover and resistance were consistent with our conceptual model with the highest resistance and lowest cover of cheatgrass in the coldest areas (cryic to frigid). The cold winter temperatures that characterize high mountain to mountain types often exceed the physiological tolerance of cheatgrass and limit germination, growth, or reproduction of the annual grass (Chambers et al., 2007; Bykova and Sage, 2012; Compagnoni and Adler, 2014; McMahon et al., 2020). In contrast, the lowest resistance and greatest cover of cheatgrass were in warm to very warm uplands and semideserts with a winter precipitation regime, which have among the highest cheatgrass cover (Bradley et al., 2018) and estimated cheatgrass presence (McMahon et al., 2020) in the western U.S. Resistance was higher in areas with either higher precipitation or summer moisture. This can be attributed to greater competition with cheatgrass due to higher productivity of grasses and forbs in winter moist areas (Bansal and Sheley, 2016; Wainwright et al., 2020) and to dominance by rhizomatous and other grasses in summer moist areas (Bradford and Lauenroth, 2006; Prevéy and Seastadt, 2014; Larson et al., 2017). Moderate resistance and low cheatgrass cover for hypermesic areas that are summer moist and have very low precipitation may indicate low climate suitability or soil limitations across these deserts (e.g. Duniway et al., 2023).

4.2. Patterns of cheatgrass cover and burn probabilities

The patterns illustrated for the annual burn probabilities resembled those observed for the sagebrush biome (Holdrege et al., 2024). Mesic and hypermesic areas that were winter moist, especially semideserts and uplands with moderately low to moderate resilience, were at greatest risk of wildfire as indicated by high annual burn probabilities. Frigid mountain types with moderately high resilience, especially those receiving higher precipitation (>547 mm), were also at risk. Like Holdrege, et al. (2024), summer moist areas had generally low annual burn probabilities that increased with temperature.

Cheatgrass cover was not directly related to the annual burn probabilities. The mesic and hypermesic areas with relatively high cover of cheatgrass and presumably high climate suitability for cheatgrass also had relatively high burn probabilities. The combination of these two factors can result in annual grass-fire cycles, especially if the perennial grasses and forbs that promote recovery have been depleted or fire frequency exceeds the recovery capacity of the dominant shrubs (Brooks et al. 2004, 2007).

4.3. Recent changes in the resilience and resistance classes

The changes in climate regimes and decreases in R&R that we observed reflect recent trends reported for the southwest U.S. An analysis of daily meteorological data from 1976 to 2019 for the western U.S. showed increases in daily maximum (0.2 °C ± 0.01 °C/decade) and minimum temperatures (0.2 °C ± 0.01 °C/decade; Zhang et al., 2021). Total annual precipitation decreased by about − 2.3 ± 1.5 mm per year per decade and interannual precipitation variability increased (Zhang et al., 2021), a trend also observed in streamflow (Ho et al., 2017). Hydrological modeling and 1200-year tree-ring reconstructions of summer soil moisture demonstrated that the years 2000–2018 were the second driest 19-year period since 800 CE in the southwest U.S. (Williams et al., 2020). The productivity and stability of forested and other ecological types depends on the intensity and length of drought and the drought resilience of trees and other species (Zhang et al., 2022, Zhao et al., 2024). Reconstruction of past precipitation in the southwest U.S. from tree rings indicated that increases in variability of cool-season precipitation resulted in roughly a twofold increase in the probability of large negative growth anomalies (Dannenberg et al., 2019). Projections of current and future patterns in soil temperature and moisture conditions from a process-based ecosystem water balance model reflected our results and indicated that higher temperatures would expand the areas of mesic (including hypermesic) and thermic (hot) soil temperature regimes and reduce those with cryic and frigid regimes across western North America drylands (Bradford et al., 2019). Less frequent and more variable precipitation events as well as drier soils were expected across most of the study area. Soil temperature and moisture regimes from the USDA Natural Resources Conservation Service Soil Survey are static measures that reflect the conditions when they were assessed. Land classification systems based on these regimes will need to periodically assess and update the ESDs and State-and-Transition Models (STMs) developed from them to accurately illustrate the effects of both disturbances and management actions as climate change continues to unfold.

The dominant plant functional groups are likely to have a strong influence on R&R in the future. We found the C4 grasses to be key indicators of summer moist areas and therefore generally higher R&R than winter moist and dry areas. In contrast, the C3 annual cheatgrass was the most frequently observed herbaceous species across frigid, mesic, and hypermesic areas that were either winter moist or dry. Warmer temperatures are already resulting in lower resistance to cheatgrass and elevational ascent of the species in these climate regimes (Smith et al., 2022). In areas that decline in climatic suitability for cheatgrass due to higher temperatures, other invasive plants, such as red brome (*Bromus rubens*) and common stork's bill (*Erodium ciconium*), may increase (Brooks et al., 2007; Bradley et al., 2016).

An evaluation of the effects of climate change on plant functional types in the sagebrush biome using a process-based soil water balance model and Global Circulation Models indicated declines in perennial C3 grass and perennial forb biomass across most of the study area, and widespread, consistent, and sometimes large increases in perennial C4 grasses (Palmquist et al., 2021). This was attributed to decreases in soil water availability in surface layers and the photosynthetic advantage of C4 grasses in warm conditions. Our results show that this likely represents an increase in summer relative to annual precipitation as indicated by the monsoon index. An increase in C4 grass species could help maintain or increase R&R but will depend on the capacity of these species to migrate and expand across the area. Past research shows that rhizomatous C4 and other grasses in summer moist areas can increase resistance to cheatgrass and resilience to disturbances (Bradford and Lauenroth, 2006; Prevéy and Seastadt, 2014; Larson et al., 2017) but additional research will be needed to determine the accuracy of the model predictions and of the R&R indicators.

The effects of climate change will also depend on the type and extent of future disturbances. Soil disturbances decrease resistance to cheatgrass more than wildfire in summer moist areas (Seipel et al., 2018), and aeolian disturbances are increasingly common across the drier portions of the study area (Nauman et al., 2023). Management strategies to maintain or increase resilience and resistance could include minimizing disturbances to the soil surface and assisted migration of C4 grasses, such as blue grama and James' galleta, by including them in restoration seed mixes in areas where establishment is possible.

Relative wildfire severity and the potential for vegetation type change will influence future R&R. The relationships between burn severity data and temperature, precipitation, and vapor pressure deficit (VPD), a measure of aridity, were used to evaluate changes in climate-fire relationships in forest and woodland ecosystems from 1984 to 2015 in Arizona and New Mexico (Mueller et al., 2020). Increasing temperature and VPD and decreasing precipitation were associated with increasing area burned and especially the area burned at high severity. The link between increasing aridity and increasing wildfire activity suggests a future with more wildfire in forests and woodlands that are already losing R&R. Management actions, such as managed fire and fuel reduction treatments, will be necessary to reduce the likelihood of uncharacteristic and large high-severity fires and maintain more resilient ecosystems.

4.4. Conclusions

The R&R indicators provide spatially explicit and climate sensitive information on the recovery potential of ecosystems and their susceptibility to cheatgrass invasion across southwest U.S. dryland landscapes. The climate regimes and multiclass R&R indicators that we developed allowed us to account for precipitation seasonality and thus to provide more accurate information on the likely responses to disturbances and climate suitability to the widespread invasive annual, cheatgrass. The evaluation of changes in climate regimes from 1980 to 1999 to 2000–2019 showed that climate change had already resulted in decreases in both R&R across > 10 % of the study area with the largest losses generally occurring in high mountain, mountain, and upland types and the greatest gains occurring in semidesert types with summer moist precipitation regimes. Indicators of R&R provide important information for strategic planning and can be used to develop prioritization strategies for fire prevention and management, invasive species management, and conservation of species habitat (Chambers et al., 2017, 2019; Ricca et al., 2018; Ricca and Coates, 2020; Crist et al., 2019; Rodhouse et al., 2021) for large landscapes, and to evaluate restoration success at more local scales (Rignos et al., 2023). For example, climate-sensitive R&R indicators were used recently to develop treatment response groups for fire risk management (Chambers et al. 2023c) and conservation and restoration strategies for areas with varying ecological integrity in the sagebrush biome (Chambers et al. 2023b). Assessments of the predictive capabilities of the R&R indicators can provide the information necessary for their refinement over time. The change in climate regimes and R&R in recent decades indicates the need to assess the direction and rate of climate change within the focal region and to consider the likely effects on R&R when developing management strategies.

CRediT authorship contribution statement

Jeanne C. Chambers: Writing – original draft, Supervision, Conceptualization. **Jessi L. Brown:** Writing – review & editing, Formal analysis, Data curation. **Steve Campbell:** Validation, Resources. **Shane A. Green:** Writing – review & editing, Validation. **Matthew C. Reeves:** Resources, Methodology. **Daniel R. Schlaepfer:** Writing – review & editing, Resources. **Vaughn Thacker:** Writing – review & editing, Validation.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112749.

Data availability

The climate regime and resilience and resistance indicator data are available in Chambers et al. 2024a, b, c, d.

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