Rangeland Ecology & Management 97 (2024) 25–40

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama

Climate Change Amplifies Ongoing Declines in Sagebrush Ecological Integrity

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A R T I C L E I N F O

Article history:
Received 26 January 2024
Revised 29 April 2024
Accepted 8 August 2024

Key Words:
Artemisia tridentata
global warming
invasive annuals
sagebrush
wildfire

A B S T R A C T

Understanding how climate change will contribute to ongoing declines in sagebrush ecological integrity is critical for informing natural resource management, yet complicated by interactions with wildfire and biological invasions. We assessed potential future changes in sagebrush ecological integrity under a range of scenarios using an individual plant-based simulation model, integrated with remotely sensed estimates of current sagebrush ecological integrity. The simulation model allowed us to estimate how climate change, wildfire, and invasive annuals interact to alter the potential abundance of key plant functional types that influence sagebrush ecological integrity: sagebrush, perennial grasses, and annual grasses. Our results suggest that climate driven reductions in sagebrush ecological integrity may occur over broader areas than increases in sagebrush ecological integrity. Declines in sagebrush ecological integrity were most likely in hot and dry regions while increases were more likely in cool and wet regions. The most common projected transitions of sagebrush ecological integrity classes were declines from Core Sagebrush Area to Growth Opportunity Area and from Growth Opportunity Area to Other Rangeland Area. Responses varied considerably across projections from different global climate models, highlighting the importance of climate uncertainty. However, our projections tended to be robust in areas that currently have the highest sagebrush ecological integrity. Our results provide a long-term perspective on the vulnerability of sagebrush ecosystems to climate change and may inform geographic prioritization of conservation and restoration investments. The results also suggest that ongoing threats, such as the continued invasion by annual grasses and increased wildfire frequency, are likely to be amplified by climate change, and imply that the current imbalance between capacity for conservation to address threats to sagebrush will grow as the climate warms.

Introduction

Climate change is having numerous impacts on plant communities and wildlife habitat, and those effects are projected to intensify in the coming decades (Nolan et al., 2018; IPCC, 2022). At the most fundamental level, the distribution and abundance of

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https://doi.org/10.1016/j.rama.2024.08.003
1550-7424/

plant species are likely to shift in response to long-term changes in the conditions that support those species (Chen et al., 2011). More rapid changes are already occurring due to enhanced extreme climate events, including heat waves and droughts, that lead to plant mortality and promote ecological transformation (Allen et al., 2010; Renne et al., 2019b). Climate change also interacts with other agents of change, notably by accelerating invasion of nonnative plant species (D'Antonio and Vitousek, 1992; Abatzoglou and Kolden, 2011) and enhancing the frequency and severity of wildfire (Westerling et al., 2006; Abatzoglou and Kolden, 2011; Donovan et al., 2017). In combination, these processes are likely to have substantial and widespread consequences, from shifts in the relative abundance of plant species and functional types to wholescale transformations of ecosystems resulting in entirely different plant communities. Anticipating and adapting to these climate change impacts is a growing challenge for natural resource managers (Bestelmeyer and Briske, 2012), and implementing adaptive strategies requires informed perspectives on likely future ecological conditions.

Anticipating climate change impacts and interactions with other stressors is particularly important in sagebrush (primarily big sagebrush, *Artemisia tridentata*) dominated rangelands for three reasons. First, sagebrush rangelands are widespread across western North America and currently occupy approximately 76 million hectares (Rigge et al., 2021). These sagebrush dominated ecosystems contain some of the largest undeveloped areas in the contiguous U.S. (Theobald et al., 2020), provide vital habitat for a range of wildlife species (Knick et al., 2003; Connelly et al., 2004; Manier et al., 2013), and provide ecosystem services including forage for domestic livestock and recreation (Davies et al., 2018). Second, the distribution and ecological integrity of sagebrush plant communities have been declining over the past several decades, driven primarily by cheatgrass (*Bromus tectorum*) invasion and increases in wildfire frequency (Knick et al., 2003; Balch et al., 2017; Palmquist et al., 2021; Doherty et al., 2022). These declines have highlighted the need for systematic, range-wide assessments of past trends, future trajectories, and conservation opportunities in the sagebrush rangelands (Connelly et al., 2004; Remington et al., 2021). Third, climate change is likely to substantially alter sagebrush plant communities, because their structure and function are closely tied to soil moisture and temperature (Noy-Meir, 1973; Sala et al., 1997; Schlaepfer et al., 2012a; Renne et al., 2019a). Within the sagebrush region conditions will become warmer and while there is uncertainty about direction and magnitude of changes in total precipitation, increased precipitation variability and altered precipitation seasonality is likely, including a shift toward cool-season precipitation in the northeastern portion of the region (Bradford et al., 2020; USGCRP, 2023). These changes in climate are in turn expected to alter soil moisture availability for plants (Bradford et al., 2020; USGCRP, 2023). Ecosystem responses may include shifts in the distribution and abundance of plant functional types (Palmquist et al., 2021), decreased ecological resistance to biological invasions and resilience to disturbance (Schlaepfer and Bradford, 2024), and increased potential for ecological transformation (Renne et al., 2019b). At least in some portions of the region, climate change is also likely to be a "multiplier" of existing threats by, for example, increasing the prevalence of wildfire and spread of invasive annual grasses (Boyte et al., 2016; Crist et al., 2023).

In this era of rapid change, retention of large sagebrush landscapes with high ecological integrity has emerged as a primary conservation strategy (Doherty et al., 2022). Large, intact high-quality areas are more likely to resist forces of transformation while serving as landscape-scale anchors for ecological connectivity (Connelly et al., 2000; Knick et al., 2013; Theobald et al., this issue). Doherty et al. (2022) defined an index "sagebrush ecological integrity" (SEI) that is positively related to the amount of sagebrush, and perennial forbs and grasses, and negatively related to the amount annual forbs and grasses, trees, and human modification on the landscape. In areas of high sagebrush ecological integrity the abundance of sagebrush, and perennial grasses and forbs, varies in relative importance according to climate, soil properties, land-use history, and wildfire frequency (West, 1983; Pennington et al., 2019). Shifts in the abundance of these plant functional types, driven by climate, increases in wildfire activity, annual grass invasion, and/or other stressors, will influence the intact habitats that are critical to support the greater sage-grouse (*Centrocercus urophasianus*) and other sagebrush-obligate and sagebrush-dependent wildlife species (Dumroese et al., 2015). Thus, understanding the responses of these plant functional types to changing climate conditions and interacting stressors over large geographic areas is critical to identify where areas with high sagebrush ecological integrity will be located in the future.

These climate-driven shifts highlight the need to effectively prioritize conservation and restoration investments toward areas with long-term potential to sustain high-quality habitat. Doherty et al., (2022) recently quantified sagebrush ecological integrity across the western United States to help enable strategic conservation to "defend and grow" core sagebrush landscapes. Such strategic conservation is necessary because of the large-scale decline of sagebrush ecosystems (rate of loss of ~1% per year over the last 20 years; Doherty et al., 2022; Mozelewski et al., this issue). The RAD (Resist, Accept, Direct) ecological management paradigm provides a relevant framework for considering these types of management decisions (Lynch et al., 2021; Schuurman et al., 2022). "Resist" aims to preserve or restore ecosystems to their historical state, "accept" recognizes inevitable changes and adapts management goals accordingly, and "direct" involves actively steering ecosystems towards desired future states. Long term durability of conservation efforts depends on resisting ecological change in areas that retain the potential for high-ecological integrity sagebrush landscapes even under increasingly warmer, seasonally drier, and more variable climatic conditions (Bradford et al., 2020), which may become more vulnerable to cheatgrass-wildfire dynamics (Crist et al., 2023). Understanding where high quality habitat is today can inform managers to prioritize areas for near-term conservation; understanding how climate change can impact these ecosystems can inform managers to identify areas with near-term, long-term, or near- and long-term management goals. Climate change may make some sagebrush habitats especially difficult to restore, thereby requiring managers to "accept" or "direct" ecological change (Schuurman et al., 2022). Some of today's high-quality sagebrush areas with decreased long-term potential may still warrant near-term to mid-term management efforts, for instance, to increase spatio-temporal connectivity between near-term and long-term areas of high-quality habitats (Theobald et al., this issue). Alternatively, there will likely be areas, especially in the cool and wet portions of the sagebrush region, where climate change may increase habitat suitability and therefore where conservation actions taken today may be most durable.

Uncertainty is a central challenge for long-term natural resource planning given climate change. Despite a well-established understanding of climate physics and how greenhouse gasses increase temperature (IPCC, 2021; USGCRP, 2023), important sources of uncertainty remain when projecting ecological responses to climate futures. A large source of variation in climate projections over the next few decades arises from differences among climate models. Variation in long-term climate projections (e.g., at the end of 21st century) is more strongly influenced by alternative scenarios which represent hypothetical futures that are determined by socio-economic actions and policy on greenhouse gas emissions. Additional important sources of uncertainty arise from our limited understanding of whether ecological change will keep pace with climate change, or whether vegetation and climate will be in a disequilibrium (Felton et al., 2022). A proven method to assess the relative importance of understudied sources of uncertainty are what-if scenarios that compare model outcomes under contrasting assumptions (Oreskes, 2003). Adequate sampling and assessments of these sources of uncertainty are needed to identify robust climate signals and to be useful sources of information for decision-making.

Our overall objective was to understand how climate change and interacting stressors (wildfire and annual grass invasion) will affect the ecological integrity of sagebrush rangelands. We assessed how sagebrush ecological integrity (as defined by Doherty et al. 2022) may respond to different climate change scenarios in combination with wildfire and annual grass invasion. We combined remotely sensed data with results from an individual plant simulation model to address four key questions: 1) How will the abundance of sagebrush ecological integrity classes change in the future? 2) How much uncertainty is there in these changes across climate futures? 3) What plant functional types are driving changes in ecological integrity, and what are the implications for managing wildfire and invasive annual grasses? 4) How sensitive are our results to modeling assumptions including the incorporation of vegetation-wildfire feedbacks, migration ability of warm-season perennial grasses to track climate, and the effects of elevated CO_2 on plant water use?

Methods

Study area

The study area for this project was the entire sagebrush biome in the United States, which is found in 13 states in the western United States (Fig. 1; Jeffries and Finn 2019). Within the biome, only areas defined as sagebrush rangelands were included in analyses (see Doherty et al. 2022 for details).

Modeling approach

We simulated future responses of sagebrush plant communities using STEPWAT2, an individual-based plant demographic simulation model (Palmquist et al., 2018), along with climate change projections from global climate models (GCMs). STEPWAT2 simulates the establishment, growth, and mortality of individual plants for multiple species and functional types. STEPWAT2 is an analysis platform that combines a plant demographic module with an annual timestep (STEPPE, Coffin and Lauenroth, 1990) with a daily timestep soil water dynamics module (SOILWAT2, Schlaepfer et al., 2012a). STEPWAT2 has been validated for big sagebrush plant communities with data from 15 sites throughout the big sagebrush region (Palmquist et al., 2018; Pennington et al., 2019).

STEPWAT2 requires inputs of daily precipitation and temperature, monthly climatic averages, soil characteristics for each soil layer, and life-history traits for plant species and functional types (Palmquist et al., 2018). Daily soil water is simulated for each soil layer with the soil water model (SOILWAT2), summarized by months and soil layers, and using active rooting depth data for plant functional types, converted to annual amounts of available water within the rooting depth of each plant functional type. Available water is the driving variable for establishment, growth, and mortality of individual plants and is allocated to individuals within a species (intraspecific competition) based upon size with large individuals receiving water before small ones. Interspecific competition is represented by differences in resource capture based on phenology and rooting depth distributions. Output from STEPWAT2 includes annual aboveground biomass by species and functional type as well as daily, monthly, and annual climate and soil water variables.

STEPWAT2 represents the effects of elevated carbon dioxide (eCO_2) on plant-level water-use efficiency via two mechanisms. First, transpiration is adjusted in SOILWAT2 based on annual values of CO_2 (ppm) from the historical record or of a given representative concentration pathway (RCP, Meinshausen et al., 2011) using an equation derived from data published in several meta-analyses (Palmquist et al., 2018). A reduction in transpiration is implemented as CO_2 increases, representing stomatal closure and reduced stomatal conductance that has been widely documented under higher CO_2 concentrations (Wang et al., 2022). Second, plant-level water-use efficiency is adjusted in STEPPE for each functional type based on CO_2 (ppm) of a given climate scenario. Using data from a meta-analysis that quantified plant-level water-use efficiency under ambient and elevated CO_2 (Wang et al., 2022), we fit equations between biomass response ratios and CO_2 for C_3 or C_4 species separately. These equations were then used to calculate plant-level water-use efficiency for each STEPPE functional type depending on CO_2 (ppm) of a given climate scenario and whether the functional type was C_3 or C_4. For more details on the implementation of CO_2 effects within STEPWAT2, see Appendix A.

Disturbances are simulated within STEPWAT2, including wildfire and livestock grazing. Wildfire is simulated based on a simple closed form equation that calculates annual wildfire probability based on site-specific fine fuels and climate (Holdrege et al., 2024a). This equation was fit using wildfire occurrence data from the U.S. Geological Survey combined wildland fire dataset (Welty and Jeffries, 2021), gridded Daymet climate data (Thornton et al., 2016), and remotely sensed biomass estimates from the Rangeland Analysis Platform (RAP, (Jones et al., 2021). Wildfire probability is a function of mean temperature (K), annual precipitation (mm), the proportion of precipitation received in summer (June-August), biomass of annual herbaceous plants (g/m^2), and biomass of perennial herbaceous plants (g/m^2). These six variables were calculated as three-year running averages (e.g., mean temperature across the current and previous 2 years) to capture antecedent climate and fine fuels conditions (Pilliod et al., 2017). In general, the equation predicts the highest wildfire probabilities in areas with high mean temperatures, intermediate annual precipitation, low summer precipitation, high biomass of annuals, and intermediate biomass of perennials (Holdrege et al., 2024a). Consistent with the well documented invasive annual grass fire cycle in this region (D'Antonio and Vitousek, 1992; Balch et al., 2013), the amount of annual biomass has a strong positive impact on predicted wildfire probability. The wildfire probability equation was used to calculate wildfire probability within STEPWAT2 separately for each year based on antecedent conditions. Wildfire is simulated stochastically, and wildfire is simulated in the given year when a random number drawn from a uniform [0, 1] distribution is less than the calculated wildfire probability for that year. When wildfire occurs, we simulated complete mortality and no recovery for big sagebrush or succulents (i.e., plants with fleshy tissues used for water storage) after wildfire, a 50% recovery of forb and other shrub biomass after wildfire, and an 80% recovery of grass biomass after wildfire. We simulated no recovery of big sagebrush because it does not resprout after fire, and must rely on germination from seed to re-establish (Schlaepfer et al., 2014). Livestock grazing is implemented by specifying a frequency of grazing and the proportion of functional type biomass removed by grazers.

STEPWAT2 simulation design

STEPWAT2 simulations were conducted for 200 big sagebrush sites used in our previous work (Holdrege et al., 2023; Palmquist et al., 2021) that span the geographic extent and the climatic space

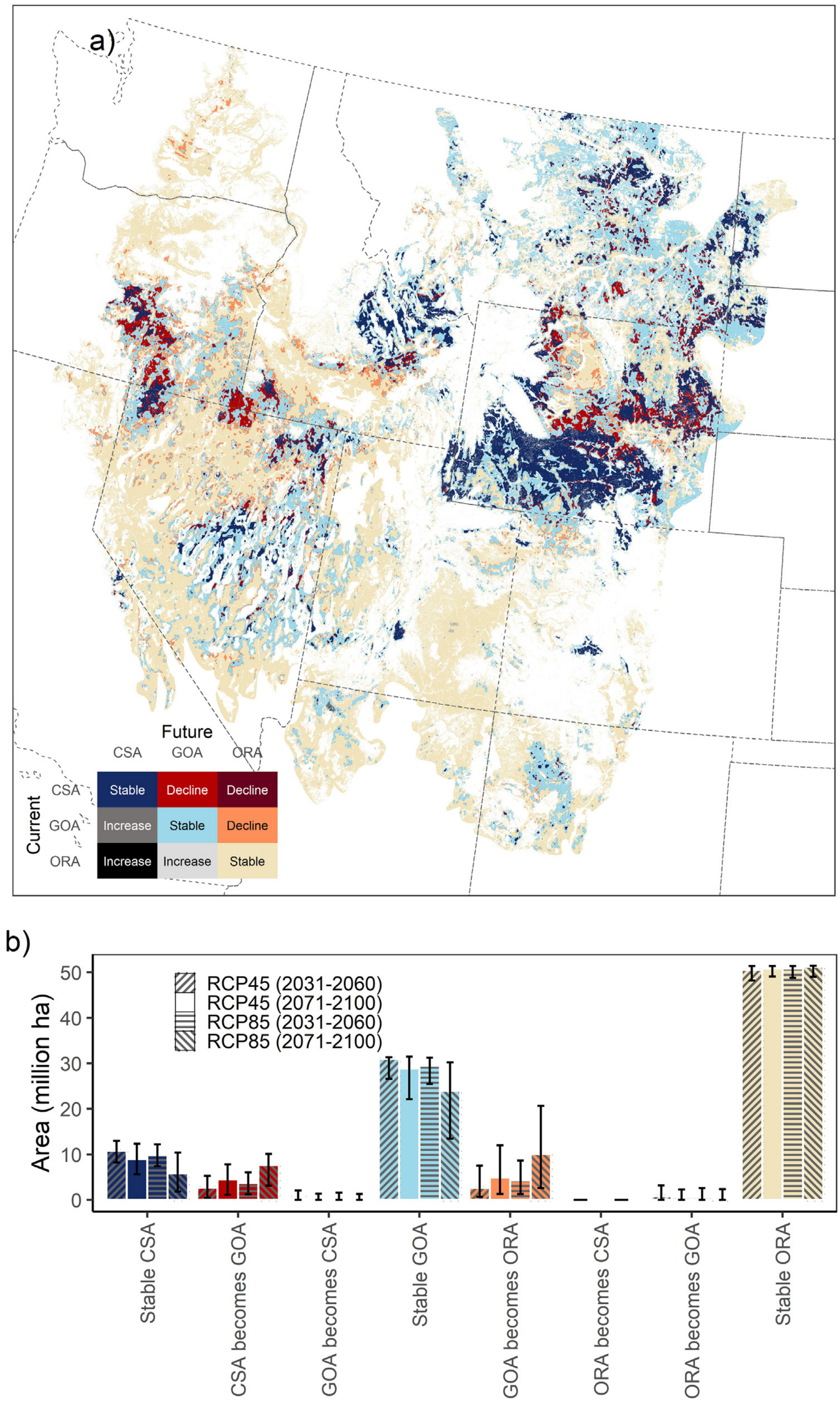

Figure 1. (A) Median change in sagebrush ecological integrity (SEI) classification from current (2017–2021) to future (RCP 4.5, 2071–2100) climate conditions for the "default" modeling assumptions (dynamic wildfire, C_4 grass expansion, but no CO_2 effects on plant-level water-use efficiency). (B) Total area in the nine possible changes of SEI classification for two emissions scenarios (RCP4.5 and RCP8.5) and two time periods (2031–2060, 2071–2100). The bars with no hash marks (RCP4.5, 2071–2100) correspond to the areas shown in the map in panel a. Bars show the area based on calculating the median future SEI across 13 global climate models at each grid-cell. Error bars show the range in area based on using the 2nd lowest and 2nd highest SEI values across GCMs at each grid-cell. Note that while nine changes in sagebrush ecological integrity classification are possible, the "ORA becomes CSA" (black) and "CSA becomes ORA" (dark red) categories do not appear on the map (because they represent approximately zero area). Abbreviations: CSA, Core Sagebrush Area; GOA, Growth Opportunity Area; ORA, Other Rangeland Area.

that big sagebrush ecosystems occupy. All simulations were conducted with annual livestock grazing at light grazing intensities (0% biomass removal for big sagebrush, other shrubs, and succulents, and 24% reductions in biomass for all herbaceous functional types). We simulated each site with soil properties that correspond to a silt loam (30% sand, 18% clay), which is the most frequent soil type for big sagebrush plant communities (Palmquist et al., 2021).

Simulations were implemented in a factorial design to evaluate the effects of climate change (without any wildfire represented), and the combined effects of climate change and wildfire, and climate change, wildfire, and CO_2. In addition, simulations were also implemented for each combination of assumptions (climate change, wildfire, CO_2) with and without the expansion of C_4 grasses under future conditions. Simulations with C_4 grass expansion allowed C_4 grasses to establish if climate became suitable in the future (based on published climate-functional type relative abundance equations described below), even if climate was not suitable for C_4 grasses in that site under current conditions. This set of simulations assumes that C_4 grasses will be able to track changing climate conditions and disperse to and establish in sites that are climatically suitable. There is considerable uncertainty regarding the ability of C_4 grasses to track changing climate and establish amidst an existing plant community, therefore, simulations were also implemented without C_4 grass expansion: C_4 grasses were not simulated under future conditions if a site was not climatically suitable for C_4 grasses under current conditions. Unless otherwise noted, we focus on presenting results where the effects of climate change, wildfire, and C_4 grass expansion are represented, but the effects of CO_2 fertilization are not (hereafter "default"). We chose to focus primarily on results where the effects of CO_2 on plant-level water-use efficiency are not represented as there is considerable uncertainty in the direction and magnitude of long-term plant productivity responses to eCO_2 (Smith et al., 2014; Wang et al., 2020; Maschler et al., 2022; McDowell et al., 2022). This work directly builds on data presented in Doherty et al. (2022) where only the effects of climate change were considered, not the combined effects of climate change, wildfire, and CO_2 fertilization.

To represent the effects of climate change, we simulated each site under current climatic conditions (1981–2010) and future climatic conditions derived from 13 GCMs for representative concentration pathways RCP4.5 and RCP8.5 for mid-century (2031–2060) and end-century (2071–2100). The 13 GCMs (CanESM2, CESM1-CAM5, CSIRO-Mk3-6-0, FGOALS-g2, FGOALS-s2, GISS-E2-R, HadGEM2-CC, HadGEM2-ES, inmcm4, IPSL-CM5A-MR, MIROC5, MIROC-ESM, and MRI-CGCM3) were chosen from those that perform well in the western U.S. (Rupp et al., 2013) and to represent the family of GCMs in existence (Knutti et al., 2013). For each site, we extracted current climate data from Daymet (Thornton et al., 2016) and future climate data from CMIP5 for each GCM from the Downscaled CMIP3 and CMIP5 Climate and Hydrology Projects archive (http://gdo-dcp.ucllnl.org/downscaled_cmip_projections; Maurer et al., 2007). We implemented hybrid-delta downscaling to generate future daily weather from current daily weather data and monthly future projections (Hamlet et al., 2010; Tohver et al., 2014).

Big sagebrush plant communities were simulated as 1 m^2 patches, which is roughly the average belowground resource space that an individual big sagebrush occupies (Sturges, 1977; Palmquist et al., 2018). Simulations were run for 200 iterations and 150 years, thus, the conditions represented by each 1 m^2 patch are far more general than the spatial scale might suggest. Plant communities were simulated for 150 years as STEPWAT2 is initiated without vegetation and it takes ~100 years for the vegetation to reach steady-state conditions. A first-order Markov weather generator in SOILWAT2 was used to produce 150 years of weather data that were representative of the 30-year current (1981–2010) or future time periods (2031–2060, 2071–2100) described above. Ten plant functional types were simulated as described in our previous work (Holdrege et al., 2023; Palmquist et al., 2021). Functional type relative abundance varied across the 200 sites under both current and future conditions: relative abundance was adjusted based on each site's climate and according to published climate-relative abundance equations (Paruelo and Lauenroth, 1996; Teeri and Stowe, 1976; Brummer et al., 2016). For more details on adjustment of vegetation parameters that resulted in differences in plant functional type relative abundance, see Palmquist et al. (2021). Here we focus on simulation output for six plant functional types each represented by a single species that is both widely distributed and locally abundant in big sagebrush ecosystems: big sagebrush, perennial C_3 grasses (*Pseudoroegneria spicata*), perennial C_4 grasses (*Bouteloua gracilis*), annual C_3 grasses (cheatgrass), perennial C_3 forbs (*Phlox hoodii*), and annual C_3 forbs (*Cryptantha* sp.) (Palmquist et al. 2021).

Interpolating STEPWAT2 results

To create continuous gridded datasets, we interpolated STEPWAT2 biomass output from the 200 sites to every grid-cell within our study area (Fig. 1) using a multivariate matching algorithm (Renne et al., 2024). The algorithm uses a nearest neighbor approach, and each grid-cell was matched with one of the 200 sites that had the most similar climate, based on six different climate variables (mean annual temperature [°C], mean annual precipitation [mm], temperature seasonality [standard deviation of monthly temperature], precipitation seasonality [standard deviation of monthly precipitation], mean temperature of the driest quarter [°C], and mean precipitation of the warmest quarter [mm]). These six climate variables were derived from Daymet climate data that has a 1 km resolution, therefore our resulting rasters also had a 1 km resolution. Using this interpolation approach, we created rasters of aboveground biomass of big sagebrush, perennial grasses and forbs (hereafter "perennials"), and annual grasses and forbs (hereafter "annuals") for historical climate conditions and 52 future conditions (13 GCMs x 2 RCPs x 2 time-periods). To evaluate the quality of our interpolations, we calculated a 'matching quality' metric (Appendix B). This metric represents how climatically similar each grid cell is to the site it was matched with, from which the simulated biomass results were derived.

Prior to further analysis we converted the rasters of simulated biomass to cover using equations that, for each of the three plant functional types (big sagebrush, perennials, annuals), related biomass to cover (Appendix C). For each of the 52 future climate scenarios and for each combination of modeling assumptions (wildfire, CO_2, C_4 grass expansion), we then calculated the simulated proportional change in cover from historical to future conditions (Eq. 1).

$$\text{Proportion change} = [(\text{simulated future cover} - \text{simulated historical cover})/\text{simulated historical cover}]. \quad (1)$$

Calculating future sagebrush ecological integrity

We calculated sagebrush ecological integrity (SEI), using the approach described in Doherty et al. (2022). SEI is a multiplicative function that is positively related to the abundance of sagebrush and perennials, and negatively related to the abundance of annuals, trees and human modification. To calculate "future" SEI we relied on estimates of future cover (C_{future}) of big sagebrush, perennials, and annuals instead of directly using remotely sensed cover estimates as is done when calculating SEI for a current or recent time-period. We used remotely sensed estimates of cover of annuals and perennials (and trees, which we did not estimate C_{future} for) from the RAP dataset (Allred et al., 2021), and sagebrush cover from RCMAP (Rigge et al., 2021). To reduce the effects of interannual variation, we used mean cover across years from 2017 to 2020 (Doherty et al., 2022). The remotely sensed estimates of cover have a native resolution of ~30 m, but smoothing was done within a 560 m radius, to create the final cover layers used ($C_{current}$; Doherty et al., 2022). We estimated "future" cover (C_{future}) by multiplying $C_{current}$ by the simulated proportional change in cover of those plant functional types as a response to climate change (Eq. 2). For example, if under a future climate scenario, we simulated 20% more sagebrush cover then under historical climate conditions, our estimate of 'future' sagebrush cover was the 2017-2020 average cover (smoothed to 560 m) multiplied by 1.2.

$$C_{future} = C_{current} * (1 + \text{proportion change}) \tag{2}$$

$$Q_{future} = f(C_{future}) \tag{3}$$

For big sagebrush, perennials, and annuals, C_{future} was converted to a "Q" or quality score, which is a score ranging between 0 and 1, that is based on expert derived functional relationships (Eq. 3, Doherty et al. 2022). We assumed that tree cover and human modification remained at current levels, because those components were not simulated within STEPWAT2 and data are lacking on their expected change under future conditions (i.e., C_{future} equaled $C_{current}$ for trees and human modification). To calculate future SEI_{560} (future SEI that has the same degree of smoothing [560 m] as the Q values), the product of the five Q scores (future sagebrush, future annuals, future perennials, trees, human modification) was calculated (Eq. 4). The Q scores of sagebrush, and perennials are positively related to their respective covers, while the Q scores of the other three components are negatively related to their respective covers (Doherty et al., 2022).

$$SEI_{560,future} = Q_{future,\ big\ sagebrush} * Q_{future,\ perennials} * Q_{future,\ annuals} * Q_{current,\ trees} * Q_{current,\ human\ modification} \tag{4}$$

This $SEI_{560,\ future}$ score was further smoothed within a 2000 m radius, to calculate the final $SEI_{2000,future}$ score (hereafter we use 'SEI' to refer to SEI_{2000}). The $SEI_{2000,future}$ score was then also binned into three categories: Core Sagebrush Areas, Growth Opportunity Areas, and Other Rangeland Areas (Doherty et al., 2022). Core Sagebrush Areas were defined as areas having SEI values that fall within the top 20% of the range in SEI (based on SEI calculated for the period 2017–2020), thus representing the remaining highest quality areas (Doherty et al., 2022). The next 30% of the range in SEI was defined as Growth Opportunity Areas (intermediate sagebrush ecological integrity), and the bottom 50% of the range was Other Rangeland Areas (lowest sagebrush ecological integrity).

Uncertainty across climate futures

For each RCP and time-period, we present results that are based on the median across the 13 simulation runs that used climate inputs from 13 different GCMs. For example, that median "future" SEI was calculated for each grid-cell for RCP4.5, 2071-2100 as the median of the 13 "future" SEI values estimated based on climate inputs from 13 GCMs. To characterize the uncertainty in our results due to projected climate variability among GCMs, we also summarized results for the 2nd lowest and 2nd highest SEI values at each pixel. We also assessed the robustness of our median projections of stable or declining SEI class. Results were considered robust if at least 12 out of 13 GCMs agreed on a change in SEI class. For example, if results from at least 12 out of 13 GCMs projected that a Core Sagebrush Area would remain Core in the future, we considered that a "robust" signal of stability. Similarly, if results from at least 12 out of 13 GCMs projected that the Core Sagebrush Area would become a Growth Opportunity Area or Other Rangeland Area we considered that a robust signal of projected declines in SEI class in response to climate change.

Plant functional type drivers of projected changes in sagebrush ecological integrity

For a given area where changes in SEI were projected, we wanted to understand whether big sagebrush, perennials, or annuals, (or a combination of these three) were driving changes in SEI. Specifically, we focused on areas with three types of changes in classification: (1) areas that are Core Sagebrush Areas now but were projected to decline in quality (become Growth Opportunity or Other Rangeland Areas), (2) Growth Opportunity Areas projected to decline (become Other Rangeland Areas), and (3) Growth Opportunity or Other Rangeland Areas projected to increase in quality. For grid-cells falling into each of these three categories of change, we determined which component (big sagebrush, perennials, or annuals) had the largest median change in Q [in the direction of the change in SEI_{560}], and therefore was the most important contributor to that change. To focus results on areas that had substantial changes in SEI, we present the dominant driver of change only in areas with a $|\Delta SEI| \geq 0.01$. We then calculated the total area where changes in big sagebrush, perennials or annuals were the primary driver of the change in SEI class. Additionally, to visualize the contribution of each of the three components (big sagebrush, perennials, or annuals) to the overall change in SEI, we created a map where each pixel was colored as a mix of red, green, and blue. Here, the amount of red was defined by the median relative proportion change in Q1 (sagebrush), green by Q2 (perennials), and blue by Q3 (annuals). Therefore, if a pixel is blue on the map, the change in SEI_{560} in that location was entirely due to projected changes in the abundance of annuals. Note, for the purposes of the colored map, if a given Q changed in the opposite direction of the overall change in SEI_{560} (e.g., it improved while SEI_{560} declined), it was defined as having zero change.

Sensitivity of projected changes in sagebrush ecological integrity to model assumptions

To investigate the influence of varying modeling assumptions, we systematically altered key aspects of our STEPWAT2 simulations and compared differences in projected SEI. Specifically, we conducted a series of sensitivity analyses by: (1) excluding the simulation of wildfire events, to understand the impact of fire disturbance; (2) preventing the expansion of C_4 grasses, to assess the implications of restricting species range shifts; and (3) incorporating the effects of increased atmospheric CO_2 levels on plant-level water-use efficiency. We compared these alternative modeling assumptions against our "default" modeling assumptions, and for each pixel calculated the difference in projected SEI and whether there was a difference in projected SEI class.

Results

Projected changes in sagebrush ecological integrity classes

About 13.5 million ha (14%) of the sagebrush region is currently classified as Core Sagebrush Area, which are areas with the highest sagebrush ecological integrity (Appendix D). An additional 34.1 million ha (35%) is classified as Growth Opportunity Area (intermediate sagebrush ecological integrity), and the remainder (51.4

million ha, 52%) is classified as Other Rangeland Area (lowest sagebrush ecological integrity). Most of the current Core Sagebrush Areas or Growth Opportunity Areas are projected to remain stable (no change in classification) under altered climate conditions, but there were also many areas of projected decline. Under RCP4.5 at the end of the century (2071-2100), 66% (median projection across GCMs) of Core Sagebrush Areas areas are projected to remain stable, and 34% are projected to decline in quality and become Growth Opportunity Areas (Fig. 1; Appendix D). The largest areas of projected stable core were in southwest Wyoming, which is also where the largest intact portions of Core Sagebrush Areas are currently located (Fig. 1). Montana and Nevada also have substantial areas of stable Core Sagebrush Areas and stable Growth Opportunity Areas. We projected the largest areas of losses of Core in the northern Great Basin and in central and eastern Wyoming. We also projected that 85% of Growth Opportunity Areas will remain stable, while 15% will decline in quality and become Other Rangeland Areas. Many of these declines were located in the Great Basin (Fig. 1). Very few areas have projected increases in ecological integrity classification in response to climate change. Under RCP4.5 (2071-2100), <1% of areas that are currently Growth Opportunity Areas are projected to become Core Sagebrush Areas, and 1% of areas that are currently Other Rangeland Areas are projected to become Growth Opportunity Areas (Fig. 1).

Uncertainty across climate futures

We found considerable variation in the area projected to remain stable as Core Sagebrush Area or Growth Opportunity Area, versus area that is projected to decline in ecological integrity depending on the RCP-time-period combination (Appendices D and E). Under RCP4.5 2031-2060, (the near-term time period and least severe climate scenario), we projected a median 20% loss of Core Sagebrush Areas and 8% loss of Growth Opportunity Areas. In comparison, RCP8.5 2071-2100 (the most severe climate scenario) resulted in median projected losses of 57% of Core Sagebrush Areas and 30% of Growth Opportunity Areas. Additionally, the spread in projections across GCMs also tended to be larger for the more severe climate scenarios, suggesting greater uncertainty (see error bars in Fig. 1B).

There was also considerable variability among GCMs, which differ in the amount of projected warming and in the direction and magnitude of changes in precipitation (Fig. 1B, Appendix F). Under RCP4.5, 2071-2100, our estimate of the percent of Core Sagebrush Areas that will decline and become Growth Opportunity Areas ranged from 9% to 58% (Fig. 1B, Appendix D). These estimates represent the 2nd highest and 2nd lowest projected SEI, respectively, across 13 GCMs calculated for each grid-cell individually. Similarly, for RCP4.5 2071-2100, the projected percent of Growth Opportunity Areas that will decline and become Other Rangeland Areas ranged from 4% to 35%.

While projected SEI differed among GCMs, our projections tended to be robust in areas where we projected stability of Core Sagebrush Areas and Growth Opportunity Areas (i.e., no projected change in habitat classification) (Fig. 2). For instance, under RCP4.5 2071-2100, there was strong agreement among GCMs (results from at least 12 out of 13 GCMs agree) in 76% of the area where the median projection was stable Core Sagebrush Area (Fig. 2). A large continuous portion of this robust stable Core Sagebrush Area is evident in southwestern Wyoming (Fig. 2). Similarly, there was strong agreement among GCMs in 85% of the area where our median results projected stable (or improved) Growth Opportunity Areas. In comparison, there was less agreement among GCMs in places where median results projected declines in ecological integrity classification: there was strong agreement in just 18% of the area where we projected loss of Core Sagebrush Areas, and in 25% of the area where we projected loss of Growth Opportunity Areas (Fig. 2).

Plant functional type drivers of projected changes in sagebrush ecological integrity

Overall we found that the dominant drivers of decline in SEI varied spatially, but these declines were commonly driven by reductions in big sagebrush or increases in annuals over most of the study area (Fig. 3). Declines in big sagebrush were commonly the driver of declines in SEI in the northern Great Basin and increasing annuals were the primary driver of declines in the Great Plains (eastern Wyoming and Montana; Figs. 3 and 4). While not as impactful overall, perennials were the dominant driver of change in parts of the southern Great Basin (Fig. 3A). Projected perennial grass declines had limited impact on declines in Core Sagebrush Areas and Growth Opportunity Areas. However, perennial grass increases were an important driver in the limited area with potential ecological integrity increases (Fig. 3B).

Median projected declines in big sagebrush abundance (expressed as Q ["quality"] scores, which are a function of cover) were largest in the Great Basin and in the Snake River Plain (Fig. 4A), while the greatest increases in annuals occurred in the Great Plains and northern Great Basin (Fig. 4C). Fairly large declines (> 25%) in Q scores of big sagebrush and annuals were projected in some areas. In contrast, most changes in Q scores of perennials were generally smaller (Fig. 4B). These changes in individual Q scores resulted in the greatest projected declines in SEI in the northern Great Basin as well as in the Great Plains (Fig. 4D).

Sensitivity of projected changes in sagebrush ecological integrity to model assumptions

Changing our "default" STEPWAT2 modeling assumptions by not including any wildfire, not allowing C_4 grass expansion, or representing the effects of increased CO_2 on plant-level water-use efficiency, had only modest effects on estimated future SEI (Figs. 5 and 6). Importantly, in most places, the same future SEI and future SEI class were projected regardless of the three alternate modeling assumptions (gray areas in Fig. 5). In some areas, slightly better or slightly worse future SEI was projected under the three alternative modeling assumptions, but the future projected classification was identical (light blue and light pink areas in Fig. 5). There were differences in only a few places in the future projected SEI class as a result of these three alternative modeling assumptions (dark blue and maroon areas in Fig. 5). The effects of these modeling assumptions were generally smaller than differences among GCMs, RCPs, and time-periods (Fig. 6).

The effects of wildfire in our model were heterogeneous. When wildfire was not simulated, projected future SEI tended to be higher across the Great Basin and in parts of Wyoming (Fig. 5A). However, there were places which covered slightly less area, where excluding wildfire caused projected SEI to be slightly lower, yet most of those areas remained in the same future SEI class (Fig. 5A). When wildfire was not simulated, declines in big sagebrush were less frequently the dominant driver of declines in ecological integrity (Appendix G). This reflects the fact that simulated wildfire driven mortality of big sagebrush increased in some areas in response to climate change.

Not allowing the range of C_4 grasses to expand in response to warming caused projected future SEI to be slightly lower in many locations (Fig. 5B). In our "default" simulations, warmer temperatures under future climate conditions allowed C_4 grasses to establish in places we did not simulate their presence under historical conditions. As a result, those locations had higher simulated abundance of perennial grasses in the future, especially in the western

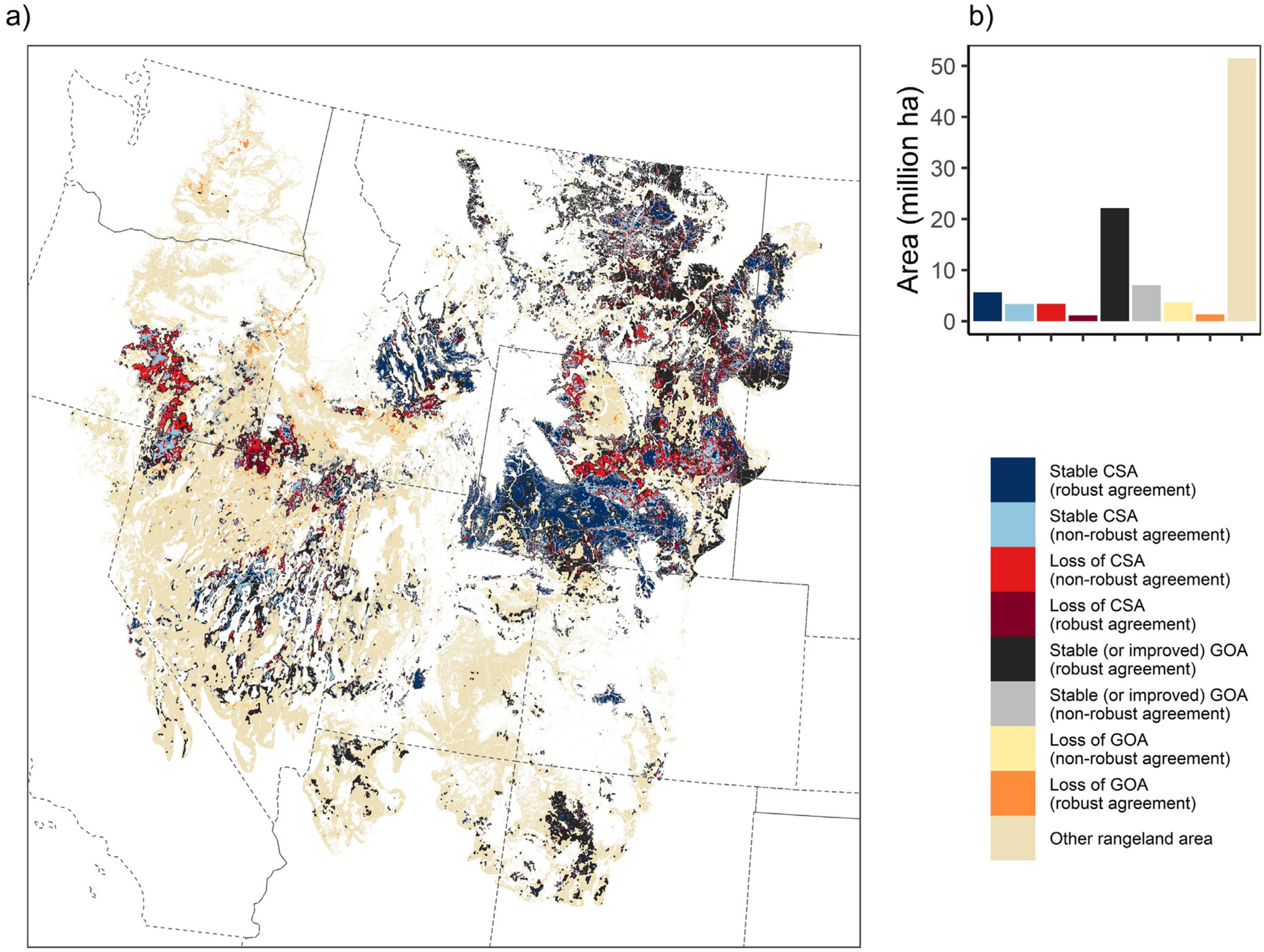

Figure 2. A, Agreement among climate models for change in sagebrush ecological integrity classification (under RCP4.5 2071–2100) for areas that are currently Core Sagebrush Areas (CSA) or Growth Opportunity Areas (GOA). B, Area of the categories shown in panel a. "Non-robust agreement" indicates agreement among 7–11 models out of 13 (light colors, not a robust signal), and 'robust agreement' means agreement among 12–13 models (dark colors, a robust signal). Loss of CSA means future classification is GOA or ORA. Loss of GOA means future classification is ORA. Results are for the "default" modeling assumptions (dynamic wildfire, C_4 grass expansion, but no CO_2 effects on plant-level water-use efficiency).

portion of the sagebrush region, which increased SEI. Additionally, when C_4 grass range expansion did not occur, perennial grasses were less frequently the dominant driver of projected increases in SEI, and were slightly more frequently the dominant driver of declines in SEI (Appendix G).

Incorporating the effects of elevated CO_2 on plant-level water-use efficiency increased future SEI (Figs. 5 and 6) by increasing plant biomass. Elevated CO_2 particularly benefited big sagebrush by allowing individual plants to grow larger over many years. For this reason, declines in big sagebrush abundance were also less commonly the driver of declines in SEI when the effects of elevated CO_2 were represented (Appendix G). This same increase in biomass was not realized by annuals, likely because within the model cheatgrass biomass is largely driven by the number of individuals established as the maximum biomass for this species is relatively small (5 g). Annual grass biomass did increase slightly under elevated CO_2, but the increases were not as large as for sagebrush because the maximum density of annuals was not affected by elevated CO_2 and there was no accumulation of biomass from one year to the next. Experimental results suggest potentially neutral effects of elevated CO_2 on invasive annuals during dry years, with positive effects restricted to wetter periods (Smith et al., 2014).

Discussion

Understanding the long-term trajectories of ecosystems under climate change is both critical for effective conservation and complicated by multiple sources of uncertainty. In light of ongoing habitat degradation, understanding potential sagebrush ecosystem responses to climate change and additional stressors is important for informing decision-making about where to resist, accept, or direct ecosystem change (Schuurman et al., 2022). Here we used an individual plant simulation model coupled with remotely sensed estimates of vegetation to project sagebrush ecosystem responses to climate change, while considering several important sources of uncertainty. Our projections indicate that the majority of Core Sagebrush Areas will remain "stable", by which we mean the climate will continue to be suitable for Core Sagebrush Areas to persist in those areas. However, our projections indicate that reductions in sagebrush ecological integrity (SEI) will also be common, due to climate-driven expansion of cheatgrass and climate- and wildfire-driven reductions in big sagebrush abundance. Overall, these results were reasonably robust across different climate futures and modeling assumptions.

Under an intermediate climate scenario (RCP4.5, 2071-2100) approximately 66% of the area currently identified as Core Sagebrush

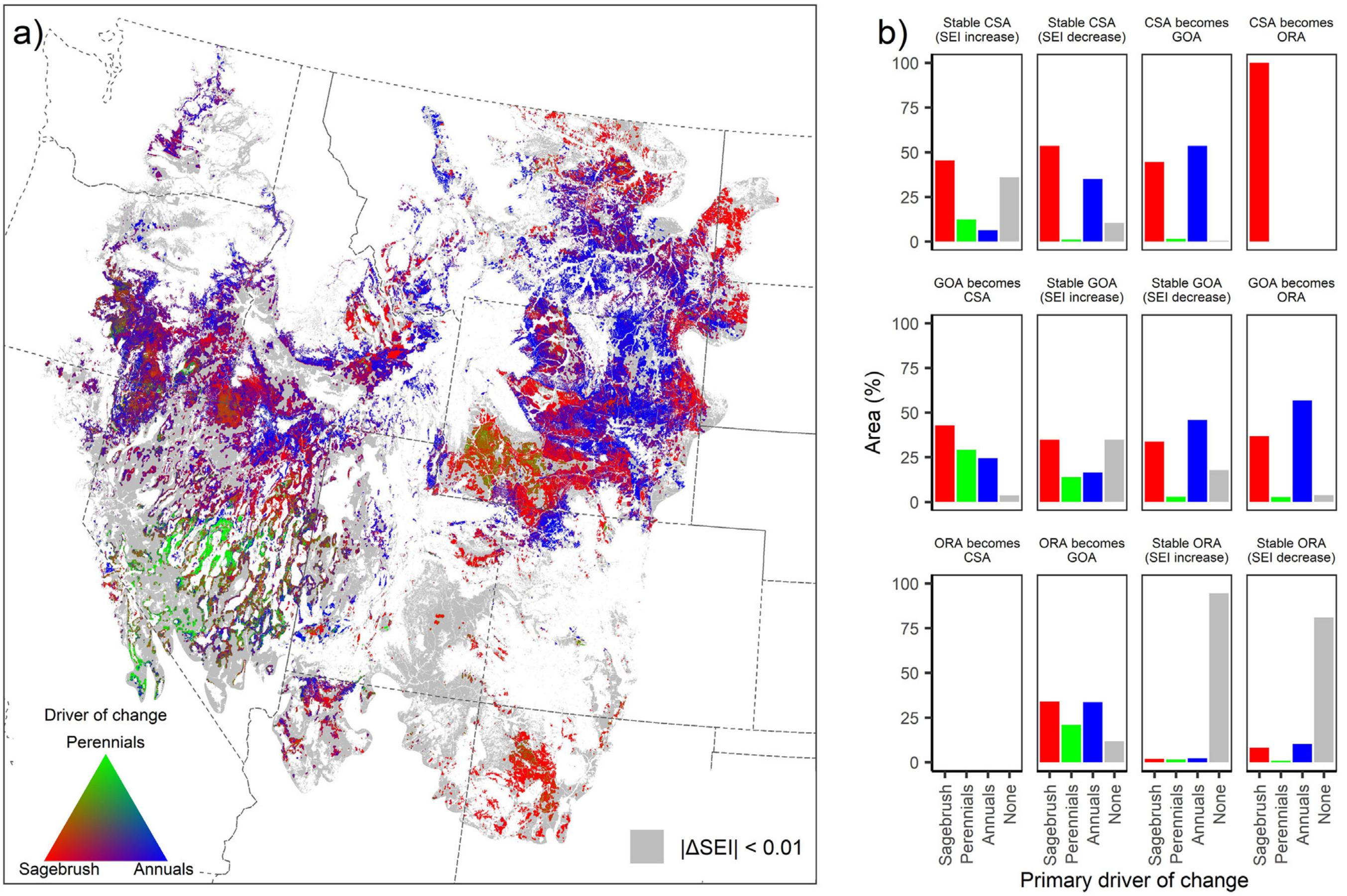

Figure 3. A, Median relative contribution of changing abundance of sagebrush (red), perennial grasses (green), and annual grasses (blue) to changes in sagebrush ecological integrity (SEI), for RCP4.5 2071–2100. B, Region-wide area most impacted by changes in each component for each SEI class change category. The primary driver of change was defined as the plant functional type that had the greatest proportional change in its Q ("quality") score in a given grid-cell. Gray areas on the map (and gray bars in panel b) represent places with little or no change in SEI (|ΔSEI| < 0.01). Results are for the "default" modeling assumptions (dynamic wildfire, C_4 grass expansion, but no CO_2 effects on plant-level water-use efficiency). Abbreviations: CSA, Core Sagebrush Area; GOA, Growth Opportunity Area; ORA, Other Rangeland Area.

Area or Growth Opportunity Area is projected to remain climatically suitable, most of which is located in southwestern Wyoming (Fig. 1). Where we projected changes in SEI class, they were almost entirely declines, and these declines were most common in the northern Great Basin and central Wyoming. This projected loss of SEI was primarily driven by a combination of decreasing sagebrush and/or increasing annual grass abundance, with the relative importance of those two factors varying spatially. These results suggest that climate change is likely to amplify ongoing losses of sagebrush habitat.

Climate change amplifies existing stressors

Approximately 360,000 ha of Core Sagebrush Areas have been lost per year between 2001 and 2020 (Doherty et al., 2022; see also Boyd et al., this issue). For perspective, our median projected habitat loss under RCP4.5 (2071–2100) translates to roughly 70,000 ha/year of Core Sagebrush Area due to climate change between 2020 and 2085 (greater projected losses of ~ 118,000 ha/year for the more severe climate change conditions of RCP 8.5; Appendix D). We do not mean this to imply that without intervention sagebrush habitat loss will be lower in the future than over the past two decades. The greatest ongoing direct threats to sagebrush ecosystems are predominantly invasion by invasive annual grasses and the subsequent annual grass fire cycle (D'Antonio and Vitousek, 1992; Remington et al., 2021; Smith et al., 2023), but it is not known how much these factors are influenced by ongoing climate change. However, threats such as invasion by annual grasses would almost certainly continue to be problems even if today's climate were constant (Smith et al., 2022). In portions of the sagebrush region where we project climate driven declines in ecological integrity, it is probably best to view climate change as having a negative effect that adds to or amplifies these existing stressors.

Wildfire is an important stressor in sagebrush ecosystems that may be amplified by climate change (Abatzoglou and Kolden, 2011; Crist et al., 2023). In our simulations, the interaction between climate change and wildfire tended to be small and was more frequently negative than positive. In a few locations in the northern Great Basin, excluding wildfire from our model led to an improved future SEI class, indicating that mitigating fire risks could be crucial in combating the combined effects of wildfire and climate change in those areas. Supporting this, Crist et al. (this issue) also found that the expected average annual area burned to remain high in the northern Great Basin under contemporary fire weather conditions. The declines in SEI under climate change were more frequently caused by loss of sagebrush when wildfire was simulated, which is consistent with the well documented pattern of poor sagebrush re-establishment post-fire (Schlaepfer et al., 2014). Overall, our simulated responses of wildfire to climate change may be conservative because our wildfire probability estimates relied on mean climate and vegetation conditions (Holdrege et al., 2024a). Therefore, if extreme fire weather conditions increase to a greater degree than can be captured by mean climatic conditions our simulated future wildfire frequency may be too low.

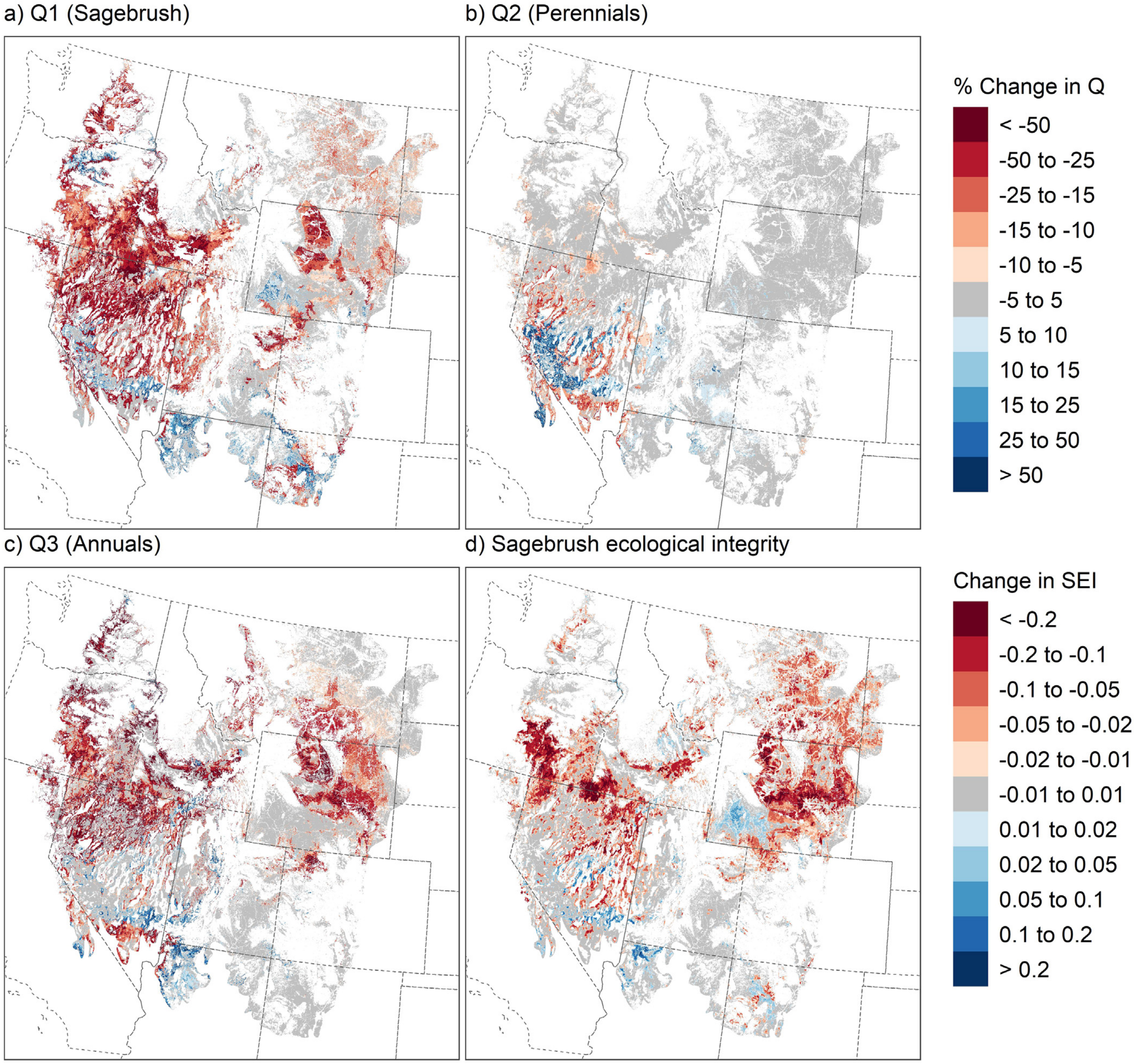

Figure 4. Median percent changes in Q values for (A) big sagebrush, (B) perennial grasses and (C) annual grasses, and d) median absolute change in sagebrush ecological integrity (SEI), for RCP4.5 2071–2100. Note that the Q score of annuals is inversely related to the cover of annuals, so areas shown in red in panel c denote projected increasing annual cover (and thereby a decreasing "quality" score). Results are for the "default" modeling assumptions (dynamic wildfire, C_4 grass expansion, but no CO_2 effects on plant-level water-use efficiency).

Implications for climate adaptation

We identified the locations of current Core Sagebrush Areas and Growth Opportunity Areas that are projected to remain "stable". There are areas where strategies aimed at resisting climate impacts may prove effective. Within sagebrush rangelands, the "defend and grow the core" strategy, described elsewhere in this issue (Kumar et al.; Mozelewski et al.; Theobald et al.), provides a focal point for climate adaptation. This strategy encompasses a dual focus: protecting and enhancing the ecological integrity of existing Core Sagebrush Areas while also restoring Growth Opportunity Areas that show promise for expanding core areas. The ~66% of Core Sagebrush Areas identified as stable (dark blue areas in Fig. 1) have long-term potential to provide climatically resilient conservation anchors of high-quality core sagebrush. Likewise, ~85% of Growth Opportunity Areas are projected to remain stable (light blue areas in Fig. 1). Efforts to grow the core may be most successful in these locations because they are more likely to have climatic conditions that can support high ecological integrity sagebrush in the future.

Our results also identify portions of the sagebrush region where "resist" strategies may not be feasible under climate change. In contrast to Core Sagebrush Areas or Growth Opportunity Areas with potential for sustained high quality, we found that most of the widespread Other Rangeland Areas (low SEI) are likely to remain in that category under future climate. This suggests that environmental conditions in these areas are unlikely to change in a way that promotes increased SEI. Given changing climate condi-

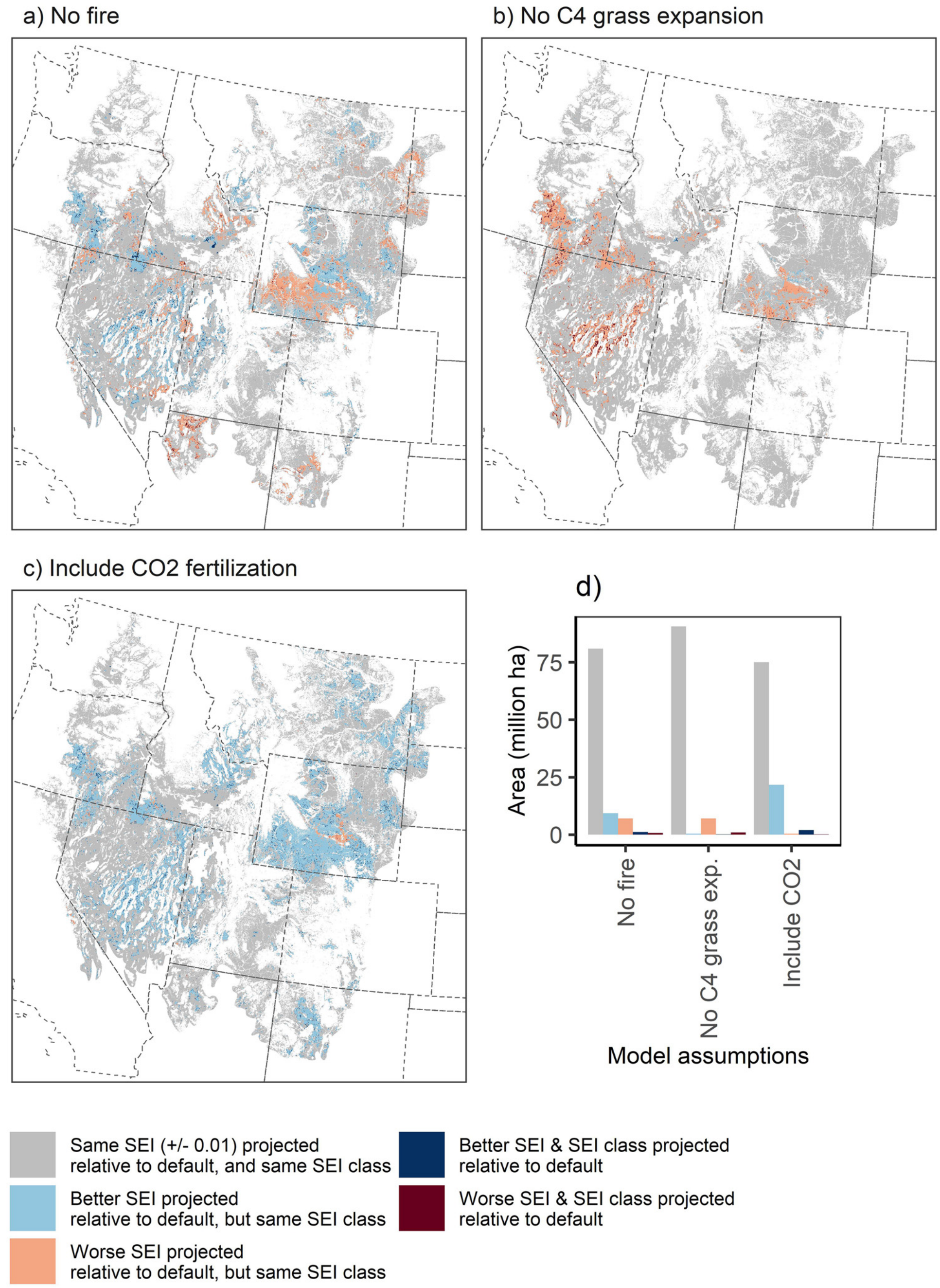

Figure 5. The spatial effects of modeling assumptions. Maps show how future sagebrush ecological integrity (SEI), and future SEI classification are different when (A) wildfire is not incorporated in the model, (B) the extent of C4 (warm-season) grasses is not allowed to expand, and (C) when the effect of CO_2 fertilization is included in the model. (D) Total area of the categories shown in panels a–c. Median results for RCP4.5 2071–2100 are shown here.

tions, restoring ecological integrity in these areas will be increasingly difficult in the coming decades. Even under contemporary climate, restoration is challenging in sagebrush rangelands, particularly in areas that have suffered multiple forms of degradation, such as significant loss of sagebrush and perennial grasses (Davies et al., 2011). Restoration efforts face even greater hurdles in hotter and drier locations (Shriver et al., 2018). In such cases, the ecological realities dictated by a changing climate may mean that adopting "accept" or "direct" strategies will be most feasible.

Limitations of the "resist" strategy are also apparent in some currently high-quality sagebrush areas. Where we projected changes in the SEI category, changes were mostly negative (e.g., from Core Sagebrush Area to Growth Opportunity Area and from Growth Opportunity Area to Other Rangeland Area). For example, under a moderate emissions scenario (RCP4.5, 2071-2100) our median results project a loss of 34% of Core Sagebrush Area and a 15% loss of Growth Opportunity Areas. These are places where resist strategies such as "defend and grow the core" will likely become increasingly challenging. Embracing adaptation strategies like "accept" or "direct" in these currently high-quality areas may represent the most socially difficult climate adaptation decisions because they involve acknowledging the potential future decline of currently valuable resources.

Management strategies may vary geographically because projected changes in SEI were driven by different plant functional types in different parts of the region. Losses of big sagebrush and increases in annuals were primarily responsible for projected transitions from Core Rangeland Areas to Growth Opportunity Areas

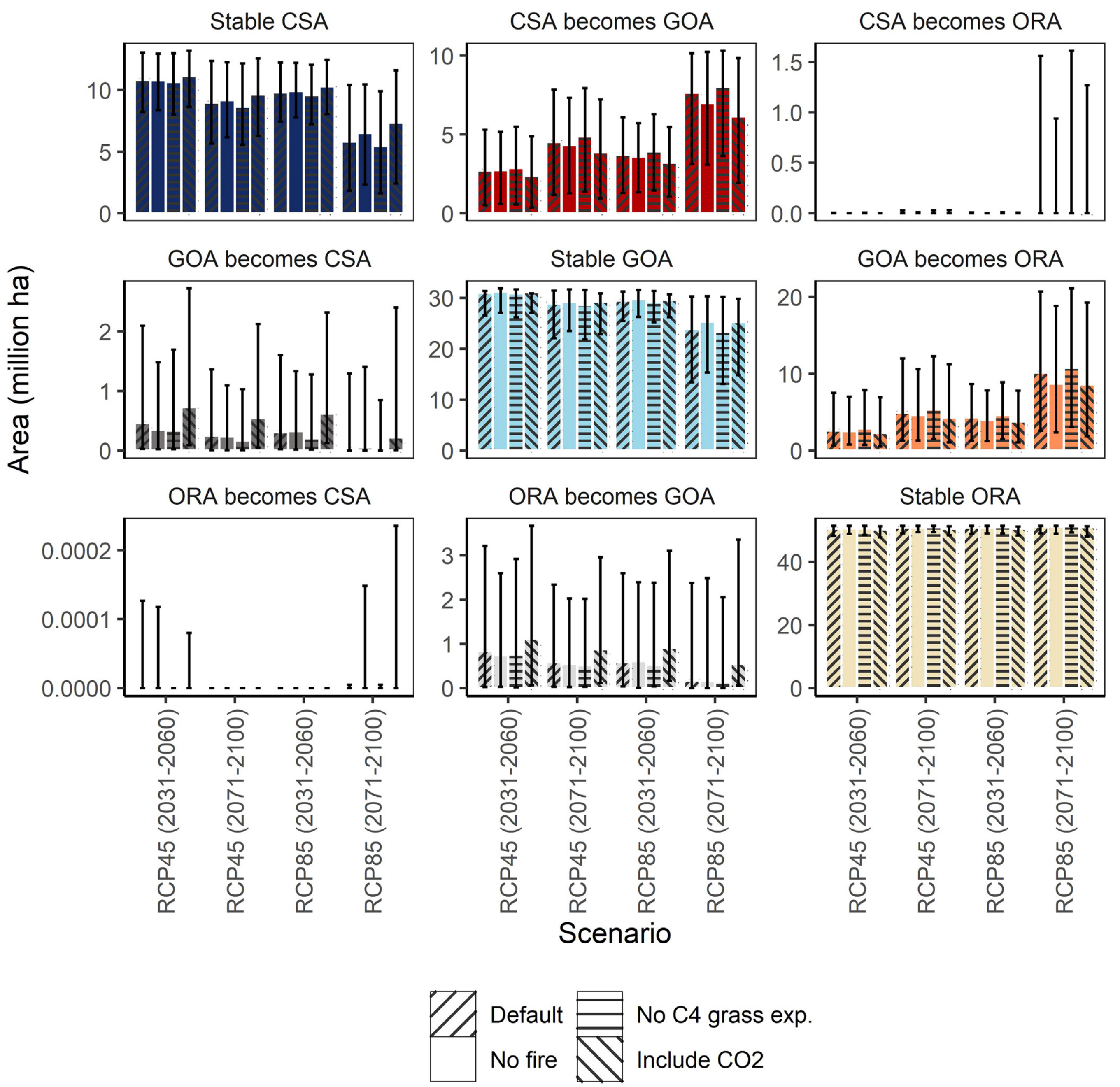

Figure 6. The effects that modeling assumptions have on the total amount of area represented by nine types of changes in sagebrush ecological integrity (SEI) classification. Patterning in bars denotes simulations done with four different modeling assumptions. Results are shown for two emissions scenarios (RCP4.5 and RCP8.5) and time-periods (2031–2060 and 2071–2100). Bars show the area based on calculating the median future SEI across 13 global climate models at each grid-cell. Error bars show the range in area based on using the 2nd lowest and 2nd highest future SEI values across GCMs at each grid-cell. Note, y-axis ranges differ between panels. Abbreviations: CSA, Core Sagebrush Area; GOA, Growth Opportunity Area; ORA, Other Rangeland Area.

or from Growth Opportunity Areas to Other Rangeland Areas. Increases in annuals were a major driver of SEI declines in general (Fig. 3B), especially in the northeastern portion of the region (Fig. 4C), consistent with previous work about the potential impact of climate change on cheatgrass (Boyte et al., 2016; Bradley, 2009; Zimmer et al., 2021). Declines in big sagebrush abundance were greatest in the northern Great Basin (Fig. 4A), an area where other studies identified sagebrush as vulnerable to climate and wildfire interactions (Schlaepfer et al., 2012b; Still and Richardson, 2015; Crist et al., 2023). However, sagebrush did increase in abundance in a few locations, and it was the primary component that caused SEI to improve in some Core Sagebrush Areas (Fig. 3B). Changes in the abundance of perennial grasses generally had less of an impact than sagebrush or annuals in areas where there were changes in SEI class. However, increases in perennials did have positive effects in some areas, including in stable Other Rangeland Areas with increasing SEI (i.e., Other Rangeland Areas that are improving, but not enough to change SEI class). Perennial grasses were also important in locations where Growth Opportunity Areas were projected to become Core Sagebrush Areas, consistent with the other research demonstrating the importance of perennial grasses for resisting annual grass invasion (Davies et al., 2010). Overall, these results suggest that in some locations ongoing efforts to restore sagebrush or perennial grasses, or suppress invasive annual grasses may become more difficult with climate change, and the plant functional types driving declines are likely to vary.

Sources of uncertainty and implications for management

Our results about areas of stability and change were fairly consistent across GCMs within a given RCP and time-period, with most stable Core Sagebrush Areas having a “robust” signal, meaning that simulation results from >90% of GCMs agreed the given grid-cell would remain a Core Sagebrush Area. However, we found that the magnitude of uncertainty among GCMs was greater for more extreme climate change scenarios, notably RCP8.5 2071–2100 (Figs E.2 and E.3). A few climate models suggested much worse outcomes for SEI than the median would indicate, which highlights the need to consider the full range of climate projections for comprehensive assessments. Additionally, we projected greater declines of Core Sagebrush Areas under more severe climate scenarios, illustrating the potential importance of societal decisions about greenhouse gas emissions and the potential benefits of avoiding the more severe RCP8.5 climate conditions (Tebaldi and Wehner, 2018). For instance, the decline in Core Sagebrush Area was about 69% greater under an extreme scenario (RCP 8.5, 2071-2100) than under a moderate scenario (RCP4.5, 2071-2100); similarly, projected losses were greater by the end of the 21st century compared to the middle of the 21st century. Despite overall variability in responses among climate models and scenarios, in some areas changes in SEI class were fairly consistent. Under both moderate and extreme scenarios much of the Core Sagebrush Area in western Wyoming was projected to remain capable of supporting high SEI into the future. However, under the extreme scenario more of the Core Sagebrush Area in the northern Great Basin and eastern Wyoming were projected to be lost.

Comparisons of model simulations representing different assumptions about ecosystem responses suggest that in general, our results are reasonably robust to those assumptions, but differences highlight some potentially important management consequences (Fig. 6). Understanding the long-term, landscape-scale impact of climate change on ecosystems is challenging because of multiple, interacting processes, and these comparisons among simulations with contrasting assumptions provide some perspective on the magnitude of that ecological uncertainty. We quantified the impacts of three ecological assumptions on our results, wildfire (which we discussed above), CO_2 fertilization, and warm-season grass expansion. The long-term implications of CO_2 fertilization on ecosystem water use efficiency remain poorly understood (Wang et al., 2022; Li et al., 2023). CO_2 fertilization increased simulated sagebrush biomass because increased water use efficiency allowed the plants to grow more given the same water availability, which is in line with generally short-duration experimental results that indicate CO_2 fertilization can reduce the effects of drought on plants while not necessarily reducing their water use (Wang et al., 2022). Therefore, under the assumption of an ongoing CO_2 fertilization effect, our results suggest almost universally positive impacts on projected SEI changes compared to an assumption of saturating CO_2 fertilization. These impacts moderate projected SEI declines under all time periods and RCPs, but are most pronounced under the RCP8.5 2071–2100 conditions which have the highest atmospheric CO_2 concentrations.

Similar to our results, previous studies have found that climate change may decrease suitability for cool-season (C_3) perennial grasses, which are most abundant across most of the sagebrush region, while increasing suitability for warm-season (C_4) perennial grasses (Palmquist et al., 2021; Havrilla et al., 2023). However, the ability of warm-season perennial grasses to track changing climate suitability remains poorly understood (Palmquist et al., 2021; Havrilla et al., 2023). Our default simulations assumed that increases in warm season grasses would not be limited by dispersal to new areas and subsequent population increase. When we tested the influence of that assumption by limiting the increase of warm season grasses to areas where they already exist, we projected more widespread future habitat declines particularly in parts of the Great Basin and SW Wyoming. This implies that migration and/or increase of warm season perennial grass populations may be needed to maintain high SEI. Therefore, intentionally increasing the relative abundance of locally present warm-season perennial grasses in seed mixes could promote perennial grass abundance in some locations.

Our analysis represented uncertainty in many aspects of the interacting global change drivers that impact these ecosystems, but there are several limitations to our results. There are various approaches to developing projections of climate impacts on ecosystems. We chose to use a process-based modeling approach which allowed us to include many sources of uncertainty, including energy forcing (RCPs), climate response (GCMs), and ecological dynamics (model assumptions). However, in our simulations we assumed that plant communities had adequate time to adjust to a given climate scenario, which is somewhat akin to a space-for-time substitution. That assumption can be an important source of uncertainty because some slow responses, such as changes in species composition, particularly for long-lived species such as big sagebrush in the absence of catastrophic mortality events, may not occur over the time-horizon of interest (Adler et al., 2020; Felton et al., 2022; Perret et al., 2024).

Our projections of changes in SEI incorporated the potential direct and indirect effects of climate change on sagebrush, perennials, and annuals. However, we did not account for the fact that the other determinants of SEI, i.e., conifer abundance and human modification, will likely change in the future as well. Conifer responses to climate change are likely to differ across the wide climate space occupied by the sagebrush region, and this is an area where further research is needed. While the long term viability of trees in many ecosystems remains uncertain due to drought induced mortality (McDowell et al., 2022), our projections of SEI are likely optimistic in places where conifer invasion will continue under climate change. Reinhardt et al. (this issue) highlights that conifer expansion is an ongoing management concern in sagebrush ecosystems. Conifer removal efforts in sagebrush rangelands are underway, as are efforts to control invasive annual grasses and restore burned areas, that if more strategically targeted and expanded could reverse predicted declining trajectories (Mozelewski et al., this issue). Similarly, there are no published socio-economic scenarios that project how human modification in sagebrush ecosystems may change in the future. For example, changes in land use such as conversion to cropland could cause continued habitat loss (Bedrosian et al., this issue), while changes to grazing regimes via targeted grazing approaches could help mitigate the destructive annual grass-fire cycle (Davies et al., 2022).

While not addressed here, our analysis framework could be used to identify degraded sites that have unrealized “climatic potential”. We quantified the growth potential of sagebrush, annuals, and perennials and projected change in SEI under future relative to current climate conditions. For example, a site may have both a current and projected future climate that could support high SEI according to our analysis; however, this site may actually be classified as Other Rangeland Area instead of as a high-quality Core Sagebrush Area purely due to degradation caused by land use or disturbance history (e.g., recent fire) which are not represented by the growth potential from our simulations. Further research would be needed to identify these types of degraded areas with “climatic potential” where recovery might be more likely and where it may be promoted by targeted management actions.

Implications

The area occupied by sagebrush ecosystems and their ecological integrity has declined substantially over the past half century primarily as a result of annual grass invasion, strengthened by enhanced wildfire dynamics. Understanding the potential future of these changes is both critical for informing natural resource management, and complicated by interactions between wildfire, biological invasions, and climate change. We used a plant community dynamics model that represents many of these interactions to evaluate how sagebrush ecological integrity (SEI) may change over the remainder of the 21st century. We found that climate change is likely to promote additional declines in SEI, amplifying the ongoing detrimental influence of annual grass invasion and wildfire. Our results can inform climate adaptation efforts within sagebrush ecosystems. Specifically, we identified locations of current high quality sagebrush rangelands that also have potential to remain high quality in the future. They represent potential opportunities to resist climate change impacts. By contrast, we identified broad areas where future climatic conditions are unlikely to support all components of SEI. These areas include both currently high and low SEI, and may be places where accepting or directing may be appropriate climate adaptation strategies. The extent and severity of SEI declines were greater under scenarios with a high magnitude of climate change, which included conditions at the end of the 21st century and higher-emissions scenarios (RCP8.5 vs. RCP4.5). Our results suggest that the current imbalance between capacity for conservation and threats will grow as the climate warms, and these results may also be used to strategically inform where conservation investments will be most appropriate.

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.

CRediT authorship contribution statement

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Acknowledgments

We thank Dave Theobald for his advice and providing code that we adapted for calculating future sagebrush ecological integrity. We thank Scott Carpenter for fitting the equation we used that related big sagebrush cover to biomass, and Stella Copeland for providing feedback on a draft of the manuscript. We thank everyone who has contributed to the Assessment, Inventory and Monitoring (Bureau of Land Management) and Natural Resource Inventory (Natural Resources Conservation Service) datasets which are essential for generating the landcover information used in our analyses. Support for this research was provided by the U.S. Fish and Wildlife Service Science Applications Program, the U.S. Geological Survey (USGS) Ecosystems Mission Area, and the USGS Northwest Climate Adaptation Science Center. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. The findings and conclusions in this report are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the authors. It does not imply its approval to the exclusion of other products that may also be suitable. USDA is an equal opportunity provider and employer.

Data Availability

The spatial data presented in this manuscript are available on the ScienceBase repository at https://doi.org/10.5066/P13RXYZJ (Holdrege et al., 2024b). Code used for analyses is available on the Zenodo repository at https://doi.org/10.5281/zenodo.12775518 (Holdrege and Schlaepfer, 2024).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at 10.1016/j.rama.2024.08.003.

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