

Combining resilience and resistance with threat-based approaches for prioritizing management actions in sagebrush ecosystems

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Abstract

The sagebrush biome is a dryland region in the western United States experiencing rapid transformations to novel ecological states. Threat-based approaches for managing anthropogenic and ecosystem threats have recently become prominent, but successfully mitigating threats depends on the ecological resilience of ecosystems. We used a spatially explicit approach for prioritizing management actions that combined a threat-based model with models of resilience to disturbance and resistance to annual grass invasion. The threat-based model assessed geographic patterns in sagebrush ecological integrity (SEI) to identify core sagebrush, growth opportunity, and other rangeland areas. The resilience and resistance model identified ecologically relevant climate and soil water availability indicators from process-based eco-hydrological models. The SEI areas and resilience and resistance indicators were consistent—the resilience and resistance indicators showed generally positive relationships with the SEI areas. They also were complementary—SEI areas provided information on intact sagebrush areas and threats, while resilience and resistance provided information on responses to disturbances and management actions. The SEI index and resilience and resistance indicators provide the basis for prioritizing conservation and restoration actions and determining appropriate strategies. The difficulty and time required to conserve or restore SEI areas increase as threats increase and resilience and resistance decrease.

KEYWORDS

conservation planning, ecological integrity index, ecological resilience, prioritization, resistance to invasion, restoration, sagebrush ecosystems

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1 | INTRODUCTION

Across the globe ecosystems are being altered by anthropogenic threats to biodiversity and rapid and interacting changes in natural processes. Strategic planning and prioritization of conservation and restoration actions are needed to ensure the persistence and recovery of species and ecosystems, many of which are declining globally (Brondizio et al., 2019). However, available resources are inadequate to manage all existing threats (Gerber et al., 2018), uncertainty exists around how best to abate the different types of threats, and decision-makers often have inadequate information for prioritizing conservation and restoration actions across large, diverse landscapes (Herrick et al., 2019; Mendoza-Ponce et al., 2020).

Over the last two decades threat-based approaches for developing prioritization schemes to manage these threats have come into prominence (e.g., Carwardine et al., 2019; Salafsky & Margoluis, 1999). In general, these threat-based approaches begin by identifying the components of the landscape (i.e., species, ecosystems) to be targeted for management, the metrics that will be used for evaluating change (e.g., condition, extent, or persistence), and the anthropogenic and persistent ecosystem threats to these components (see Carwardine et al., 2019). This information is then used to evaluate the management and economic feasibility of different actions, assess cobenefits, and determine appropriate management strategies. This type of approach is being used to evaluate threats and devise approaches for conserving biodiversity in systems ranging from Sub-Saharan African lakes experiencing the effects of increased agricultural development (Danaher et al., 2022) to areas burned in the 2019–2020 Australian megafires (Ward et al., 2022).

The capacity of a system to recover following removal of threats or changes in management to address threats depends on several factors, including the nature of the threat, the ecological resilience of the system to the threat, and ongoing changes in climate. Threat management is often most successful when individual, specific threats to species, such as predators, pollutants, or over-utilization have been removed from the system or managed successfully (e.g., Giovacchini et al., 2022). More challenging are the chronic, expanding threats to ecosystems and increases in habitat modification resulting from greater environmental stochasticity due to a warming climate, species invasions, and altered disturbance regimes. For example, in terrestrial ecosystems experiencing progressive invasions of flammable grasses and development of grass-fire cycles, it may not be possible to completely remove the threat and stop its expansion (Rossiter et al., 2003; D'Antonio et al., 2011; Gorgone-Barbosa et al., 2015; Fusco et al., 2019; Pausas & Keeley, 2021; Kleinhesselink et al., 2023).

The likelihood that management actions can successfully mitigate threats depends on the ecological resilience of the ecosystem to the threat. Ecological resilience concepts and measures are increasingly used to understand the environmental conditions influencing the responses of ecosystems to threats and develop management strategies to address them (Chambers, Bradley, et al., 2014; Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019; Rodhouse et al., 2021; Ricca & Coates, 2020). Ecological resilience (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 altered fire regimes (Holling, 1973). An understanding of resistance to invasive plant species is increasingly important because of the potential of the invaders to modify habitat and transform ecosystems. 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 & Thomsen, 2004). Threat-based assessments provide information on an area's current ecological conditions as indicated by the extent of intact versus degraded areas and magnitude of the predominant threats; indicators of resilience and resistance provide information on the same area's potential to recover and ability to resist plant invasions (Chambers, Beck, et al., 2017; Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019). Thus, assessments of regional threats can be coupled with indicators of resilience and resistance to prioritize areas on the landscape for conservation and restoration management investments where success is most likely (Chambers, Maestas, et al., 2017; Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019).

The sagebrush biome (Jeffries & Finn, 2019) is an extensive dryland region in the western United States (~1186, 900 km²) that is experiencing rapid transformations to novel ecological states due to the combination of anthropogenic and ecosystem threats (Knick et al., 2011; Coates et al., 2016). Major anthropogenic threats to sagebrush ecosystems include urban and exurban expansion and associated infrastructure, land conversion to agriculture, and oil and gas development (Knick et al., 2011). The primary ecosystem threats to sagebrush ecosystems are habitat modification due to invasion of exotic annual grasses, expansion of pinyon and juniper tree species into the shrublands, and concomitant changes in fire regimes (Miller et al., 2013, 2019). Climate warming is exacerbating invasion by exotic annual grasses (Bradley et al., 2016) and resulting in longer and hotter fire seasons and a new era of mega-fires (Abatzoglou & Kolden, 2013; Bradley et al., 2018).

A relatively high proportion of the sagebrush biome is managed by state and federal agencies, ranging from 80.1% in the state of Nevada to 29.0% in Montana. The co-

mingled nature of public-private lands have required land and natural resource management agencies, private landowners, and other partners to work together to develop effective concepts and strategies for addressing the threats to sagebrush ecosystems (Maestas et al., 2022). Key elements have been managing for resilient and resistant ecosystems (Chambers, Beck, et al., 2017; Chambers, Brooks, et al., 2019; Crist et al., 2019; Remington et al., 2021) and, more recently, core sagebrush areas with high ecological integrity (Doherty, Theobald, Bradford, et al., 2022).

To develop a spatially explicit approach for prioritizing management actions across sagebrush landscapes, we combined a new threat-based model of current ecological conditions or integrity (Doherty, Theobald, Bradford, et al., 2022) with new resilience and resistance indicators of the potential to recover from disturbances and resist plant invasion (Chambers et al., 2023a). Previous prioritization schemes used contiguous cover of big sagebrush (*Artemisia tridentata*), a widespread, keystone plant species, to indicate current ecological conditions, and a combined index of resilience and resistance based on soil temperature and moisture regimes, to inform selection of areas for conservation and restoration actions (Chambers, Pyke, et al., 2014; Chambers et al., 2016; Chambers, Beck, et al., 2017; Chambers, Maestas, et al., 2017; Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019; Maestas et al., 2016). Recognition of the need to better account for the factors that contribute to current ecological conditions motivated development of the sagebrush ecological integrity (SEI) index (Doherty, Theobald, Bradford, et al., 2022). The new threat-based model, referred to as the Conservation Design, assessed geographic patterns in SEI and used those patterns to identify core sagebrush areas, growth opportunity areas, and other rangeland areas (Doherty, Theobald, Bradford, et al., 2022). Sagebrush ecological integrity was developed based on changes to the ecosystems that directly impaired the biotic components of ecological integrity (Salafsky et al., 2008). The combined index of resilience and resistance has been used successfully in assessments of threats to high-value ecosystems, including sage-grouse breeding habitat, National Parks, and other conservation areas (e.g., Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019; Ricca et al., 2018; Ricca & Coates, 2020; Rodhouse et al., 2021). However, prior research indicated that the index was static in nature, sometimes differed across state boundaries, and could not be used in projections of climate change effects (Bradford et al., 2019). Therefore, new indicators of resilience and resistance were developed that are based on climate and soil water availability variables derived from process-based ecohydrological models and that are both ecologically relevant and climate responsive (Chambers et al., 2023a).

To gain the understanding of the combined SEI index and resilience and resistance indicators needed to

develop an effective approach for landscape prioritization, we asked three questions. (1) How are the SEI categories related to resilience to disturbance and resistance to invasion by cheatgrass (*Bromus tectorum*)? (2) What is the current level of cheatgrass invasion in the SEI areas and how is it related to resilience and resistance? (3) What is the wildfire risk for SEI areas and how is it related to resilience and resistance and the current level of cheatgrass invasion? We used the results of our analyses to build on our prior work and to provide a landscape prioritization scheme for focusing management actions that considers the relative resilience and resistance of the SEI areas and magnitude of the primary threats.

2 | METHODS

2.1 | Study area

This study included seven Level III EPA ecoregions representing the range of environmental characteristics and ecosystem attributes within the sagebrush biome: Northern Basin and Range, Snake River Plain, Central Basin and Range, Wyoming Basins, Colorado Plateau, Middle Rockies, and Northwestern Great Plains (Wiken et al., 2011; US EPA, 2022). The western Cold Desert ecoregions (Northern Basin and Range, Snake River Plain, Central Basin and Range) have mid-latitude climates with warm to hot summers, cold winters, and winter-dominated precipitation, and are characterized largely by shrubland vegetation. The eastern Cold Desert ecoregions (Wyoming Basins, Colorado Plateau) have a continental climate with warm to hot and dry summers and cool to cold and wet winters. Summer precipitation increases from west to east with the west characterized largely by shrublands and the east transitioning to warm-season grasses. The Middle Rockies in the Western Cordillera has cool to warm, short summers, very cold winters, and relatively high precipitation. Upper elevations have coniferous forests, the foothills are partly wooded or shrub-dominated, and the intermontane valleys are grass- or shrub-covered. The Northwestern Great Plains in the West-central Semi-arid Prairies has a mostly dry, mid-latitude climate characterized by warm to hot summers and cold winters. Sagebrush species are present, but climate patterns favor grass dominance.

2.2 | Spatial data for resilience, resistance and sagebrush ecological integrity

We evaluated the relationships among the SEI categories and resilience and resistance categories by overlaying

and comparing the three spatial layers. The new SEI categories were based on a synthetic variable that was modeled using five indicators of the current ecological conditions of sagebrush ecosystems (see Doherty, Theobald, Bradford, et al., 2022). Two of the indicators (percent sagebrush foliar cover and percent perennial grass cover) were assumed to contribute to integrity, whereas the other three indicators (percent annual grass cover, percent tree [conifer] cover, and an index of human modification) represented threats that reduce integrity. These indicators were combined to define three categories of SEI, including Core Sagebrush Areas (CoreSage) representing the highest SEI, Growth Opportunity Areas (Growth) representing intermediate SEI, and Other Rangeland Areas (OtherRange) with the lowest SEI (Figure S1).

The updated resilience and resistance categories were based on models relating the relative resilience and resistance of the dominant ecological types in the focal ecoregions to climate and soil water availability indicators derived from ecohydrological simulations (see Chambers

et al., 2023a). Ecological types (a category of land with distinctive environmental components: climate, geology, geomorphology, soils, and potential natural vegetation) were developed from the Soil Survey Information (USDA NRCS, 2022a) and Ecological Site Descriptions (USDA NRCS, 2022b) that are widely used by managers across the sagebrush biome, and then categorized according to their relative resilience and resistance. Resilience categories were based primarily on the abiotic characteristics that determine an ecological type's potential response to disturbance (Chambers, Bradley, et al., 2014; Chambers, Brooks, et al., 2019). Resistance categories were derived largely from climate and soil suitability of an ecological type to cheatgrass, but resource availability and competition from perennial herbaceous species were also considered (Chambers, Bradley, et al., 2014; Chambers, Brooks, et al., 2019). Resistance categorization focused on cheatgrass because it is the most widespread and problematic exotic annual grass in the sagebrush biome (McMahon et al., 2021). The climate and soil water availability variables that best predicted the categories of

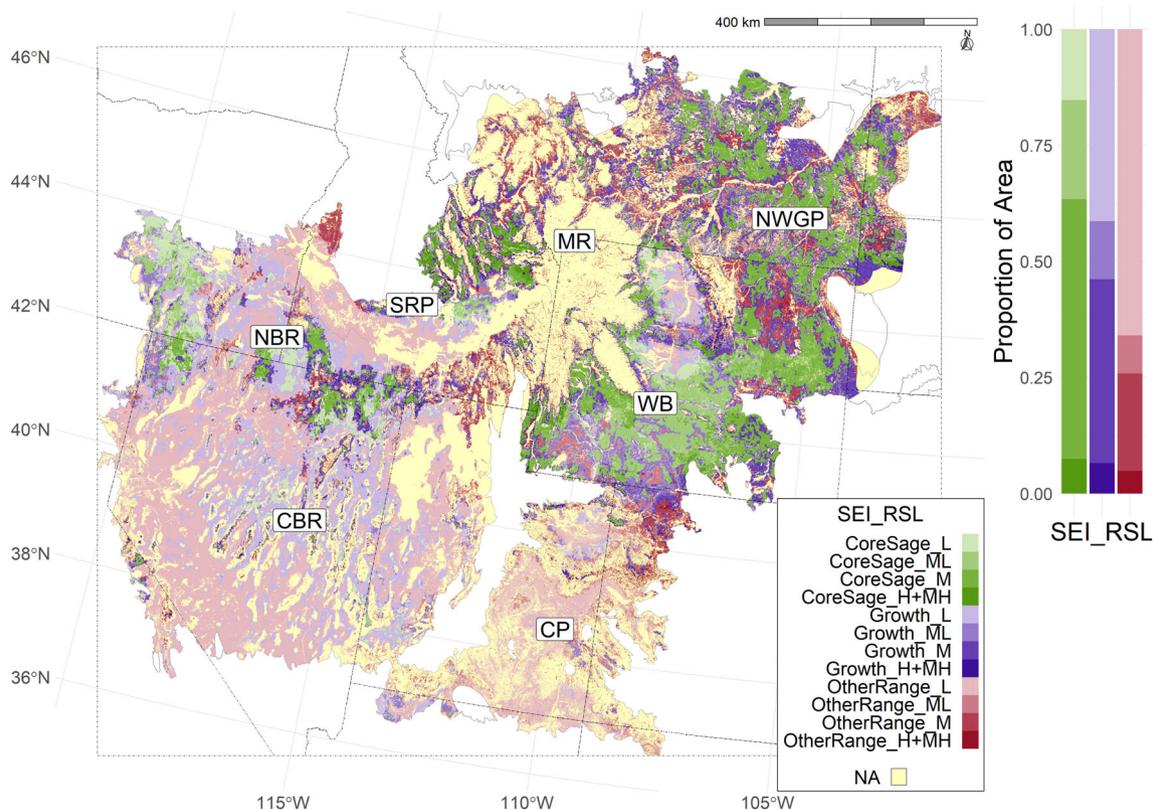


FIGURE 1 Resilience (RSL) of CoreSage, Growth, and OtherRange sagebrush ecological integrity (SEI) areas in ecoregions representing the range of environmental conditions in the sagebrush biome. More intense colors depict higher levels of resilience. Ecoregional boundaries are depicted by thinner black lines and the sagebrush biome boundary by a thicker black line. US state boundaries are shown by dashed lines. Ecoregions are the Northern Basin and Range (NBR), Snake River Plain (SRP), Central Basin and Range (CBR), Colorado Plateaus (CP), Wyoming Basin (WB), Middle Rockies (MR), and Northwestern Great Plains (NWGP). The bar graph shows relative proportions of the area of the resilience (RSL) categories by sagebrush ecological integrity (SEI) categories. H + MH, high + moderately high; M, moderate; ML, moderately low; L, low.

resilience and resistance were identified from random forest models. Resilience and resistance categories were low (L), moderately low (ML), moderate (M), and moderately high to high (H + MH) (Figure S2).

Climate and soil water availability were chosen as indicators of resilience and resistance because they are primary determinants of vegetation dynamics in sagebrush ecosystems (Chenoweth et al., 2022; Gremer et al., 2015; Lauenroth et al., 2014; Schlaepfer et al., 2012) and strongly influence species invasions and fire risk (Chambers, Brooks, et al., 2019). Prior indicators of resilience and resistance based on soil climate regimes (soil temperature and moisture) have been widely used to develop prioritization strategies for fire prevention and management, invasive species management, habitat conservation, and restoration (Chambers, Pyke, et al., 2014; Chambers et al., 2016; Chambers, Beck, et al., 2017; Chambers, Maestas, et al., 2017; Chambers, Allen, et al., 2019; Chambers, Brooks, et al., 2019; Crist et al., 2019; Ricca et al., 2018; Rodhouse et al., 2021), and are indicative of

treatment outcomes (Riginos et al., 2023). These prior indicators are useful in illustrating current resilience and resistance, but are static in nature, change across state boundaries due to differences in soil mapping protocols, and have algorithms that prevent accurate projections of climate change effects (Bradford et al., 2019). The new climate and soil water availability indicators used here have patterns similar to the prior soil climate indicators but represent a significant advancement. The updated indicators were based on widely available climate data and soil water availability metrics derived from process-based ecohydrological models and facilitate greater understanding of the effects of climatic conditions and ecological drought on ecosystem recovery (Chenoweth et al., 2022).

The spatial data layers of the resilience and resistance categories (Chambers et al., 2023b) and SEI categories (Doherty, Theobald, Holdrege, et al., 2022) were mapped at 30-m resolution and reflected areas occupied by sagebrush and pinyon-juniper ecosystems within the rangelands data layer (Reeves & Mitchell, 2011). Portions of

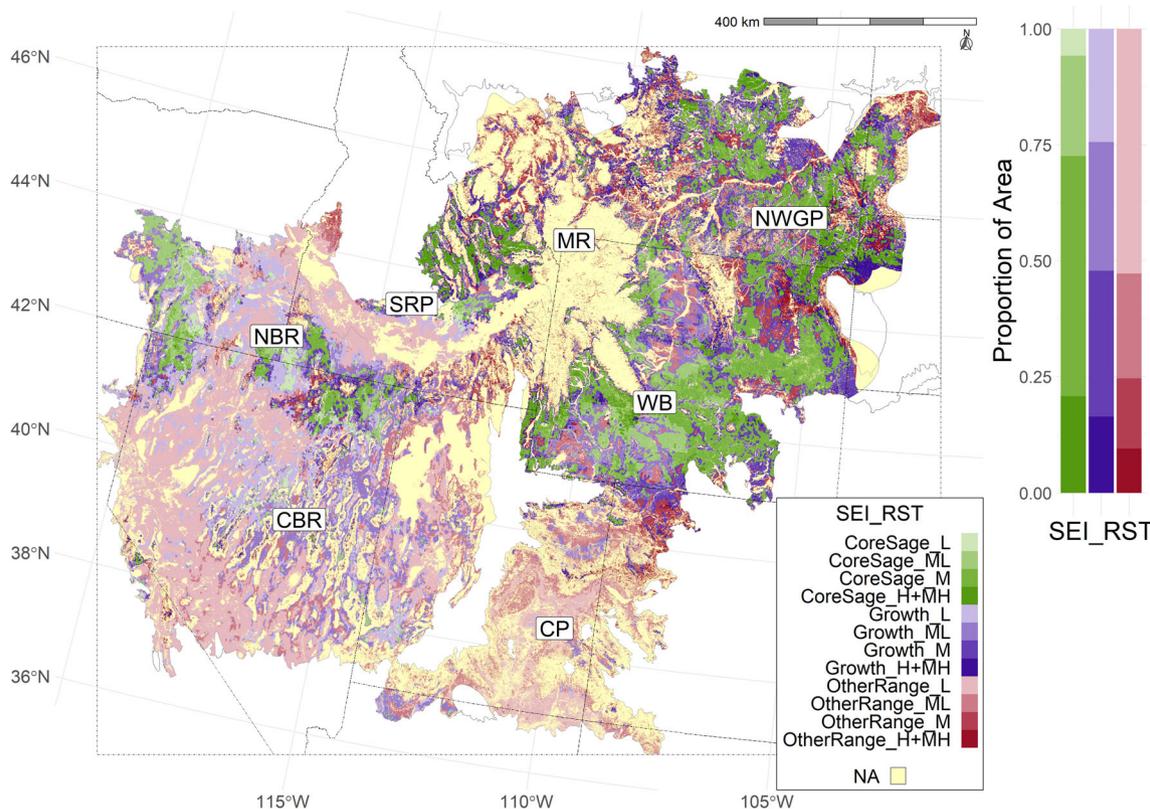


FIGURE 2 Resistance (RST) of CoreSage, Growth, and OtherRange sagebrush ecological integrity (SEI) areas in ecoregions representing the range of environmental conditions in the sagebrush biome. More intense colors depict higher levels of resistance. Ecoregional boundaries are depicted by thinner black lines and the sagebrush biome boundary by a thicker black line. US state boundaries are shown by dashed lines. Ecoregions are the Northern Basin and Range (NBR), Snake River Plain (SRP), Central Basin and Range (CBR), Colorado Plateaus (CP), Wyoming Basin (WB), Middle Rockies (MR), and Northwestern Great Plains (NWGP). The bar graph shows relative proportions of the area of the resistance (RST) categories by sagebrush ecological integrity (SEI) categories. H + MH, high + moderately high; M, moderate; ML, moderately low; L, low.

the ecoregions that fell outside of the sagebrush biome perimeter were excluded (Chambers et al., 2023b).

2.3 | Relationships among resilience, resistance, SEI, cheatgrass cover, and wildfire risk

We evaluated the SEI categories in conjunction with the resilience and resistance categories by overlaying the spatial data layers in R (Hijmans, 2023; R Core Team, 2022). We determined the area extent of the resilience and resistance categories within each SEI category for the entire study area and within each ecoregion. We also examined patterns of absolute area covered as well as proportional area.

The current level of cheatgrass invasion and fire risk in the SEI areas and their relationships to resilience and resistance were evaluated using the estimated cover of cheatgrass and annualized burn probability estimates. We developed a spatial data layer representing mean cheatgrass cover during 2016–2020 at 30-m resolution from the mean values of remotely-sensed annual cover for that time period (Dahal et al., 2022) (Figure S3).

Annual burn probability was derived using a geospatial fire modeling application (Finney et al., 2011) and ca. 2020-vintage landscape data calibrated specifically for use in quantitative wildfire risk assessment for the sagebrush biome (Short et al., 2023) (Figure S4). For each resilience and resistance category and SEI category, we calculated summary statistics of cheatgrass cover and wildfire probability and generated boxplots representing the distribution of the data.

3 | RESULTS

3.1 | Resilience and resistance of sagebrush ecological integrity areas

Across the ecoregions, the different SEI areas were characterized by similar proportions of the resilience and resistance categories but had slightly higher resistance to cheatgrass than resilience to disturbance overall. Across the SEI areas, CoreSage comprised 22% of the total area, and had the greatest proportional areas of H + MH and M resilience (63%) and resistance (73%) and the smallest areas of ML and L resilience (37%) and resistance (27%)

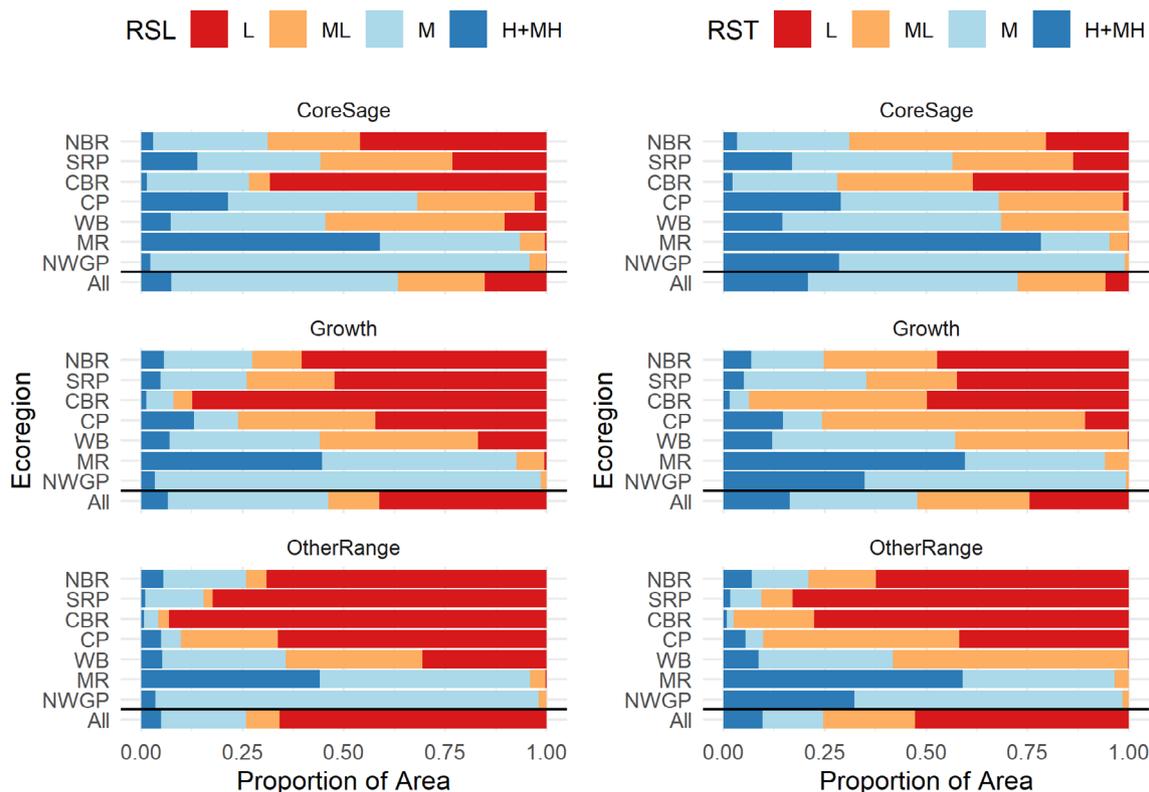


FIGURE 3 Relative proportions of the area of the resilience (RSL; left) and resistance (RST; right) categories by sagebrush ecological integrity (SEI) category and ecoregion. All ecoregions combined are indicated by “All.” Ecoregions are the Northern Basin and Range (NBR), Snake River Plain (SRP), Central Basin and Range (CBR), Colorado Plateaus (CP), Wyoming Basin (WB), Middle Rockies (MR), and Northwestern Great Plains (NWGP).

(Figures 1 and 2). Growth areas were 36% of the total area and had intermediate areas both of H + MH and M resilience (46%) and resistance (48%) and of ML and L resilience (54%) and resistance (52%). Other Range

comprised the greatest amount of the area (42%) and had the largest areas of ML and L resilience (74%) and resistance (75%) and smallest areas of H + MH and M resilience (26%) and resistance (25%).

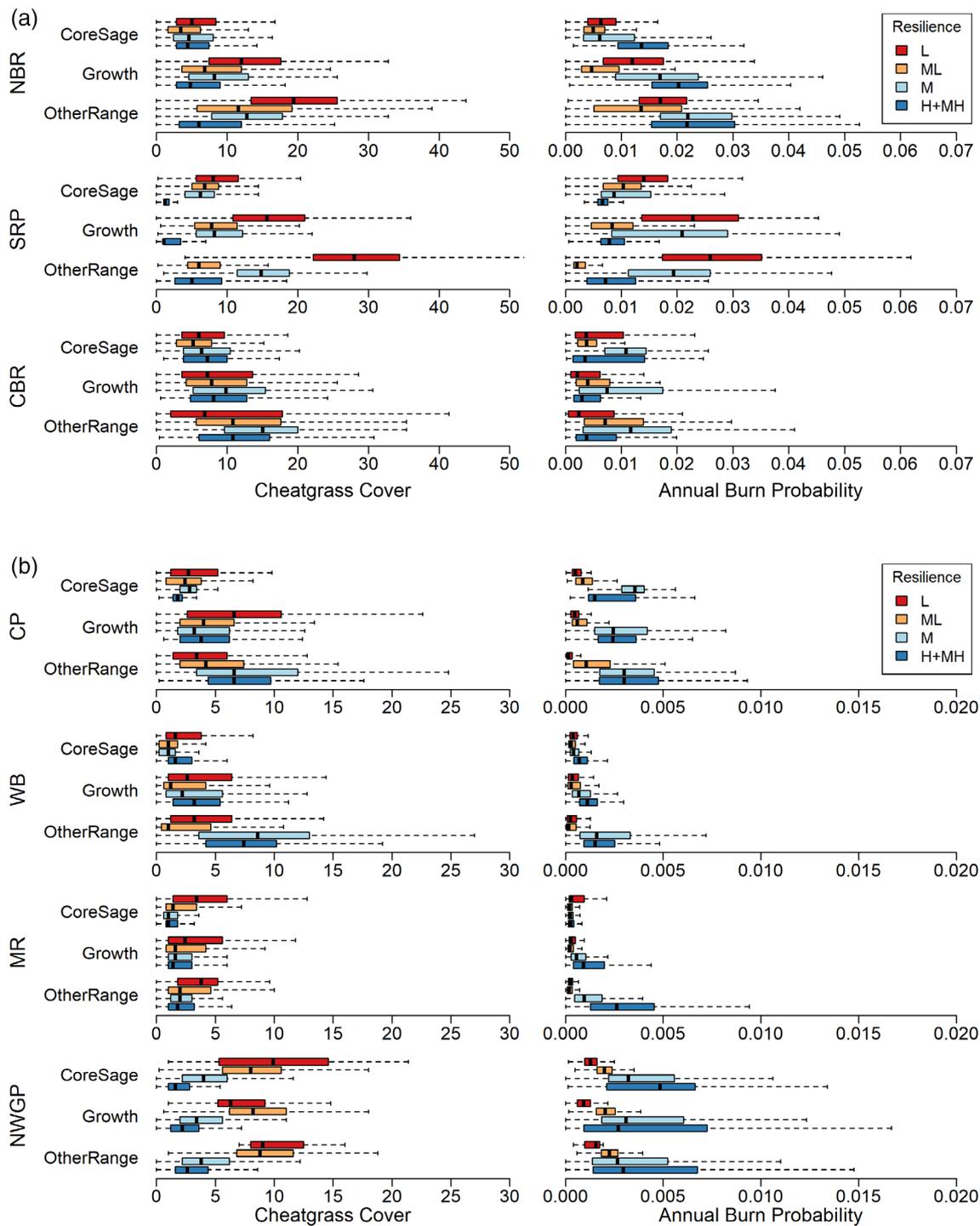


FIGURE 4 Cheatgrass cover (left) and annual burn probability (right) of the combined resilience (RSL) and sagebrush ecological integrity (SEI) categories for the western ecoregions (a) and eastern ecoregions (b). Center lines of boxplots indicate the median value of a sample of up to 1e5 raster cells, hinges show the first and third quartiles, and whiskers show minimum and maximum values. Western ecoregions are the Northern Basin and Range (NBR), Snake River Plain (SRP), Central Basin and Range (CBR); eastern ecoregions are the Colorado Plateaus (CP), Wyoming Basin (WB), Middle Rockies (MR), and Northwestern Great Plains (NWGP).

Large differences existed among ecoregions in the areas of CoreSage, Growth, and OtherRange (Figure S5, Table S1) and in the proportional areas of the different resilience and resistance categories (Figure 3). The proportional areas of H + MH and M resilience and

resistance comprised over 95% in the CoreSage areas of the coldest and wettest ecoregions (Middle Rockies and Northwestern Great Plains) but were less than 25% for all other ecoregions (Figure 3). The proportion of CoreSage area with ML and L resilience and resistance was highest

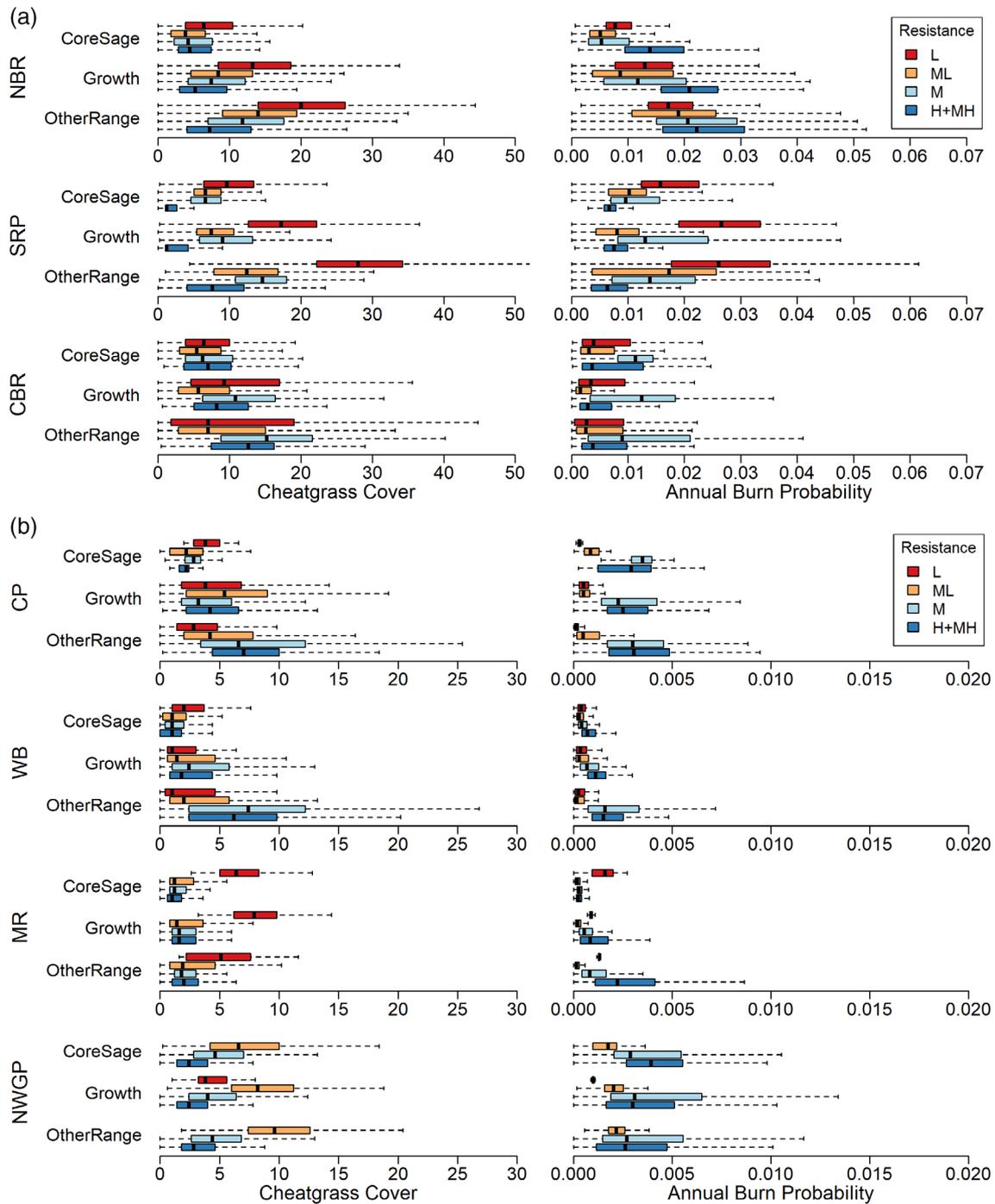


FIGURE 5 Cheatgrass cover (left) and annual burn probability (right) of the combined resistance (RST) and sagebrush ecological integrity (SEI) categories for the western ecoregions (a) and eastern ecoregions (b). Center lines of boxplots indicate the median value of a sample of up to 1e5 raster cells, hinges show the first and third quartiles, and whiskers show minimum and maximum values. Western ecoregions are the Northern Basin and Range (NBR), Snake River Plain (SRP), Central Basin and Range (CBR); eastern ecoregions are the Colorado Plateaus (CP), Wyoming Basin (WB), Middle Rockies (MR), and Northwestern Great Plains (NWGP).

for the relatively warm and dry Central Basin and Range (73% and 72%, respectively) and was 50% or more for both resilience and resistance in the other western ecoregions (Northern Basin and Range and Snake River Plain). The resilience and resistance categories for Growth and OtherRange areas followed a pattern similar to that of the CoreSage areas, with progressively more ML and especially L in Growth and OtherRange areas. Exceptions were the Middle Rockies and Northwestern Great Plains where the resilience and resistance categories differed little among SEI areas.

3.2 | Relationship of cheatgrass cover and wildfire risk to resilience, resistance, and sagebrush ecological integrity areas

The median cover of cheatgrass was generally highest in L and lowest in H + MH resilience and resistance categories across SEI areas (Figures 4 and 5, Figure S3, Tables S2 and S3). In addition, progressively higher cheatgrass cover occurred in Growth and OtherRange areas than CoreSage areas across resilience and resistance categories in almost all ecoregions. Large ecoregional differences existed with the western ecoregions (Northern Basin and Range, Snake River Plain, and Central Basin and Range) having higher cheatgrass cover across both SEI categories and resilience and resistance categories than the eastern ecoregions.

Median annual burn probabilities were universally higher in the western than eastern ecoregions corresponding to generally higher median covers of cheatgrass (Figures 4 and 5, Figure S4, Tables S4 and S5). In the Central Basin and Range and especially Northern Basin and Range, M or H + MH resilience and resistance categories tended to have the highest annual burn probabilities despite relatively lower cheatgrass cover for all SEI areas. This pattern was also true for most of the eastern ecoregions, even though they had relatively lower burn probabilities overall. In contrast, in the Snake River Plain, L resilience and resistance areas had the highest annual burn probabilities for all SEI areas and the highest covers of cheatgrass. Annual burn probabilities tended to increase progressively from CoreSage to OtherRange areas across resilience and resistance categories in the Northern Basin and Range. The Northwestern Great Plains had low but detectable probabilities of burning for the M and H + MH resilience and resistance categories.

4 | DISCUSSION

The SEI areas provided information on the extent of intact vs degraded sagebrush areas and magnitude of the predominant threats, while the resilience and resistance

indicators provided information on the recovery potential of the SEI areas to both disturbances and conservation and restoration management actions. We found that the resilience and resistance indicators and SEI index showed overall positive relationships and therefore were generally consistent, supporting the validity of each other. Higher resilience and resistance tended to co-occur with higher SEI areas, while lower resilience and resistance largely co-occurred with lower SEI areas suggesting similar management strategies. The resilience and resistance indicators and SEI index also were complementary in that they provided information that was additional to each other. For example, CoreSage areas with high SEI occurred that were characterized by low resilience and resistance with little recovery potential suggesting the need for special management considerations. The consistent yet complementary nature of these two spatially explicit information sources indicates that they can be integrated and used together to better inform landscape prioritization of conservation and restoration investments across sagebrush ecosystems.

4.1 | Relationship of SEI areas to resilience and resistance indicators

The similarities and differences in the resilience and resistance indicators and SEI index can be explained largely by (1) the strong influence of environmental conditions on sagebrush ecosystems and their relative resilience and resistance, and (2) the interactions among patterns of environmental conditions and land use and development. Both resilience and resistance and the SEI areas were strongly affected by the environmental gradients that exist across the sagebrush biome. A temperature gradient exists from north to south where the southern-most ecoregions (Central Basin and Range and Colorado Plateau) had warmer mean and winter temperatures, the lowest amount of CoreSage, and generally lower resilience and resistance than the more northern ecoregions (Chambers et al., 2023a). In these southern ecoregions large OtherRange areas were characterized by vegetation types other than sagebrush, such as salt desert, and had low resilience and resistance. They also tended to have relatively higher covers of cheatgrass in the M and H + MH resistance categories. A precipitation seasonality gradient exists from east to west where the north-eastern ecoregions (Northwestern Great Plains and Wyoming Basin) received a higher proportion of precipitation in summer (Chambers et al., 2023a), had the largest area of CoreSage, and had generally higher resilience and resistance than the western ecoregions. Higher proportions of perennial grasses in areas with more summer precipitation and relatively low climatic water deficits typically result

in greater competition with cheatgrass and other annual invaders as well as more rapid recovery from disturbances (Bradford & Lauenroth, 2006; Larson et al., 2017; Prevéy & Seastedt, 2014). Topographic gradients are primary determinants of SEI areas and resilience and resistance indicators in more mountainous ecoregions, and both CoreSage areas and M and H + MH increase with elevation due to decreases in temperature and climatic water deficits and increases in precipitation (Roundy & Chambers, 2021). This is particularly evident in the western ecoregions, where CoreSage areas with M and H + MH resilience and resistance are often associated with mountain ranges and occur at higher elevations.

Although patterns of resilience and resistance are the underlying determinants of ecosystem recovery potentials, current ecological conditions, as indicated by the SEI index, strongly influence management options. Patterns of land ownership, use, and development differ across the biome (Knick et al., 2011), and while this has little to no effect on patterns of resilience and resistance (Chambers et al., 2023a), it has a large effect on patterns of SEI (Doherty, Theobald, Bradford, et al., 2022). For example, areas with relatively high covers of sagebrush and/or perennial grasses and low threat levels may be categorized as CoreSage but have L or ML resilience and resistance. In contrast, areas with lower levels of sagebrush and/or perennial grasses or alternatively higher levels of threats may have M or H + MH resilience and resistance and be categorized as OtherRange. Patterns of historical land uses and their interactions with relative resilience and resistance help explain these differences. For example, heavy, historical livestock grazing combined with the introduction of cheatgrass in sagebrush ecosystems with relatively low resilience and resistance resulted in progressive expansion of the invader and development of invasive grass–fire cycles (Pyke et al., 2016). This is particularly evident in the western ecoregions which did not evolve with grazers and had high climatic suitability to cheatgrass. However, livestock grazing in sagebrush ecosystems with moderate relative resilience and resistance has not resulted in the same levels of cheatgrass invasion in the eastern ecoregions. The eastern ecoregions evolved with grazers, are often dominated by competitive grasses, and are generally less climatically suitable to the invader (Pyke et al., 2016).

4.2 | Level of annual grass invasion in SEI areas and relationship to resilience and resistance

Patterns of cheatgrass cover reflected the concepts used to develop the SEI index and the resilience and resistance

indicators as well as the differences among ecoregions. Low cover of invasive annuals was a criterion for developing the SEI areas (Doherty, Theobald, Bradford, et al., 2022) and CoreSage areas had generally low cover of cheatgrass for all resilience and resistance categories. Growth and OtherRange areas had progressively more cheatgrass, which was reflected in larger areas of lower resilience and resistance due to warmer and drier conditions. Exceptions were in the relatively warm and dry southern ecoregions where higher levels of cheatgrass cover in M and H + MH resilience and especially resistance may reflect recent climate change and observations of increased cheatgrass on cooler and moister sites at higher elevations (Bradley et al., 2016; Smith et al., 2022). However, these were often small areas where three different spatial layers were intersected (e.g., 164 km² of M resistance and 122 km² of H + MH resistance in CoreSage within the Colorado Plateaus, Appendix S6) and this finding should be interpreted with caution. Similarities in the resilience and resistance categories corresponded to the environmental conditions and ecosystem attributes that determine resilience to disturbance and resistance to cheatgrass in sagebrush ecosystems (Chambers, Bradley, et al., 2014; Chambers, Brooks, et al., 2019). Because invasive annual grasses in the sagebrush biome differ in the climatic and environmental conditions suitable for invasion (McMahon et al., 2021), resistance to these other invaders differs from that of cheatgrass (Brooks et al., 2016). For example, a common invasive annual grass in the cooler and moister areas of Northwestern Great Plains is Japanese brome (*B. japonicus*).

4.3 | Fire risk in SEI areas and relationship to resilience and resistance

Patterns of annual burn probabilities across the ecoregions are affected by seasonal climatic regimes, ignitions, and historical as well as current fire regimes. Western Cold Deserts receive little summer precipitation, have long and hot fire seasons with high ignition probabilities, and thus high annual burn probabilities (Abatzoglou & Kolden, 2013; Westerling, 2016). The Middle Rockies, Northwestern Great Plains, and large parts of the Wyoming Basin and Colorado Plateau receive relatively more summer precipitation, most fires burn either before or after the summer rains, and both ignition and burn probabilities are lower (Chambers, Brooks, et al., 2019). Cooler and wetter sagebrush ecosystems have higher productivity (fuel loads) and shorter historical fire return intervals (e.g., Nelson et al., 2014) helping to explain why SEI areas with high resilience and resistance have relatively high annual burn probabilities in the western

ecoregions. The Snake River Plain is an exception because it has large areas of high invasive annual grass cover which burn more frequently and can transmit fire to CoreSage and Growth areas (Bradley et al., 2018).

4.4 | Using an understanding of the relative resilience and resistance of the SEI areas to prioritize conservation and restoration actions

The consistent yet complementary nature of the resilience and resistance indicators and SEI index provides the basis for developing a framework to evaluate management priorities and strategies for sagebrush ecosystems. Resilience and resistance indicators based on soil temperature and moisture regimes have been used successfully in assessments of threats to high-value ecosystems, including sage-grouse breeding habitat, National Parks and other conservation areas, and they provide valuable information for prioritizing management actions (e.g., Chambers, Allen, et al., 2019; Ricca et al., 2018; Ricca & Coates, 2020; Rodhouse et al., 2021). Combining the new ecologically relevant and climate sensitive resilience and resistance indicators with the SEI areas provides an important landscape scale decision tool that can enhance existing frameworks for prioritizing sagebrush ecosystems for conservation and restoration actions (e.g., Chambers, Maestas, et al., 2017; Chambers, Brooks, et al., 2019; Crist et al., 2019; Doherty, Theobald, Bradford, et al., 2022).

Our analyses of the relationships among the SEI index and resilience and resistance indicators were intended to provide the information needed to develop an effective approach for prioritizing resource investments across large landscapes. As in all spatial landscape analyses, uncertainties exist due to the data sources, models used, and spatial projections (Neuendorf et al., 2018). Assessments of planning or project areas at smaller, local scales will require more in-depth analyses using local data on factors such as ecological site types and current ecological conditions (Chambers, Beck, et al., 2017).

The framework for evaluating management priorities and strategies based on the new SEI index and resilience and resistance indicators (Figure 6) builds on our prior work (Chambers, Beck, et al., 2017; Chambers, Maestas, et al., 2017; Crist et al., 2019). The SEI areas provide information on the extent of relatively intact versus degraded sagebrush areas and magnitude of threats, while the resilience and resistance indicators provide information on the likely responses of these areas to both disturbances and management actions. The extent of intact sagebrush, levels of threats, and relative resilience and resistance strongly influence the amount of management intervention required

to conserve and restore sagebrush ecosystems (Chambers, Beck, et al., 2017; Chambers, Maestas, et al., 2017; Crist et al., 2019).

In general, areas with high to moderate (H + MH and M) resilience and resistance are characterized by cooler and wetter conditions with low climatic water deficits (Chambers et al., 2023a), are generally more productive, have higher covers of sagebrush and perennial grasses (positive indicators of SEI), and recover more quickly from disturbances like wildfires (Chambers, Bradley, et al., 2014; Chambers, Brooks, et al., 2019). In addition, they are less suitable climatically to invasive annual grasses like cheatgrass (Bansal & Sheley, 2016; Chambers et al., 2007; Wainwright et al., 2020). In contrast, areas with moderately low to low (ML and L) resilience and resistance are characterized by warmer and drier conditions with high climatic water deficits (Chambers et al., 2023a), generally have lower sagebrush and perennial grass cover (Chambers, Pyke, et al., 2014) and, as observed here, have higher percentages of cheatgrass cover in many ecoregions.

CoreSage areas have the largest extents of intact sagebrush, lowest levels of threats and have generally H + MH and M resilience and resistance. The CoreSage H + MH and M resilience and resistance areas comprised 22% of the study area and are high priorities for protective management aimed at minimizing disturbance, maintaining ecosystem connectivity, and preventing development of uncharacteristic fire regimes. Strategies may include reducing or eliminating disturbances from land uses and development, establishing conservation easements, practicing early detection and rapid response to invasives, and proactive fire management (Chambers, Bradley, et al., 2014; Chambers et al., 2016; Chambers, Beck, et al., 2017; Chambers, Brooks, et al., 2019; Crist et al., 2019). CoreSage areas with ML and L resilience and resistance comprised 6 to 8% of the study area, occurred primarily in the western ecoregions, and are considered among the highest priorities for protective management. The degree of difficulty and time frame required to restore sagebrush ecosystems increases as resilience and resistance decrease, and many ecosystems with ML and L resilience and resistance are at high risk of transitioning to alternative states dominated by invasive annuals (Kleinhesselink et al., 2023).

Growth areas have moderate extents of intact sagebrush, intermediate levels of threats, and occur in both the western and eastern ecoregions. These areas comprised 36% of the study area—17% of the study area was characterized by Growth areas with H + MH and M resilience and resistance while 19% had ML and L resilience and resistance. Connectivity and ecological conditions can be improved in many growth areas, but the

		CoreSage Sagebrush dominated – low modification, PJ or cheatgrass	Growth Moderate sagebrush cover – moderate modification, PJ or cheatgrass	OtherRange Low sagebrush cover – high modification, PJ or cheatgrass
Resilience and Resistance	High	RESTORATION/RECOVERY POTENTIAL HIGH <i>Native grasses and forbs often sufficient for recovery after disturbance</i> <i>Risk of annual invasive grasses becoming dominant is low</i> <i>Seeding/transplanting success typically high</i>		
		Minimal intervention; preventative management to maintain function	Some intervention to enhance connectivity and improve function	Significant intervention to increase/maintain sage. Other types may require different strategies.
	Moderate	RESTORATION/RECOVERY POTENTIAL MODERATE <i>Native grasses and forbs often adequate for recovery after disturbance</i> <i>Risk of annual invasive grasses becoming dominant is moderate</i> <i>Seeding/transplanting success often good</i>		
		Some intervention to minimize risk of invasion; preventative management to maintain function	Moderate intervention to minimize invasive risks, enhance connectivity, and improve function	Significant intervention to increase/maintain sage. Other types may require different strategies
Moderately Low	RESTORATION/RECOVERY POTENTIAL VARIABLE <i>Native grasses and forbs often may be inadequate for recovery after disturbance</i> <i>Risk of annual invasive grasses becoming dominant is moderately high</i> <i>Seeding/transplanting success depends on site characteristics</i>			
	Moderate amount of intervention to minimize risk of invasion and maintain and enhance function	Moderately high intervention to minimize invasive risks, enhance connectivity, and improve function	Recovery of sage and other types difficult without significant intervention over long timeframe	
Low	RESTORATION/RECOVERY POTENTIAL LOW <i>Native grasses and forbs often inadequate for recovery after disturbance</i> <i>Risk of annual invasive grasses becoming dominant is high</i> <i>Seeding/transplanting may require multiple interventions</i>			
	Moderate-to-high amount of intervention to minimize risk of invasion and maintain function	High intervention to minimize invasive risks, enhance connectivity, and improve function	Recovery of sage and other types unlikely without multiple interventions over long timeframe	

FIGURE 6 A framework for evaluating management priorities and strategies based on sagebrush ecological integrity (Doherty, Theobald, Bradford, et al., 2022) combined with ecological resilience to disturbance and resistance to the invasive annual grass, cheatgrass (Chambers et al., 2023a).

amount of intervention required increases with the magnitude of the threats and as resilience and resistance decrease. Management activities may include identifying and correcting improper livestock grazing, reducing or eliminating new infestations of invasive plants, removing pinyon and juniper in tree expansion areas, and actively restoring habitats following wildfire and other disturbances (Chambers, Bradley, et al., 2014; Chambers, Beck, et al., 2017; Crist et al., 2019).

OtherRange areas typically have low amounts of intact sagebrush and/or high threat levels. These areas comprised the largest proportion of the study area (42%)—10% of the study area had OtherRange areas with H + MH and M resilience and resistance while 32% had ML and L resilience and resistance. OtherRange areas with low landscape cover of sagebrush may not have the characteristics to support high value sagebrush resources due to either ecosystem or anthropogenic disturbances. These areas are typically lower priority for implementing

conservation and restoration activities to maintain or restore sagebrush, except where they can provide important habitat connectivity, maintain refugia, or sustain socio-economic values. Both Growth and OtherRange areas that support ecosystem types other than sagebrush, such as salt desert shrublands and persistent pinyon and juniper woodlands, are important components of the landscape that require additional assessment and may benefit from conservation and restoration actions.

4.5 | Synthesis

Assessments of resilience and resistance in conjunction with SEI provide important insights into the environmental conditions that determine the success of conservation and restoration actions. The new resilience and resistance indicators and SEI index for sagebrush ecosystems are both consistent and complementary; together, they

capture the importance of environmental conditions in driving the structure and function of sagebrush ecosystems and the interactions among patterns of environmental conditions with land use and development. Large differences in SEI areas and the resilience and resistance indicators exist among ecoregions. In the western ecoregions where CoreSage areas are generally small, it will be necessary to prioritize protective management across resilience and resistance categories to conserve sagebrush ecosystems. In many ecoregions large growth areas indicate potential to maintain or improve ecological integrity through proactive management. Extensive OtherRange SEI areas indicate a need to more critically assess the prevalence of other vegetation types, the biological diversity of these types, and species at risk. Many of these areas are relatively warm and dry, have low resilience and resistance, and are highly vulnerable to climate change (Chambers et al., 2023a; Palmquist et al., 2021). Evaluating how resilience and resistance are projected to change with climate warming can provide insights for the management of all SEI areas. In areas where climate change effects are projected to be severe, management actions may need to help ecosystems transition to new climatic regimes (Lynch et al., 2021; Schuurman et al., 2022).

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DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories (Chambers et al., 2023b; Doherty, Theobald, Holdrege, et al., 2022).

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SUPPORTING INFORMATION

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

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