



# Well-Connected Core Areas Retain Ecological Integrity of Sagebrush Ecosystems Amidst Overall Declines From 2001–2021



David M. Theobald<sup>1,2,\*</sup>, Alexander V. Kumar<sup>3</sup>, Kevin Doherty<sup>4</sup>, Katherine A. Zeller<sup>5</sup>, Todd B. Cross<sup>6,7</sup>

<sup>1</sup> Conservation Planning Technologies, Colorado State University, 1113 W. Olive St., Fort Collins, CO 80521, USA

<sup>2</sup> Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80526, USA

<sup>3</sup> US Fish and Wildlife Service, Fort Collins, CO 80526, USA

<sup>4</sup> US Fish and Wildlife Service, Lakewood, CO 80439, USA

<sup>5</sup> USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, Missoula, MT 59801, USA

<sup>6</sup> Crosswinds Ecological Consulting, LLC, Hartland, VT 05048, USA

<sup>7</sup> Fedy Wildlife and Molecular Ecology Lab, School of Environment, Resources and Sustainability, University of Waterloo, Waterloo, ON N2L 3G1, Canada

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## ABSTRACT

Conservation of species' mobility and ecological integrity is necessary for the productivity of the sagebrush biome in the western United States. Building on the recently developed Sagebrush Conservation Design (SCD) that mapped sagebrush ecological integrity (SEI)—defined as the higher cover of sagebrush and perennial grass and reduced threats due to invasive annual grass, tree encroachment, and human disturbance—we modeled the structural connectivity of sagebrush ecosystems to better incorporate the role of landscape-level processes into assessments of integrity. Because integrity can vary spatially, as well as temporally, we quantified both interannual variability and trends in variability in SEI from 2001–2021. We used the resultant map to identify areas with high structural landscape connectivity (i.e., “well-connected cores”), then determined the coincident core sagebrush areas (CSAs) that represent functioning sagebrush ecosystem with few landscape threats, and growth opportunity areas (GOAs) that represent functioning systems impacted by one or more threats as originally defined and mapped in the SCD. We found that CSAs were located in areas with higher landscape connectivity, and the biome-wide average of SEI declined by 30% from 2001 to 2021, although the structural connectivity biome-wide declined one-third less (by 20%). CSAs located in areas with high connectivity had 25% higher SEI values on average than those with low connectivity, and the trend in declining SEI values was slower. Our datasets of landscape connectivity can be combined with other SCD products to provide a broader ecosystem context—both spatially and temporally. Our results can be used to inform, refine, focus, and prioritize conservation and management efforts to those CSAs and GOAs we identified as particularly well connected and which may be more resilient to recently altered dynamics and declines—those that will serve to anchor efforts to conserve the sagebrush biome in light of changing land use and climate.

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## Introduction

The Sagebrush Conservation Design (SCD) collaboratively developed maps of sagebrush ecological integrity (Doherty et al. 2022, and further discussed in Doherty et al. (2024)). A key product of the SCD was a map showing quantified biome-wide sagebrush ecological integrity (SEI), as a function of sagebrush, perennial grass, annual grass, tree encroachment, and human disturbance. SEI was

used to identify core sagebrush areas (CSAs) that represent functioning sagebrush ecosystem with few landscape threats, growth opportunity areas (GOAs) that represent functioning systems impacted by one or more threats, and other rangeland areas (ORAs) that represent low-functioning and/or higher levels of landscape threats. The CSAs and GOAs are central to the “defend the core” strategy of the SCD (Maestas et al. 2022).

Still lacking is a better understanding of the broad, landscape-level connectivity of CSAs (i.e., the “core of cores” or “backbone”), and inter-annual trends in connectivity. To further support the key premise of the “defend the core” strategy as described by Doherty et al. (2024), we examine the working premise that areas identi-

\* Correspondence: David M. Theobald, Conservation Planning Technologies, Colorado State University, Fort Collins, CO 80521, USA.

E-mail address: [dmt@davidmtheobald.com](mailto:dmt@davidmtheobald.com) (D.M. Theobald).

fied as high-integrity (especially CSAs) are strongly correlated over time (on an annual basis), in large part due to the structural connectivity of these areas. In addition to connectivity, recent analyses inspired by the SCD include invasive and perennial grass dynamics (Smith et al. 2023; Boyd et al. 2024), conifer treatment prioritization (Reinhardt et al. 2024), wildlife responses (Prochazka et al. 2024; Kumar et al. 2024), and wildfire probability (Crist et al. 2023; Crist et al. 2024).

Ecological connectivity is consistently identified as a key component of high-functioning landscapes (Heller and Zavaleta 2009; Krosby et al. 2010; Hilty et al. 2020) and protecting, maintaining, and restoring areas of connectivity are primary tools available to land managers seeking to retain biodiversity, minimize the potentially fragmenting impacts of land use (Schmitz et al. 2015) and facilitate climate adaptation (Elsen et al. 2023). Structural connectivity considers the permeability of the landscape based on its structural characteristics, whereas functional connectivity considers the permeability of the landscape for specific species, considering their behavioral responses (Kindlmann and Burel 2008; Keeley et al. 2021). Functional connectivity models developed for specific species in the sagebrush biome include pronghorn (*Antilocapra americana*, Zeller et al. 2021), greater sage-grouse (*Centrocercus urophasianus*, Crist et al. 2017; Row et al. 2018; Cross et al. 2023), and pygmy rabbit (*Brachylagus idahoensis*, Dilts et al. 2023). Here we analyze the structural connectivity of the sagebrush biome.

Sagebrush ecosystems are dynamic and show year-to-year variability (Shi et al. 2018; Buchholtz et al. 2023a) due particularly to climatic conditions, and interrelated, wildfire and invasive species (Buchholtz et al. 2023b), primarily annual grasses (Bradford et al. 2023). In the face of these dynamics, identifying relatively stable and well-connected landscapes is valuable to inform conservation management of the sagebrush biome. Recently, consideration of “dynamic” connectivity has been encouraged (e.g., Zeller et al. 2020), because it captures the inherently dynamic ecological and socio-ecological processes and their effect on landscape-level patterns by highlighting potential intra- and inter-annual variations of ecosystem conditions such as seasonality, disturbance, human development, and climate change. Importantly, by exploring these spatio-temporal changes, it is possible to identify areas of connectivity that have withstood perturbations from natural or human-caused landscape dynamics, and that may continue to do so into the future. Here we model dynamic structural connectivity to understand the spatial and temporal fluctuations of areas of well-connected high-integrity sagebrush within the US sagebrush biome. We build on the SEI datasets generated from recent modeling of the ecological integrity of the sagebrush ecosystem (Doherty et al. 2022) by calculating structural connectivity (which we call *SEI-C* hereafter) to better understand how ecological connectivity likely adds to the overall integrity of the sagebrush biome.

To inform key products of the SCD, we examined the structural landscape connectivity which forms the ecological context for the previously identified CSAs and GOAs. More specifically, we quantified the structural landscape context of previously identified CSAs and GOAs, in order to provide additional information for strategic natural resource management and to anticipate possible sensitivity to drivers of change such as land use, wildfire, and climate variability. We anticipate that this new dataset and information will support further assessments and analyses, including those raised during the development of the SCD, many of which are described within this special issue.

Our overall objective to inform the planning and management of the sagebrush ecosystem was composed of two related elements. First, we identified areas within the sagebrush biome that have high dynamic structural connectivity at the landscape level, determined whether these well-connected cores are stable or vari-

able between years, and determined whether there exists a directional trend (i.e., increase or decrease) over recent years (2001–2021). Second, we examined the landscape context using *SEI-C* by identifying the areas with the highest overall connectivity, as well as the CSAs and GOAs that are particularly important to maintaining connectivity.

## Methods

To address our objective, we modeled the structural connectivity of Sagebrush Ecological Integrity (*SEI-C*) for each year from 2001–2021 and quantified the spatial patterns for each year and across time, as well as the temporal trends of the landscape-level cores per pixel and for the overall biome. Then, to identify important areas that are also well-connected (i.e., landscape-level cores that form the “backbone” of the dynamic sagebrush ecosystem) to provide additional context to support the prioritization of future conservation efforts, we overlaid these landscape connectivity maps on the maps of sagebrush areas (CSAs, GOAs, and ORAs identified for the 2021 time step by Doherty et al. 2022).

### Study area

Our study area consisted of the sagebrush biome in the western contiguous United States as used in the SCD (Doherty et al. 2022)—defined as the sagebrush biome boundary (Jeffries and Finn. 2019), with nonrangeland land cover (e.g., forests, lakes, urban areas, and cropland) and alpine areas removed. Three subregions within the biome were identified that reflect important regional differences, based on the grouping of ecoregions (Dinerstein et al. 2017): the Great Basin, Intermountain West, and Great Plains. We expanded the biome by 20 km to include areas adjacent to the biome to minimize any potential edge effects on our structural connectivity results.

### Structural connectivity modeling

We built the structural connectivity model on 90-m ecological integrity datasets produced by the SEI model (as described in Doherty et al. 2022). Briefly, SEI was modeled so that high integrity was defined as areas with abundant sagebrush, native understories, and minimal threats (invasive annual grasses, expanding conifers, and human modification). Two of the five variables (percent sagebrush cover and percent perennial grasses and forbs cover) contribute to integrity, whereas three variables (percent annual grasses and forbs cover, percent tree [conifer] cover, and an index of human modification) represent “threats” that detract from integrity. Because there can be considerable year-to-year variability in the sagebrush ecosystem (Buchholtz et al. 2023a), we calculated 4-year averages for each variable. For example, the percent cover of perennial grasses and forbs for 2021 was calculated as the pixel-wise average value for the years 2018 through 2021.

We recalculated the SEI model using revised and updated annual datasets of sagebrush from the USGS Rangeland Condition, Monitoring, Assessment, and Projection dataset (RCMAP; Rigge et al. 2021); perennial grasses and forbs, and annual grasses and forbs from the Rangeland Analysis Platform (RAP v3) from 2001 through 2021 (Allred et al. 2021); and the degree of human modification (Theobald et al. 2020; Doherty et al. 2022) generated for 2001, 2006, 2011, 2016, 2019, and 2020. RAP v3.0 represents the most recent available data source for mapping *SEI-C*, and our work anticipates the next-phase application and evolution of the SCD. More specifically, we used the SEI model output (specifically the *SEI*<sub>560</sub> data layer) that estimates ecological integrity prior to smoothing with a 2-km radius used to generate the CSAs, GOAs, and ORAs (Doherty et al. 2022).

We calculated SEI-C assuming that higher structural connectivity exists in areas with high ecological integrity that are also well-connected at a landscape level. Thus, the  $SEI_{560}$  data were transformed to resistance values ( $R$ ), following a standard approach (Theobald et al. 2012; Dickson et al. 2017):

$$R = (1 - SEI_{560} + 1)^a \quad (1)$$

where  $a=2$  reflects moderate resistance to locations with low ecological integrity yielding values between 1 (low resistance) and 4 (high resistance).

We applied a resistant-kernel (RK) modeling approach, commonly used to model both species-specific (Compton et al. 2007) and species-agnostic connectivity (i.e., landscape or coarse/meso-filter: Hunter 2005; Krosby et al. 2015; Marrec et al. 2020). Resistant kernels calculate cost distance from source pixels distributed across the landscape with the accumulation of kernels representing densities of potential movement. In this framework, which results in a synoptic connectivity surface across a study area, no destination locations are required. Recently, Kumar and Cushman (2023) and Lumia et al. (2024) found that RK was more accurate and appropriate for modeling connectivity for systems without discrete source-destination locations than Circuitscape (McRae and Beier 2007), and so are better suited to mapping landscape permeability (Theobald et al. 2012) to identify well-connected areas (Anderson et al. 2023). In this way, the RK approach differs from the Omniscape approach (applying Circuitscape from a gradient perspective; Schloss et al. 2021) that is typically used to highlight potential corridors and “pinch points” that may restrict connectivity (Schloss et al. 2022; Belote et al. 2022). RK has been found to be a relatively simple and readily-interpretable modeling approach that eases communication and application of results in conservation practice (e.g., Cushman et al. 2013; Krosby et al. 2015).

We calculated kernels with maximum “dispersal” distances based on minimum cost distances calculated using resistance values. The kernels were defined so that the Gaussian distribution of  $SD=3$  equaled the dispersal distance (30 km used) typical of estimates of long-distance dispersal by Greater sage grouse (Cross et al. 2017)—a primary species of conservation interest in the sagebrush biome. Following standard practice, each RK was normalized to a sum to 1.0 (Landguth et al. 2012).

We calculated a RK for each point from a uniform-random grid of “source” points spaced at 910 m (every third cell at 270-m resolution, which is roughly half the habitat distance of 560-m radius used by Doherty et al. 2022). We summed the RK results from all source points to obtain a surface of cumulative RKs which we used as the final connectivity data layer for each year (i.e., SEI-C). Following methods from Landguth et al. (2012) and Plunket (2022), the RK model was implemented in the LandSCaPeN library (<https://groups.google.com/g/gee-landscapen>) using Google Earth Engine (Gorelick et al. 2017).

### Analyses

We conducted four primary analyses on the SEI-C results and comparisons with CSAs and GOAs. First, we identified locations within the biome where landscape connectivity was stable or varying over time. We did this by calculating, for each pixel  $i$ , the arithmetic mean  $X_i$  [Eq. 2] and standard deviation  $\sigma_i$ , through time for each year  $y$  [Eq. 3]:

$$X_i = \sum_{y=2001}^{2021} (C_{i,y})/21 \quad (2)$$

$$\sigma_i = \sqrt{\frac{\sum_{y=2001}^{2021} (X_i - X_i)^2}{21}} \quad (3)$$

We quantified the inter-annual variability as the pixel-wise standard deviation through time. To calculate a Z-score for each pixel [Eq. 4], we normalized the SEI-C value at each pixel  $X_i$  by the average SEI-C value across the biome [Eq. 5], using:

$$Z_i = \frac{X_i - \mu}{\sigma_i} \quad (4)$$

$$\mu = \sum_{i=1}^n (X_i)/n \quad (5)$$

Second, to understand temporal trends for the biome as a whole (and 3 subregions separately), we calculated the mean SEI-C value ( $X$ ) using the SEI-C value ( $C$ ) for all pixels ( $n$ ) across the biome  $b$  for each year  $y$ . Separately, we also calculated the mean  $SEI_{560}$  for all pixels ( $n$ ) across the biome  $b$  for each year  $y$ .

We calculated the simple rate of change between the first and last year of our dataset as:

$$X_{b,2001-2021}^* = (X_{b,2021} - X_{b,2001})/X_{b,2001} \quad (6)$$

Additionally, we fit a linear trend line (simple linear regression) through all years of  $X_b$ . We also calculated trends in SEI-C, restricted to the pixels within CSAs, and separately, restricted to the pixels within GOAs.

Third, we identified high connectivity locations on the SEI-C maps that serve as landscape cores within the broader sagebrush biome (similar to the idea of network “nodes”), by classifying the SEI-C pixel values ( $C_i$ ) using 10 class breaks obtained from a heads-tails classification (HT; Jiang 2013) for 2021 ( $C_{i,2021}$ ). HT is particularly appropriate for data with heavy-tailed distributions and characterizes the underlying hierarchical structure in spatial patterns (Jian and Yin 2014). We applied the heads-tails class breaks obtained from the structural connectivity layer for 2021 to all previous years (i.e., the breaks were held consistent so landscape cores were relative to those in 2021).

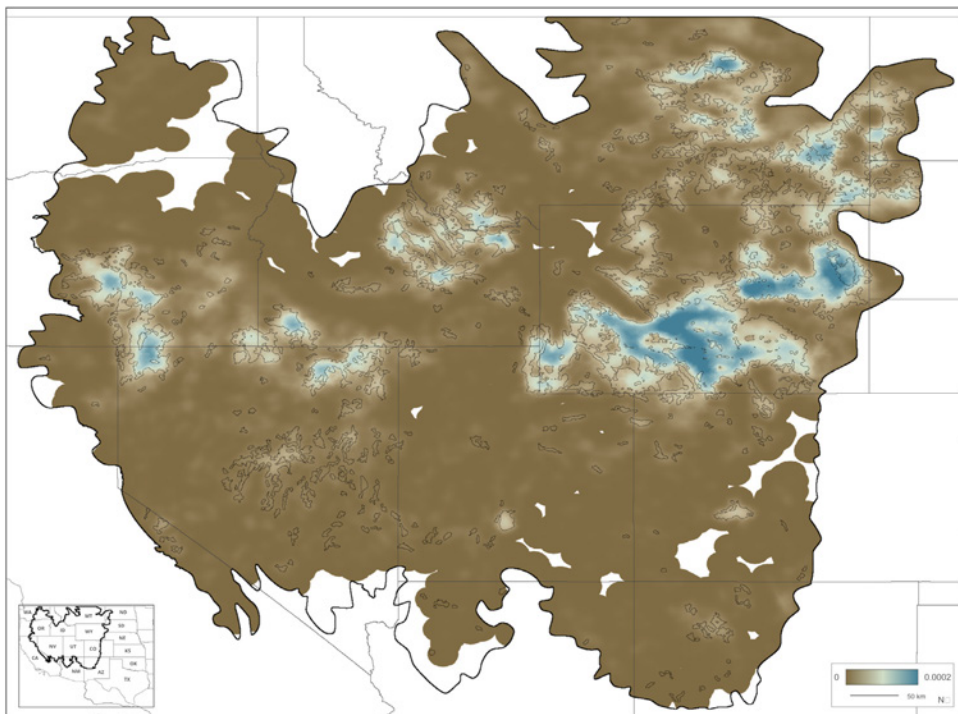
Fourth, we identified CSAs and GOAs that also were high landscape-level SEI-C (i.e., “well-connected cores”) by finding the spatial intersection of the CSA and GOA polygons, then attributing each polygon with the highest (most connected) level of the landscape core classes.

### Results

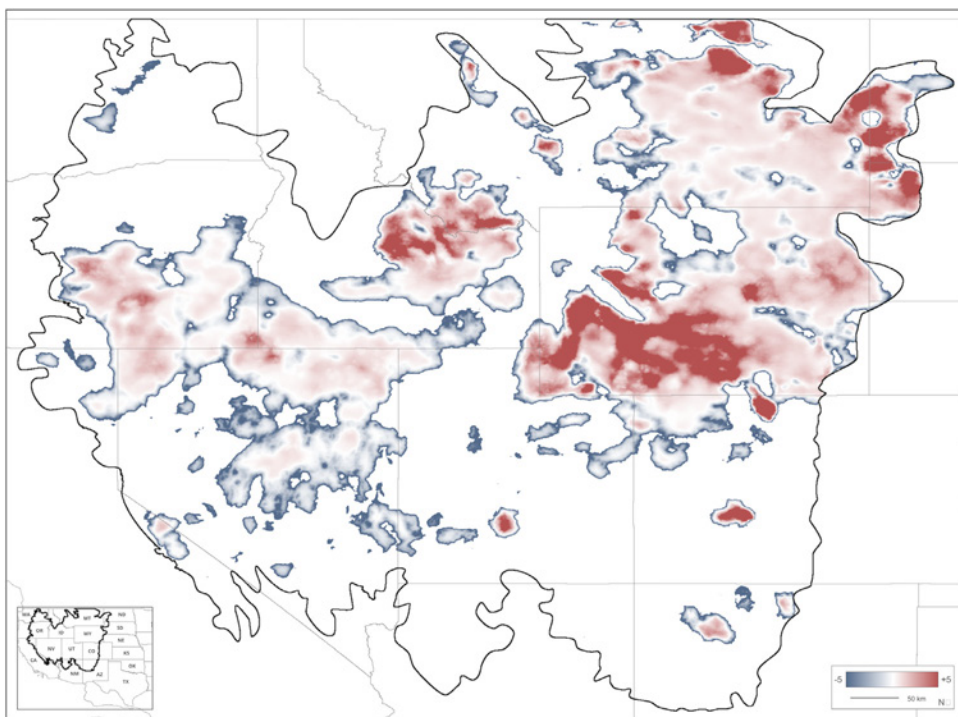
Areas with high structural landscape connectivity (i.e., high SEI-C values), which we call landscape cores, were especially prominent in southwestern and northeastern Wyoming, south-central Oregon, and the plains of Montana (Fig. 1). The CSAs, and to a lesser extent GOAs, were generally spatially coincident with these landscape cores. Landscape connectivity was higher for the CSAs (mean = 1.08e-04; SD = 5.41e-05) and, to a lesser extent, GOAs (mean = 4.30e-05; SD = 4.15e-05), as compared to the full biome (mean = 5.84e-05; SD = 4.08e-05). The interannual variability of landscape connectivity, as summarized for pixels within CSAs or GOAs, was slightly higher (measured as the standard deviation of the pixel-wise mean values) for the CSAs (SD = 5.59e-06) compared to the variability for the full biome (SD = 5.24e-06) and the GOAs (SD = 4.31e-06). Many of the CSAs were located where landscape connectivity was both high and stable (i.e., high positive Z values, see Eq. 5, shown in Fig. 2).

The average landscape connectivity of the sagebrush biome, as measured by the biome-wide mean value of SEI-C, declined by 20.2% from 2001 to 2021 (1.3% annually). Landscape connectivity for the CSAs declined by 13.2% (1.0% annually), while for the GOAs SEI-C declined by 21.2% (1.3% annually). By ecoregion, the declines in connectivity for the CSAs were greatest in the Great Plains region (19.9%, with a maximum rate of change in a given year of

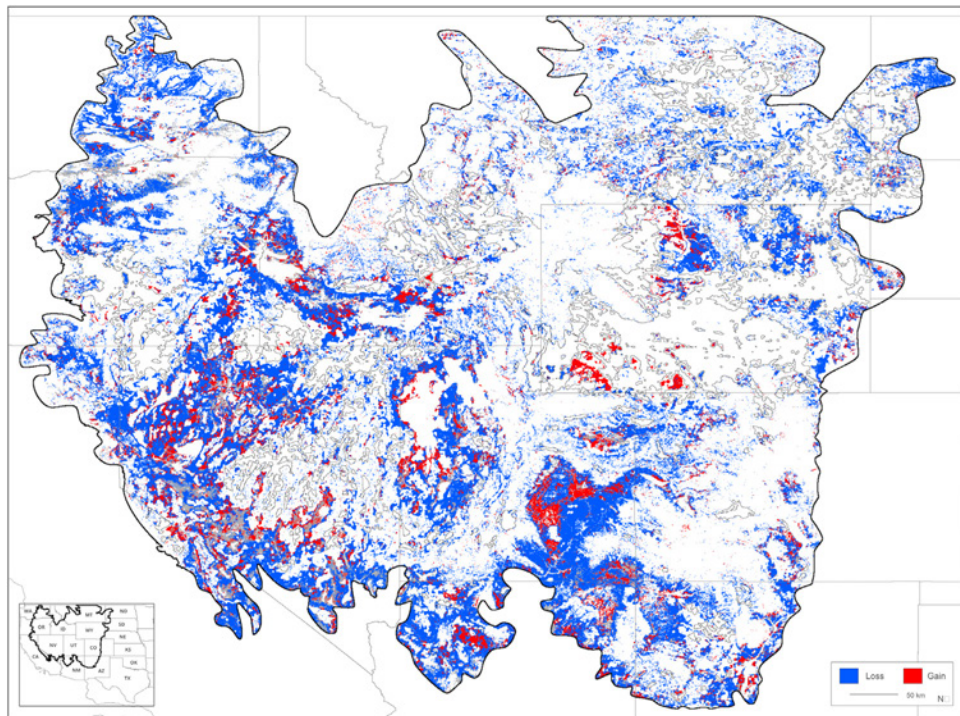




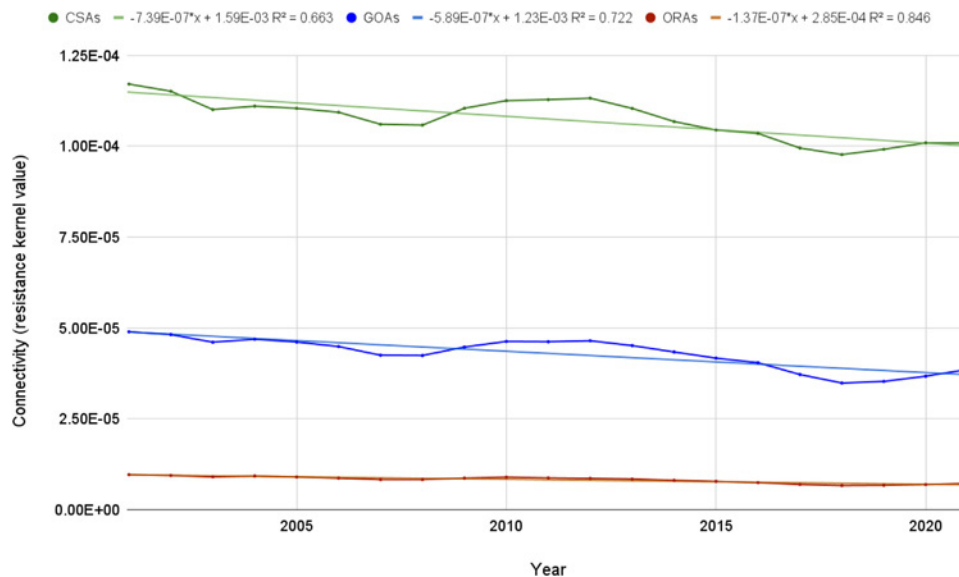
**Figure 1.** A map of sagebrush biome-wide structural connectivity modeled by resistant-kernel modeling at a 30 km radius for 2021 (low = brown, high = blue) with core sagebrush areas (CSAs;  $>50 \text{ km}^2$ ) outlined.



**Figure 2.** Landscape-level cores, indicated by red, are found in locations that have relatively high landscape connectivity (i.e., SEI-C values) and that are stable over time as calculated by Z-scores (from 2001–2021); red areas indicate areas that have higher than average SEI values and that have relatively stable landscape connectivity values over time, blue areas indicate lower connectivity and/or not stable over time, and areas beyond the blue edges are also low SEI-C and relatively unstable (but not shown for clarity). Values are calculated using Eq. 5. Black outlines indicate core sagebrush areas (CSAs;  $>50 \text{ km}^2$ ).



**Figure 3.** The gain and loss of ecological integrity (used to calculate landscape structure), are shown by the difference of  $SEI_{560}$  values from 2001 to 2021 (blue is loss, red is gain). The biome-wide mean declined from 0.375 in 2001 to 0.263 in 2021, a decline of 30.0%.

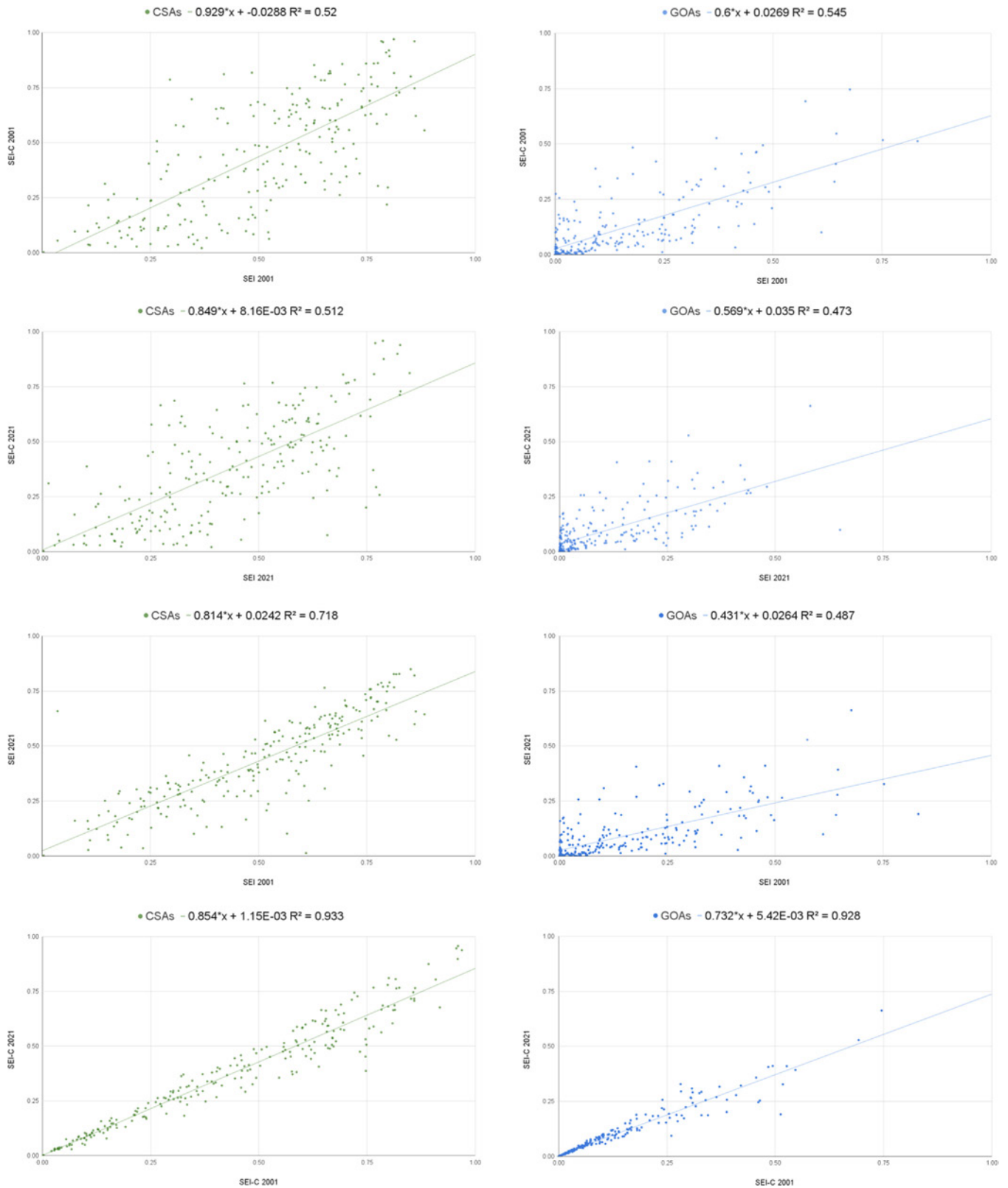


**Figure 4.** Declines in structural landscape connectivity modeled by a resistant kernel approach at a 30-km radius for the sagebrush biome. Core sagebrush areas (CSAs) had higher connectivity and the rate of decline was greater (larger slope of the trendline) compared to growth opportunity areas (GOAs) and other rangeland areas (ORAs).

24.7%), followed by the Great Basin (18.2%, max 31.9%), with a lower decline in the Intermountain region (9.7%, max 13.8%), with an annual average decline of 1.7%, 1.1%, and 0.9%, respectively. The  $SEI_{560}$  values used to calculate connectivity declined by 30% from 2001 to 2021 (Fig. 3).

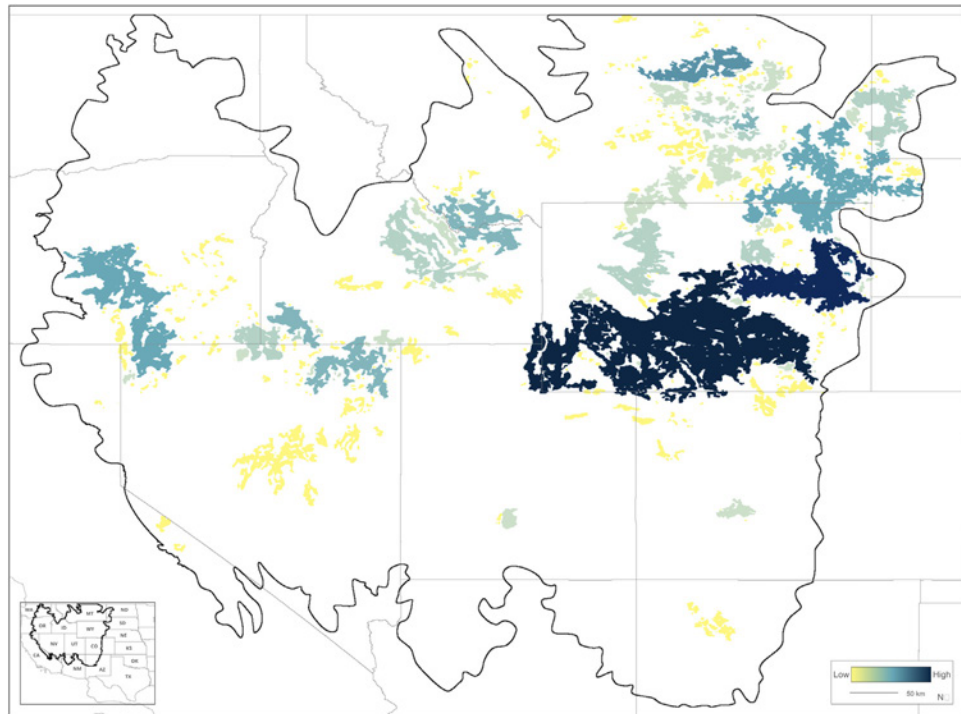
The decline in connectivity from 2001 to 2021 is also apparent in the linear trendlines fit through the biome-wide averages of connectivity for each year (Fig. 4). CSAs had higher connectivity values than GOAs and ORAs, and the rate of decline for CSAs (slope =  $-7.39e-07$ ) was slightly greater than that of the GOAs (slope =  $-5.89e-07$ ) and ORAs (slope =  $-1.37e-07$ ).

Scatterplots (Fig. 5) show important differences between the SEI and SEI-C variables. Overall, SEI-C values were slightly lower than SEI values (i.e., the linear trends show slopes  $<1.0$ ), which is more pronounced in locations within CSAs (0.85–0.93) than within GOAs (0.57–0.6), and have fairly weak relationships ( $R^2 = 0.47$ – $0.54$ ), and these relationships have slightly weakened from 2001 to 2021. Within CSAs, the decline in SEI values was slower for better-connected CSAs (Fig. 6), defined as class 5 and above (linear regression  $-2.71e-03$ ,  $R^2 = 0.474$  vs.  $-4.56e-3$ ,  $R^2 = 0.683$ ). The area of overlap of CSAs, GOAs, and ORAs with landscape cores increased from relatively low levels of connectivity (high SEI-C values, class



**Figure 5.** Scattergrams of the relationship between sagebrush ecological integrity (SEI) and the derived landscape structure (SEI-C), show generally weaker relationships in 2021 compared to 2001.





**Figure 6.** Core sagebrush areas (CSAs) in 2021 that are well-connected at a landscape level (i.e., landscape cores) are shown in dark blue and those less-well connected are shown in yellow.

**Table 1**

The intersection of CSAs, GOAs, and ORAs from the SCD for 2020 with the levels of landscape cores for 2001 and 2021.

| Landscape core level | Area (km <sup>2</sup> ) in 2001 |         |        |         | Area (km <sup>2</sup> ) in 2021 |         |        |         |
|----------------------|---------------------------------|---------|--------|---------|---------------------------------|---------|--------|---------|
|                      | CSAs                            | GOAs    | ORAs   | All     | CSAs                            | GOAs    | ORAs   | All     |
| 10                   | 3 128                           | 523     |        | 3 651   | 289                             |         |        | 289     |
| 9                    | 1 055                           | 324     |        | 1 378   | 382                             | 2       |        | 384     |
| 8                    | 1 638                           | 398     |        | 2 036   | 821                             | 10      |        | 831     |
| 7                    | 2 745                           | 426     | 1      | 3 172   | 1 753                           | 43      |        | 1 796   |
| 6                    | 6 083                           | 1 500   | 9      | 7 592   | 3 424                           | 221     |        | 3 645   |
| 5                    | 11 423                          | 3 265   | 72     | 14 759  | 7 223                           | 864     | 2      | 8 089   |
| 4                    | 18 757                          | 10 207  | 363    | 29 326  | 14 719                          | 3 433   | 22     | 18 174  |
| 3                    | 27 390                          | 24 994  | 1 140  | 53 525  | 27 189                          | 13 244  | 389    | 40 822  |
| 2                    | 32 944                          | 52 495  | 7 736  | 93 176  | 41 962                          | 47 363  | 2 673  | 91 998  |
| 1                    | 24 159                          | 115 579 | 55 271 | 195 009 | 30 482                          | 127 227 | 41 392 | 199 100 |
| Total                | 129 323                         | 209 711 | 64 591 | 403 625 | 128 244                         | 192 407 | 44 477 | 365 128 |

Higher-level landscape cores (e.g.,  $\geq 5$ ) have greater landscape connectivity and so could be considered to contribute the most to the landscape connectivity of the sagebrush ecosystem (also see Fig. 6).

1) to the highest level of connectivity (high SEI-C values, class 10; Table 1). Well-connected landscape cores occupy a relatively small portion of the landscape but play a critical role in connecting the ecosystem. CSAs occupy a higher proportion of the higher level (connected) landscape cores (e.g., in 2021, 97.6% at class 7, down to 50% in class 3). The spatial configuration of the landscape cores, and the CSAs/GOAs that overlap them, are shown in Fig. 6. There was a decline in overall landscape core area from 403 625 to 365 128 km<sup>2</sup> from 2001 to 2021, reflecting a decline in landscape connectivity due to lower ecological integrity of the sagebrush biome more recently (2021). Within CSAs, the decline in SEI values was slower for well-connected CSAs (defined as classes 5–10 vs. classes 1–4, where the slope in linear regression is:  $-2.71\text{e-}03$ ,  $R^2 = 0.474$  vs.  $-4.56\text{e-}3$ ,  $R^2 = 0.683$ ).

Although there are important ecoregional differences between the Great Basin, Intermountain, and Great Plains subregions, generally they follow general patterns and declines in SEI and connectivity over the recent past, similar to the biome-wide patterns and trends.

## Discussion

As expected and consistent with the SCD findings, the general patterns of CSAs and GOAs were coincident with high SEI-C values (i.e., landscape cores) and were generally found in the same locations of the CSAs (Fig. 1). This in general provides a confirmation that the CSAs, on average, are placed within structurally-connected locations that have high ecological integrity. Not surprisingly, several very large areas of CSAs dominate the sagebrush biome, such as southwestern Wyoming and east-central Oregon, and these areas are among the best connected within the sagebrush biome.

The interannual variability was greater than expected for both high-integrity areas (SEI) and landscape connectivity (SEI-C, though muted slightly), particularly compared to previous interpretations of sagebrush ecosystem dynamics from 5-year snap-shots. Interestingly, the interannual variability of landscape connectivity was slightly greater for the CSAs, which may be due in part because the CSAs overall had higher integrity and connectivity ( $X_{CSA} = 1.08\text{e-}04$  vs.  $X_{GOA} = 4.3\text{e-}05$ ), and therefore had “more to lose.” A key find-

ing is that many CSAs are located in areas with high connectivity and integrity and minimal interannual variability. These areas can potentially be identified as particularly important today, and likely relatively robust into the near future. Some CSAs have high connectivity and SEI but also have relatively high interannual variability, which might suggest lower conservation priority. Additional analyses are needed to tease out whether the interannual variability itself is increasing or decreasing over time, and to focus on particular areas of interest because of the spatial variability of these trends.

We found strong evidence that, in general, the sagebrush biome declined in Sagebrush Ecological Integrity (SEI) and in structural connectivity (SEI-C), although there are short-term (2–5 years) ups and downs that complicate the dynamics. The biome-wide average SEI declined by 30% from 2001 to 2021 (Fig. 3), though, importantly, SEI-C biome-wide declined by one-third less (by 20%). CSAs located in high connectivity areas (landscape classes 5–10) had 25% higher SEI values on average than low connectivity areas (classes 1–4), and the trend in declining SEI values was slower.

Our findings also augment the SCD products and delineation of CSAs and GOAs in particular, by additionally providing SEI-C values summarized within specific CSAs. We attributed the CSAs and GOAs with the level of their structural connectivity to help provide important contextual information—specifically to help identify specific CSAs that are also landscape cores. Furthermore, more detailed and specific analyses that compare the SEI vs. SEI-C values apart from CSA and GOA polygons can be accomplished using the datasets produced. Generally, pixels with both high connectivity and integrity (i.e., both high ranked SEI-C values and SEI values) are both currently and likely in the future to be important for their ecological values and might be high conservation priority. Locations that are highly connected but with moderate integrity (SEI-C > SEI values) indicate that they provide particular value for movement between high-integrity locations, and thus may be a higher priority for conservation as GOAs. Locations that are not highly connected but have high integrity (SEI-C < SEI) identify localized high-integrity areas but may be less resilient because of their lack of landscape structural connectivity (particularly those smaller islands that are at the fringe of the sagebrush biome). A comparison of the differences in the SEI-C and SEI values between CSAs and GOAs might also be valuable to guide potential trade-offs between conserving CSAs with low SEI-C but high SEI values versus GOAs that have high SEI-C but low SEI.

We believe that well-connected cores provide particular ecological value and so could serve as locations that may provide particular value to “anchor” conservation efforts within the broader ecosystem. Map products developed in this work (e.g., Fig. 6 shows an example of CSAs colored by connectivity level) provide granular data that can be readily, and powerfully combined with other data products from the broader SCD process (other papers in this issue).

Additional future analyses would be of particular value to help inform conservation strategies, include:

1. Identify areas with high Z-values (Fig. 2) and prioritize GOAs that 1) are adjacent to and serve to connect landscape cores; 2) have high integrity (SEI); 3) have low inter-annual variability, and have undergone minimal declines recently; or 4) that would be good candidates for restoration. Because these locations have high SEI-C, they are likely to be more able to adapt to potential/likely climate change.
2. Calculate trends in  $SEI_{560}$  and SEI-C for specific areas of interest (e.g., management area or project site). We caution that such analyses should be avoided at project-level extents below  $\sim 100 \text{ km}^2$ .

3. Consider ways to incorporate the spatial variability within CSAs, or further refine their boundaries, particularly for very large ones (e.g., southwestern Wyoming).
4. Examine how well-connected CSAs may be affected by projected climate change effects (Holdrege et al. 2024).

#### *Comparison to other processes and species-specific results*

We found that the spatial patterns and temporal trends were generally consistent with previous findings from the SCD and other related work. For example, SEI was found to strongly predict sage grouse (Prochazka et al. 2024) and sagebrush-obligate songbird (Kumar et al. 2024) population dynamics. We also note that our findings that CSAs have higher and more stable connectivity are in agreement with findings from Buchholtz et al. (2023a)—though there are important differences that make it difficult to conduct a strict comparison. Most notably, we focus on the sagebrush ecosystem (that includes the components and spatial configuration of sagebrush, perennial grass, annual grasses, and land use threats) whereas Buchholtz’s work focuses on the percent cover of sagebrush. Additionally, there were spatial and temporal scale differences between the two approaches; we used a resistant-kernel connectivity approach with a 30-km threshold annually while Buchholtz et al. (2023a) used an Omniscape approach with a 75-km radius every 5 years.

#### *Implications*

The general locations, patterns, and trends identified in the SCD are strongly consistent with our findings based on modeling structural connectivity over time. Our findings underscore the urgency and the scale of recent declines, especially that from 2001–2021 sagebrush ecological integrity declined by  $\sim 30\%$ . We have, however, identified specific parts of the landscape, particularly well-connected and of high ecological integrity (CSAs) to focus conservation that have declined only 13%. Additional analyses of specific CSAs and portions of CSAs can be completed to further refine and bolster confidence in sagebrush ecosystem “anchors,” by identifying places with high levels of structural connectivity, lower inter-annual variability, and lower rates of recent and forecasted declines. These will also bring added value to other insights from work on invasive species, conifer encroachment, fire regimes, and other products discussed in this issue.

Finally, we suggest that the SEI-C metric provides additional, complementary information that is consistent with other recent research (Smith et al. 2023) that we are losing sagebrush biome habitat at a rapid pace, adding urgency for the need to prioritize efforts for protecting anchor areas and focusing on restoration, particularly of GOAs, that are important to maintain/improve landscape-level resiliency.

#### **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**

**David M. Theobald:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Alexander V. Kumar:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Kevin Doherty:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Katherine A. Zeller:** Conceptualization, Methodology, Writing – original draft, Writing – review



& editing. **Todd B. Cross:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

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## Corrigendum

# Corrigendum to “Well-Connected Core Areas Retain Ecological Integrity of Sagebrush Ecosystems Amidst Overall Declines From 2001–2021” [Rangeland Ecology & Management Volume 97, November 2024, Pages 41–50]



David M. Theobald<sup>1,2,\*</sup>, Alexander V. Kumar<sup>3</sup>, Kevin Doherty<sup>4</sup>, Katherine A. Zeller<sup>5</sup>, Todd B. Cross<sup>6,7</sup>

<sup>1</sup> Conservation Planning Technologies, Colorado State University, 1113 W. Olive St, Fort Collins, CO 80521, USA

<sup>2</sup> Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80526, USA

<sup>3</sup> US Fish and Wildlife Service, Fort Collins, CO 80526, USA

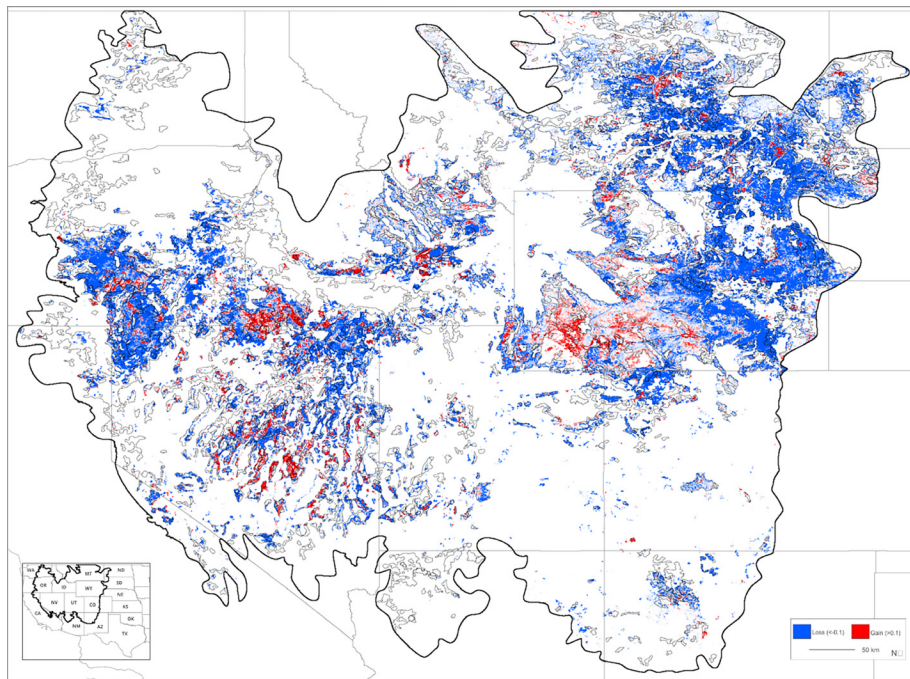
<sup>4</sup> US Fish and Wildlife Service, Lakewood, CO 80439, USA

<sup>5</sup> USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, Missoula, MT 59801, USA

<sup>6</sup> Crosswinds Ecological Consulting, LLC, Hartland, VT 05048, USA

<sup>7</sup> Fedy Wildlife and Molecular Ecology Lab, School of Environment, Resources and Sustainability, University of Waterloo, Waterloo, ON N2L 3G1, Canada

The authors regret that there was an error in [Figure 3](#). Please see the updated [Figure 3](#) image and its legend below.



**Figure 3.** The gain and loss of ecological integrity used to calculate landscape structure for all classes (core sagebrush areas, growth opportunity areas, and other rangelands), as shown by the difference of SEI560 values from 2001 to 2021.

The authors apologize for any inconvenience caused.

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\* Corresponding author.

E-mail address: [dmt@davidmtheobald.com](mailto:dmt@davidmtheobald.com) (D.M. Theobald).

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