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ORIGINAL RESEARCH

Leveraging local habitat suitability models to enhance restoration benefits for species of conservation concern

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Abstract

Efforts to restore habitats and conserve wildlife species face many challenges that are exacerbated by limited funding and resources. Habitat restoration actions are often conducted across a range of habitat conditions, with limited information available to predict potential outcomes among local sites and identify those that may lead to the greatest returns on investment. Using the Gunnison sage-grouse (*Centrocercus minimus*) as a case study, we leveraged existing resource selection function models to identify areas of high restoration potential across landscapes with variable habitat conditions and habitat-use responses. We also tested how this information could be used to improve restoration planning. We simulated change in model covariates across crucial habitats for a suite of restoration actions to generate heatmaps of relative habitat suitability improvement potential, then assessed the degree to which use of these heatmaps to guide placement of restoration actions could improve suitability outcomes. We also simulated new or worsening plant invasions and projected the resulting loss or degradation of habitats across space. We found substantial spatial variation in projected changes to habitat suitability and new habitat created, both across and among crucial habitats. Use of our heatmaps to target placement of restoration actions improved habitat suitability nearly fourfold and increased new habitat created more than 15-fold, compared to placements unguided by heatmaps. Our decision-support products identified areas of high restoration potential across landscapes with variable habitat conditions and habitat-use responses. We demonstrate their utility for strategic targeting of habitat restoration actions, facilitating optimal allocation of limited management resources to benefit species of conservation concern.

Keywords *Centrocercus minimus* · Gunnison sage-grouse · Habitat management · Habitat suitability · Sagebrush · Resource selection function

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Introduction

Habitat loss and degradation are leading drivers of global species declines and are forecasted to intensify given future human land-use and climate change projections (Visconti et al. 2016; Johnson et al. 2017; Powers and Jetz 2019). Effective species conservation increasingly relies on habitat restoration to reverse these declines and prevent extinctions (Shackelford et al. 2013; Jones et al. 2018). Efforts to restore degraded habitats can increase species' use, improve demography, and contribute to viable and persistent populations (Borgmann and Conway 2015), but these efforts face a multitude of logistical, academic, and economic challenges (Scott et al. 2010; Collier and Johnson 2015). Some examples of such challenges include the inadequacy of decision-making resources (Ortega-Argueta et al. 2017) at suitable spatial and temporal resolutions, barriers to practical use of available conservation products or tools (Guisan et al. 2013), and uncertainty imposed by a changing world (Van Horne and Wiens 2015). These problems are exacerbated by limited funding and resources (Jacobsen et al. 2007; Dayer et al. 2016; Hare et al. 2019) and an often-urgent need for interventions to prevent extinction of vulnerable species (Legge et al. 2021; Mason et al. 2021). Both of these further complicate the dilemma of determining where valuable restoration resources should be optimally deployed to stem or reverse species losses.

Habitat restoration actions (i.e., treatments) are often focused in areas that are accessible to, and either currently or formerly used by wildlife (Scott et al. 2001). However, the selection and use of habitats by animals within these areas (including restoration sites) can vary substantially. Habitat-use relationships are complex, and species respond to multiple habitat features (Manly et al. 2002). This means that different restoration sites formerly used by a species may not provide equivalent returns on investment, even for the same habitat restoration actions. Restoration planning efforts that do not consider the potential for spatial variation in realized benefits to species (e.g., improvements in habitat suitability) risk the inefficient use of valuable management funding and resources. By contrast, strategic planning that targets actions in areas that are expected to provide the greatest benefits for species may help maximize efficiency (Arkle et al. 2014). However, this requires an understanding of how species use resources across landscapes (Boyce 2006; McGarigal et al. 2016; Marini et al. 2019; Northrup et al. 2021) and consideration of local variation in habitats and habitat-use relationships among populations (Shirk et al. 2014; Saher et al. 2022).

Resource selection functions (RSFs) are widely used to quantify habitat suitability across space for wildlife species and provide valuable information that can direct habitat management for species of conservation concern (Avgar et al. 2017; Shoemaker et al. 2018; Northrup et al. 2021). Resource selection functions characterize the relative probability of selection across space, based on locations of known use (compared to those available) and the underlying resource conditions on the landscape (Boyce and McDonald 1999; Manly et al. 2002; Johnson et al. 2006). They can additionally be mapped to increase usability of the results (Morris et al. 2016). Recent applications of RSFs have enhanced our understanding of species-habitat relationships and helped guide strategic management of wildlife populations and their habitats. Models that are developed for specific geographic locations (e.g., populations or sub-populations), rather than an entire species range, can consider unique habitat-use relationships at those sites. Such RSFs may be of great value for strategic restoration planning because they allow differentiation between seemingly similar sites and bring clarity to expected returns on habitat management investments, an important consideration when populations differ in selection response to variable habitat characteristics (e.g., Shirk et al. 2014; Saher et al. 2022). While the resulting suitability layers can be used to identify candidate sites for habitat restoration action, they stop short of indicating where limited restoration resources might be best allocated across the landscape. This information may be critical in cases where immediate, targeted actions are required to stem population declines.

The Gunnison sage-grouse (*Centrocercus minimus*, hereafter GUSG) is currently listed as threatened under the United States Endangered Species Act (1973; USFWS 2014). The species has experienced substantial and continuing declines in range-wide abundance and distribution (Schroeder et al. 2004), primarily due to loss and degradation of habitat (U.S. Fish and Wildlife Service [USFWS] 2019, 2020a) and is now restricted to eight populations in southwestern Colorado and eastern Utah that span six ecoregions with varying habitat characteristics (USFWS 2019). The Gunnison, and the closely related greater sage-grouse (*Centrocercus urophasianus*), are sagebrush obligate species that depend upon large areas of contiguous sagebrush habitats year-round (Connelly et al. 2011; Wisdom et al. 2011; Young et al. 2020), as well as sufficient native herbaceous cover and mesic habitats important for nesting and brood-rearing (Connelly et al. 2000a, 2011; Donnelly et al. 2016, 2018). They face a multitude of known and persistent threats, including invasive plants that alter fire regimes, conifer expansion into sagebrush habitats, human development and infrastructure, improper grazing practices, and alteration of habitats by climate change (Remington et al. 2021; USFWS 2014).

Resource selection functions have been a focus of recent efforts to help support sage-grouse conservation by advancing scientific knowledge of habitat suitability and important environmental variables associated with habitat use (Aldridge et al. 2012; Coates et al. 2016; Walker et al. 2016; Heinrichs et al. 2017; Doherty et al. 2018; Brussee et al. 2022) and have been used to directly inform management of the greater sage-grouse (e.g., Doherty et al. 2016; LeBeau et al. 2017; Ricca et al. 2018; Smith et al. 2019). However, similar applications have not yet been developed to improve habitats for the GUSG. Two recent publications, Saher et al. (2022) and Apa et al. (2021), produced RSF maps identifying important habitat requirements for GUSG, and quantifying seasonal suitability across crucial habitats. While these mapping efforts provided critical insights into population-specific habitat characteristics of importance and spatial variation in habitat suitability, they did not indicate where restoration actions could be prioritized across the landscape. We sought to fill this knowledge gap for GUSG, thereby facilitating more optimal placements of habitat restoration actions to maximize returns on management investment given limited funding and resources.

We used existing RSFs for GUSG to assess spatial variability in habitat responses to specific restoration actions and assess where those actions might be best applied on the landscape to increase effectiveness of local management plans for recovery of the species. Specifically, 1) we generated heatmaps of improvement potential for commonly used, local-scale land management actions across crucial habitats within the remaining Colorado satellite populations and 2) assessed their potential for improving management outcomes by simulating decisions on placement of habitat restoration actions, made with and without the heatmaps, and comparing the resulting improvements in habitat suitability. We demonstrate the utility of this approach to aid strategic habitat restoration planning and discuss broader applications of this approach to other species and ecological systems.

Methods

Study area

Our study focused on the six GUSG satellite populations in southwest Colorado: Crawford, Cerro Summit-Cimarron-Sims Mesa (CCS), Piñon Mesa, Poncha Pass, San Miguel, and Dove Creek (Fig. 1). As of 2019, each of these populations were declining or already below conservation targets (GUSG Rangewide Steering Committee [GSGRSC] 2005) with an estimate of < 5000 birds remaining range wide (with 2019's 3-year estimates for the Gunnison Basin population at 3787 birds, and 554 birds across the satellites; USFWS 2019, 2020a). The 2020 USFWS Final Recovery Plan (FRP; USFWS 2020a) and Recovery and Implementation Strategy (RIS; USFWS 2020b) outline steps needed to improve species viability in the long-term, based on concepts of resiliency, redundancy, and representation (i.e., the 3Rs; USFWS 2016, Smith et al. 2018). While the Gunnison Basin population largely satisfies the resiliency requirement due to its relative size and stability (USFWS 2019), considerable concern surrounds the persistence of the satellite populations (Saher et al. 2022), which are critical to maintaining redundancy and representation, and may provide significant adaptive capacity to future environmental change (USFWS 2019). In addition to highlighting the importance of conserving remaining habitats within these

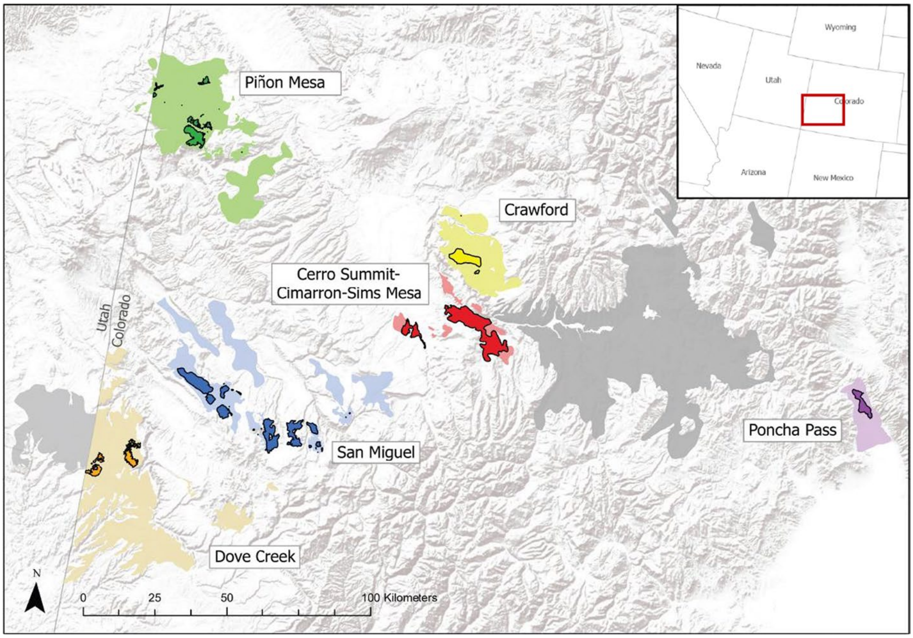

Fig. 1 Distribution of the six Gunnison sage-grouse (*Centrocercus minimus*) satellite populations in south-western Colorado, USA. Dark-shaded, color polygons represent crucial breeding patch habitat extents (Saher et al. 2022; the focus of this study), and lighter shades represent the U.S. Fish and Wildlife Service's currently recognized range for each population (USFWS 2020b), for spatial context. The Gunnison Basin core population (Colorado) and Monticello satellite population (Utah; gray polygons) were not part of this study but included here for reference. Map image is the intellectual property of Esri and is used herein under license. Copyright © 2022 Esri and its licensors. All rights reserved

populations, the FRP and RIS also invoke restoration of habitats as critical to improving habitat quantity and quality across the species' range, underscoring the importance of such actions. We did not include the Gunnison Basin core population or the Monticello satellite population in Utah in our analysis because reference RSF models (see below) were not available for these populations. See the Supplemental for additional details on the study area.

Leveraging existing resource selection function models

As the spatial scale of habitat selection responses can be influential, we chose a previously developed suite of RSF models (Saher et al. 2022; hereafter "reference models") that characterize GUSG habitat selection responses at multiple scales based on contemporary vegetation spatial products (Rigge et al. 2020). We used these empirically driven, season-specific models and inputs to assess the habitat improvement potential (or degradation) for specific habitat actions aimed at improving habitat conditions for the six remaining GUSG satellite populations in Colorado. All modifications of spatial data layers and model runs were conducted using ArcGIS® Pro [v.2.8.0, 2021 Esri Inc.]. We restricted our analysis to crucial habitats (Fig. 1) defined by the corresponding "patch-scale" models of Saher et al. (2022; representing 95% of currently utilized habitats) because this best represented the spatial scale at which most land-management actions are applied (e.g., pinyon-juniper removal, invasive weed control, sagebrush seeding/planting, restoration of mesic habitats, etc.).

The reference models generated by Saher et al. (2022) used the exponential form of an RSF (Manly et al. 2002), but their sum of linear responses could not be exponentiated when generating mapped predictions because some locations had incalculably large values, so they simply mapped the linear predictor and scaled between 0–1, to visualize the habitat suitability predictions. The linear formula by itself does not directly reflect a true probability of selection (i.e., compared to a Resource Selection Probability Function [RSPF] estimated using logistic regression) and, thus, is a relative function related to the true probability of selection (Manly et al. 2002). For this reason, we transformed the RSF suitability indices into ranks based on the number of habitat use locations that were observed at or below that RSF value. This was similar to a percentile, but rather than 100 bins the number of bins was determined by the number of use locations (that differed for each satellite population and model). For each RSF map, we extracted the RSF values at habitat use locations used in that model, and calculated the proportion of observations that were less than or equal to the RSF value (Range 0–1). This resulted in each model having its own unique classification, where the RSF values at each use location were assigned 0–1 percentile ranks (see the supplemental for table examples). Each model's RSF surface was then reclassified using this table as a series of thresholds for binned ranks. Following Saher et al. (2022), we defined "habitat" as those pixels with habitat suitability ranks exceeding the value that captured 95% of use locations in the reference models; those falling below were considered "non-habitat". The resulting map suitability values (MapRSF) for habitats ranged >0.00 to 0.95, with smaller values indicating higher ranked habitats (i.e., if there were 100 observations, all mapped RSF values between the 2nd-greatest estimated use location and greatest estimated use location would receive a rank of 0.02). The difference in suitability scores between the reference and modified maps represents the change in value based on binned percentiles for habitat use locations ($<1\%$ increments). Change in habitat suitability could therefore respond non-linearly to change in RSF values, with the steepest increases in suitability occurring where smaller increasing RSF values caused greater increases in the number of use locations captured.

Mapping effects of single management actions on habitat suitability

We categorized each covariate in the reference models as having a positive or negative relationship to habitat suitability and determined whether that relationship was linear or quadratic based on marginal effects predictions from Saher et al. (2022). Covariates generally summarized spatial layers representing habitat conditions over moving window buffer radius or distance decay scales ranging 45 m to 570 m (Saher et al. 2022). For most habitat variables, we only assessed breeding season models because summer reference models were unavailable for all satellite populations; however, when available (i.e., for all satellite populations except Dove Creek), we also assessed summer models. These seasonal comparisons of mesic improvements are valuable to consider because of their critical importance in the summer when broods depend on these habitats for food and cover.

We simulated changes in habitat characteristics that were expected to result from habitat restoration actions (e.g., an increase in sagebrush percent cover resulting from seeding or planting sagebrush) by modifying values in the original 30-m × 30-m geospatial input layers (i.e., pre-moving window) used in the reference models, within a 1-km buffer of each population's spatial extent. We only evaluated management actions that could (1) improve habitat suitability for GUSG in the satellite populations based on these relationships (see Connelly et al. 2011; Wisdom et al. 2011; Aldridge et al. 2012; Knick et al. 2013; Young et al. 2020; Walker et al. 2016), and (2) be reasonably modified using current on-the-ground management actions to improve GUSG habitats (e.g., those employed by the BLM, Table 1). Additional details on covariate modifications can be found in the Supplemental. After generating the modified input layers that simulated management action outcomes across the landscape for each satellite population, we recalculated all moving window and decay function values, substituted them one-at-a-time into the reference model equations (Supplemental Table S1), and reran the models using the ArcPy package in ArcGIS® Pro to generate a comparative RSF layer for each action. For models that included multiple covariates calculated from the same original geospatial input layer (e.g., percent mesic cover [moving window] and distance to mesic [decay function] in Dove Creek), we substituted both covariates simultaneously. To generate our final RSF map, we reclassified each model output from the linear RSF into percentile bins of habitat use locations, using the reclassification table derived from the *original* RSF model.

Mapping effects of paired management actions on habitat suitability

Management agencies may apply multiple actions that overlap across space into their management strategies for improving GUSG habitats. We extended our single-covariate breeding season assessments by creating maps representing combined actions to investigate the potential to further improve suitability (e.g., increasing sagebrush cover plus annual herbaceous removal). We used the same methodologies as with single covariates above but instead substituted pairs of modified covariates that spatially coincided with the reference models. We simulated only a subset of possible paired actions to demonstrate how habitat improvement heatmaps can further inform strategic management planning, selecting pairs likely to result in the greatest improvements to habitat suitability based on single action heatmaps.

Table 1 List of habitat management actions for Gunnison sage-grouse (*Centrocercus minimus*) in southwest Colorado for which projected change in habitat suitability was assessed (based on actions impacting habitat covariates that were determined to be reasonably modifiable and expected to have either a preferential impact on habitat suitability or stakeholder interest in outcomes)

Satellite population	Covariate	Description	Scale of influence	Raw or moving window*input (1-km patch buffer)		Relationship to suitability	Habitat action
				Mean	SD		
Crawford	% sage	Percent sagebrush cover	120-m	11.71	7.05	Positive	Increase 1-SD
	% < 5% conifer-pj	Presence of 1–4% pinyon-juniper cover	570-m	10.89*	10.47*	Negative quadratic	Removal
	% annual herb	Percent annual herbaceous cover	570-m	0.07	0.60	Negative	Removal
	% mesic	Percent mesic cover	570-m	na	na	Negative	Improvements
	dist. to mesic (summer)	Distance decay function to mesic	570-m	na	na	Negative	Improvements
Cerro Summit-Cimarron-Sims Mesa (CCS)	% sage	Percent sagebrush cover	120-m	5.71	6.33	Positive	Increase 1-SD
	% < 5% conifer-pj	Presence of 1–4% pinyon-juniper cover	570-m	16.72*	11.40*	Negative quadratic	Removal
	% annual herb	Percent annual herbaceous cover	570-m	0.98	1.93	Negative	Removal
	% mesic	Percent mesic cover	570-m	na	na	Negative	Improvements
	dist. to mesic (summer)	Distance decay function to mesic	570-m	na	na	Positive	Improvements
Piñon Mesa	shrub height	Mean shrub height (all shrubs)	390-m	37.69	41.36	Negative	Decrease 1-SD
	dist. to 5–10% conifer-pj	Distance decay function to 5–10% pinyon-juniper cover	570-m	0.79*	0.20*	Negative	Removal
	% mesic	Percent mesic cover	120-m	na	na	Positive quadratic	Improvements
	% mesic (summer)	Percent mesic cover	270-m	na	na	Positive quadratic	Improvements
	sage height	Mean sagebrush height	390-m	11.29	13.51	Positive	Increase 1-SD
	% litter	Percent litter cover	570-m	8.92	9.06	Positive quadratic	Increase 1-SD

Table 1 (continued)

Satellite population	Covariate	Description	Scale of influence	Raw or moving window*input (1-km patch buffer)		Relationship to suitability	Habitat action
				Mean	SD		
Poncha Pass	% non-sage shrub	Percent non-sagebrush shrub cover	390-m	10.53	9.64	Positive quadratic	Increase 1-SD
	% non-sage shrub	Percent non-sagebrush shrub cover	390-m	10.53	9.64	Positive quadratic	Decrease 1-SD
	% mesic	Percent mesic cover	570-m	na	na	Positive	Improvements
	% mesic (summer)	Percent mesic cover	390-m	na	na	Negative quadratic	Improvements
	% annual herb	Percent annual herbaceous cover	570-m	0.21	0.58	Negative	Removal
San Miguel	sage height	Mean sagebrush height	570-m	17.76	17.53	Positive quadratic	Increase 1-SD
	% 5–10% conifer-pj	Presence of 5–10% pinyon-juniper cover	570-m	7.94*	7.88*	Negative quadratic	Removal
	% mesic	Percent mesic cover	570-m	na	na	Complex quadratic	Improvements
	% mesic (summer)	Percent mesic cover	570-m	na	na	Complex quadratic	Improvements
	% annual herb	Percent annual herbaceous cover	570-m	1.76	2.82	Negative	Removal
	% herb	Percent herbaceous cover	570-m	11.82	9.64	Positive	Increase 1-SD
	% non-sage shrub	Percent non-sagebrush shrub cover	570-m	9.11	9.59	Complex quadratic	Increase 1-SD
	% non-sage shrub	Percent non-sagebrush shrub cover	570-m	9.11	9.59	Complex quadratic	Decrease 1-SD
Dove Creek	% other sage	Percent non-big sagebrush	570-m	3.38	4.13	Positive	Increase 1-SD
	% mesic/dist. to mesic	Percent mesic cover/distance to mesic	570-m	na	na	Positive/negative	Improvements
	% annual herb	Percent annual herbaceous cover	390-m	1.34	2.71	Negative	Removal

All covariates represent those for crucial breeding season habitats unless labeled otherwise. Scale of influence for each covariate is reported, along with the mean and standard deviation (SD) of input values within a 1-km buffer of the crucial habitat extent and the expected relationship to habitat suitability as informed by the current Sage-grouse literature and margin plots, from Saher et al. (2022)

Mapping effects of new or worsening plant invasions on habitat suitability

Prioritizing monitoring efforts for invasive species can lead to more effective management of invasions (Tarbox et al. 2022). To identify where habitats might be most sensitive to increases in invasive plant cover, and therefore where monitoring and rapid response might be most valuable, we created an additional set of heatmaps that simulated new or worsening annual herbaceous and pinyon-juniper invasions. Our annual herbaceous heatmaps *increased*, rather than decreased, the raw covariate percent cover values by 1 standard deviation (SD) of the values in the buffered crucial habitat extents. To simulate new or worsening pinyon-juniper encroachment (represented by binary presence/absence raw layers of < 5% or 5–10% encroachment), we increased the moving window inputs by 1 SD of the buffered extent. We capped values in the modified layers at 100% cover to remain within logical bounds.

Calculating change in habitat suitability

We calculated change in habitat suitability using the ArcPy package in ArcGIS® Pro as:

$$\text{Change in habitat suitability} = -1 * \left(MapRSF_{\text{modified}} - MapRSF_{reference} \right) \quad (1)$$

We created two sets of heatmaps for each habitat action scenario to serve as decision-support tools for habitat restoration planning. We first generated *uncategorized* maps using values generated by Eq. 1. We then produced final, *categorized* maps, using nested conditional statements to identify areas where new habitat was created (i.e., that transitioned from non-habitat to habitat) and areas that remained non-habitat despite simulated management interventions. Some model covariates (e.g., percent mesic cover, mean sagebrush height) had a positive but quadratic (decreasing) relationship to suitability, meaning habitat improvement actions would be beneficial, but only to a point. Beyond this threshold, further increases in the variable are expected to be reduce habitat use. For this reason, we visualized resulting negative impacts on habitat suitability in our heatmaps because we expected very high proportions of these habitat characteristics to be detrimental to GUSG.

Assessing the utility of our heatmaps for improving management strategies

To gauge how using our habitat improvement heatmaps could improve returns on restoration investments, we simulated habitat improvement actions guided by our heatmaps and compared outcomes to those not guided by these maps. We employed an independent technician, without prior knowledge of our heatmap predictions or the reference models, to develop two sets of hypothetical treatment locations: *non-targeted* scenarios based on past BLM treatment data and *targeted* scenarios that used our heatmaps to inform placement of treatments (see the Supplemental for detailed methods) to maximize habitat suitability improvement outcomes for GUSG (Table 2). We assessed three types of actions for which sufficient management records or planning data existed: reduction of non-sagebrush shrub cover, pinyon-juniper removal, and mesic improvements. We limited the simulated reduction of non-sagebrush shrub cover to within San Miguel because this was the only satellite

Table 2 Comparison of non-targeted versus spatially targeted model-specific habitat management action outcomes for five Gunnison sage-grouse (*Centrocercus minimus*) satellite populations in southwestern Colorado

Satellite population	Management action	Action type	Change in habitat suitability			New habitat created				
			Mean projected change	Percent change (%)	Improvement factor	30-m^2 Pixels	km^2	Increase in km^2	Percent change (%)	Improvement factor
				(From non-targeted)				(From non-targeted)		
Crawford	conpj4 removal	Non-targeted	0.00704			1005	0.90			
		Targeted	0.01679	138.4	2.38	2194	1.97	1.07	118.3	2.18
Cerro Summit-Cimarron-Sims Mesa (CCS)	conpj4 removal	Non-targeted	0.01543			*Not assessed*				
		Targeted	0.03808	146.8	2.47					
Piñon Mesa	conpj10 removal	Non-targeted	0.00669			693	0.62			
		Targeted	0.02968	343.9	4.44	4442	4.00	3.37	541.0	6.41
	mesic improvements	Non-targeted	0.00106			58	0.05			
		Targeted	0.00454	329.7	4.30	922	0.83	0.78	1489.7	15.90
Poncha Pass	mesic improvements	Non-targeted	0.00122			31	0.03			
		Targeted	0.00117	**− 3.6**	**0.96**	57	0.05	0.02	83.9	1.84
San Miguel	pnss reduction	Non-targeted	**− 0.00620**			42	0.04			
		Targeted	0.00806	130.1	2.30	2114	1.90	1.86	4933.3	50.33
	conpj10 removal	Non-targeted	0.00015			43	0.04			
		Targeted	0.00217	1299.6	14.00	1391	1.25	1.21	3134.9	32.35
	mesic improvements	Non-targeted	0.00839			3708	3.34			
		Targeted	0.00631	**− 24.9**	**0.75**	5233	4.71	1.37	41.1	1.41

Table 2 (continued)

Satellite population	Management action	Action type	Change in habitat suitability			New habitat created				
			Mean projected change	Percent change (%)	Improvement factor	30-m^2 Pixels	km^2	Increase in km^2	Percent change (%)	Improvement factor
				(From non-targeted)				(From non-targeted)		
	Non-targeted Mean	0.00422			797	0.72				
	Targeted Mean	0.01335	295.0	3.95	2336	2.10	1.39	1477.5	15.77	

We investigated mean projected change in breeding habitat suitability (quantified as the change in percentile of habitat selection likelihoods based on values from the Saher et al. (2022) reference resource selection function models) and new habitat creation for each of eight satellite population-specific management actions: removal of < 5% or 5–10% pinyon-juniper cover (conpj4 or conpj10 removal, respectively), reducing percent non-sagebrush shrub cover (e.g., serviceberry [*Amelanchier alnifolia*] or Gambel Oak [*Quercus gambelii*]; pnss reduction), and construction of rock dams or other installations to create or restore mesic habitats (mesic improvements). *Non-targeted* actions represent how management entities currently place treatments on the landscape, and *Targeted* actions simulate placement additionally informed by the categorized heatmaps generated by this study. Improvement outcomes for targeted actions are compared to the non-targeted baseline with negative outcomes shown in bold population where models indicated removal could have a beneficial impact on suitability at local sites.

To simulate areas with mesic improvement potential within the satellite populations, we used a stream reach valley bottom polygon layer developed by The Nature Conservancy (Nagel et al. 2014, Data contact Teresa Chapman); see Supplemental for details). We used these pre-defined polygons to generate our set of *non-targeted* mesic action polygons by selecting the ten largest stream segments that did not overlap areas of substantial existing mesic, water, wetland, or agriculture cover, based on the reference map covariate layers used in the reference models. We then used our heatmaps to inform selection of our targeted polygon set, again with the aim of maximizing habitat suitability outcomes by improving the availability of mesic habitat resources for GUSG.

We used the resulting restoration action polygon sets to simulate changes on the landscape following realistic habitat restoration actions, this time only modifying the covariate values within the treatment polygons (rather than the entire landscape). We mapped improvements and calculated improvement metrics two ways for each set, including: (1) the overall projected improvement in habitat suitability across the patches, and (2) the total projected area of new habitat created, calculating for each the percent gain of the targeted action polygon sets over the corresponding non-targeted sets.

Results

Overall trends

We observed considerable spatial variability in projected change in habitat suitability values across the crucial breeding season habitats for most habitat restoration action scenarios, as well as large differences in the magnitude of change among many action types. Our *categorized* maps for the Crawford, Piñon Mesa, Poncha Pass, and San Miguel satellite populations [Figs. 2, 3, 4, 5 (also see Supplemental Fig. S1)] highlight areas where 32 simulated management actions had maximal or minimal projected benefits for improving breeding and summer habitat suitability. They illustrate areas where: (1) new habitat could be created, (2) existing habitat could be improved, or (3) areas were likely to remain non-habitat despite management interventions. Results for the CCS and Dove Creek satellite populations involved numerous modeling and interpretation caveats and are reported exclusively in the Supplemental (Figs. S2–S4). *Uncategorized* RSF percentile change maps show calculated values from Eq. 1 for each 30-m^2 pixel for each satellite population (Supplemental Figs. S5–S8).

Several notable trends were seen in responses to habitat actions across multiple satellite populations. Increasing sagebrush cover and height, litter cover, and herbaceous cover generally resulted in widespread improvements in habitat suitability (Figs. 2f, 3a, f, and 5e, h [also see Supplemental Figs. S3f, and S4b]). Paired management actions resulted in greater improvements for all satellite populations compared to single actions (Figs. 2g, 3h, and 4g [also see Supplemental Fig. S1a, S2d, and S3g]), and increased the overall area of new habitat that could be created by an average of 30.1% compared to the next best single action.

Removal of annual herbaceous grasses generally resulted in large improvements in habitat suitability but with variable outcomes among satellite populations (Figs. 2a, 4f, and 5a [also see Supplemental Fig. S3a S4a]). New or worsening annual herbaceous invasions

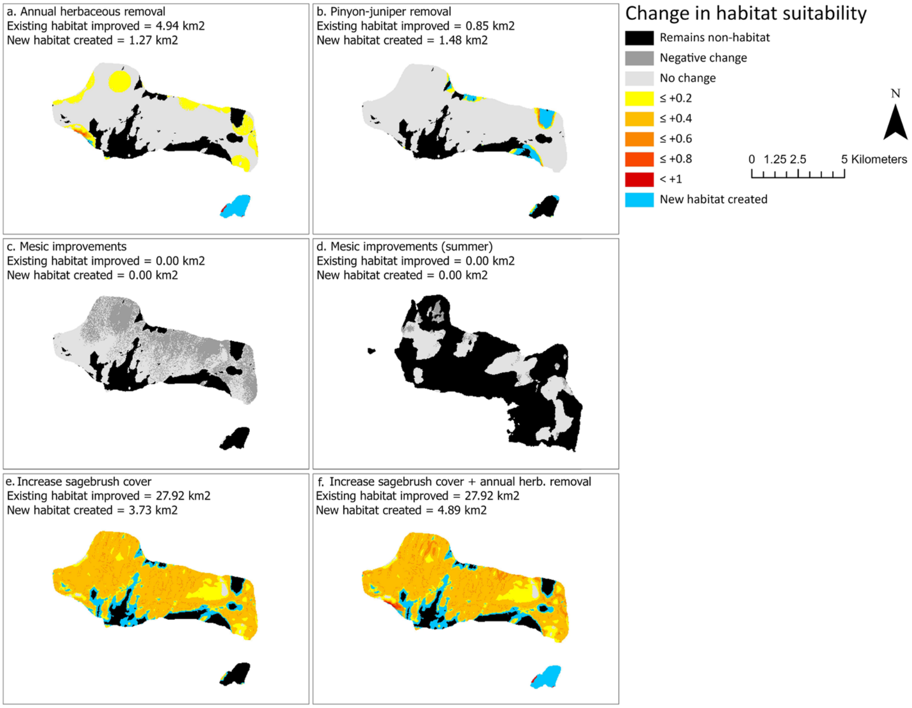

Fig. 2 Categorized heatmaps showing projected change in habitat suitability resulting from habitat restoration actions (or pairs of actions) in the Crawford satellite population of Gunnison sage-grouse (*Centrocercus minimus*). Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. The heatmaps show change in suitability for each 30-m^2 pixel, except for areas where (1) new habitat was projected to be created, (2) non-habitat was projected to remain non-habitat despite intervention, or (3) negative impacts to suitability were projected to occur. Habitat was defined as those pixels with habitat suitability ranks exceeding the value that captured 95% of use locations in the Saher et al. (2022) reference models. All heatmaps represent changes for crucial habitats in the breeding season, except for a single summer-season action (mesic improvements)

(simulated by increasing covariate values within the buffered extents) eliminated nearly all existing habitats (i.e., habitats that transitioned to non-habitat) within crucial habitat extents (Fig. 6a, b), except for San Miguel (Fig. 6c) where cheatgrass (*Bromus tectorum*, a pervasive and non-native annual herbaceous grass) cover was already relatively substantial in crucial habitats. Pinyon-juniper removal also resulted in large gains in suitability across varying extents [Figs. 2b, 3b (also see Supplemental Fig. S3b)], except for San Miguel where existing pinyon-juniper cover was relatively limited within the crucial habitats (Fig. 5b). New or worsening pinyon-juniper encroachment showed considerable spatial variation in potential impacts (Figs. 7a–c). These patterns appear to be relative to the magnitude of current invasion or encroachment within each satellite population.

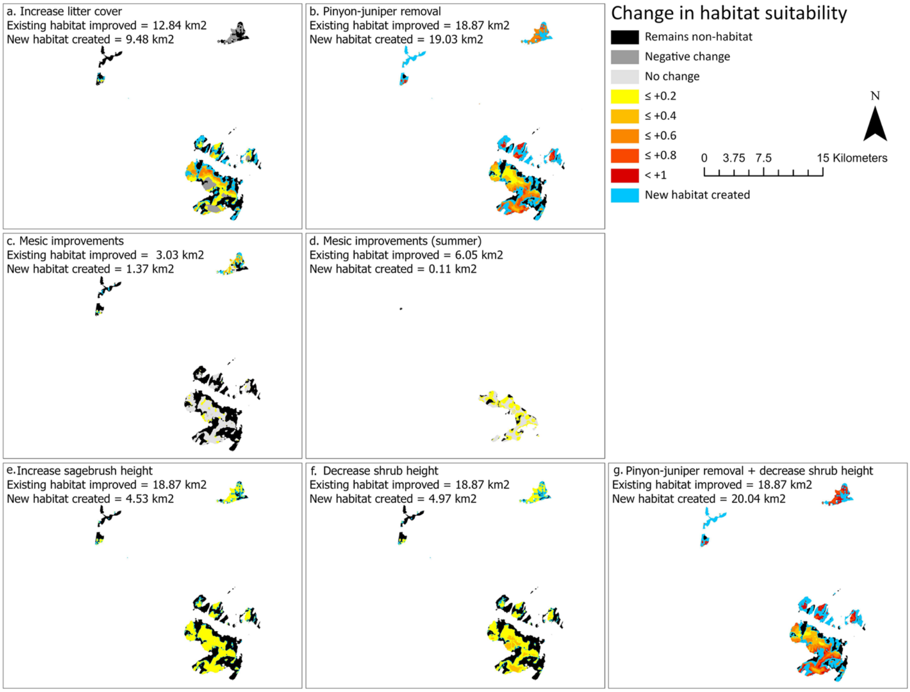

Fig. 3 Categorized heatmaps showing projected change in habitat suitability resulting from habitat restoration actions (or pairs of actions) in the Piñon Mesa satellite population of Gunnison sage-grouse (*Centrocercus minimus*). Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. The heatmaps show change in suitability for each 30-m^2 pixel, except for areas where (1) new habitat was projected to be created, (2) non-habitat was projected to remain non-habitat despite intervention, or (3) negative impacts to suitability were projected to occur. Habitat was defined as those pixels with habitat suitability ranks exceeding the value that captured 95% of use locations in the Saher et al. (2022) reference models. All heatmaps represent changes for crucial habitats in the breeding season, except for a single summer-season action (mesic improvements)

Satellite populations

In the Crawford satellite population, the greatest amount of overall improvement in suitability of existing habitats was projected to occur from management actions that increased sagebrush cover and could benefit much of the crucial habitat extent (Fig. 2f). However, removal of annual invasive grasses (Fig. 2a) and pinyon-juniper (Fig. 2b) were also expected to have relatively large impacts in isolated areas. Projected improvements and new habitat created from pinyon-juniper removal generally complemented areas improved by increasing sagebrush cover and annual herbaceous removal. While some single actions were projected to result in the creation of new habitats, the total area with this potential was relatively small (max of 4.89 km^2 for the combined actions) compared to the total area where existing habitats could be improved (max of 27.92 km^2).

In Piñon Mesa, we projected pinyon-juniper removal could create the most habitat and result in the greatest improvements in habitat suitability across crucial habitats of any single management action (Fig. 3b). Increasing litter cover (e.g., by modifying grazing

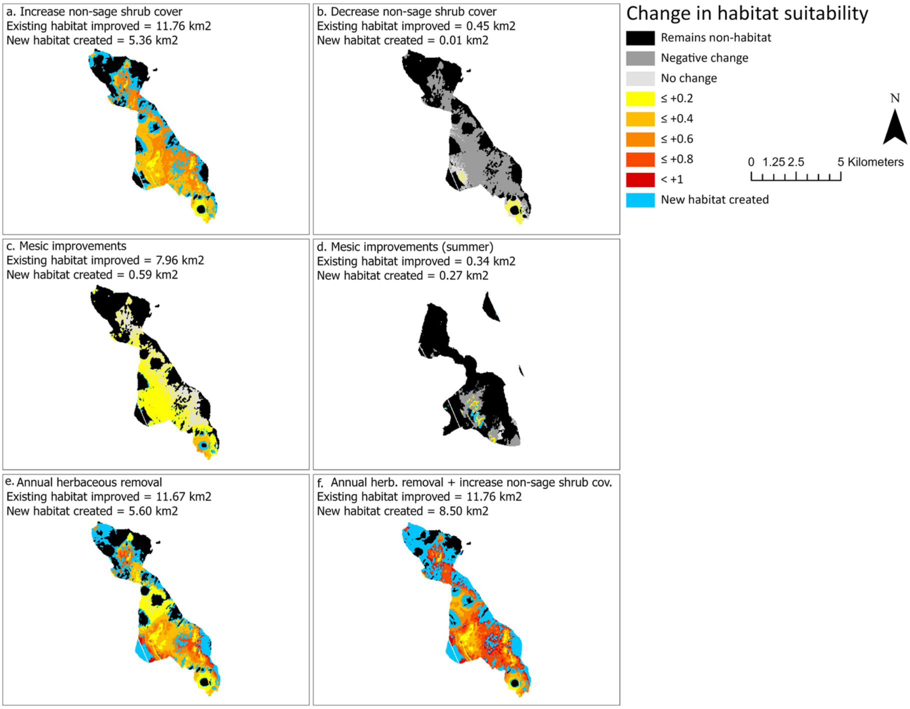

Fig. 4 Categorized heatmaps showing projected change in habitat suitability resulting from habitat restoration actions (or pairs of actions) in the Poncha Pass satellite population of Gunnison sage-grouse (*Centrocercus minimus*). Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. The heatmaps show change in suitability for each 30-m^2 pixel, except for areas where (1) new habitat was projected to be created, (2) non-habitat was projected to remain non-habitat despite intervention, or (3) negative impacts to suitability were projected to occur. Habitat was defined as those pixels with habitat suitability ranks exceeding the value that captured 95% of use locations in the Saher et al. (2022) reference models. All heatmaps represent changes for crucial habitats in the breeding season, except for a single summer-season action (mesic improvements)

practices) was projected to result in large gains overall that were largely complementary to pinyon-juniper removal, though also reduce suitability in some areas (Fig. 3a). Increasing sagebrush height and decreasing shrub height (e.g., reducing non-sagebrush shrubs) resulted in similar outcomes, though with relatively moderate benefits across much of the crucial habitat extent (Fig. 3f, g). Pairing pinyon-juniper removal with decreasing shrub height led to very strong improvements across the entire extent (Fig. 3h).

In Poncha Pass, removing annual herbaceous cover (Fig. 4f) and increasing non-sagebrush shrub cover (Fig. 4a) were projected to result in the greatest and most widespread habitat suitability improvements and new habitat created. Paired actions resulted in substantial and widespread gains (Fig. 4g). Our simulations indicated that decreasing non-sagebrush shrub cover in this satellite population would result in widespread negative impacts to habitat suitability across most of the crucial habitat extent (Fig. 4b). Mesic improvements in the breeding season were expected to result in habitat suitability gains in many areas (Fig. 4c), but the areas seeing the most benefit in this season differed from those in the summer/brood-rearing season (Fig. 4d). Projected breeding

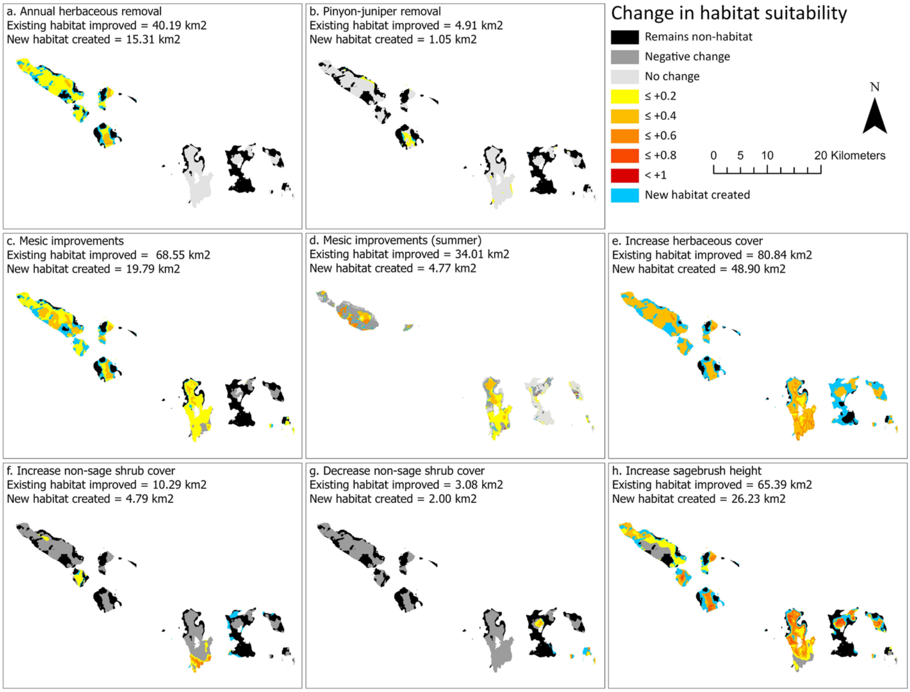

Fig. 5 Categorized heatmaps showing projected change in habitat suitability resulting from habitat restoration actions (or pairs of actions) in the San Miguel satellite population of Gunnison sage-grouse (*Centrocercus minimus*). Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. The heatmaps show change in suitability for each 30-m^2 pixel, except for areas where (1) new habitat was projected to be created, (2) non-habitat was projected to remain non-habitat despite intervention, or (3) negative impacts to suitability were projected to occur. Habitat was defined as those pixels with habitat suitability ranks exceeding the value that captured 95% of use locations in the Saher et al. (2022) reference models. All heatmaps represent changes for crucial habitats in the breeding season, except for a single summer-season action (mesic improvements)

season gains in suitability resulted in negative impacts to suitability in the summer (i.e., late brood-rearing) season.

In San Miguel, increasing herbaceous cover (Fig. 5e) and sagebrush height (Fig. 5h) had the largest and most widespread gains in suitability and new habitat created. Mesic improvements were projected to substantially improve breeding habitat suitability across the western half of crucial habitats and the westernmost of the eastern habitat patches (Fig. 5c), though some of these actions resulted in negative impacts on suitability in summer in those same areas (Fig. 5d). Because of the complex quadratic relationship between non-sagebrush shrub cover and habitat suitability, simulated increases and decreases in shrub cover (a 1-SD directional change) both resulted in negative impacts across much of the extent, with a few isolated areas of relatively large gains in habitat suitability (Fig. 5f, g). Annual herbaceous removal resulted in relatively large benefits in the western half of the crucial habitat extent, where cheatgrass was already well-established (Fig. 5a).

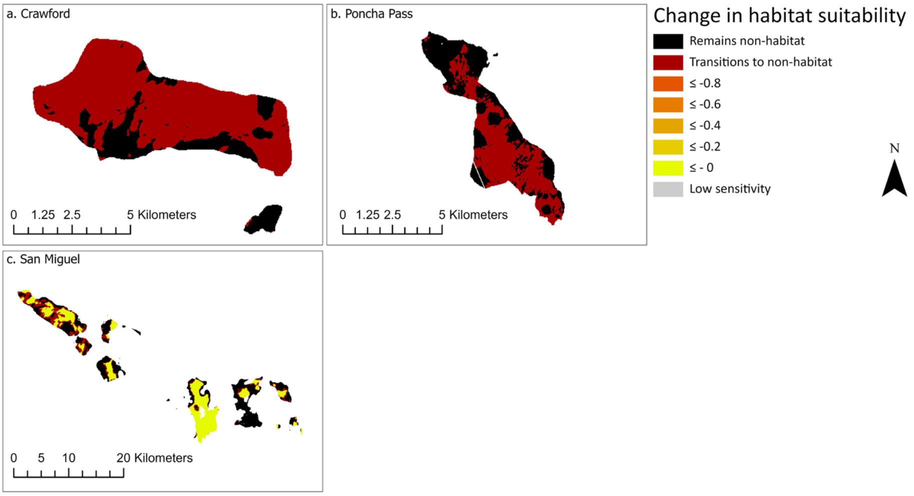

Fig. 6 Categorized heatmaps showing projected change in habitat suitability in crucial breeding-season habitats resulting from new or worsening annual herbaceous (predominately cheatgrass) invasions in the Crawford, Poncha pass, and San Miguel Gunnison sage-grouse (*Centrocercus minimus*) satellite populations. Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. Non-habitat was defined as those pixels with habitat suitability ranks below the value that captured 95% of use locations in the Saher et al. (2022) reference models

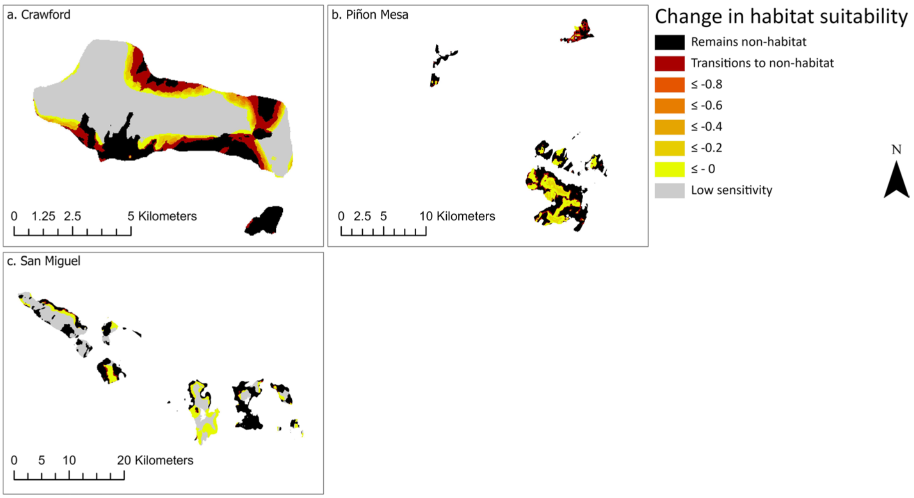

Fig. 7 Categorized heatmaps showing projected change in habitat suitability resulting from new or worsening pinyon-juniper encroachment in crucial breeding-season habitats of the Crawford, Piñon Mesa, and San Miguel Gunnison sage-grouse (*Centrocercus minimus*) satellite populations. Change in suitability values were quantified as the change in binned percentile from the *reference* resource selection function (Saher et al. 2022) maps to the *modified* maps, based on habitat use locations from the Saher et al. (2022) models. Non-habitat was defined as those pixels with habitat suitability ranks below the value that captured 95% of use locations in the Saher et al. (2022) reference models

Benefits of targeting habitat actions with heatmaps

Spatially targeting treatment polygons using our categorized heatmaps resulted in a nearly fourfold increase in habitat suitability values (improvement factor = 3.95) and more than a 15-fold increase in habitat created (improvement factor = 15.77) compared to non-targeted polygons (Table 2). The mean projected change in habitat suitability for each set of simulated population-specific management actions and the total area of new habitat created for targeted and non-targeted actions, as well as the percent increase in these metrics that resulted from targeting, are reported in Table 2. Targeting treatment polygons using our uncategorized heatmaps (i.e., *RSF percentile change* maps showing the calculated values from Eq. 1) resulted in larger overall improvements in habitat suitability compared to targeting guided by our categorized maps (improvement factor = 4.18), but slightly lower improvements in habitat created (improvement factor = 14.38; see full comparative results in Supplemental Table S2.

Discussion

We developed a novel approach to evaluate potential habitat restoration efforts in a spatial context with the aim of improving site conditions for a species of critical conservation concern. Using GUSG to demonstrate its utility, we found divergent responses to simulated change in habitat characteristics following restoration actions across satellite populations, further highlighting the need for management strategies tailored to populations with unique habitat-use relationships and adaptive divergence (Zimmerman et al. 2019; Oyler-McCance et al. 2021; Apa et al. 2021; Saher et al. 2022), and that face differing levels of future threats (Van Schmidt et al. 2024). The heatmaps generated by our approach predict habitat improvement potential at management-relevant scales and identify hotspots where management is likely to result in the greatest return on conservation investment across multiple, unique satellite populations and ecoregions. In doing so, they effectively highlight the need for site-specific management prescriptions, particularly when habitats are not uniform across space and may serve as valuable resources for developing long-term conservation strategies, as well as prioritizing restoration sites in the short-term. Our approach is transferable, thus providing a blueprint for managers looking to optimize their habitat restoration dollars. Ultimately, using these data-driven and satellite population-specific resource selection models should increase the efficiency and success of management actions targeted at improving habitat conditions for species of conservation concern.

Our work represents the first effort to map and compare predicted habitat suitability responses across space for a diverse suite of habitat restoration actions, thereby facilitating the optimal allocation of habitat restoration actions, for a species of critical conservation concern. While the exact applications of our heatmaps will depend on the specific management goals being considered, they are intended to aid managers in a complex decision-making process that optimizes use of limited financial and other resources for restoring habitats for at-risk species. Our comparison of targeted versus non-targeted restoration actions suggests these heatmaps can support the spatial targeting of restoration action sites intended to improve or create habitats. Critically, non-linear responses for some habitat covariates (e.g., non-sagebrush shrub) meant that placement of habitat interventions in some areas could degrade existing habitats if the full landscape and seasonal contexts were not considered (for example, in San Miguel). This is vital to ensuring that management actions intended to benefit species do not have unintentional detrimental impacts. We also demonstrated several extensions to our base heatmaps that may further facilitate optimal placement of restoration actions and may be transferrable to other species or systems. These include (1) projections for paired restoration actions applicable to multi-approach management strategies and (2) invasion maps that forecast the relative severity of habitat degradation across space from the spread of native and non-native plants and could be used to target priority areas for monitoring and early response. The workflow for our targeted actions assessments can serve as a tool to simulate actions within smaller, customized extents, thereby allowing managers to assess the relative impacts of proposed management actions. These extensions can be applied to any system or species for which RSF models exist and the potential impacts of management actions on habitat characteristics are known. Additionally, our heatmaps could be used with decision-support resources to enhance strategic planning that considers future projections across the species' range, such as the habitat vulnerability assessment maps generated by Van Schmidt et al. (2024).

Seasonal RSFs often demonstrate varying selection relationships to the same covariates at different times of year. Therefore, effective habitat management planning may require balancing potential improvements in suitability in one season with degradation in another. For example, mesic habitats are used by GUSG in the late brood-rearing season in summer where herbaceous plants (critical sources of food and cover for chicks) persist, compared to other upland habitats that have senesced (Fischer et al. 1996; Connelly et al. 2011). However, the presence of mesic habitats can displace other important habitat features such as sagebrush cover, which is critical for survival and reproduction, because sagebrush conceals nesting hens in the breeding season and provides forage and concealment in other seasons (Aldridge and Boyce 2007, 2008; Connelly et al. 2011). Seasonal tradeoffs are demonstrated in the San Miguel and Poncha Pass seasonal mesic heatmaps, which projected varying spatial responses to mesic habitat improvements between seasons, both in the magnitude and direction of change in habitat suitability across the landscape. While mesic improvement actions may have a substantial benefit at local sites in one season, the result may be detrimental in another season and should be strategically targeted as a result. Similarly, GUSG are dependent on sufficient sagebrush cover for survival in the winter months (Schroeder et al. 1999; Connelly et al. 2000b; Crawford et al. 2004), so management actions that reduce sagebrush cover to make way for other important cover types in the warmer seasons may have unintended impacts on winter habitats and, therefore, survival. Although winter RSF models were not available for use in this study, such maps could provide insight into other potential seasonal tradeoffs, allowing managers to target treatments with full consideration of year-round seasonal requirements for GUSG.

Several caveats should be considered when translating results of our study for real-world applications. First, as with all analyses incorporating remotely sensed data, the input layers used in our models all have some error associated with them (including potential misclassifications of habitat features) and limitations related to capturing rapidly changing habitat features. For example, annual herbaceous layers considered in RSF models were based on 2015 imagery (see Saher et al. 2022) and there is the potential for rapid expansion and spread of invasions, so both the extent and cover of this habitat feature have likely changed since then. However, the time period within which our heatmaps will remain relevant for management will depend on the speed of change across the landscape. For this reason, we recommend that users verify on-the-ground habitat conditions as part of the decision-making process and suggest that the data inputs describing habitat covariates for these models be updated, as needed, to renew their relevance for conditions on the landscape. This is more important in cases where suitability is non-linearly related to habitat characteristics, such as non-sagebrush shrub in our study (Fig. 5f, g). In such cases, managers could cross-reference field observations with estimated response thresholds (i.e., from marginal effects plots; Saher et al. 2022) prior to modifying habitats. Second, attempts to forecast the potential success of treatments (i.e., vegetation seedings or plantings) were not possible given available data at the time of our study and were therefore beyond its scope. We instead applied measures of static change (expected to result from successful restoration actions) to eligible pixels and assumed equal restoration success among the various management actions. We did, however, attempt to minimize possible overestimation of improvement potential by masking areas where habitat improvements were unlikely to occur (e.g., developed areas, large bodies of water, and unsuitable topographies). For this reason, our heatmaps are intended to be used in combination with local expert knowledge on whether specific actions would be successful at local sites as part of the strategic restoration planning process.

While the maps generated in our study represent valuable decision-making resources designed to improve spatial prioritization of habitat management actions, they stop short of incorporating important demographic information for species of conservation concern. Future efforts to build this spatial prioritization approach could assimilate these types of data to better understand how management actions affect life stages critical to satellite population persistence and recovery. This information could link back to seasonal predictions of habitat suitability improvement and the relationship to specific demographic rates of interest to maximize potential population growth. For example, chick survival has been demonstrated as a key factor driving population growth of greater sage-grouse (Taylor et al. 2012) and it is important to ensure that resources selected by animals, and thus managed for, are not ecological traps that pose fitness consequences (Aldridge and Boyce 2007). Planting sagebrush may help directly improve breeding, nesting, or winter habitat (thereby improving rates of adult and nest survival), but it may not necessarily alleviate factors limiting chick survival (e.g., the presence of mesic habitats adjacent to sufficient sagebrush "escape" cover). These types of relationships could be identified and tested using integrated population models (i.e., IPMs) or matrix models (Taylor et al. 2012; Coates et al. 2018; Mathews et al. 2018). Synthesizing these models with our approach to management applications could help managers further target specific action types and application sites, effectively maximizing satellite population growth potential by additionally targeting factors with the greatest influence on productivity or survival.

Summary

We provide a practical approach for leveraging RSF models to develop spatially varying and satellite population-specific predictions of change in habitat suitability for species of conservation concern. These data are intended to support resource managers tasked with developing strategic habitat restoration plans that maximize returns on restoration investments, particularly when limited funding and resources require highly efficient and targeted conservation efforts to generate maximum benefits for species. We found that applying specific restoration treatments in seemingly similar sites could yield vastly different consequences in terms of change in habitat suitability. This indicates that the multi-variable conditions that comprise and improve habitats can be difficult to identify without the use of habitat analyses. Analytical resources that are designed to uncover the locations, actions, and contexts that make efficient use of restoration resources may provide another method of anticipating restoration benefits before actions are planned and undertaken. These types of analyses have the potential for broader application across a wide range of ecological systems and species for which habitat suitability models exist or could be developed. Importantly, restoration analyses that anticipate the range of restoration benefits can support strategic planning that focuses on the specific needs of species in unique locations and thereby contribute to conserving species in dynamic and changing landscapes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02886-x.

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Author contributions All authors contributed to the study's conception and design. Material preparation, data collection and analysis were performed by Jessica Shyvers, Nathan Van Schmidt and D. Joanne Saher. The first draft of the manuscript was written by Jessica Shyvers and all authors provided feedback and revisions to subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data generated as part of this study are available through a U. S. Geological Survey data release (Shyvers et al. 2024) https://doi.org/10.5066/P9VBT1ER.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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