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Targeting conifer removal to create an even playing field for birds in the Great Basin

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ABSTRACT

The encroachment of pinyon-juniper woodlands into sagebrush habitat in the Great Basin Ecoregion of the western USA, represents a potential source of habitat degradation for sagebrush-associated wildlife species. To restore sagebrush habitat, managers are conducting large-scale conifer removal efforts within the Great Basin, particularly within Greater Sage-Grouse (*Centrocercus urophasianus*) priority areas for conservation. Such large-scale habitat modification efforts may result in unintended ecological trade-offs for wildlife. To investigate these trade-offs, we used community science data to develop species distribution models for two sagebrush and three pinyon-juniper associated bird species of conservation concern in the Great Basin. We evaluated the predictive performance of our models with an independent dataset of presence locations derived from systematic monitoring programs. We then simulated conifer removal across the Great Basin and mapped habitat gains and losses for our study species. Despite differing land cover associations, 31%–51% of suitable habitat for our study species coincided with Greater Sage-Grouse priority areas for conservation. Our conifer removal scenario increased suitable habitat by 6%–17% for sagebrush associates and reduced habitat by 11%–41% for pinyon-juniper associates. We identified areas of the Great Basin where conifer removal expanded habitat for sagebrush associates without concurrent habitat loss for pinyon-juniper associates. Our results provide guidance for conducting vegetation management in the Great Basin while addressing the habitat needs for multiple focal species. Our methods, which use freely available community science data and geospatial layers, can easily be transferred to other species and ecoregions.

1. Introduction

The Great Basin Ecoregion (hereafter "Great Basin"), North America's largest desert, faces many threats including altered fire regimes, intensive grazing, drought, invasive species, and climate change (Miller et al., 2008; Pellant et al., 2004). Additionally, in recent decades, pinyon-juniper woodlands have exhibited atypical patterns of expansion that reduce or degrade adjacent sagebrush shrublands (Miller et al., 2008). This conifer "encroachment" has been identified as a threat to sagebrush-dependent species like the Greater Sage-Grouse (*Centrocercus urophasianus*; Baruch-Mordo et al., 2013), a declining species of conservation concern that has been extirpated from half of its historic range (Garton et al., 2011). Despite some suggestions that pinyon-juniper expansion may be part of a longer-term natural dynamic of this ecoregion or a consequence of reestablishment of woodlands after clearing in the early western settlement period (Ko et al., 2011; Miller et al., 2019), conifer removal to restore sagebrush habitat is a primary management objective in the Great Basin and throughout the Greater Sage-Grouse range (Reinhardt et al., 2020). Since 2012, conifers have been removed on 450 km^2 in the Great Basin portions of Nevada, Utah, and Idaho (C. Witt, unpublished USFS data), and removal is expected to continue in the future (Reinhardt et al., 2020), especially in Greater Sage-Grouse Priority Areas for Conservation (PACs; U.S. Fish and Wildlife Service, 2013), which cover approximately 31% of the Great

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Basin.

Any large-scale habitat modification effort, such as conifer removal across the Great Basin, may result in ecological trade-offs for wildlife. Research has shown that Greater Sage-Grouse function as an umbrella species for other sagebrush obligates (Donnelly et al., 2017; Hanser and Knick, 2011; Rowland et al., 2006) and that conifer removal can have positive effects on these species (Holmes et al., 2017). However, the benefits of conifer removal may only hold for strict sagebrush obligates (Rowland et al., 2006) and will likely have negative effects on conifer-associated species of conservation concern, like the Pinyon Jay (*Gymnorhinus cyanocephalus*; Boone et al., 2021; Magee et al., 2019; Rosenberg et al., 2016). Given these likely trade-offs, the high degree of conservation concern associated with conifer- and sagebrush-associated species (Partners In Flight 2016), the large-scale efforts to implement conifer removal, and the desire to integrate management across the entire Great Basin (Chambers et al., 2008; Chambers and Wisdom, 2009), land managers would benefit from information about the responses of multiple species to these treatments. Tools to identify areas where treatments could benefit sagebrush-associated species without adversely impacting conifer-associated species would be particularly valuable.

Understanding species' responses to treatments requires detailed knowledge of the relationship between relative habitat quality and key habitat characteristics. Habitat suitability models and species distribution models (SDMs) represent popular techniques to identify these relationships. These models require substantial data to derive robust relationships across large geographic extents; data which are often not available through traditional systematic data collection techniques (Dickinson et al., 2010). For many species, community science data (also known as citizen science data, or public participation in scientific research; Shirk et al., 2012) is becoming increasingly available and represents an alternate data source to supplement our knowledge regarding species occurrence, abundance, and distribution (Bonney et al., 2009). Community science data has also been used to model occupancy, species richness, population trends, and to generate SDMs (Hochachka et al., 2012). Though there are some concerns about the ability of these data to provide robust and valid inference regarding species distribution and abundance (Dennis et al., 1999; Hassall, 2012; Hochachka et al., 2012), incorporating recent advances in SDMs such as ensemble SDMs (Grenouillet et al., 2011) and multi-scale SDMs (McGarigal et al., 2016; Shirk et al., 2018) can increase model performance and reliability.

To improve the conservation community's collective understanding of ecological trade-offs regarding sagebrush and conifer-associated species' response to conifer removal in the Great Basin, we (1) leveraged community science data to develop multi-scale SDMs across the Great Basin ecoregion for five sagebrush- or conifer-associated bird species of conservation concern: Brewer's Sparrow (*Spizella breweri*), Gray Flycatcher (*Empidonax wrightii*), Juniper Titmouse (*Baelolophus ridgwayi*), Pinyon Jay, and Sagebrush Sparrow/Bell's Sparrow (*Artemisiospiza nevadensis/Artemisiospiza belli*), (2) evaluated modeled relationships with independent data collected using a probabilistic sampling design, (3) predicted changes in habitat suitability for our five focal species under a simulated conifer removal scenario, and (4) evaluated the extent to which suitable habitat for our focal species was associated with PACs, which are deemed essential to the conservation of Greater Sage-Grouse.

This work is representative of a larger trend towards ecoregion-wide analysis and planning that are increasingly being promoted to bring independent agendas under a single umbrella, encourage multi-species management, and allow ecological understanding of larger spatial processes (Anderson, 2010; Groves, 2003). In addition, our work provides detailed maps for biologists, managers, and land use planners that can be used to identify locations where conifer treatments would benefit sagebrush obligates while reducing negative impacts on several conifer-associated species. The use of freely available community science data and geospatial layers makes our approach accessible to others and transferable to other species and ecoregions.

2. Methods

2.1. Study area and species

Our study area covered the Great Basin ecoregion as defined by the intersection of the Great Basin Landscape Conservation Cooperative (LCC) program and availability of geospatial layers (see below; Fig. 1). The 515,276 km^2 Great Basin study area is a temperate desert with basin and range topographic characteristics, encompassing parts of Oregon, Nevada, California, Idaho, and Utah. Typical vegetation in the Great Basin includes sagebrush and salt desert shrublands in valleys, pinyon-juniper woodlands in surrounding foothills and middle-elevation slopes, and various mountain shrub and forest types at the highest elevations (Miller et al., 2014).

We selected bird species that were either pinyon-juniper (Gray Flycatcher, Juniper Titmouse, and Pinyon Jay) or sagebrush (Brewer's Sparrow and Sagebrush Sparrow/Bell's Sparrow) associated. These species were identified in meetings with state and federal land managers as species of interest or were listed as species of conservation concern in the Great Basin (Partners in Flight 2016). We combined data for Sagebrush and Bell's Sparrow (hereafter "Sage Sparrow") because these were only recently identified as two separate species and because of difficulties in discerning these species in the field.

2.2. Bird data

We identified presence and absence points for our focal species from the eBird database (eBird, 2017; Sullivan et al., 2009). We restricted our data query to include only comprehensive lists from eBird to ensure the species recorded represented the full suite of species detected at a location. For each species, we used typical breeding season (April 15th - July 15th) locations of eBird-approved sightings from 1990 to 2016 as the presence points. We defined absence points for each focal species as points where a complete list was tabulated but the species was not detected during the same inter- and intra-annual time period. This 'focal-group background' method has been shown to account for sampling bias and outperform randomly selecting pseudo-absence points across the study area (Phillips et al., 2009).

To further account for sampling bias, we removed any duplicate points and spatially rarefied the presence and absence points by creating a 1 km grid over the study area and randomly retaining one point in every grid cell (Fourcade et al., 2014). Table S1 contains the final number of presence and absence points used for each species.

2.3. Environmental variables

We selected a suite of land cover, topographic, climatic, soil, and human development variables we hypothesized may affect habitat use of our focal species (Table S2) and resampled all variables to a 90 m pixel size. The geospatial data for some of the vegetation layers, like percent shrub and herbaceous cover were available for most, but not all the Great Basin ecoregion. We therefore restricted our analyses to the spatial extents of the layers with smaller geographic footprints within the Great Basin (Fig. 1).

We smoothed each variable at eight different spatial scales to identify the appropriate scale of effect for each variable and construct multi-scale models (McGarigal et al., 2016). We felt this was critical, as previous studies have shown that multi-scale models are more representative of habitat use for species and outperform single-scale models (Johnson et al., 2004; Wheatley and Johnson, 2009; Zeller et al., 2014). We used the *smoothie* package (Gilleland, 2013) in the R software environment (R Core Team, 2019) to apply a Gaussian smooth to each environmental variable with the following bandwidths: 90 m, 180 m,

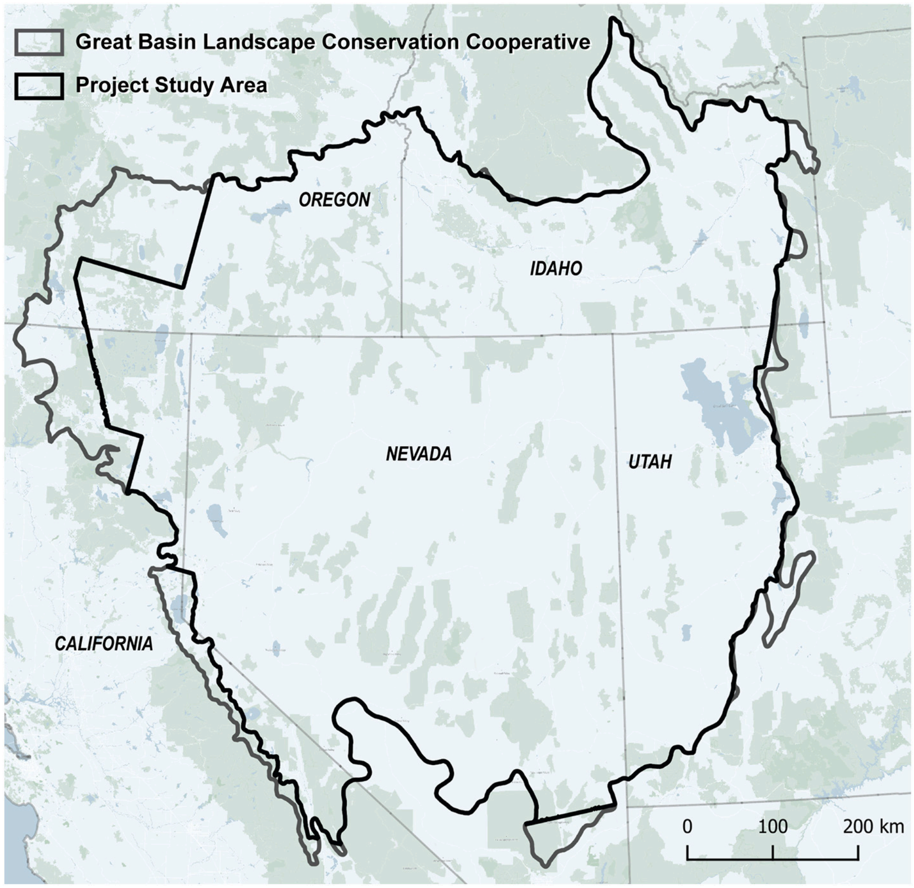

Fig. 1. Extent of Great Basin Landscape Conservation Cooperative and project study area.

360 m, 720 m, 1440 m, 2880 m, 5760 m, and 11,520 m.

2.4. Multi-scale species distribution models

A flowchart of our multi-scale species distribution modeling approach is provided in Fig. S1.

Following methods developed by Shirk et al. (2018), we performed *t*-tests on the values associated with each presence and absence point for each species, environmental variable, and scale combination. We retained the scale of each environmental variable with the lowest p-value for possible inclusion in the multivariate models. We then removed any variable that had a p-value >0.01. We assessed pairwise Spearman's rank correlations between all remaining variables. When a pair of variables had a correlation greater than $|0.6|$, we removed the variable with the higher p-value from the prior step. We used the remaining variables to develop the SDMs for each focal species.

Many SDM modeling approaches are considered appropriate for analyzing presence-absence data – all with various advantages and disadvantages (Franklin, 2010). Therefore, we selected a suite of SDMs, Generalized Linear Models (GLMs), Multivariate adaptive regression splines (MARS), Maximum Entropy (MAXENT), Random Forests (RF), and Boosted Regression Trees (BRT), to assess habitat suitability for our species. We used the *BIOMOD2* package in R (Thuiller et al., 2019) to develop SDMs for each bird species.

We performed a 10-fold cross validation to assess each model's predictive ability. Across the 10 folds, we calculated the Area Under Receiver operating characteristic curve (AUC; Hanley and McNeil, 1982) and used the AUC values to formally rank our models. Due to a large number of similarly-performing SDMs, as evaluated by AUC values, we combined our entire suite of SDM models into a final 'ensemble' model using the BIOMOD2 package in R (Grenouillet et al., 2011). We then predicted habitat suitability for each bird species across the study area using the final ensemble model.

We further assessed the performance of the ensemble models with an independent data set of presence points for each species. These presence points (hereafter, 'validation points') were collected from point-transect surveys conducted by the Great Basin Bird Observatory (GBBO) and the Integrated Monitoring in Bird Conservation Regions (IMBCR) partnership, mainly in the Idaho, Nevada, and Oregon portions of the Great Basin LCC (Fig. S2). The GBBO surveys were conducted during the breeding season months of April, May, June, and July from 2006 to 2017. The IMBCR surveys were conducted during the breeding season months of May, June, and July from 2013 to 2017 (Hanni et al., 2012). We rarefied all validation points to 1 km which resulted in 643, 260, 160, 220, and 319 validation points for Brewer's Sparrow, Gray Flycatcher, Juniper Titmouse, Pinyon Jay, and Sage Sparrow respectively.

We rescaled the ensemble habitat suitability surfaces from 0 to 1 and extracted the values of the validation points on the rescaled surfaces. We then used the Boyce Index (Boyce et al., 2002; Hirzel et al., 2006) to compare the expected frequency of observed values at the validation points with the expected values based on a random distribution across the study area for a range of habitat suitability classes. To calculate the Boyce Index, we used the *ecospat* package in R (Broennimann et al., 2018) with 10 bins (Hirzel et al., 2006). The Boyce index is the Spearman's rank correlation coefficient between the observed/expected ratios and the bins. Higher values indicate better predictive ability of the model.

2.5. Habitat continuity metrics and overlap with areas of Greater Sage-Grouse habitat restoration

We derived binary suitability surfaces from the SDM output for each species using the maximum test sensitivity plus specificity values. For Brewer's Sparrow, Gray Flycatcher, Juniper Titmouse, Pinyon Jay, and Sage Sparrow these values were 0.44, 0.48, 0.59, 0.68, and 0.51 respectively. On each binary habitat suitability surface, we calculated the proportion of the Great Basin representing suitable habitat for each species. We also calculated six landscape metrics that summarize habitat continuity using the *landscapemetrics* package in R (Hesselbarth et al., 2019). These metrics included mean patch area, largest patch index, core area index, aggregation index, contiguity, and the radius of gyration (McGarigal and Marks, 1995). We set the edge depth to 250 m for the core area index calculations.

To determine where Greater Sage-Grouse restoration activities will be coincident with habitat for each species, we overlaid "Priority Areas for Conservation" (PAC) polygons (U.S. Fish and Wildlife Service, 2013), and calculated the proportion of habitat for each species contained within the PACs.

2.6. Predicting suitable habitat after conifer removal

With the exception of Juniper Titmouse, all species had either pinyon-juniper or tree cover in their final models. To simulate the effects of conifer removal on these species, we set the conifer variables to zero and then re-predicted habitat suitability across the study area with the final SDMs. We did not have data on the type and location of future conifer treatments therefore, we simulated total conifer removal, which is an unlikely scenario across the entire study area but is still appropriate for examining treatment effects on a per-pixel basis. We created binary habitat suitability maps from the habitat projections, as described above, and calculated area and percent of habitat gained and lost for each species. We then summed the amount of habitat created for sagebrush-associated species which would not reduce the amount of suitable habitat for pinyon-juniper-associated species.

3. Results

The scales of selection for the different environmental layers varied among bird species as did the variables selected for the multivariate ensemble SDMs (Tables 1, S3). Shrub height, percent herbaceous cover, and streams were in the final models for all species (Table 1), and species had differing responses to these variables (Fig. S3). At least two anthropogenic variables were present in each species' model (Table 1). Responses to anthropogenic variables were generally negative, with the exception of Pinyon Jays having a positive response to agricultural landcover and Gray Flycatcher and Juniper Titmouse having a positive response to higher densities of transmission lines (Fig. S3). All our bird models included at least one soil variable and, except for Sage Sparrow, at least one topographic variable (Table 1). Other variables included in the final SDMs differed among the species (Table 1, Fig. S3).

The varying relationships of our focal species to our habitat covariates resulted in apparent differences in the predicted habitat suitability surfaces (Fig. 2). For example, our Brewer's Sparrow and Gray Flycatcher models predicted high habitat suitability across much of the Great Basin, whereas our models predicted restrictive habitat suitability for Juniper Titmouse and Pinyon Jay (Fig. 2). However, there were also large areas of overlap within and among the sagebrush and the pinyon-juniper associates (Fig. 3).

Within-sample model performance of the ensemble models ranged from an AUC of 0.74–0.90 (Table S4). Our evaluation of the ensemble models using the independent set of validation points resulted in a Boyce Index Spearman's rank correlation of 0.83, 0.93, 0.94, 0.95, and 0.86 for Brewer's Sparrow, Gray Flycatcher, Juniper Titmouse, Pinyon Jay, and Sage Sparrow, respectively.

Brewer's Sparrow had the highest proportion of suitable habitat across the Great Basin. This was followed by Gray Flycatcher, Sage Sparrow, Pinyon Jay, and Juniper Titmouse (Table 2). Brewer's Sparrow also had the highest habitat continuity metrics of all our study species except for the largest patch index, which was highest for Gray Flycatcher (Table 2). Gray Flycatcher had the lowest values for mean core area index, contiguity, and mean radius of gyration, indicating the patches have a large amount of edge, small cores, and are relatively small in size. Although Juniper Titmouse had the least amount of suitable habitat in the Great Basin, values for mean core area index, contiguity, and mean radius of gyration were high, indicating that the suitable habitat that is present is relatively continuous.

Percent of suitable habitat overlapping Greater Sage-Grouse PACs was highest for Brewer's Sparrow at 51%. This was followed by Sage Sparrow (41%), Juniper Titmouse (41%), Gray Flycatcher (37%), and Pinyon Jay (31%).

Our conifer removal scenario increased the amount of suitable habitat for Brewer's Sparrow and Sage Sparrow and decreased the amount of suitable habitat for Gray Flycatcher and Pinyon Jay (Table 3, Fig. S4). Sage Sparrow showed the largest potential habitat gains from conifer removal while Pinyon Jay showed the largest potential habitat losses. We overlaid the gains of the sagebrush-associated species with the losses of the pinyon-juniper-associated species to identify locations where conifer removal can provide benefits to sagebrush-associates without negatively affecting pinyon-juniper associates (Fig. 4, sagebrush associate gains, no pinyon-juniper associate losses; Fig. S4).

Our conifer removal scenario created 36,228 km^2 of suitable habitat for our focal sagebrush-associated species across the entire study area, with 14,399 km^2 of that area occurring within PACs. Conversely, 52,184 km^2 of suitable habitat for our pinyon-juniper associated species was removed from the landscape under our hypothetical conifer removal scenario, with 22,912 km^2 of that area occurring within PACs. We identified a total of 26,551 km^2 and 6712 km^2 where suitable habitat could be created for our focal sagebrush species under the conifer removal scenario, without eliminating suitable habitat for our focal pinyon-juniper associated species, across the entire study area and PACs; respectively.

4. Discussion

Habitat management in the Great Basin has primarily focused on a small number of species, particularly Greater Sage-Grouse, and has employed conifer removal as a preferred vegetation management tool. In this study, we consider how this paradigm could affect a wider suite of species of conservation concern. Our findings support previous assertions that conifer removal presents ecological trade-offs for wildlife (Bombaci and Pejchar, 2016; Holmes et al., 2017; Magee et al., 2019), and that conifer removal at scale is likely to generally benefit sagebrush associated species while reducing the amount of suitable habitat for pinyon-juniper associated species. Notably, our total conifer-removal treatments, if conducted with no consideration of pinyon-juniper-associated species, have the potential to eliminate over 40% of remaining Pinyon Jay habitat within the Great Basin. However, our findings also suggest that for the species we modeled, there are spatial offsets in their respective concentrations of high-quality habitat, and that by taking full advantage of these offsets, net responses of multiple bird species to conifer removal can be improved, perhaps considerably. Greater Sage-Grouse PACs, where the majority (53%) of conifer removal efforts are occurring (Reinhardt et al., 2020), deserve special attention in this regard, given that they encompass 31% of Pinyon Jay suitable habitat and 37% of Gray Flycatcher suitable habitat. It may therefore be particularly important to assess and incorporate habitat requirements of pinyon-juniper associated species when conifer removal is conducted within PACs, something that has not been a focus in conifer removal prioritization efforts to date (Miller et al., 2017; Reinhardt et al., 2017).

The habitat relationships we developed largely correlated with

Table 1
Final variables and scales included in multivariate species distribution models for each of five focal bird species in the Great Basin Landscape Conservation Cooperative ecoregion. The t- and *p*-values below were generated using *t*-tests from the univariate models. The variables for each species were ordered by t-value. Response curves are provided in Fig. S3.

Brewer's Sparrow			
Variable	Scale (m)	t-value	p-value
Agriculture	2880	28.89	9.73E-171
Shrub height	360	27.13	9.42E-146
Elevation	360	22.09	1.74E-99
Percent bare ground	180	21.60	1.81E-95
Major roads	2880	20.30	2.21E-86
Transmission lines	11,520	19.15	3.84E-77
Percent herbaceous cover	180	16.68	7.40E-59
Percent impervious surface	180	15.32	1.65E-50
Mean pH	180	14.71	3.25E-46
Normalized difference vegetation index	720	14.67	3.70E-46
Litter cover	720	14.18	2.42E-43
Depth to restricted layer	1440	13.38	1.27E-38
Percent silt	360	13.20	1.39E-37
Percent sand	5760	13.08	6.20E-37
Slope	5760	11.71	7.35E-30
Annual precipitation	2880	7.82	8.36E-14
Intermittent streams	11,520	5.55	3.59E-07
Percent pinyon-juniper	180	5.10	3.73E-06
Year since last fire	90	4.68	2.96E-05
Perennial streams	1440	3.74	0.001698

Pinyon Jay			
Variable	scale (m)	t-value	p-value
Agriculture	11,520	33.00	5.79E-180
Saturated soil water content	360	32.27	1.29E-135
Elevation	360	28.66	1.28E−115
Residual soil water content	1440	22.13	9.53E-79
Percent bare ground	2880	19.80	1.18E-67
Shrub height	720	18.23	7.69E-59
Compound topographic index	1440	17.77	9.02E-57
Slope	11,520	17.54	3.23E-55
Solar radiation	180	15.60	2.44E-45
Transmission lines	11,520	14.99	1.01E-43
Perennial streams	5760	14.97	1.05E-42
Major roads	11,520	14.00	2.10E-39
Percent pinyon-juniper	360	12.82	5.59E-32
Percent impervious surface	360	9.19	4.51E-18
Calcium carbonate	360	7.87	1.80E−13
Percent herbaceous cover	360	7.62	9.48E-13
Organic matter	11,520	7.36	6.42E-12
Annual water deficit	11,520	7.31	1.00E-11
Percent big sagebrush	90	6.43	2.72E-09
Year since last fire	11,520	4.15	0.000335
Bulk density	90	3.87	0.001051
Intermittent streams	90	3.72	0.001859

Gray Flycatcher			
Variable	Scale (m)	t-value	p-value
Agriculture	11,520	36.51	3.34E-249
Temperature seasonality	90	26.63	4.96E-119
Percent silt	2880	19.20	8.62E-69
Shrub height	1440	15.72	7.87E-49
Compound Topographic index	1440	11.27	1.39E-26
Transmission lines	11,520	10.49	2.06E-23
Height above river	11,520	9.11	5.83E-18
Percent pinyon-juniper	360	8.52	8.09E-16
Solar radiation	180	8.05	2.85E-14
Annual water deficit	11,520	6.23	7.16E-09
Mean March snowpack	2880	6.15	1.20E-08
Percent impervious surface	90	5.91	4.59E-08
Perennial streams	11,520	5.74	1.23E-07
Percent herbaceous cover	90	5.38	8.91E-07
Intermittent streams	180	4.72	2.48E-05
Percent cheatgrass	90	3.88	0.000952

Sage Sparrow			
Variable	Scale (m)	t-value	p-value
Agriculture	2880	28.67	2.91E-144
Major roads	11,520	26.32	7.50E-121
Percent bare ground	720	25.89	8.05E-105
Shrub height	720	19.77	1.22E-69
Actual evapotranspiration	90	19.50	1.68E-68
Percent impervious surface	720	17.25	8.15E-60
Percent sand	11,520	16.32	4.55E-50
Seasonal temperature	90	12.76	2.42E-32
Available water capacity	180	12.76	2.64E-32
Percent tree cover	360	12.13	2.67E-30
Perennial streams	5760	10.48	9.63E-23
Organic matter	180	10.39	1.24E-22
Bulk density	11,520	8.74	2.22E-16
Solar radiation	11,520	8.53	1.24E-15
Percent cheatgrass	11,520	8.15	2.24E-14
Litter	11,520	7.73	4.97E-13
Annual herbaceous cover	180	7.56	1.77E-12
Mean pH	11,520	7.35	7.42E-12
Year since last fire	11,520	7.12	3.50E-11
Depth to restricted layer	1440	5.30	1.82E-06
Intermittent streams	11,520	5.25	2.43E-06
Precipitation, seasonality	11,520	4.76	2.59E-05

Juniper Titmouse			
Variable	Scale (m)	t-value	p-value
Elevation	720	18.80	5.10E-52
Solar radiation	360	13.83	1.31E-33
Shrub height	180	12.47	1.16E-27
Soil water content at field capacity	180	11.57	2.34E-24
Major roads	5760	10.23	3.20E-20
Perennial streams	5760	9.46	1.72E-17
Temperature, seasonality	90	7.71	3.75E-12
Transmission lines	5760	7.70	3.15E-12
Precipitation, coldest quarter	11,520	7.35	3.48E-11
Normalized difference vegetation index	720	5.87	1.50E-07
Percent herbaceous cover	11,520	4.71	4.55E-05
Intermittent streams	11,520	4.22	0.0003790

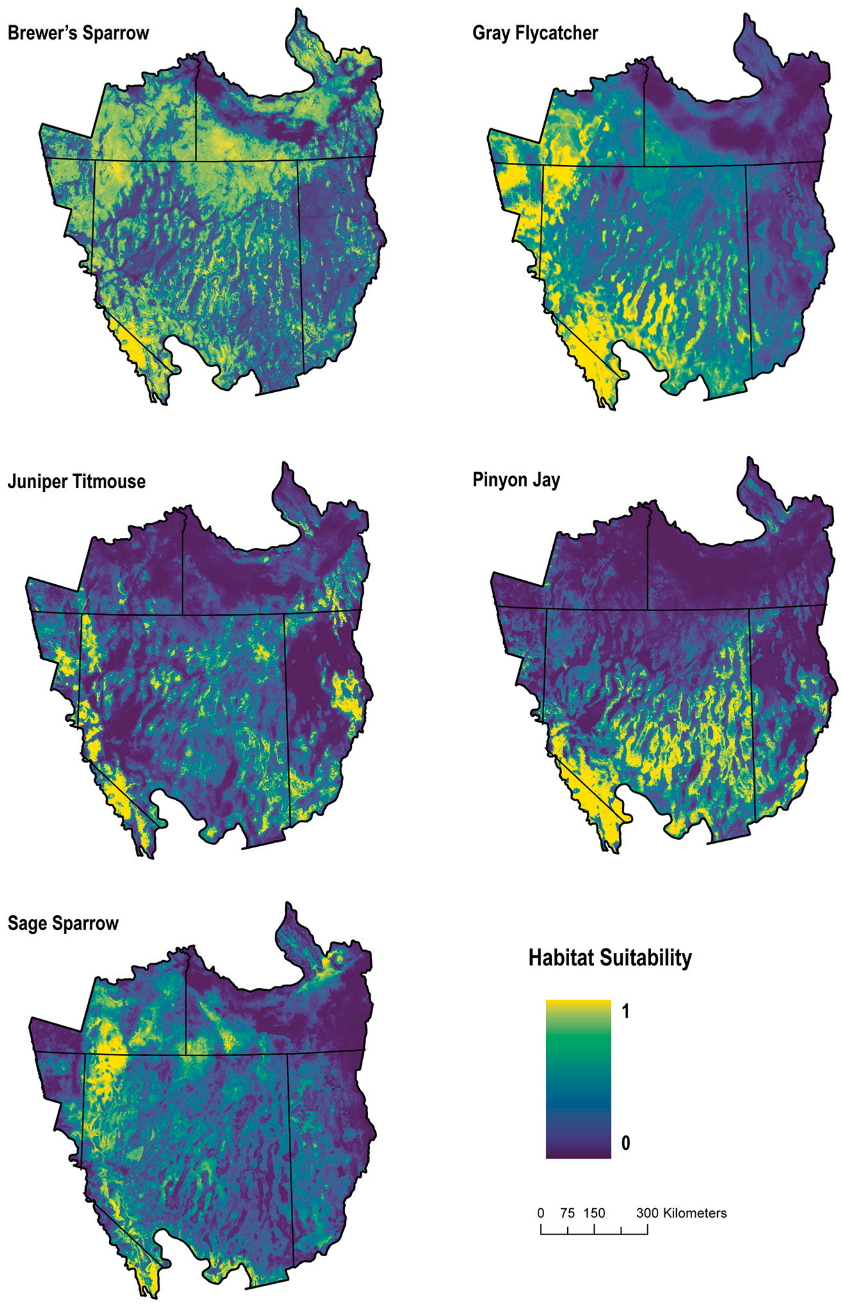

Fig. 2. Habitat suitability predictions derived from multi-scale ensemble species distribution models for five focal bird species across the Great Basin.

previous modeling efforts of our focal species. Like Knick et al. (2008) and Donnelly et al. (2017), our final species suitability models contained habitat, topographical, and anthropogenic variables, which underscores the need for future habitat modeling efforts to incorporate these elements. Our inclusion of additional anthropogenic features, transmission lines, and roadways, in our analysis expanded upon the effort of Knick et al. (2008). One or more of these anthropogenic variables were included in our final model for each focal species, which aligns with most prior research demonstrating general avoidance of roads and developed regions by our focal species (Francis et al., 2009; Ingelfinger and Anderson, 2004; Mutter et al., 2015).

Our work demonstrates the utility of merging opportunistic data with data collected through standardized monitoring programs to develop and evaluate habitat suitability models. The benefits of less expensive, large and broad-ranging datasets of opportunistic occurrences compared to more expensive data collected across smaller geographic extents from standardized monitoring efforts has been a frequent topic of discussion (Hochachka et al., 2012; Janousek et al., 2019; Rondinini et al., 2006). The extensive eBird data set provided the opportunity to explore habitat suitability relationships for a larger number of variables at broader spatial scales than would have been possible with data from more structured monitoring efforts alone. The eBird data set also allowed us to incorporate multiple scales in our analytic framework to ensure our SDMs reflected an appropriate scale of selection of each landscape variable, while using an ensemble approach allowed for the incorporation of multiple SDMs into a single output. Based on AUC values, these ensemble models generally performed the same or better than any individual model on its own (Grenouillet et al., 2011). We were able to further investigate model performance with independent datasets that employed robust, systematic sampling designs to ensure our habitat models were not biased by the limitations of opportunistic data collection (Phillips et al., 2009; Yoccoz et al., 2001).

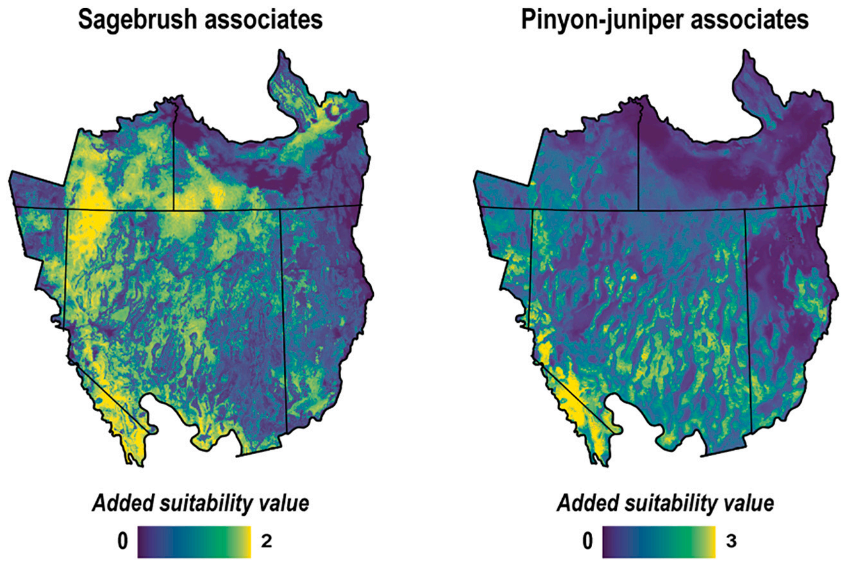

Fig. 3. Summed habitat suitability surfaces for sagebrush and pinyon-juniper associated species in the Great Basin Landscape Conservation Cooperative. The sagebrush associated species were Brewer's Sparrow and Sage Sparrow and the pinyon-juniper associated species were Gray Flycatcher, Juniper Titmouse, and Pinyon Jay.

Table 2
Landscape metrics describing habitat continuity for our five focal species across the Great Basin. The largest patch index is the percent of the landscape covered by the largest patch of suitable habitat. The core area index is the percentage of core area in relation to patch area. The aggregation index equals 0 when suitable habitat is disaggregated and 100 when habitat is maximally aggregated. Contiguity assesses the spatial connectedness of pixels in patches; equals 0 for one-pixel patches, and 1 for fully connected patches. The radius of gyration measures the distance of each cell in a patch to the patch centroid.

Species	Percent of suitable habitat in the Great Basin	Mean patch area (km^2)	Largest patch index (%)	Mean core area index (%)	Mean aggregation index	Mean contiguity	Mean radius of gyration (m)
Brewer's Sparrow	41.3%	12.85	10.2	4.27	98.2	0.35	289
Gray Flycatcher	38.4%	3.62	29.9	0.29	98.0	0.14	74.6
Juniper Titmouse	12.1%	4.79	1.34	4.03	96.5	0.35	270
Pinyon Jay	14.1%	1.68	3.95	0.41	94.7	0.17	90.3
Sage Sparrow	26.4%	8.10	6.77	3.50	97.9	0.31	249

Table 3
Habitat gains and losses for four bird species from wholesale conifer removal across the entirety of the Great Basin Landscape Conservation Cooperative (LCC) study area and within Greater Sage-Grouse Priority Areas for Conservation (PACs) in the Great Basin LCC.

Great Basin LCC						
Species	Suitable habitat (km^2)	Suitable habitat with conifer removal (km^2)	Suitable habitat added (km^2)	Suitable habitat lost (km^2)	Percent change	
Brewer's Sparrow	212,743	223,976	13,007	1,904	6 %	
Sage Sparrow	112,961	136,220	23,221	132	17 %	
Gray Flycatcher	197,922	176,872	1,655	22,538	−11 %	
Pinyon Jay	72,558	44,014	1,061	29,646	−41 %	
Greater Sage-Grouse PACs in Great Basin LCC						
Species	Suitable habitat (km^2)	Suitable habitat with conifer removal (km^2)	Area added (km^2)	Area lost (km^2)	Percent change	Net change in the Great Basin from treating only PACs
Brewer's Sparrow	107,441	112,070	5,240	657	5 %	2.46 %
Sage Sparrow	45,913	55,074	9,159	47	20 %	8.11%
Gray Flycatcher	73,217	64,483	974	9,672	−13 %	−4.89%
Pinyon Jay	22,617	9,435	82	13,240	−58 %	−18.25%

The predictive power of these tools was highlighted in our high Boyce Index values from out of sample, systematically-collected, data from the region.

We recognize that though our models had high predictive performance, there are caveats to their use. On the one hand, our brute force scenario of complete conifer removal exceeds what is likely to occur. On

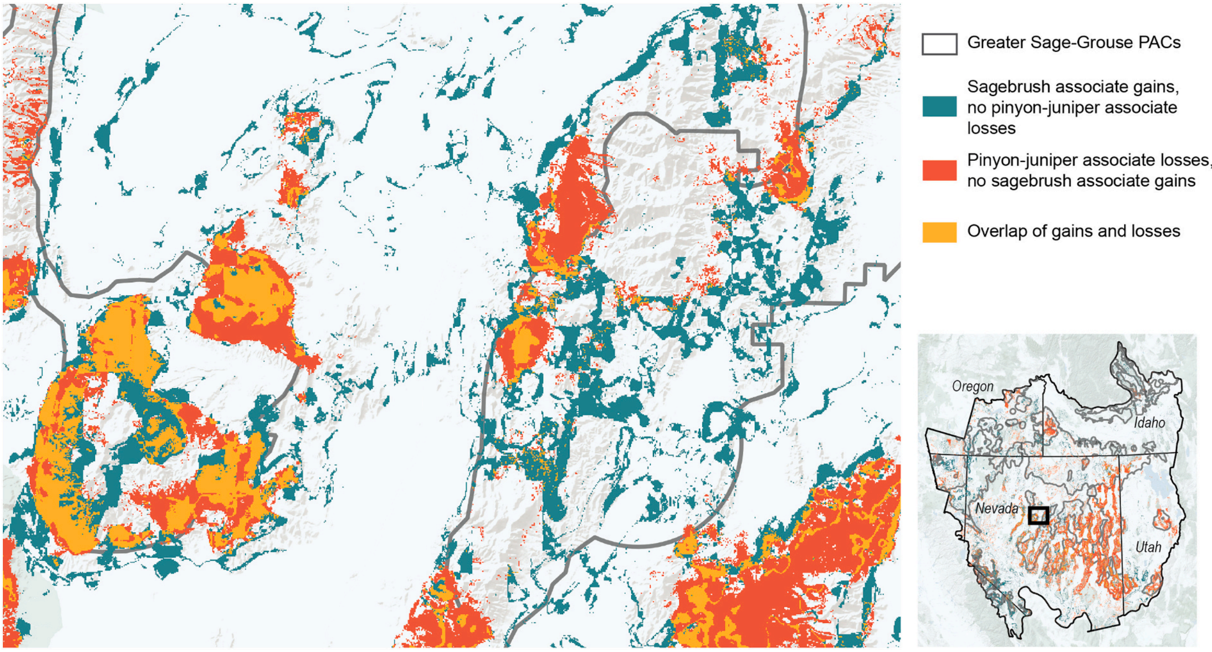

Fig. 4. Subset of Great Basin Landscape Conservation Cooperative study area showing Greater Sage-Grouse priority areas for conservation (PACs), and habitat gains for sagebrush associates (Brewer's Sparrow and Sage Sparrow) and habitat losses for pinyon-jay associates (Gray Flycatcher and Pinyon Jay) under wholesale conifer removal.

the other hand, our habitat suitability models include predictors that likely serve as proxies for tree cover even when the tree cover attribute was reduced to zero. These two factors may to some extent offset one another. Other subtleties include the fact that actual conifer removal treatments are often targeted at areas with relatively low canopy cover and fewer mature trees (Miller et al., 2017), which we did not account for in our removal scenario. For these reasons, a more nuanced approach that simulates conifer removal at different extents and scales and that incorporates the characteristics of targeted woodlands may provide additional information. Despite these limitations, our maps can serve as coarse project-level tools for managers seeking to identify potential areas where conifer removal would improve habitat for sagebrush species while mitigating unwanted negative impacts on pinyon-juniper species of conservation concern.

Large-scale habitat alteration programs, like conifer removal in the Great Basin, require integrated research and management to promote a full ecological understanding of their system-wide effects (Chambers et al., 2008). In contrast, reliance on a single species to serve as an indicator of ecological benefit can be limiting. For example, while Greater Sage-Grouse have been found to be a good surrogate species for other sagebrush obligates, this may not be the case for sagebrush associates (Carlisle and Chalfoun, 2020; Rowland et al., 2006) and is certainly not the case for pinyon-juniper associates. Other research suggests that carefully selecting multiple focal species for conservation and management produces better results than emphasizing a single umbrella species (Fleishman et al., 2001; Simberloff, 1998). Further, enlarging the suite of focal species increases the likelihood that they collectively provide a useful representation of the biological communities in which they exist.

Our results suggest there is significant potential in the Great Basin to create a new and effective paradigm for vegetation management that is informed by a set of multiple focal species. The pragmatic urgency of pursuing these changes is emphasized in particular by the pronounced rate of long-term Pinyon Jay population decline in western coniferous forests (Boone et al., 2018; Sauer et al., 2017), the relatively small amount of suitable habitat within the region for this species, the potential threat of climate change to future pinyon nut production (Redmond et al., 2012), and other threats to the species (Jolly et al., 2015; Westerling et al., 2006). Under this new paradigm, conifer management in the Great Basin could incorporate core area concepts for multiple species and pursuit of landscape-scale mosaics that maximize ecosystem function, diversity, and resilience. In addition to siting considerations, the on-ground parameters of conifer management could potentially be enhanced such that they not only create sagebrush habitat, but also improve the habitat value of the pinyon-juniper woodlands that remain. These considerations, when integrated with existing products to inform vegetation management planning (e.g. Chambers et al., 2017; Crist et al., 2016; Reinhardt et al., 2020), could provide managers with a rich set of tools to better achieve integrated ecosystem management.

CRediT authorship contribution statement

Katherine Zeller: Conceptualization, Methodology, Formal analysis, Writing – original Draft, Writing – review & editing, Visualization, **Samuel Cushman:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition, **Nicholas Van Lanen:** Conceptualization, Validation, Writing – original Draft, Writing – review & editing, **John Boone:** Conceptualization, Validation, Writing – original Draft, Writing – review & editing, **Elisabeth Ammon:** Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109130.

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