Landsc Ecol (2023) 38:1971–1989
https://doi.org/10.1007/s10980-023-01672-4

RESEARCH ARTICLE

Pygmy rabbit habitat network reveals threats and opportunities for management and conservation

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Received: 21 June 2022 / Accepted: 24 April 2023 / Published online: 8 May 2023

Abstract
Context Identifying core habitat areas and corridors is a first step to ensuring suitable areas are available to support movement and gene flow. The pygmy rabbit (*Brachylagus idahoensis*) is a species of concern and a sagebrush obligate of the arid Great Basin, yet a habitat network of core areas and corridors for this species has not been assessed.
Methods Using a multiscale habitat modeling approach, we mapped pygmy rabbit habitat suitability and identified important variables that define habitat suitability. Movement pinch points in the Snake River plain and from Nevada west to Oregon/Idaho were identified from our connectivity analyses.
Results Vegetation and climate variables were key for predicting pygmy rabbit habitat suitability constituting 38% and 31% of total variable importance respectively. Vegetation variables were consistently selected at fine spatial scales (90–720 m) whereas all other types of variables varied in their spatial scale. The level of protection for corridors compared to core areas differed depending upon the metric. Core areas had a greater percentage of sage-grouse priority Habitat Management Area but a lower percentage of total Habitat Management Area compared to corridors.

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-023-01672-4.

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Threats were consistently higher for corridors compared to core areas across a wide range of metrics.

Conclusions The network of corridors and core areas from this analysis provide land managers with a starting point to develop site-specific plans to enhance pygmy rabbit habitat and connectivity. Corridors tended to have less protection under the sage-grouse priority areas than core areas and appear to be potentially more susceptible to climate-change range retraction.

Keywords Biogeography · Dispersal · Landscape genetics · Microsatellites · Resistance surfaces

Introduction

Conserving core areas and ecological corridors to support species movement have been key strategies in the global conservation movement (Merriam 1990; Jongman 1995; Opdam et al. 1995) with recent high-level commitments from the US government and other nations to conserve 30% of land and 30% of waters for preserving biodiversity (USDOI 2021). Maintaining connectivity is critical to promoting wildlife movements, including those related to breeding and gene flow (Hanski and Simberloff 1997) and for facilitating a species' response to climate change (Keeley et al. 2018).

Ecological corridors have been defined as "linear landscape features that connect two or more habitat patches and function to facilitate movement" (Soule and Gilpin 1991). Corridors have alternately been characterized as critical for upholding network-wide connectivity (Gilbert-Norton et al. 2010; Saura et al. 2014; Resasco 2019) or representing a trade-off in which lower quality habitat is prioritized for conservation over higher quality core habitat (Simberloff and Cox 1987; Sawyer et al. 2011; Haddad et al. 2014; Travers et al. 2021). Therefore, there is considerable scientific debate about the relative importance of core areas and corridors (Noss and Harris 1986) and habitat loss versus habitat fragmentation per se (Fahrig 2003; Lindenmayer and Fischer 2007). For example, several studies have found that improving matrix quality may be critically important for species, perhaps even more important than increasing the size of habitat patches (Prugh et al. 2008; Haddad et al. 2015; Rybicki et al. 2020; Ramírez-Delgado et al. 2022). Corridors are commonly located outside of protected areas and frequently occur in sink habitats that may facilitate movement, but are unable to sustain long-term persistence (Mateo-Sánchez et al. 2015). Therefore, corridors may be subject to a greater degree of anthropogenic change than core areas due to factors such as roads, agriculture, wildfire, invasive annual grasses, and climatic conditions. Typically, threats are only assessed for core areas or habitat patches, but assessing the types and prevalence of threats in corridors is also necessary for developing effective habitat management plans. Here, we propose a framework in which both threats and levels of protection are assessed for both core areas and corridors.

Sagebrush ecosystems in western North America and sagebrush-dependent species are rapidly declining (Davies et al. 2011) due to a number of stressors including climate change (Schlaepfer et al. 2012; Shriver et al. 2018), increased fire occurrence (Balch et al. 2013; Pilliod et al. 2021), invasive annual grasses (Bradley and Mustard 2005; Boyte and Wylie 2017), an expanding human footprint (Leu et al. 2008; Germaine et al. 2020), tree expansion (Olsen et al. 2021), and novel predators (Howe et al. 2014). Sagebrush obligate species include the Greater Sage-grouse (*Centrocercus urophasianus*) (hereafter referred to as sage-grouse) (Connelly and Braun 1997; Rowland et al. 2006), pygmy rabbit (*Brachylagus idahoensis*) (Shipley et al. 2006), Brewer's sparrow (*Spizella breweri*) (Rottler et al 2015), sage sparrow (*Artemisiospiza nevadensis*), and the sage thrasher (*Oreoscoptes montanus*). Of these species the sage-grouse has received the most conservation attention, and population declines of this species have been well documented (Connelly and Braun 1997) and linked to sagebrush-related declines (Knick et al. 2013). Pygmy rabbits have received less attention, but studies have increasingly shown that their population numbers are also sensitive to changes in habitat quality and anthropogenic stressors (Crawford et al. 2010; Germaine et al. 2017).

Although the two species share many similar habitat needs and have overlapping ranges (Smith et al. 2019) they also differ in important ways (Smith et al. 2021). Sage-grouse chicks require late-summer forbs making them reliant upon mesic habitats such as wet meadows and riparian areas (Donnelly et al. 2016), while pygmy rabbits do not differ strongly in their seasonal habitat selection (McMahon et al. 2017). In particular, Smith et al. (2021) discussed that protections for sage-grouse may protect pygmy rabbit habitat patches, but pygmy rabbit populations may decline and opportunities for natural immigration and emigration may be limited without also conserving connectivity among habitat patches. Therefore, because of the differences in habitat requirements, movement abilities, and functional connectivity for these species, there is a need to develop pygmy rabbit-specific habitat and connectivity models to assess whether sage-grouse can serve as a suitable umbrella species for pygmy rabbits.

We leveraged already-collected presence-only data to model multi-scale habitat suitability and connectivity for the pygmy rabbit across the Great Basin Ecoregion in the western U.S. (hereafter Great Basin). In order to understand the factors controlling the distribution of pygmy rabbits and to allow managers to prioritize management based on habitat amount and connectivity, we developed multi-scale habitat suitability and connectivity models across the study area. Objectives of this study include 1) examining the scale of effect (Jackson and Fahrig 2014) for a range of habitat predictor variables, 2) developing habitat suitability and connectivity models, 3) mapping a habitat network for pygmy rabbits in the Great Basin, and 4) comparing the amount of protection and threats in core habitat areas, corridors, and other reachable habitat (defined as habitat to which the species could possibly disperse from known or likely starting points).

We predict a priori that pygmy rabbits will respond primarily to vegetation variables related to sagebrush cover and climatic variables describing the climatic niche of sagebrush, and that selection for these variables will occur at broad spatial scales (> 10 km). We base our predictions of pygmy rabbit connectivity on past modeling of sage-grouse, another sagebrush obligate (Crist et al. 2017). We expect that core areas will be located in southeastern Oregon/Nevada, Idaho/Nevada, eastern Nevada, and Idaho north of the Snake River Plain, based on previous studies (Larrucea and Brussard 2008; Smith et al. 2019). Pinch points (areas within corridors where movement is constricted due to a lack of suitable habitat) are most likely to occur between these core areas because of the presence of anthropogenic features, such as roads, urban development, and agricultural areas, as well as secondary impacts of human development that may include increased fire and invasive species. Corridors for many species contain lower levels of protection (Kastza et al. 2020; Stahl et al. 2020) and greater levels of threat (Nandy et al. 2007; Ntongani et al. 2010; Martin et al. 2019) compared to core areas. Confirmation of these predictions would indicate that separate management actions may be required for corridors as opposed to core areas with corridors potentially requiring land acquisition, barrier removal, and habitat restoration and the management of core areas focused more on the maintenance of large tracts of sagebrush.

Methods

Study area

Our study area encompassed three level 3 ecoregions: the central Great Basin, northern Great Basin, and Snake River Plain (Omernik and Griffith 2014) as shown in Fig. 1. The Great Basin ecoregion is a large temperate desert with basin and range topographic characteristics which encompasses most of Nevada and parts of Oregon, California, Idaho, and Utah. The dominant vegetation is salt desert scrub with sagebrush shrublands in the valleys and lower elevation areas, and pinyon-juniper woodlands, open conifer forests and mountain sagebrush in the mountainous higher elevation areas. Although nearly the entire Great Basin is considered arid with an average annual precipitation ranging from 123—353 mm in the valleys (PRISM Group 2010) distinct gradients of aridity exist. Many areas of northern Nevada and southern Idaho are considered sagebrush steppe, a vegetation type that includes a wider range of perennial forbs and grasses, and parts of central and eastern Nevada are sagebrush desert, a vegetation type that has far fewer forbs and grasses. The southeastern portion of the Great Basin is subject to summer monsoonal storms whereas the northern and western portions of the Great Basin are in a winter-dominated precipitation regime. Datasets containing several important environmental covariates (e.g. sagebrush cover, herbaceous cover, etc.) were not available for the entire study region. Therefore, our study area was refined to encompass areas that had all geospatial covariates at the time this study was undertaken (Fig. 1).

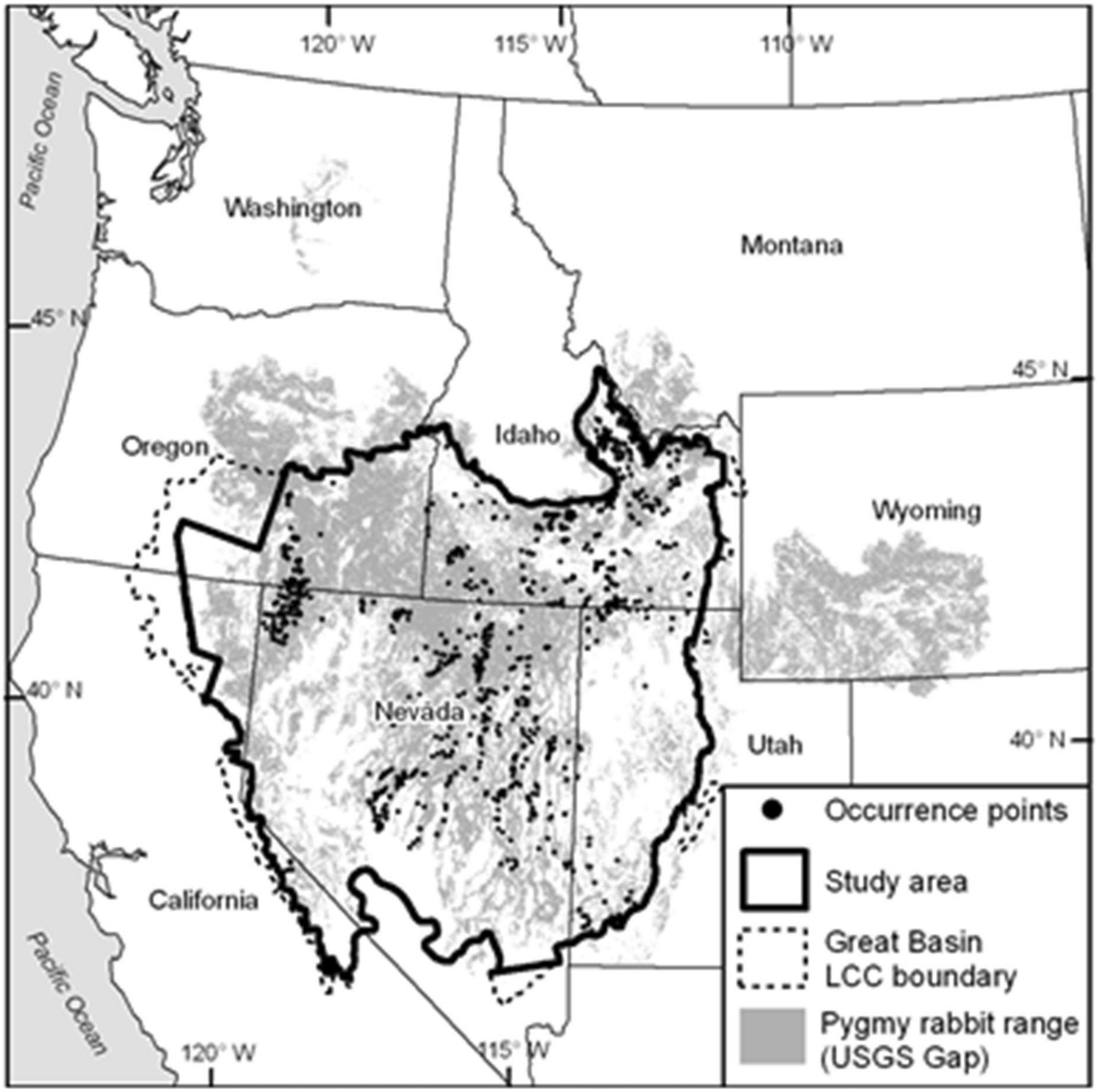

Fig. 1 Map showing the range of pygmy rabbit (USGS GAP) in the intermountain western United States in gray, the Great Basin boundary (dashed line), and the study area extent (bold black line). Occurrence points used for modeling are shown as small black dots

Presence / Pseudoabsence data

Presence data for pygmy rabbit (n = 2630) were derived from a number of sources including (1) recent surveys by the University of Nevada, Reno as part of a pygmy rabbit habitat modeling and demography project (Crowell et al. 2020), (2) Larrucea and Brussard (2008), (3) locations from the BLM Inyo Office (Bishop, California), (4) survey data from the Sheldon-Hart Mountain Refuge Complex, (5) locations from the Idaho and Utah Natural Heritage databases, (6) survey data from the Nevada Department of Wildlife, (7) data collected by consulting companies during Ruby Pipeline surveys, and (8) museum records from the Arctos database.

To reduce spatial correlation in the data, we gridded the entire Great Basin study area into 1-km grid cells and recorded presences and that fell within each grid cell. When multiple agencies had records located within a grid cell we prioritized the data according to the agency which had the most current and complete records. The University of Nevada, Reno, surveys were given the highest priority since they took place in 2016–2017 and data from Larrucea and Brussard (2008) were given second highest priority. The next highest priority was given to data from the BLM Inyo Office followed by data from the Sheldon-Hart Mountain Refuge Complex. The Idaho and Utah Natural Heritage Databases were given the next highest priority followed by the NDOW database, the Ruby Pipeline dataset, and finally the Arctos data. This spatial rarefication process resulted in 1,340 presence points for use in the analysis. Pseudo-absences were created by randomly sampling from within the range of pygmy rabbit in the Great Basin (USGS GAP data) in a 10:1 ratio with the presence data. All pseudo-absence points were sampled so that they were 1 km away from each other.

Geospatial variables

We selected 14 climate, three topographic, 13 soil, 14 vegetation, four human development, and four water-related variables that may affect pygmy rabbit habitat suitability (Table 1). We resampled all geospatial variables to a 90-m grid resolution. We also smoothed each variable at eight spatial scales. Exploring a variety of different smoothing factors allows for the identification of the appropriate scale of effect for each variable and the construction of multi-scale models (McGarigal et al. 2016). We used the *smoothie* package (Gilleland 2013) in the R software environment (R Core Team 2016) to apply a Gaussian smooth to each environmental variable with the following bandwidths: 90 m, 180 m, 360 m, 720 m, 1440 m, 2880 m, 5760 m, and 11,520 m.

Multiscale species distribution models

We used the scale optimization approach described in Shirk et al. (2018) to identify the characteristic scale of selection for each variable and obtain a final variable set for the SDMs in a manner similar to what has been done for other species (Zeller et al. 2021a, 2021b). For each environmental variable at each scale, we performed student t-tests to evaluate the difference in means between values at the presence and pseudo-absence points. We then removed any scaled variable that had a p-value $>$ 0.01. For each variable, we retained the scale that resulted in the highest t-value. We then assessed pairwise Spearman's rank correlations among all remaining variables and removed the variable with the lower t-value from any pair that had a correlation greater than 0.6. We used the remaining variables to develop the SDMs.

We fit SDMs for pygmy rabbit with two regression methods [Generalized Linear Models (GLMs); Multivariate adaptive regression splines (MARS)], and three machine-learning methods [Random Forests (RF); Boosted Regression Trees (BRT); Maximum Entropy (MAXENT)], with the BIOMOD2 package in R (Thuiller et al. 2016). For each model, we performed a tenfold cross validation procedure to assess each model's predictive ability using 80% of the data for training and 20% for testing. Across the 10 folds, we calculated the Area Under Receiver operating characteristic curve (AUC; Hanley & McNeil 1982) and used the averaged AUC values to formally rank our models. Due to the absence of a single SDM model that was clearly superior to all others, we combined our entire suite of SDM models into a final 'ensemble' model by calculating a weighted average with the weights based on the AUC values. Ensemble models have been shown to outperform individual SDMs and their use has thus been proposed as the optimal way to estimate presence-pseudo-absence models (Grenouillet et al. 2011). We then projected the ensemble model across the Great Basin to predict habitat suitability across the study area. Finally, we thresholded the habitat maps using maximum True Skill Statistic (maxTSS; Liu et al. 2016) to create a binary map of suitable and unsuitable habitat.

We also assessed the predictive ability of our models with the Boyce Index (Boyce et al. 2002; Hirzel et al. 2006). The points removed during the spatial rarefication procedure were used as hold-out points for this calculation. The Boyce Index compares the expected frequency of observed values at the hold-out points with the expected values based on a random distribution across the study area for a range of habitat suitability classes. The final performance summary statistic is the spearman rank correlation coefficient between the observed/expected ratios and the

Table 1 Environmental variables used in the pygmy rabbit species distribution models. Source / derivation, data year, and citation are provided

Variable	Source/derivation	Year	Citation
Topography and water			
Elevation	National Elevation Dataset	2009	USGS (2009)
Slope in degrees	Derived from the National Elevation Dataset	2009	USGS (2009)
Compound topographic index	Derived from the National Elevation Dataset	2009	USGS (2009)
Intermittent streams	National Hydrography Dataset	2012	USGS (2008)
Perennial streams	National Hydrography Dataset	2012	USGS (2008)
Stream distance	National Hydrography Dataset	2012	USGS (2008)
Height above nearest drainage	Derived from the National Elevation Dataset and the National Hydrography Dataset	2009	Nobre et al. (2011) and Dilts and Yang (2015)
Vegetation			
Annual grass cover, percent	Herbaceous annual cover	2017	Boyte and Wylie (2017)
Total grass cover, percent	National Land Cover Database	2013/2014	Xian et al. (2015)
Bare ground, percent	National Land Cover Database	2013/2014	Xian et al. (2015)
Cheatgrass cover, percent	Boyte and Wiley	2015	Boyte and Wiley (2015)
Litter cover, percent	National Land Cover Database	2013/2014	Xian et al. (2015)
Big sagebrush, percent	National Land Cover Database	2013/2014	Xian et al. 2015
Sagebrush, percent	National Land Cover Database	2013/2014	Xian et al. (2015)
Sagebrush height	National Land Cover Database	2013/2014	Xian et al. (2015)
Shrub cover, percent	National Land Cover Database	2013/2014	Xian et al. (2015)
Shrub height	National Land Cover Database	2013/2014	Xian et al. (2015)
Pinyon-Juniper, percent	Falkowski et al. (2017)	2012/2013	Falkowski et al. (2017)
Tree cover, percent	National Land Cover Database	2011	Coulston et al. (2012)
Year since last fire	Monitoring Trends in Burn Severity and Geospatial Multi-Agency Coordination	2018	Eidenshink et al. (2007) and Walters et al. (2008)
Normalized Difference Vegetation Index	Landsat/Climate Engine	2017	Tucker (1979) and Huntington et al. (2017)
Human development			
Agricultural cover, percent	National Land Cover Database	2011	Homer et al. (2015)
Primary & secondary roads	TIGER line files	2015	U.S. Census Bureau (2015)
Impervious surface, percent	National Land Cover Database	2011	Xian et al. (2011)
Transmission lines	S&P Global Platt		S&P Global Platt
Climatic			
Actual evapotranspiration	Dobrowski et al. (2013)	2013	Dobrowski et al. (2013)
Degree days above 5 °C	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Annual precipitation	PRISM Climate Data	1981–2010	PRISM Climate Group 2010
Precipitation, coldest quarter	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Precipitation, seasonality	PRISM Climate Data	1981–2010	PRISM Climate Group 2010
Precipitation, warmest quarter	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Mean March snowpack, 30 yr nrml	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Solar radiation	Derived from the National Elevation Dataset	2009	McCune and Keon (2002) and Fu and Rich (2002)
Temperature range	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Temperature, seasonality	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)

Table 1 (continued)

Variable	Source/derivation	Year	Citation
Temperature, warmest month	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Temperature, warmest quarter	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Temperature, annual mean	PRISM Climate Data	1981–2010	PRISM Climate Group (2010)
Annual mean water deficit	Dobrowski et al. (2013)	2013	Dobrowski et al. (2013)
Soil			
Available water capacity	POLARIS	2016	Chaney et al. (2016)
Bulk density	POLARIS	2016	Chaney et al. (2016)
Calcium carbonate	POLARIS	2016	Chaney et al. (2016)
Clay, percent	POLARIS	2016	Chaney et al. (2016)
Organic matter	POLARIS	2016	Chaney et al. (2016)
Mean pH	POLARIS	2016	Chaney et al. (2016)
Soil depth	POLARIS	2016	Chaney et al. (2016)
Sand, percent	POLARIS	2016	Chaney et al. (2016)
Silt, percent	POLARIS	2016	Chaney et al. (2016)
Soil water content at wilting point	POLARIS	2016	Chaney et al. (2016)
Soil water content at field capacity	POLARIS	2016	Chaney et al. (2016)
Residual soil water content	POLARIS	2016	Chaney et al. (2016)
Saturated soil water content	POLARIS	2016	Chaney et al. (2016)

bins. Values closer to one indicate better predictive ability of the model. To calculate the Boyce Index, we used the ecospat package in R (Broennimann et al. 2017; Hirzel et al. 2006). Uncertainty maps were created by taking the standard deviation of the predictions from the five modeling approaches used in the ensemble model.

Connectivity modeling

We used the UNICOR package (Landguth et al. 2012) to model cumulative resistant kernel connectivity (Compton et al. 2007) across the Great Basin. Resistant kernels calculate cost and distance from source points and are summed to create a cumulative kernel surface. The output surface can be interpreted as the probability of dispersal or movement across each grid cell on the landscape. We modeled resistant kernel connectivity among 2000 source points that were distributed proportionally to habitat suitability across the Great Basin in areas known to be currently occupied by pygmy rabbit. In some rare instances (e.g. White Mountains of California), we noted areas in which habitat appeared to be suitable but no known occurrence existed. To avoid including suitable habitat that did not contain known occurrences we created a 12 km buffer around occurrence points. Contiguous habitat areas not falling within the 12 km were not included as potential source points for the resistant-kernel analysis.

The resistance surface was the linear inverse of the habitat suitability surface, range re-scaled from 1 to 100. UNICOR allows the incorporation of edge distances into the connectivity calculations. These edge distances can be used to stop the kernel from spreading beyond the dispersal distance of a species, based on cumulative cost distance values. Known pygmy rabbit dispersal distances are approximately 12 km (Estes-Zumpf and Rachlow 2009) and we conducted a sensitivity test with UNICOR that identified 96,000 as the edge distance that would result in a kernel spreading 12 km on average. Combining the resistant-kernel model with the binary habitat maps derived with the maxTSS statistic allowed us to identify areas that are considered suitable but not reachable, reachable but not suitable, and both suitable and reachable.

Core areas and corridors

Following Cushman et al. (2018), we created core areas representing the top 25% highest quality habitat (Cushman et al. 2018) located within suitable-reachable areas using a multi-step approach. First, we restricted the analysis to only assess habitat within suitable-reachable habitat. Second, we mapped the top 25% highest suitability habitat within the suitable-reachable area. Third, we grouped adjacent pixels into patches if they shared at least a single cell edge. This process resulted in our core patches. We then summarized the total habitat suitability for all patches and ranked the patches according to these sums. Fourth, we removed small patches by identifying the inflection point (elbow approach; Thorndike 1953) of a plot of cumulative habitat versus the habitat patch rank, and removing patches 230 km^2.

To map corridors, we used the Multiple Shortest Paths approach of Pinto and Keitt (2009), which is a stochastic version of the Dijkstra's algorithm. Multiple shortest paths were calculated between core areas using a custom tool in ArcGIS 10.7.1 (Dilts 2021) that added 25% random noise to the resistance surface, which, in this case, was range re-scaled from 1–100. To add 25% random noise to the raster we generated a random number for each raster cell scaled from -1 to 1, which was multiplied by 0.25 times the resistance surface and added to the original resistance surface. We mapped 20 least-cost paths between core areas and combined the least-cost paths using the Line Density tool in ArcGIS Spatial Analyst (Esri 2019) using a search distance of 1500 m. The output of the Multiple Shortest Paths included maps showing the number of overlapping paths, which allows us to identify pinch points within corridors in a manner similar to Circuitscape (McRae 2006). We created corridors by combining least-cost paths within 1500 m of each other into a single polygon. We also filled holes within the corridor polygon.

Conservation of and threats to the pygmy rabbit network

We measured the degree of protection and level of threats in pygmy rabbit core areas, corridors (from multiple shortest paths), and other reachable habitat (from resistant kernels). To assess protection, we examined overlap with all Sage-grouse Habitat Management Areas (HMAs) and priority HMAs. These HMAs have been defined by the Bureau of Land Management, US Forest Service, and US Fish and Wildlife Service to minimize surface disturbance on lands that have been mapped as critical for the sage-grouse. We calculated the percent of the pygmy rabbit network that was public land as well as an alternative measure of the degree of protection, described in more detail below. The US Geological Program Gap Analysis Program (Aycrigg et al. 2013) has mapped all public lands in the United States and has developed a classification scheme describing the level of protection ranging from 1 (wilderness) to 4 (no specific management for biodiversity). Nearly all of the lands in our study area were level 3 or higher. Status 1 lands have protections in place to keep them in their natural state (e.g. wilderness areas and national parks). Status 2 lands are primarily managed for naturalness but allow for some natural disturbances to be suppressed (e.g. wildfire). Status 3 lands manage most of their areas to maintain natural vegetative cover, but also allows for extractive uses. We mapped classes 1 and 2 together and calculated the proportion of core areas and corridors falling within those classes.

To quantify potential threats to pygmy rabbit in both corridors and core areas we calculated five metrics. The proportion agricultural land and the proportion of impervious surface were used as metrics of direct modification of habitat by humans. Agriculture data and impervious surface were derived from the National Land Cover Database 2016 (Homer et al. 2015). Impervious surface was a continuous map of cover ranging from 0 to 100%. We classified all cells with a value of 1% or greater as impervious for the purpose of this study. Invasive annual grasses, such as cheatgrass (*Bromus tectorum*), have led to reductions in sagebrush cover and an altered fire cycle that promotes more annual grass invasion (Whisenant 1990). To map annual grass cover we used the Boyte and Wylie (2017) map of annual grass cover and classified all cells with annual grass and forb greater than 10% as annual grass. Burned areas were mapped as a combination of the Monitoring Trends in Burn Severity Data (MTBS) (Eidenshink et al. 2007) and Geospatial Multi-Agency Coordinate (GeoMAC) (Walters et al. 2008) from the years 1984 to 2020. Climatic Water Deficit (CWD), defined as the difference between potential evapotranspiration and actual evapotranspiration (Stephenson 1990), can be used as a measure of aridity. High levels of CWD may indicate areas that are more prone to sagebrush range retraction (Schlaepefer et al. 2012). We calculated CWD using the Climatic Water Deficit Toolbox for ArcGIS (Dilts and Yang 2015).

Results

The scales of selection for the geospatial layers varied and ranged across the bandwidths examined from 90 to 11,520 m (Supplementary Material S1). The only consistency in characteristic scales was for vegetation variables. Pygmy rabbits selected for all vegetation variables at relatively fine scales (90–720 m). The individual SDMs all had an AUC value > 0.9, so all models were combined in the final ensemble model (Table 2). The final ensemble model contained five vegetation variables, four climate variables, three water-related variables, two soil variables, two topographic variables, one human development variable, and year since last fire (Table 3). Collectively, vegetation variables accounted for 38% of variable importance (based on summing the t-values and dividing by the total), followed by climate (31%), soil (12%), topographic (11%), anthropogenic (6%), and disturbance (2%). Response curves for each variable in the final models are provided in Fig. 2, with the most important variables (t-values > 10) being percent tree cover, mean annual temperature, elevation, percent sagebrush, percent pinyon-juniper, soil depth, distance to transmission lines, annual grass cover, precipitation of the warmest quarter, and precipitation of the coldest quarter. The predicted ensemble model indicates high habitat suitability for pygmy rabbit in the northwest corner of Nevada and north into Oregon, the northeast part of Nevada and north into Idaho, the northeastern part of the Great Basin study area, and in the basins of central and eastern Nevada (Fig. 3a). The Boyce Index of the final predictive surface was 0.88. Uncertainty in the predictions generally appeared to be highest in areas with lower suitability and where few occurrences were located (Fig. 3b).

Table 2 Model performance using the Area Under Receiver operating characteristic curve (AUC) from a tenfold cross validation for each species distribution model

Model	Presence/pseudoabsence
	AUC
Generalized linear model	0.917
Generalized additive model	0.908
Multivariate adaptive regression splines	0.913
Maximum entropy	0.916
Boosted regression trees	0.918
Random forest	0.959
Ensemble model	0.944

Table 3 Final variables and scales included in the multivariate species distribution models. The t- and p-values of the t-test for each variable are provided. Variables are listed in order of t-value from largest to smallest

Variable	scale (m)	t-value	p-value
Tree cover, percent	360	36.241	1.93E−243
Temperature annual mean	90	32.998	3.28E−181
Elevation	5760	26.909	2.34E−132
Sagebrush, percent	360	24.317	5.08E−110
Pinyon-Juniper, percent	360	23.132	8.04E−109
Soil depth	11,520	21.928	4.93E−93
Transmission lines	11,520	16.280	2.83E−54
Annual grass cover, percent	720	14.461	6.38E−44
Precipitation, warmest qtr	11,520	13.320	3.77E−37
Precipitation, coldest qtr	180	12.943	2.14E−35
Cheatgrass, percent	360	12.413	4.53E−33
Sand, percent	1440	12.183	8.47E−32
Perennial streams	11,520	9.6538	3.05E−20
Intermittent streams	5760	7.6073	6.30E−13
Solar radiation	180	7.4563	1.69E−12
Year since last fire	180	7.3598	3.57E−12
Stream distance	90	6.9282	7.38E−11
Temperature seasonality	360	5.9549	3.56E−08

The resistant-kernel model suggests that suitable-reachable pygmy rabbit habitat within the Great Basin occurs in three major regions: eastern/central Nevada, Idaho north of the Snake River Plain, and the tri-state area of Oregon, Nevada, and California with some smaller areas in eastern Oregon as shown by letters A, B, and C respectively in Fig. 3C. Twenty-seven patches accounted for 85% of suitable-reachable habitat and ranged in size from 231 to 18,006 km^2. Some suitable-reachable habitat occurred in areas that appear to be unoccupied, the largest of which is located in northeastern California followed by western Utah and a higher elevation area along the Nevada-California border as shown by letters A, B, and C respectively in Fig. 3D.

The Multiple Shortest Paths analysis identified broad corridors across the Humboldt River Plain

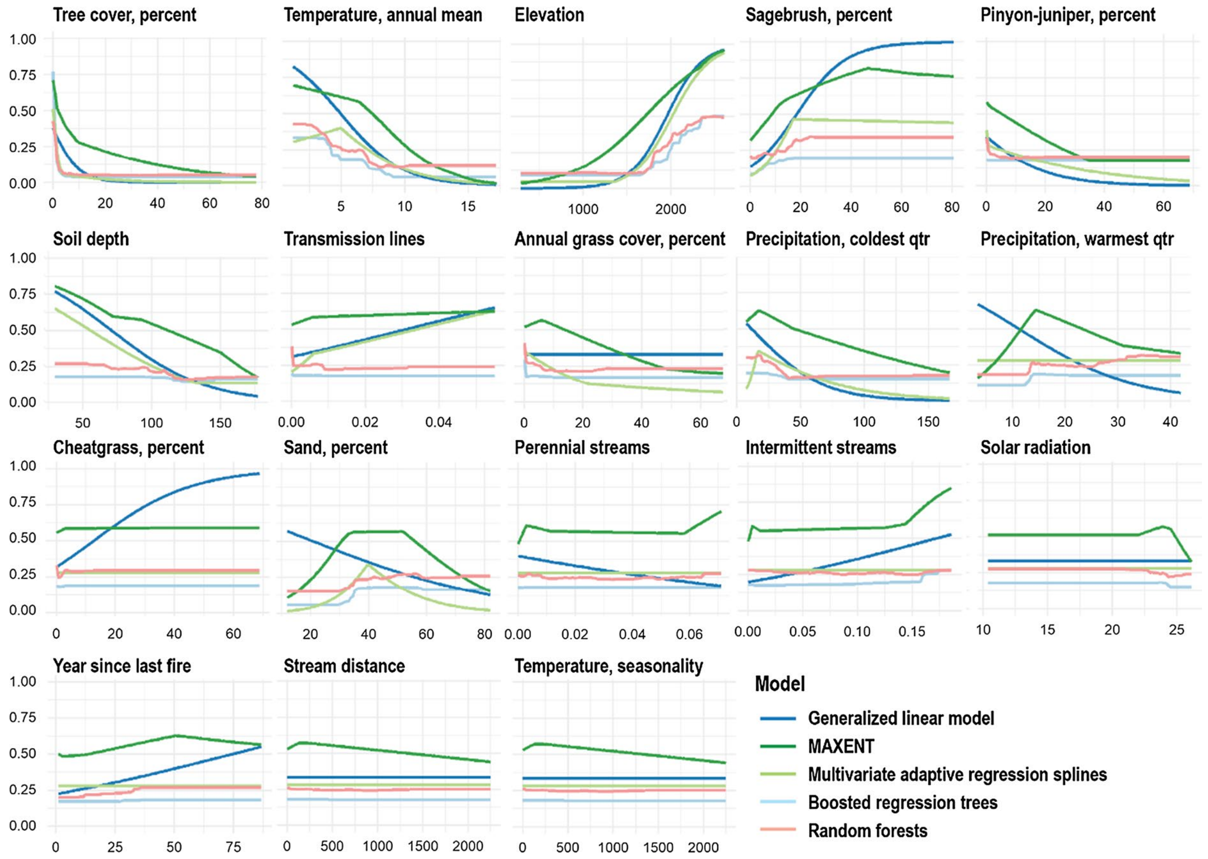

Fig. 2 Model response curves for variables in the final pygmy rabbit models

into northeastern Nevada and across the Snake River Plain into central Idaho shown with letters A and B in Fig. 3E. In contrast, the tri-state region of Oregon, Nevada, and California (letter C in Fig. 3E) appears to be disconnected from the remainder of the range. The Snake River Plain (letter A in Fig. 3F) appears to be a pinch point for potential movement with a single route that is connecting the northern Nevada and central Idaho populations of pygmy rabbits. Although the resistant-kernel analysis shows a small gap suggesting that connectivity may be limited between northern Nevada and the tri-state region (Oregon-Nevada-Idaho), we kept the single corridor connecting core areas 18 and 24 (letter B in Fig. 3F) based on expert knowledge of the study area.

Cores, corridors, and other reachable habitat differed in both levels of protection and threats (Fig. 4). Consistent with our a priori expectations, core areas were composed of a greater percentage of sage-grouse priority HMA area and a greater proportion of public lands compared to corridors and other reachable habitat. However, contrary to expectations we found that corridors and other reachable habitat had greater levels of sage-grouse HMA area and a greater proportion of GAP 1 and 2 lands. GAP 1 lands (legal protections designed to keep lands in their natural state, such as wilderness designation) were exceedingly rare in this region constituting 1.5%, 4.5%, and 4.1% for core areas, corridors, and other reachable habitat. Consistent with a priori expectations, corridors and other reachable habitat had a greater percentage of agriculture, more cheatgrass, and higher levels of Climatic Water Deficit relative to core areas.

Discussion

Our study represents the first attempt to map a habitat network for pygmy rabbit at broad spatial scales, comprised of core habitat areas, discrete corridors,

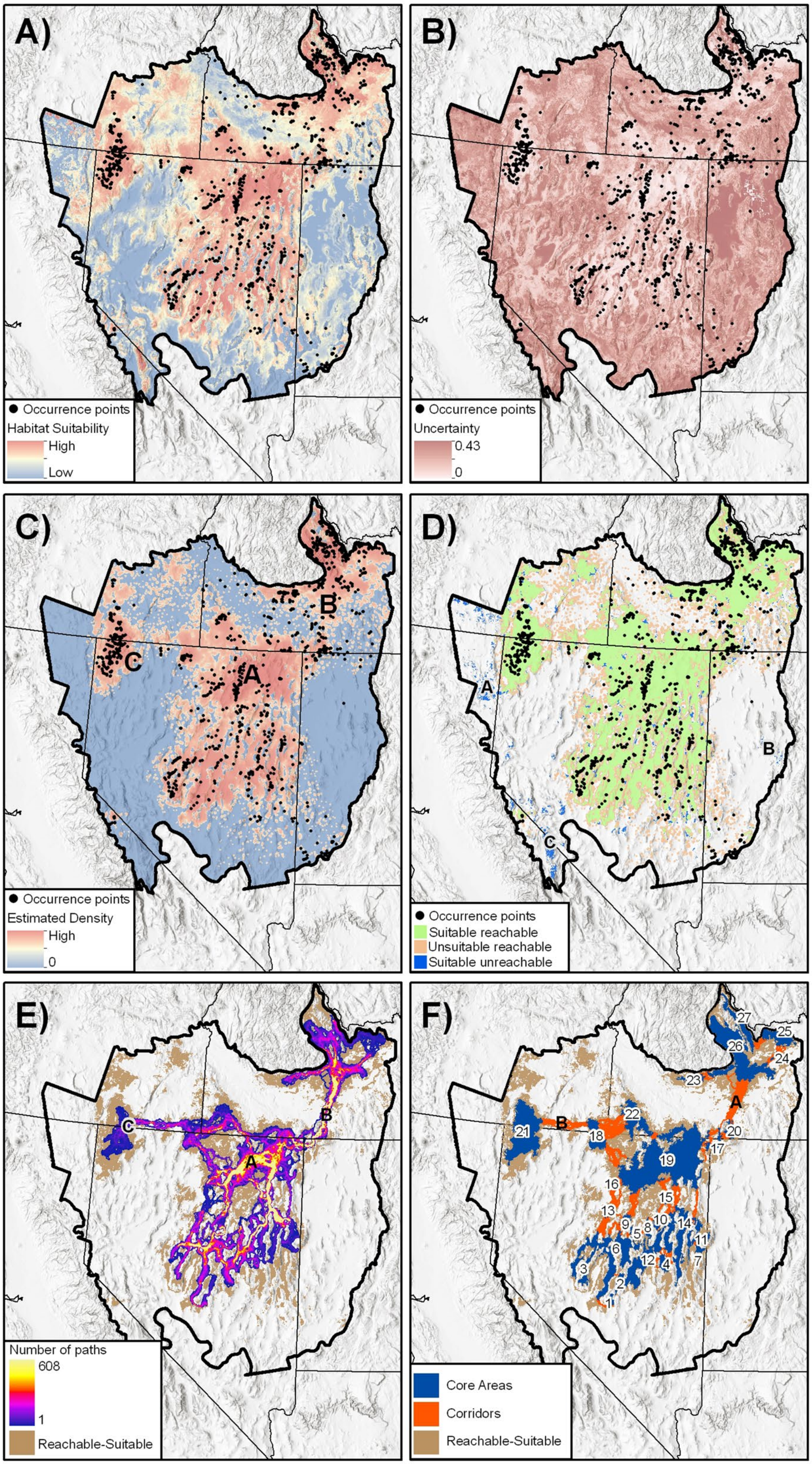

Fig. 3 **A** Pygmy rabbit (*Brachylagus idahoensis*) habitat within the Great Basin modeled using presence (black dots) and background points (not shown on the map). Red shades indicate greater relative habitat suitability and blues indicate lower suitability. **B** Pygmy rabbit habitat uncertainty as measured from the standard deviation of the average suitability with darker shades of red showing higher levels of disagreement among modeling methods and lighter shades showing more agreement. **C** Resistant-kernel of expected density of pygmy rabbit dispersers with red shades indicating greater density of dispersers and blues indicating lower densities of dispersers. **D** Habitat classified into four categories suitable (contains 95% of occurrences) and reachable (resistant-kernel predicts greater than 0 dispersers) (green), unsuitable and unreachable (gray), suitable but unreachable (brown), and unsuitable but reachable (blue, rare). **E** Total number of overlapping paths derived from the Multiple Shortest Paths analysis using 125 source points shown with a purple to yellow color ramp. The resistant-kernel is shown as a transparent gray. **F** Twenty-seven core areas (blue) and thirty-two corridors (orange). Core areas represent the highest 25% habitat suitability within reachable and suitable habitat. Corridors were mapped as Multiple Shortest Paths connecting core areas. The reachable and suitable habitat is shown as a transparent gray

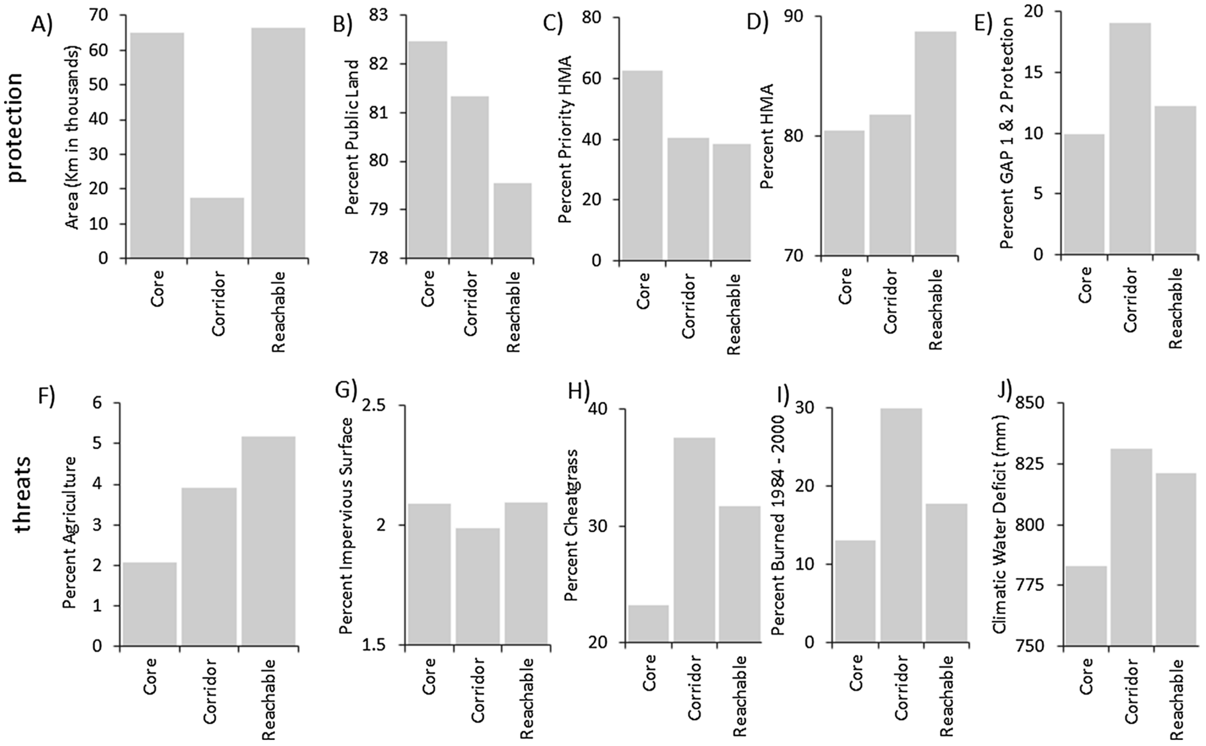

Fig. 4 Pygmy rabbit network metrics. **A** Area of pygmy rabbit core, corridor, and other reachable habitat areas (labeled as 'Reachable'), **B**–**E** percent protected, and **F**–**J** percent of pygmy rabbit network with a threat

and other reachable habitat. Within the Great Basin of North America, most habitat connectivity modeling efforts to-date have focused on the sage-grouse (Knick et al. 2013; Crist et al. 2017; Row et al. 2018). We applied commonly-used connectivity methods, such as resistant-kernels and Multiple Shortest Paths, to map corridors and connectivity for the pygmy rabbit. As such, we provide managers with detailed and species-specific information about the pygmy rabbit while providing information that allows scientists and managers to understand differences in habitat selection, movement, and existing protection between sage-grouse and pygmy rabbits.

In particular, we identified two critical pinch points to movement that may require further investigation in the field (labeled A and B on Fig. 3F). Our model predicts a single movement corridor that crosses the Snake River Plain. However, field investigation may be required for this corridor as it contains Lake Walcott in the Snake River, which may be a barrier to movement. Our model predicts that movement between the tri-state region and northern Nevada may be limited or no longer feasible in the Denio area at the Nevada-Oregon border. Here again, further field investigations are needed to determine whether pygmy rabbits are present in this valley as there is abundant sagebrush in the area. Furthermore, parts of the Denio Valley are designated as a sage-grouse GHMA (BLM 2015).

Sage-grouse and pygmy rabbits differ in terms of their specific habitat needs, with sage-grouse early brood-rearing being dependent upon mesic resources, such as meadows and interspace forbs, and pygmy rabbits having a diet that is more reliant on sagebrush itself. Despite these differences both species are considered sagebrush obligates and share habitat affinities (Smith et al. 2019, 2021). Our maps of habitat connectivity share many similarities with earlier analyses on habitat connectivity for sage-grouse. Knick et al. (2013) used the location of sage-grouse leks to develop habitat models and used Circuitscape to model population connectivity among leks. They identified the same pinch-point in the Denio Valley, although their maps also suggest that there may be other potential areas of connectivity further to the north (e.g. Steens Mountains) that may link the Nevada-Idaho-Oregon region with the Oregon-Nevada-California region further to the west. Their maps also show some support for a Snake River Plain crossing that encompasses Lake Walcott, as well as some of the same corridors connecting northeastern Nevada to eastern Nevada in the vicinity of Wells, NV. In a study using network analysis to assess the importance of sage-grouse priority habitat areas Crist et al. (2017) identified a single very large priority habitat area stretching across northern Nevada and southern Idaho west to the Nevada-California-Oregon border. This large priority habitat area includes the Denio Valley. Their study also suggests important connections between this core region and eastern Nevada as well as Idaho north of the Snake River Plain. They identify habitat connectivity between this very large core area and southwestern Wyoming as another critical connection. Our study did not consider southwestern Wyoming as this area falls outside of the Great Basin, but is within the range of pygmy rabbits (Germain et al. 2014).

Byer et al. (2021a) identified the distribution of sagebrush in the Holocene as a major driver of pygmy rabbit genetic connectivity. Our contemporary analysis using the Multiple Shortest Paths approach reveals many of the same patterns with areas north of the Humboldt River likely to have continuous and omnidirectional connectivity whereas areas south of the Humboldt River show a north–south trending pattern of connectivity characteristic of the Basin and Range geological province. Larrucea et al. (2018) noted low levels of genetic divergence among populations suggesting that the tri-state region was functionally connected to northern Nevada populations. The Byer et al. (2021a) study did not extend into Idaho, however Estes-Zumpf et al. (2010) found a level of heterozygosity in the Lemhi Valley of Idaho that was similar to what Larrucea et al. (2018) found in Nevada, which might suggest higher levels of gene flow. Furthermore, Byer et al. (2021b) found that the temporal scale of reductions in pygmy rabbit gene flow to be much more recent than previously thought with much of northern Nevada only becoming separated in the past hundreds of years. A recent range wide genomic study of pygmy rabbit shows that in addition to the Columbia Basin population being genetically distinct that southwestern Wyoming and southern Utah are also quite distinct from the Great Basin population (Nerkowski 2021). Furthermore, the Idaho populations north of the Snake River Plain appear to be genetically well-connected to the remaining populations in the Great Basin corroborating the findings of Byer et al. (2021b) that suggest that reductions in gene flow may have only occurred recently. Studies of sage-grouse genetic connectivity (Cross et al. 2018; Row et al. 2018) show similar patterns to pygmy rabbits including a genetic cluster that spans the Snake River Plain, which might suggest high levels of historical gene flow. Cross et al. (2018) identified several hub nodes of connectivity including the Lake Walcott region that our study identified.

Our study applies a multiscale habitat modeling approach for pygmy rabbit habitat mapping. Multiscale modeling approaches have become increasingly popular in recent years (McGarigal et al. 2016) as scientists have recognized that exploring multiple scales and identifying the strongest, or characteristic scale, of selection for each variable (Holland et al. 2004) allows for a more robust and nuanced estimation of habitat suitability. In addition, it has been shown that multi-scale models often outperform single-scale models (Boscolo and Metzger 2009; Kuhn et al. 2011; Sáncheza et al. 2013). Our application of the multi-scale optimization approach proposed by Shirk et al. (2018) allowed us to optimize the scales for each geospatial variable within an SDM framework and generate multi-scale SDMs. Our finding of habitat selection for vegetation variables by pygmy rabbits occurring at finer spatial scales (< 720 m) compared to other variables is consistent with models of other sagebrush obligate species in the Great Basin. For example, Zeller et al. (2021b) found that positive selection for shrub cover and negative selection for bare ground occurred at relatively fine scales (< 250 m) for pronghorn antelope. Similarly, Zeller et al. (2021a) found that selection for and against vegetation variables by the sagebrush obligate birds Brewer's sparrow and sage sparrow occurred at spatial scales less than 720 m. In contrast, selection for topographic, climatic, edaphic, and anthropogenic variables in Zeller et al. (2021a), Zeller et al. (2021b), and this study were more variable than scale selection for vegetation.

We leveraged already-collected and archived presence-only data to create baseline habitat suitability and connectivity models for pygmy rabbit (Jennings et al. 2020). This approach is promising for species of conservation concern since there are typically data that have already been collected from sources like ongoing research and monitoring projects, federal and state agencies, and natural history museums. By using archived data, habitat suitability and connectivity modeling can be done quickly and relatively inexpensively across large geographic areas since field work and data collection in the traditional sense are not needed. Though sampling biases may be present in compiling data from both research studies and opportunistically-collected data, these biases have the potential to be addressed in the modeling framework through rarefication, as we did, or other means. Model appropriateness can be confirmed through cross validation procedures or using hold-out data or data from other studies. Our models had relatively good performance with both forms of validation. These approaches are transferrable to other species and study areas and the products derived from these analyses can help with management and conservation of species of concern.

The approach outlined in this study contains a number of methodological steps that influence the ultimate location of core areas and corridors, which may influence where and how conservation resources are allocated. The biggest limitation is the fact that least-cost paths (and by extension, randomized or multiple shortest paths) will always find a solution even if it is not biologically realistic (Sawyer et al. 2011). Although these corridors probably represent historical movement paths and may offer the best option for connectivity, field-based assessments are needed to determine whether these corridors are actually usable. This may become especially imperative given future changes in climate change and land use. However, estimating potential corridors, as we have done here, provides an important starting point from which more detailed assessments can be made to ultimately inform conservation action.

Another potential limitation to the resistant kernel approach applied in this study is that we assumed that number of dispersers is proportional to habitat suitability, not abundance. Abundance models would help alleviate these concerns and more research is needed to understand how abundance is related to occurrence. However, as is the case with pygmy rabbits, most data are presence-only occurrence records. Hence, our habitat suitability models represent the relative occurrence rate and there is an explicit assumption that abundance is related to occurrence. A related issue is that due to computational limitations we seeded 2000 source points in proportion to habitat suitability in order to create the resistant kernels. The placement of such points has the potential to influence the outcome of the resistant kernels, although such a large number of points created a relatively smooth map, suggesting that 2000 points may be a large enough number for pygmy rabbits.

An additional potential limitation is that the resistant-kernel approach we used assumed that connectivity is the inverse of habitat suitability, which may not always be the case. Several studies have documented cases in which mismatches in habitat suitability and gene flow occur (e.g. Peterman et al. 2014; Mateo-Sánchez et al. 2015). Beier (2018) categorizes two types of species that use corridors, more-mobile passage species, and species with shorter dispersal ranges that he refers to as corridor dwellers. We would characterize pygmy rabbits as corridor dwellers and posit that treating the resistance surface as the inverse of habitat suitability may be more appropriate for corridor dwellers compared to passage species. Byer et al. (2021a) found that the presence of sagebrush is highly related to pygmy rabbit gene flow and almost no gene flow occurred in areas in which sagebrush was absent. Although we believe that the use of the inverse of the habitat suitability model is justified for the pygmy rabbit, more studies are needed that relate life history characteristics of species to resistance surfaces.

As with all habitat suitability models there is uncertainty that goes into every step of the process. For example, sampling is rarely done in a non-biased manner, spatial covariates may only relate to some processes of interest, and factors, such as disease, dispersal limitation, and disturbance, are not usually accounted for in the habitat modeling process. Our multiscale habitat modeling framework incorporates estimates of uncertainty, but uncertainty associated with many of the reasons above cannot be directly captured in the modeling process. Therefore, although our estimates reflect the best-available data at the time, further detailed studies using local variables and expert knowledge are suggested prior to making conservation decisions involving the use of scarce resources.

Our study provides a framework for assessing protection and threats for core areas, corridors, and other reachable habitat for pygmy rabbits and for other species globally. Kaszta et al. (2020) examined the level of protection in both core areas and corridors for the clouded leopard in southeast Asia and found only 24% of core areas and 17% of corridors to be protected, suggesting that corridors may potentially be prone to more development and anthropogenic stressors than core areas. We found mixed evidence depending on the particular metric of protection that the level of protection for corridors and other reachable habitat was less than for core areas. Corridors and other reachable habitat had lower levels of protection compared to core areas if measured by the proportion of public lands and priority HMA and higher levels of protection if measured using all HMAs and GAP status 1 and 2.

In contrast to differences in protection, differences in threats were consistently higher for corridors and other reachable habitat compared to core areas in almost all metrics. Corridors and other reachable habitat had higher levels of agriculture compared to core areas, as well as more annual grasses, burned area, and Climatic Water Deficit. Climatic Water Deficit, as a measure of atmospheric demand for water relative to supply (Stephenson 1990), suggests that corridors may be more susceptible to climate change-induced range retraction compared to core areas. Furthermore, disturbance related to changes in climate, such as fire and subsequent invasion by annual grasses, may lead to losses in sagebrush, which has been identified as being highly associated with historical gene flow for pygmy rabbit (Byer et al. 2021a). Zeller et al. (2021b) contrasted the climate change threat for both connectivity areas and habitat for pronghorn antelope in the Great Basin and found that connectivity areas were more vulnerable to climate change compared to core habitat. Our results are in-line with these findings and highlight the idea that corridors and connectivity areas may be more vulnerable to climate change for sagebrush obligate species compared to core areas and that multiple stressors may compound. Further research across a wider range of taxa and systems is needed to help determine whether corridors are inherently more vulnerable to anthropogenic and climate stressors compared to core areas. Site-specific studies can help managers determine the greatest threats and develop management plans to help mitigate specific threats.

In this study we employed a number of different connectivity modeling methods which were highly complementary to one another. The resistant-kernel modeling approach provided a continuous map that depicted the probability that a disperser might reach a given cell from a randomly-seeded start point. We used the resistant-kernels to identify core habitat as well as to divide suitable habitat into both reachable and unreachable categories, and to identify areas of general connectivity. Multiple Shortest Paths (Pinto and Keitt 2009) were used to identify potential corridors between core areas. This approach provides many of the same benefits as Circuitscape (e.g. identification of pinch points and redundant pathways) but also offers a number of additional benefits. The Multiple Shortest Paths method can be tuned to represent the level of randomization in either movement (Long 2019) or landscape (Dilts 2021) making it an ideal tool for corridor building. We found that rasters representing the cumulative number of paths easier to threshold than the cumulative current maps of Circuitscape allowing us to generate tighter more linear corridors compared to cumulative current maps which had more of an hourglass shape (broad closer to start and end points and narrow in the middle; Koen et al. 2010). However, by overlaying paths we were able to identify pinch points as well as areas where redundancy in movement pathways exists similar to McRae et al. (2008). Together, these approaches provide a comprehensive framework in which different components of habitat connectivity (core areas, corridors, suitable-reachable areas) can be assessed against potential threats as well as opportunities.

Data Archiving Statement

Data for this study are available at: to be completed after manuscript is accepted for publication.

Acknowledgements This research was made possible by grants from U.S. Fish and Wildlife, Nevada Department of Wildlife, Greater Hart Sheldon Fund, the Great Basin Landscape Conservation Cooperative, and the National Science Foundation (OIA-1826801). This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute. The findings and conclusions in this publication are those of the authors

and should not be construed to represent any official USDA or US Government determination or policy.

Author contributions TD and KZ wrote the main manuscript text. KZ and TD performed the analysis and prepared the figures. MD and EL collected data. SC and MM secured funding. All authors reviewed and contributed to the manuscript writing.

Declarations

Competing interests The authors declare no competing interests.

References

Aycrigg JL, Davidson A, Svancara LK, Gergely KJ, McKerrow A, Scott JM (2013) Representation of ecological systems within the protected areas network of the continental United States. PLoS ONE 8:e54689

Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Chang Biol 19:173–183

Beier P (2018) A rule of thumb for widths of conservation corridors. Conserv Biol 33:976–978

BLM (Bureau of Land Management) (2015) Record of decision and approved resource management plan amendments for the Great Basin region, including the Greater Sage-Grouse sub-regions of Idaho and Southwestern Montana, Nevada, and northeastern California, Oregon, Utah. U.S. Department of the Interior Bureau of Land Management, Washington, D.C., USA. https://digitallibrary.utah.gov/awweb/awarchive?item=81618 Accessed 2 Dec 2021

Boscolo D, Metzger JP (2009) Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landsc Ecol 24:907–918

Boyte SP, Wylie BK (2015) Near-real-time cheatgrass percent cover in the Northern Great Basin, USA. Rangelands 38(5):278–284

Boyte SP, Wylie BK (2017). Estimates of Herbaceous Annual Cover in the Sagebrush Ecosystem. U.S. Geological Survey data release. https://doi.org/10.5066/F7445JZ9 Accessed 23 June 23 2017

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Bradley BA, Mustard JF (2005) Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. Remote Sens Environ 94:204–213

Broennimann O, Di Cola V, Guisan A (2017) ecospat: Spatial Ecology Miscellaneous Methods. R package version 2.2.0. https://CRAN.R-project.org/package=ecospat

Byer NW, Dilts TE, Larrucea ES, Crowell MM, Shoemaker KT, Weisberg PJ, Matocq MD (2021a) Holocene-era landscape conditions affect genetic connectivity in a sagebrush obligate species, the pygmy rabbit (*Brachylagus idahoensis*). Landsc Ecol 36:3575–3590

Byer NW, Holding ML, Crowell MM, Pierson TW, Dilts TE, Larrucea ES, Shoemaker KT, Matocq MD (2021b) Adaptive divergence despite low effective population size in a peripherally isolated population of the pygmy rabbit, *Brachylagus idahoensis*. Mol Ecol 00:1–16

Chaney NW, Wood EF, McBratney AB, Hempel JW, Nauman TW, Brungard CW, Odgers NP (2016) POLARIS: A 30-meter probabilistic soil series map of the contiguous United States. Geoderma 274:54–67

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799

Connelly JW, Braun CE (1997) Long-term changes in sage grouse *Centrocercus urophasitlnus* populations in western North America. Wildlife Biol 3:229–234

Coulston JW, Moisen GG, Wilson BT, Finco MV, Cohen WB, Brewer CK (2012) Modeling percent tree canopy cover: a pilot study. Photogramm Eng Rem S 78:715–727

Crawford JA, Anthony RG, Forbes JT, Lorton GA (2010) Survival and causes of mortality for pygmy rabbits (Brachylagus idahoensis) in Oregon and Nevada. J Mammal 91:838–847

Crist MR, Knick ST, Hanser SE (2017) Range-wide connectivity of priority areas for Greater Sage-Grouse: Implications for long-term conservation from graph theory. Condor 119:44–57

Cross TB, Schwartz MK, Naugle DE, Fedy BC, Row JR, Oyler-McCance SJ (2018) The genetic network of greater sage-grouse: Range-wide identification of keystone hubs of connectivity. Ecol Evol 8:5394–5412

Crowell MM, Shoemaker KT, Matocq MD (2020) Ideal conditions for increased trapping success of pygmy rabbits (Brachylagus idahoensis) across the Great Basin. J Mammal 101:1736–1749

Cushman SA, Elliot NB, Bauer D, Kesch K, Bahaa-el-din L, Bothwell H, Flyman M, Mtare G, Macdonald DW, Loveridge AJ (2018) Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PLoS ONE 13:e0196213

Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biol Conserv 144:2573–2584

Dilts TE, Yang J (2015) Topography Tools for ArcGIS 10.1. University of Nevada Reno. http://www.arcgis.com/home/item.html?id=b13b3b40fa3c43d4a23a1a09c5fe96b9

Dilts TE (2021) Multiple shortest paths toolbox for ArcGIS 10.7. University of Nevada Reno. https://arcg.is/1TWK980

Dobrowski SZ, Abatzoglou J, Swanson AK, Greenberg JA, Mynsberge AR, Holden ZA, Schwartz MK (2013) The climate velocity of the contiguous United States during the 20th century. Glob Change Biol 19:241–251

Donnelly JP, Naugle DE, Hagen CA, Maestas JD (2016) Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions. Ecosphere 7:e01208

Eidenshink J, Schwind B, Brewer K, Zhu ZL, Quayle B, Howard S (2007) A project for monitoring trends in burn severity. Fire Ecol 3:3–21

Esri (2019) ArcGIS Desktop: Release 10.7.1. Environmental Systems Research Institute, Redlands, CA.

Estes-Zumpf WA, Rachlow JL (2009) Natal dispersal by pygmy rabbits (*Brachylagus idahoensis*). J Mamm 90:363–372

Estes-Zumpf WA, Rachlow JL, Waits LP, Warheit KI (2010) Dispersal, gene flow, and population genetic structure in the pygmy rabbit (*Brachylagus idahoensis*). J Mamm 91:208–219

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Falkowski MJ, Evans JS, Naugle DE, Hagen CA, Carleton SA, Maestas JD, Khalyani AH, Poznanovic AJ, Lawrence AJ (2017) Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecol Manag 70:15–24

Fu P, Rich PM (2002) A geometric solar radiation model with applications in agriculture and forestry. Comput Electron Agric 37:25–35

Germaine S, Ignizio D, Keinath D, Copeland H (2014) Predicting occupancy for pygmy rabbits in Wyoming: an independent evaluation of two species distribution models. J Fish Wildl Manag 5:298–314

Germaine SS, Carter SK, Ignizio DA, Freeman AT (2017) Relationships between gas field development and the presence and abundance of pygmy rabbits in southwestern Wyoming. Ecosphere 8:e01817

Germaine SS, Assal T, Freeman A, Carter SK (2020) Distance effects of gas field infrastructure on pygmy rabbits in southwestern Wyoming. Ecosphere 11:e03230

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A Meta-analytic review of corridor effectiveness. Conserv Biol 24:660–668

Gilleland E (2013) Two-dimensional kernel smoothing: Using the R package smoothie. NCAR Technical Note, TN-502+STR. http://opensky.library.ucar.edu/collections/TECH-NOTE-000-000-000-869. Accessed 23 May 2021

Grenouillet G, Buisson L, Casajus N, Lek S (2011) Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34:9–17

Haddad NM, Brudvig LA, Damschen EI, Evans DM, Johnson BL, Levey DJ, Orrock JL, Resasco J, Sullivan LL, Tewksbury JJ, Wagner SA, Weldon AJ (2014) Potential negative ecological effects of corridors. Conserv Biol 28:1178–1187

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristics curve. Radiology 143:29–36

Hanski I, Simberloff D (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanki I, Gilpin ME (eds) Metapopulation biology: ecology, genetics, and evolution. Academic Press, Cambridge, pp 5–26

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54:227–233

Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K (2015) Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogramm Eng Remote Sens 81:345–354

Howe KB, Coates PS, Delehanty DJ (2014) Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem. Condor 116:35–49

Huntington JL, Hegewisch KC, Daudert B, Morton CG, Abatzoglou JT, McEvoy DJ, Erickson T (2017) Climate Engine: cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. B Am Meteorol Soc 98:2397–2410

Jackson HB, Fahrig L (2014) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–63

Jennings MK, Zeller KA, Lewiston RL (2020) Supporting adaptive connectivity in dynamic landscapes. Land 9:295

Jongman RH (1995) Nature conservation planning in Europe: developing ecological networks. Landsc Urban Plan 32:169–183

Kaszta Ż, Cushman SA, Macdonald DW (2020) Prioritizing habitat core areas and corridors for a large carnivore across its range. Anim Conserv 23:607–616

Keeley AT, Ackerly DD, Cameron DR, Heller NE, Huber PR, Schloss CA, Thorne JH, Merenlender AM (2018) New concepts, models, and assessments of climate-wise connectivity. Environ Res Lett 13:073002

Knick ST, Hanser SE, Preston KL (2013) Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. Ecol Evol 3:1539–1551

Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5:e11785

Kuhn A, Copeland J, Cooley J, Vogel H, Taylor K, Nacci D, August PV (2011) Modeling habitat associations for the Common Loon (Gavia immer) at multiple scales in northeastern North America. Avian Conserv Ecol 6:4. https://doi.org/10.5751/ACE-00451-060104

Landguth EL, Hand BK, Glassy J, Cushman SA, Sawaya MA (2012) UNICOR: A species connectivity and corridor network simulator. Ecography 35:9–14

Larrucea ES, Brussard PF (2008) Shift in location of pygmy rabbit (Brachylagus idahoensis) habitat in response to changing environments. J Arid Environ 72:1636–1643

Larrucea ES, Robinson ML, Rippert JS, Matocq MD (2018) Genetically distinct populations of the pygmy rabbit (Brachylagus idahoensis) in the Mono Basin of California. J Mamm 99:408–415

Leu M, Hanser SE, Knick ST (2008) The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecol Evol 18:1119–1139

Lindenmayer DB, Fischer J (2007) Tackling the habitat fragmentation panchreston. Trends Ecol Evol 22:127–132

Liu C, Newell G, White M (2016) On the selection of thresholds for predicting species occurrence with presence-only data. Ecol Evol 6:337–348

Long JA (2019) Estimating wildlife utilization distributions using randomized shortest paths. Landsc Ecol 34:2509–2521

Martin EH, Jensen RR, Hardin PJ, Kisingo AW, Shoo RA, Eustace A (2019) Assessing changes in Tanzania's Kwakuchinja Wildlife Corridor using multitemporal satellite imagery and open source tools. Appl Geogr 110:102051

Mateo-Sánchez MC, Balkenhol N, Cushman S, Pérez T, Domínguez A, Saura S (2015) Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6:1–16

McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606

McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol 31:1161–1175

McMahon LA, Rachlow JL, Shipley LA, Forbey JS, Johnson TR (2017) Habitat selection differs across hierarchical behaviors: selection of patches and intensity of patch use. Ecosphere 8:e01993

McRae BH (2006) Isolation by resistance. Evolution 60:1551–1561

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

Merriam G (1990) Ecological processes in the time and space of farmland mosaics. In: Baudry J, Zonneveld IS, Forman RT (eds) Changing landscapes: an ecological perspective. Springer, New York, pp 121–133

Nandy S, Kushwaha SP, Mukhopadhyay S (2007) Monitoring the Chilla-Motichur wildlife corridor using geospatial tools. J Nat Conserv 15:237–244

Nerkowski SA (2021) A Rabbit's Tale: Genetic Monitoring, Genomic Diversity, and Habitat Selection in the Endangered Columbia Basin Pygmy Rabbit (Brachylagus idahoensis). Dissertation, University of Idaho

Nobre AD, Cuartas LA, Hodnett M, Rennó CD, Rodrigues G, Silveira A, Saleska S (2011) Height Above the Nearest Drainage—a hydrologically relevant new terrain model. J Hydrol 404:13–29

Noss RF, Harris LD (1986) Nodes, networks, and MUMs: preserving diversity at all scales. Environ Manag 10:299–309

Ntongani WA, Munishi PK, Mbilinyi BP (2010) Land use changes and conservation threats in the eastern Selous-Niassa wildlife corridor, Nachingwea, Tanzania. Afr J Ecol 48:880–887

Olsen AC, Severson JP, Maestas JD, Naugle DE, Smith JT, Tack JD, Yates KH, Hagen CA (2021) Reversing tree expansion in sagebrush steppe yields population-level benefit for imperiled grouse. Ecosphere 12:e03551

Omernik JM, Griffith GE (2014) Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environ Manag 54:1249–1266

Opdam P, Foppen R, Reijnen R, Schotman A (1995) The landscape ecological approach in bird conservation: integrating the metapopulation concept into spatial planning. Ibis 137:139–146

Peterman WE, Connette GM, Semlitsch RD, Eggert LS (2014) Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. Mol Ecol 23:2402–2413

Pilliod DS, Jeffries MA, Welty JL, Arkle RS (2021) Protecting restoration investments from the cheatgrass-fire cycle in sagebrush steppe. Conserv Sci Pract 3:e508

Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landsc Ecol 24:253–266

PRISM Climate Group (2010) Minimum, maximum, mean temperature, and annual precipitation. Oregon State University. http://prism.oregonstate.edu Accessed 28 July 2017

Prugh LR, Hodges KE, Sinclair AR, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramírez-Delgado JP, Di Marco M, Watson JE, Johnson CJ, Rondinini C, Corredor Llano X, Arias M, Venter O (2022) Matrix condition mediates the effects of habitat fragmentation on species extinction risk. Nat Comm 13:595

Resasco J (2019) Meta-analysis on a decade of testing corridor efficacy: what new have we learned? Current Landsc Ecol Rep 4:61–69

Rondinini C, Rodrigues AS, Boitani L (2011) The key elements of a comprehensive global mammal conservation strategy. Philos Trans R Soc Lond B 366:2591–2597

Rottler CM, Noseworthy CE, Fowers B, Beck JL (2015) Effects of conversion from sagebrush to non-native grasslands on sagebrush-associated species. Rangelands 37:1–6

Row JR, Doherty KE, Cross TB, Schwartz MK, Oyler-McCance SJ, Naugle DE, Knick ST, Fedy BC (2018) Quantifying functional connectivity: the role of breeding habitat, abundance, and landscape features on range-wide gene flow in sage-grouse. Evol Appl 11:1305–1321

Rowland MM, Wisdom MJ, Suring LH, Meinke CW (2006) Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biol Conserv 129:323–335

Rybicki J, Abrego N, Ovaskainen O (2020) Habitat fragmentation and species diversity in competitive communities. Ecol Lett 23:506–517

Saura S, Bodin Ö, Fortin MJ (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. J Appl Ecol 51:171–182

Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? J Appl Ecol 48:668–678

Schlaepfer DR, Lauenroth WK, Bradford JB (2012) Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. Ecography 35:374–384

Shipley LA, Davila TB, Thines NJ, Elias BA (2006) Nutritional requirements and diet choices of the pygmy rabbit (Brachylagus idahoensis): a sagebrush specialist. J Chem Ecol 32:2455–2474

Shirk AJ, Cushman SA, Waring KM, Wehenkel CA, Leal-Sáenz A, Toney C, Lopez-Sanchez CA (2018) Southwestern white pine (*Pinus strobiformis*) species distribution models project a large range shift and contraction due to regional climatic changes. For Ecol Manag 411:176–186

Shriver RK, Andrews CM, Pilliod DS, Arkle RS, Welty JL, Germino MJ, Duniway MC, Pyke DA, Bradford JB (2018) Adapting management to a changing world: Warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands. Glob Chang Biol 24:4972–4982

Simberloff D, Cox J (1987) Consequences and costs of conservation corridors. Conserv Biol 1:63–71

Smith IT, Rachlow JL, Svancara LK, McMahon LA, Knetter SJ (2019) Habitat specialists as conservation umbrellas: do areas managed for greater sage-grouse also protect pygmy rabbits? Ecosphere 10:e02827

Smith IT, Knetter SJ, Svancara LK, Karl JW, Johnson TR, Rachlow JL (2021) Overlap between sagebrush habitat specialists differs among seasons: implications for umbrella species conservation. Rangeland Ecol Manag 78:142–154

Soulé ME, Gilpin ME (1991) The theory of wildlife corridor capability. In: Saunders DA, Hobbs RJ (eds) The role of corridors in nature conservation. Surrey Beatty, Sydney, pp 91–104

Stahl AT, Fremier AK, Cosens BA (2020) Mapping legal authority for terrestrial conservation corridors along streams. Conserv Biol 34:943–955

Stephenson NL (1990) Climatic control of vegetation distribution: the role of the water balance. Am Nat 135:649–670

Thorndike RL (1953) Who belongs in the family? Psychometrika 18:267–276

Thuiller W, Georges D, Engler R, Breiner F (2016) biomod2: Ensemble Platform for Species Distribution Modeling. R package version 3.3–7. https://CRAN.R-project.org/package=biomod2

Travers E, Härdtle W, Matthies D (2021) Corridors as a tool for linking habitats—shortcomings and perspectives for plant conservation. J Nat Conserv 60:125974

Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. Remote Sens Environ 8:127–150

U.S. Census Bureau (2015) TIGER/Line Shapefiles. Geographic Products Branch, Geography Division, U.S. Census Bureau. https://www.census.gov/geo/maps-data/data/tiger-geodatabases.html Accessed 8 Aug 2017

U.S. Department of Interior (2021) Conserving and Restoring America the Beautiful. Preliminary Report to the National Climate Task Force. https://www.doi.gov/sites/doi.gov/files/report-conserving-and-restoring-america-the-beautiful-2021.pdf Accessed 21 June 2022

U.S. Geological Survey (2008) USGS National Hydrography Dataset Best Resolution (NHD) for Hydrologic Unit (HU) 4. https://www.sciencebase.gov/catalog/item/5a58a589e4b00b291cd690cd Accessed 20 April 2017

U.S. Geological Survey (2009) National elevation dataset. EROS Sioux Falls, SD. http://viewer.nationalmap.gov/viewer Accessed 30 Jan 2020

U.S. Geological Survey (2019) State Wildlife Action Plans (SWAP): A national look at Species of Greatest Conservation Need as reported in State Wildlife Action Plans. https://www1.usgs.gov/csas/swap/index.html. Accessed 25 April 2022

Walters SP, Schneider NJ, Guthrie JF (2008) Geospatial Multi-Agency Coordination (GeoMAC) wildland fire perimeters. US Geological Survey Data Series, 612(6). https://pubs.usgs.gov/ds/612/pdf/ds612.pdf Accessed 12 Mar 2020

Whisenant SG (1990) Changing fire frequencies on Idaho's Snake River Plains: Ecological and management implications. McArthur, ED (ed) Symposium on Cheatgrass Invasion, Shrub Die-off and Other Aspects of Shrub Biology and Management. Intermountain Research Station, Forest Service, US Department of Agriculture, Ogden, UT, pp 5–8

Xian GZ, Homer CG, Dewitz J, Fry J, Hossain N, Wickham J (2011) The change of impervious surface area between 2001 and 2006 in the conterminous United States. Photogramm Eng Rem S 77:758–762

Xian G, Homer C, Rigge M, Shi H, Meyer D (2015) Characterization of shrubland ecosystem components as continuous fields in the northwest United States. Remote Sens Environ 168:286–300

Zeller KA, Cushman SA, Van Lanen NJ, Boone JD, Ammon E (2021a) Targeting conifer removal to create an even playing field for birds in the Great Basin. Biol Conserv 257:109130

Zeller KA, Schroeder CA, Wan HY, Collins G, Denryter K, Jakes AF, Cushman SA (2021b) Forecasting habitat and connectivity for pronghorn across the Great Basin ecoregion. Divers Distrib 12:2315–2329