

RESEARCH ARTICLE

Forecasting habitat and connectivity for pronghorn across the Great Basin ecoregion

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Abstract

Aims: In the sagebrush ecosystems of the western United States, identifying and enhancing habitat for large ungulates has become an increased priority for many management agencies, as indicated by Department of Interior Secretarial Order 3362. Estimating and understanding current and future habitat suitability and connectivity is important for successful long-term management of these species.

Location: Great Basin ecoregion, western USA.

Methods: We focussed on pronghorn (*Antilocapra americana*) in the Great Basin ecoregion and used a variety of data sources (GPS telemetry, aerial surveys, observation locations) to develop multi-scale ensemble habitat suitability models for the current and two future time steps (years 2050 and 2070). We also developed dynamic resistant kernels to model pronghorn connectivity. We combined the habitat suitability and connectivity outputs to derive and quantify changes in pronghorn habitat networks through time as well as identify areas that are resilient to climate and land use change.

Results: We observed a 33.4% decline in highly suitable pronghorn habitat by 2070, assuming a high carbon emission scenario. Patches of suitable habitat reduced in number and size, whilst the distance amongst patches increased, indicating elevated importance of connectivity for pronghorn in the future. Future connectivity decreased to a greater degree than habitat suitability (47.2%–80.0%, depending on the pronghorn movement threshold used). We also found highly suitable habitat (70%) to be more resilient to climate change than areas of connectivity (10%–15%).

Main conclusions: Our results show a loss of high-quality pronghorn habitat and areas of connectivity with projected climate change. Connectivity was more sensitive than habitat, indicating connectivity may become a limiting factor for pronghorn populations in the Great Basin. These results can help managers prioritize resource investments and conservation efforts in areas most likely to be successful towards long-term pronghorn conservation.

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KEYWORDS

climate change, connectivity, Great Basin, habitat networks, multi-scale habitat suitability, pronghorn

1 | INTRODUCTION

Identifying and enhancing habitat for Rocky Mountain elk (*Cervus canadensis nelsoni*), mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) in the sagebrush (*Artemisia* spp.) ecosystems of the western United States has become an increased priority for many state and federal agencies due to Secretarial Order number 3362 (U.S. Department of the Interior 2018). Conservation of ungulate habitats and movement corridors is important to long-term population persistence through effects on gene flow, metapopulation dynamics and providing opportunities to respond to stochastic environmental conditions (Chetkiewicz et al. 2006; Hilty et al. 2019). Habitat and connectivity for these big game species may be compromised by anthropogenic features such as residential expansion, roads, fences and energy development (Berger, 2004; Christie et al. 2015; Jones et al. 2019; Northrup et al. 2015; Sawyer et al. 2017). Large ecological shifts caused by declining sagebrush vegetation, invasive species and climate change may also have negative effects on habitat and lead to an increase in stochastic events on western ungulate species (Bishop et al. 2009; Gedir et al. 2015; Watkins et al. 2007). Providing for landscape connectivity and integrating future changes into current planning are the two most frequently recommended strategies for adapting to these impacts (Heller & Zavaleta, 2009). Therefore, there is a need to identify how and where climate change and human development will affect habitat quality and connectivity for big game species in the western United States. This information can help coordinate management actions, minimize negative impacts to wildlife and mitigate future threats (Sinclair et al. 2018).

Pronghorn, found across shrublands and grasslands of western North America, have experienced multiple population fluctuations over the past several centuries. From an estimated 30 million individuals in the early 1800s, overhunting reduced the population to a low of an estimated 13,000 individuals in the early 1900s (O'Gara & Yoakum, 2004). Implementation of regulated harvest and augmentation efforts helped recover the population to approximately 915,000 individuals (Western Association of Fish and Wildlife Agencies, 2018). However, pronghorn are again declining in some regions (Gedir et al. 2015; Reinking et al. 2019; Trausch et al., 2020) and, due to their metabolic needs, may be threatened by activities that restrict access to forage during periods of nutritional bottlenecks (Wesley et al. 1973). For example, pronghorn avoid roads, fences and energy development (Beckmann et al. 2012; Christie et al. 2015; Jones et al. 2019; Reinking et al. 2019), which can limit access to forage (Christie et al. 2015), restrict migration between seasonal ranges (Berger, 2004; Jakes et al. 2020; Jones et al. 2019), cause population isolation (Theimer et al. 2012) and reduce available habitat (Gates et al., 2012; Jones et al. 2019). Certain fences and fenced roadways may directly limit movement for pronghorn,

either by acting as a barrier or by causing direct mortality as a result of entanglement (Harrington & Conover, 2006; Jones et al. 2018; Seidler et al. 2015). Restricted movements result in reduced connectivity amongst important resource patches and may cause malnutrition, low fawn recruitment and diminished population sizes (Jones et al. 2020; O'Gara & Yoakum, 2004).

Changes in vegetation may also negatively impact pronghorn populations. Throughout much of their range in the Great Basin Ecoregion of the United States (hereafter "Great Basin"), pronghorn are dependent on sagebrush species, which are high in protein and other nutrients, are easily digestible and more available than grasses in the winter months (Wambolt, 2004; Yoakum, 2004). However, sagebrush vegetation is declining in the Great Basin due to multiple factors, including pinyon-juniper encroachment, altered fire regimes, intensive grazing and invasive species (Miller et al., 2008; Pellant et al. 2004). Declines in sagebrush vegetation can prompt pronghorn to switch to other, poorer quality browse, which has been linked to lower recruitment and may result in reduced population sizes (Boccardi et al. 2008).

Climate change can further exacerbate the effects of habitat fragmentation and loss of sagebrush forage by causing complex interactions amongst climate, water and vegetation, and increasing uncertainty about future trends in wildlife populations (Prato, 2009). In the Great Basin, sagebrush vegetation is predicted to decrease in the central and southern portions of the ecoregion with future climate change, but increase in the northern and eastern portions (Adler et al. 2018), possibly causing a shift in the distribution of pronghorn across the region. Snowpack is also projected to decline in the Great Basin (Mote et al. 2005), and whilst this might increase the negative effects summer drought on pronghorn populations (Brown et al. 2006; Gedir et al. 2015), it could also ease movement restrictions for pronghorn in the winter and allow movement into previously unused areas, particularly in the northern and higher elevation areas of the Great Basin.

Given the sensitivity of pronghorn to loss of sagebrush vegetation, development infrastructure such as roads and fences, and uncertainty introduced by climate change, estimating current and future habitat suitability and connectivity is important for successful long-term management of pronghorn in the Great Basin. In this paper, we used data from a variety of sources (GPS telemetry, aerial surveys, observation locations) to develop multi-scale habitat suitability and connectivity models for pronghorn at two different movement thresholds and during three different time steps, current, 2050 and 2070. We combined the habitat suitability and connectivity outputs to derive pronghorn habitat networks for current and future potential conditions. We then quantified changes in these habitat networks under various scenarios through time and identified areas in the Great Basin that appeared resilient to climate

change. This information can be used to prioritize habitats for conservation and management opportunities.

2 | METHODS

2.1 | Study area

The study area encompassed most of the Great Basin Landscape Conservation Cooperative Ecoregion (GreatBasinLCC.org), but was refined slightly to coincide with our work on other species in the area (Figure 1). The dominant vegetation in this temperate desert region consists of sagebrush and other xeric shrubs at lower elevations and open conifer forests and pinyon-juniper woodlands at higher elevations. The study area measured 515,276 km² and covers most of the state of Nevada and parts of California, Idaho, Oregon and Utah.

2.2 | Environmental variables and ecological neighbourhoods

We selected a suite of vegetation, topographic, soil, temperature and precipitation variables available for the study area for both current and future scenarios (Table S1.1). Vegetation was derived from the Conterminous United States Land Cover Projections (Sohl et al., 2018), which were available annually from 2005 to 2100 at a 250 m raster resolution. Future projections included major land use/land cover types (Table S1.2) and accounted for an expanding anthropogenic footprint. The current time step was based on the historical land cover data from the year 2005. We also used two future years, 2050 and 2070, and two carbon dioxide emissions scenarios, moderate (B1) and high (A2; Nakicenovic et al. 2000). The original land cover types were combined into the following classes: water, barren, developed, deciduous forest, evergreen forest, mixed forest, shrub, grassland, agriculture and wetland (Table S1.2). Deciduous and mixed forest were dropped from the analysis due to their scarcity on the landscape (0.2% and 0.01% of the study area, respectively). We derived all topographic variables from the 30 m National Elevation Dataset (U.S. Geological Survey, 2009) and downloaded soil variables from the 30 m Polaris database (Chaney et al. 2016). We considered topographic and soil variables to be static across our 2005–2070 temporal window.

We obtained temperature and precipitation variables from the Climatology at High resolution for the Earth's Land Surface Areas (CHELSA) data base (Krager et al. 2017). These data were available at a 1-km raster resolution. To be consistent with the land cover data, we used the 1979–2013 averages for the current time step, the 2040–2060 averages for the 2050 time step and the 2061–2080 averages for the 2070 time step. The CHELSA data were not derived with the Special Report on Emission Scenarios (SRES, Nakicenovic et al. 2000), but instead used Representative Concentration Pathways (RCPs; van Vuuren et al. 2011). Therefore, we matched RCP 8.5 with SRES A2 and RCP 4.5 with SRES B1 (van Vuuren

et al. 2011). RCP 8.5 is associated with rising carbon emissions resulting in an average global rise in temperature of 4.3°C by the year 2100, whilst RCP 4.5 is associated with slowly declining carbon emissions and an average global rise in temperature of 2.4°C. For each future emissions scenario, we used five Global Climate Models (GCMs): CESM1-CAM5, FIO-ESM, IPSL-CM5A, MIROC5 and MPI-ESM-MR. We selected these GCMs following the recommendations of Sanderson et al. (2015) to use models that had the lowest amount of interdependence. All GCMs were based on Coupled Model Intercomparison Project phase 5 (Taylor et al. 2012).

The variables were clipped to our study area and resampled to a 250 m pixel size to match the land cover data. Studies have demonstrated that (1) pronghorn and other species respond to different environmental features at different scales (Jakes et al. 2020; McGarigal et al. 2016) and (2) that identifying and incorporating these scales into multi-scale models results in higher model performance than single scale models (DeCesare et al. 2012; Johnson et al. 2004; Wheatley & Johnson, 2009). Therefore, to identify the scale of effect for each variable, we applied a Gaussian smooth to each variable at the following bandwidths with the smoothie package (Gilleland, 2013) in the R software environment (R Core Team, 2019): 250, 500, 1,000, 2,000, 4,000, 8,000 and 16,000 m.

2.3 | Pronghorn data

Data on pronghorn were obtained from the U.S. Fish and Wildlife Service, the Nevada Department of Wildlife, the Utah Division of Wildlife Resources, the California Department of Fish and Wildlife, the Oregon Biodiversity Information Center and the Biodiversity Information Serving Our Nation database (Table 1). In total, 471,103 locations were obtained for the study area. To account for spatial correlation in our pronghorn location data, and to prevent model overfitting to areas with telemetry locations, we subset the locations with the following procedure. First, we extracted information from the following environmental layers at each pronghorn location: elevation, shrub, grassland, annual mean temperature and annual precipitation. We then fit a semi-variogram model for each environmental layer and identified the sill with the gstat package (Pebesma, 2004) in R. Ten kilometres was the distance beyond which environmental values at the points were no longer correlated. Therefore, we used that distance to subset our points so that points were more than 10 km from each other (Figure 1). This process retained 1,278 points for use in our models.

2.4 | Multi-scale species distribution models

In addition to detailing our species distribution model (SDM) methods below, we provide the procedure in the standardized ODMAP (Overview, Data, Model, Assessment and Prediction) protocol format in Appendix 2, as recommended by Zurell et al. (2020). We used a suite of SDMs combined into an ensemble model (Grenouillet

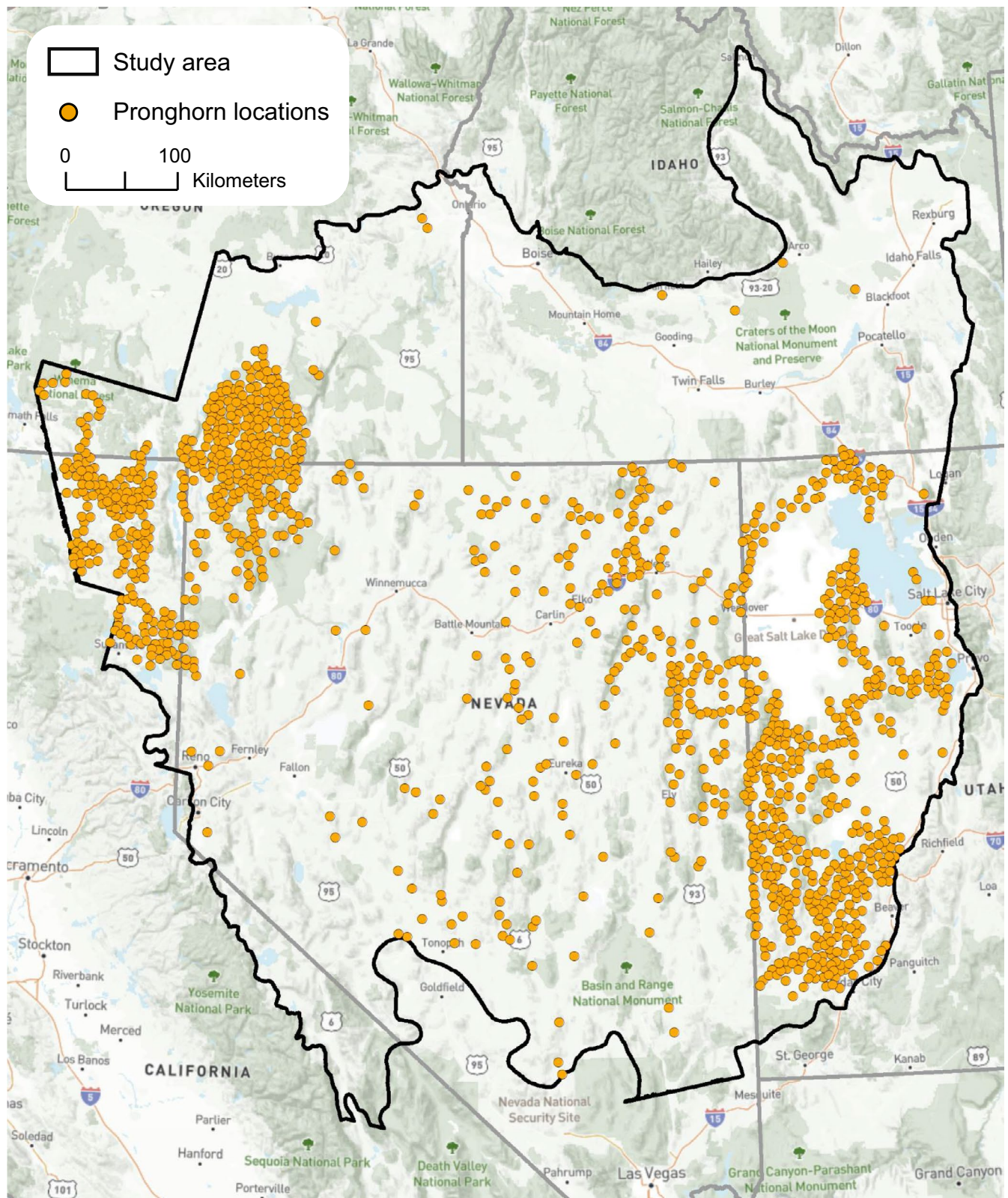


FIGURE 1 The study area in the Great Basin Ecoregion, USA, and pronghorn locations used in the analysis

et al. 2011) to predict habitat suitability for pronghorn across our study area. Models included generalized linear models (GLMs), multivariate adaptive regression splines (MARS), maximum entropy

(MAXENT), random forests (RF) and boosted regression trees (BRT). Pseudo-absence points were randomly sampled across the study area with a rule that no sampled point could be within 10 km from

TABLE 1 Pronghorn data types, provider, citation and years used in the analysis

Region	Data type	Number of point locations	Number of individuals	Years	Data provider
California	GPS collar	405,093	68	2009–2017	California Department of Fish and Wildlife
	Observations	310	NA	2000–2017	California Department of Fish and Wildlife
Great Basin	Observations	55	NA	2000–2016	Biodiversity Information Serving Our Nation
Nevada	Observations	481	NA	1971–2012	Nevada Department of Wildlife
Nevada/ Oregon	GPS collar	61,886	50	2015–2017	U.S. Fish and Wildlife Service
Oregon	Observations	56	NA	1989–2011	Oregon Biodiversity Information Center
Utah	Observations	3,222	NA	2001–2015	Utah Division of Wildlife Resources

another sampled point. This resulted in 12,655 pseudo-absence points for analysis.

To identify the scale of effect for each variable, we performed *t*-tests on the values at the presence and absence points for each environmental variable at each scale (Shirk et al. 2018). For each variable, we considered scales with *p*-values less than .01 and identified the scale with the lowest *p*-value for inclusion in the multi-scale SDMs. We ran pairwise Spearman's rank correlations between all remaining variables and, if correlations greater than |0.6| were present, we retained the variable with the lower *p*-value. With this final variable set, we used the BIOMOD2 package (Thuiller et al., 2019) in R to run all SDMs and combine them into a single ensemble model. The ensemble model is the weighted average proportional to the receiver operating characteristic curve value of the individual SDMs. The ensemble model was predicted across the study area to obtain a final habitat suitability map.

We assessed the predictive performance of our models with both a random 10-fold cross validation procedure and a block cross-validation procedure. The 10-fold cross-validation was performed as part of the BIOMOD2 code in R, and we used the Area Under Receiver operating characteristic curve (AUC; Hanley & McNeil, 1982) as our performance metric. The block cross-validation followed the procedure recommended by Roberts et al. (2017). We divided our study area into four blocks and ran a cross validation procedure where we built and predicted the model with the data from three of the blocks and calculated the continuous Boyce Index on the test data from the fourth block. We used the *ecospat* package in R (Broennimann et al., 2018) with 10 bins (Hirzel et al. 2006) to calculate the Boyce index for each block and took the average across blocks. The Boyce Index ranges from 0 to 1 and is the Spearman's rank correlation coefficient between the observed/expected ratios across the bins.

We predicted the final ensemble model for each future time step, 2050 and 2070, for each RCP and for each of our five GCMs. We averaged the habitat suitability models across GCMs for each RCP and time step. We divided the habitat suitability predictions into five bins and calculated the per cent of the Great Basin in each bin for each year and emissions scenario. We also used the maximum test sensitivity plus specificity values from the ensemble SDM to create binary maps that differentiated highly suitable pronghorn

habitat from other habitat. In creating the binary maps from the future habitat suitability surfaces, we used the same threshold value as for the current time step. No rescaling was performed on these surfaces prior to conducting the binning or thresholding procedures.

We used the *landscapemetrics* package (Hesselbarth et al. 2019) in R to calculate the following landscape metrics on the binary habitat maps: per cent of the landscape, largest patch index, number of patches, mean nearest neighbour distance and radius of gyration. Landscape per cent measures what percentage of the study area is high-quality habitat, largest patch index measures the largest sized habitat patch in the study area, number of patches measures how many habitat patches are in the study area, whilst the mean nearest neighbour distance measures how far apart these patches are. The radius of gyration measures the extent of a patch by calculating the mean distance from a patch centroid to the every other cell in a patch and can be interpreted as the mean distance one can move across a patch before reaching the edge of that patch. This suite of metrics provides information about fragmentation of habitat and landscape effects on spatial population processes (Cushman, Landguth, et al. 2012; McGarigal & Marks, 1995).

2.5 | Connectivity models

To obtain source points for the connectivity models, we range rescaled the current pronghorn habitat suitability model from 0 to 1 and sampled 10,000 points with the "Create Spatially Balanced Points" toolbox (Theobald et al. 2007) in ArcMap 10.5.1 (ESRI, 2016). This approach results in more points being sampled in higher probability suitability bins whilst providing coverage across the study area. The number of source points was a trade-off between wanting to sample a large number of points whilst maintaining reasonable computation times. We believe this is an adequate number of source points for the study area given that the pronghorn population estimate for Nevada is 28,000–30,000 (Nevada Department of Wildlife, 2020).

We obtained our resistance surface by taking the linear inverse of the habitat suitability SDM and range rescaling that from 1 to 100. There is some discussion in the literature arguing for other transformations from habitat suitability to resistance (e.g. Keeley et al. 2016;

Mateo-Sánchez et al. 2015); however, in previous work, we found that for SDMs, the linear inverse transformation outperformed other transformations for predicting connectivity (Zeller et al. 2018). We used UNICOR software (Landguth et al. 2012), to run resistant kernel connectivity models (Compton et al. 2007) from each source point. We used 500,000 and 1,000,000 as the cost distance thresholds for pronghorn (hereafter 500 and 1,000). This is equivalent to a pronghorn moving 500 or 1,000 km through a landscape with no resistance to movement. Across a resistant surface, these theoretical movement distances decrease as the thresholds are reached more quickly when resistance values are added. For example, an individual that has the capacity to move 500 km across a resistance surface of all ones may only be able to move 250 km across a resistance surface where the all pixel values equal two. Therefore, as resistance increases movement distance will decrease. Given that dispersal distance has the capacity to be 40 times the diameter of an average home range (Bowman et al. 2002) and that annual migration distances up to 888 km have been documented (Jakes et al. 2018), we consider these cost distance thresholds to be realistic lower and upper bounds for pronghorn movement our analysis. The final connectivity surfaces were obtained by summing the resistant kernels for all source points. These surfaces approximated total movement density given the two different cost distance thresholds.

To model connectivity into the future, we used a dynamic resistant kernel approach (Ash et al. 2020; Barros et al. 2019; Cushman, 2015) that seeded source points for each time step based on the resistant kernel results from the previous time step. For example, the resistant kernel results from the current time step were range rescaled from 0 to 1 and source points for the year 2050 were sampled on this surface. The source points for the year 2070 were sampled on the surface derived from running the 2050 resistant kernel connectivity models.

The number of source points for each time step was calculated based on the proportional change in habitat suitability through time. Specifically, we calculated the per cent change in the sum of the habitat suitability surfaces across time steps, and then multiplied 10,000 by that value. For the year 2050, this resulted in 9,338 and 8,440 source points for the RCP 4.5 and 8.5 emissions scenarios, respectively, and for the year 2070, this resulted in 9,276 and 7,931 source points for the RCP 4.5 and 8.5 scenarios, respectively. We assumed that the change in habitat suitability would result in a corresponding change in the number of individuals making longer-distance movements across the study area. We averaged the ensemble SDMs across all GCMs for each time step and used the range rescale procedure described above to obtain the resistance surfaces for each time step, then ran the resistant kernel connectivity models in UNICOR. In calculating the summary information below, we used the entirety of the resistant kernel output and did not threshold it as we did for the habitat suitability surfaces.

2.6 | Habitat networks and comparisons

We combined the binary habitat maps with the connectivity models to create networks of highly suitable habitat patches and

TABLE 2 Variables included in the final pronghorn species distribution models, their scales of effect, and *t*- and *p*-values from the univariate scaling process

Final layer	Scale	<i>t</i> -value	<i>p</i> -value
Per cent clay	16,000 m	34.37	4.12×10^{-208}
Bulk density	16,000 m	29.72	2.10×10^{-175}
Solar radiation	16,000 m	28.14	4.53×10^{-160}
Per cent barren	250 m	26.02	2.01×10^{-140}
Per cent shrub	250 m	25.83	1.57×10^{-138}
pH	500 m	24.82	3.14×10^{-124}
Elevation	16,000 m	21.59	3.97×10^{-94}
Temperature, warmest quarter	8,000 m	19.80	6.37×10^{-81}
Soil Depth	16,000 m	18.35	2.30×10^{-67}
Degrees slope	250 m	17.88	1.54×10^{-65}
Per cent silt	16,000 m	17.13	2.68×10^{-61}
Annual mean precipitation	16,000 m	16.84	5.53×10^{-58}
Proportion agriculture	16,000 m	15.43	1.78×10^{-50}
Proportion water	1,000 m	8.78	2.25×10^{-17}
Precipitation seasonality	16,000 m	8.20	4.60×10^{-15}
Proportion grass	2,000 m	4.44	7.36×10^{-5}

Note: Variables are listed from highest *t*-value to lowest.

their connections. We calculated the proportion of highly suitable habitat and areas of connectivity for each time step and emissions scenario. We also calculated per cent change from the current time step. To determine how the current protected area network represents pronghorn habitat and connectivity, we calculated the proportion of these areas covered by all lands identified in the Protected Areas Database of the United States (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018) as well as only those lands that were classified as an IUCN 1–6 protected area. Lastly, we identified areas that were resilient to climate and land cover change as areas that persisted from the current time step through 2070.

3 | RESULTS

The final individual SDMs had AUC values of .77, .80, .84, .83, .84 and .84 for the GLM, MARS, RF, BRT, MAXENT and ensemble model, respectively. The block cross-validation had a Boyce Index value of .76. Scales of effect differed amongst the variables in the final SDMs (Table 2). Suitable habitat for pronghorn was generally positively correlated with shrub and grassland cover, per cent clay, and soil depth and negatively correlated with solar radiation, mean temperature during the warmest quarter, per cent silt and proportion of agriculture (Figure 2). Other variables had weaker relationships and were sometimes model dependent.

Habitat suitability maps indicated areas of high habitat suitability in the south-eastern and north-western areas of the Great Basin (Figure 3). Other highly suitable habitat areas were present throughout the basin and range areas of central and northern Nevada as well as south-eastern Idaho and southern Oregon (Figure 3). We found that the per cent of highly suitable habitat generally declined with future projections, whilst the per cent of lower quality habitat increased (Figure 3). Landscape metrics indicated that highly suitable habitat patches decreased in size and number and became farther from one another in future projections (Figure 4).

Connectivity model results highlighted similar geographic areas to the habitat suitability maps in terms of importance for pronghorn (Figure S1.1). In future years, connectivity tended to concentrate in the south-eastern and north-western parts of the Great Basin with continuity between those two areas trending from south-east to north-west. Amount of connectivity was highly dependent on the cost distance threshold used. When a larger cost distance threshold was used, more of the Great Basin was suitable for connectivity (Figures 5 and 6 and Figure S1.1).

Combining the habitat suitability and connectivity maps resulted in identifying a network of highly suitable and connected habitat for pronghorn throughout the Great Basin (Figures 5 and 6). From the

current time step to 2050, 10.7% and 24.7% of high-quality habitat were lost for the RCP 4.5 and 8.5 emission scenarios, respectively. From the current time step to 2070, 12.0% and 33.4% of high-quality habitat was lost for the RCP 4.5 and 8.5 emission scenarios, respectively. Depending on the cost distance threshold used, loss of connectivity ranged from 18.9% to 57.6% in 2050 and 47.2% to 83.5% in 2070.

Overlaying these areas with the protected areas in the Great Basin revealed that 78% of these areas were under some form of protection (e.g. BLM public land), whilst only 10% of the areas are under more strict forms of protection as defined by IUCN Protected Area categories 1–6 (Table S1.3). Through time, amount of protection of the pronghorn networks remained relatively stable (Table S1.3).

The resulting maps show that areas resilient to climate and land cover change persist in the south-eastern to the north-western areas of the Great Basin, the same areas identified as being important habitats and areas of connectivity (Figure 7).

4 | DISCUSSION

We compiled pronghorn data throughout the Great Basin and modelled current and future habitat suitability and connectivity. Our

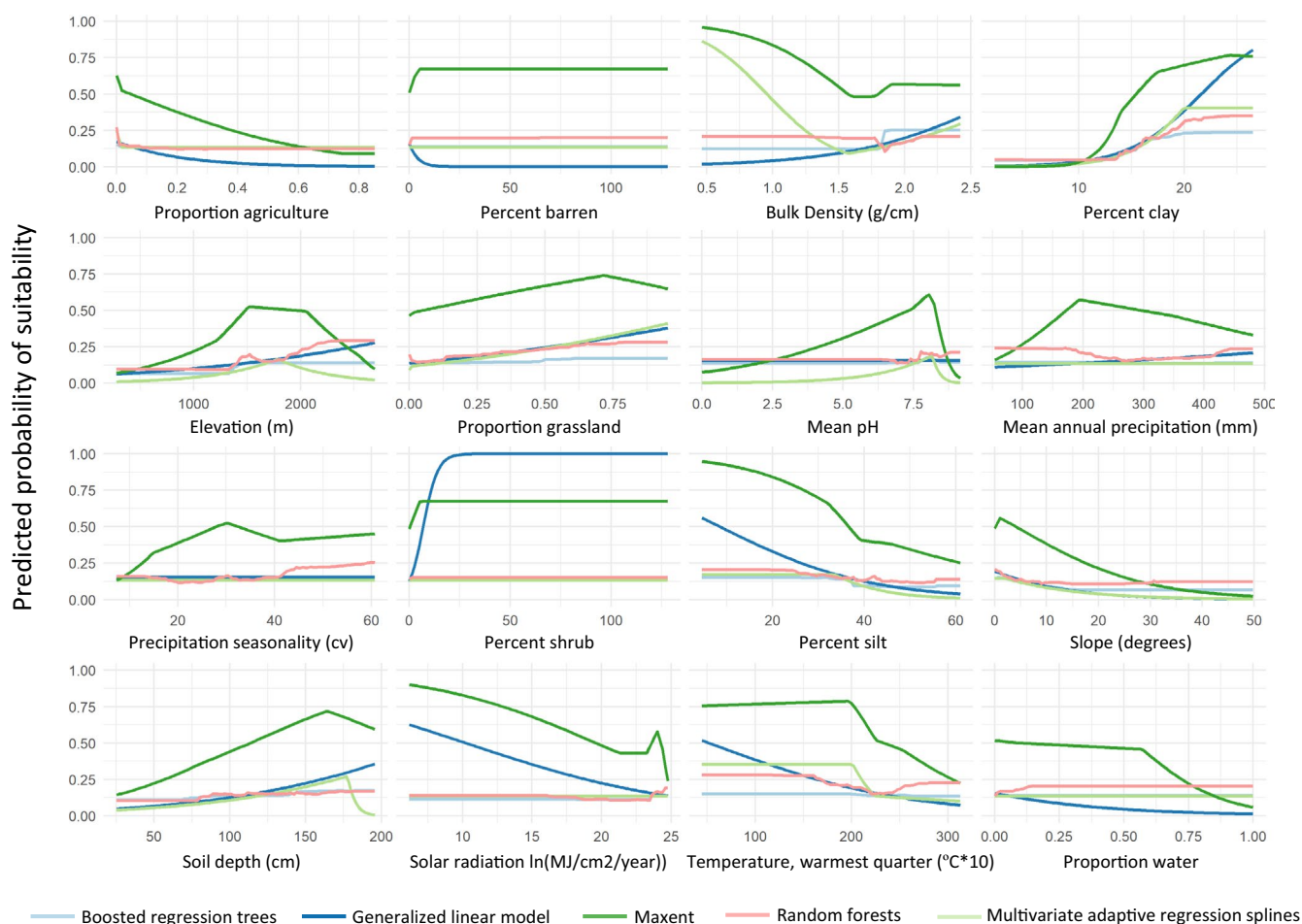


FIGURE 2 Variable response plots from the five pronghorn species distribution models used in the analysis. These five models were combined into a final ensemble species distribution model

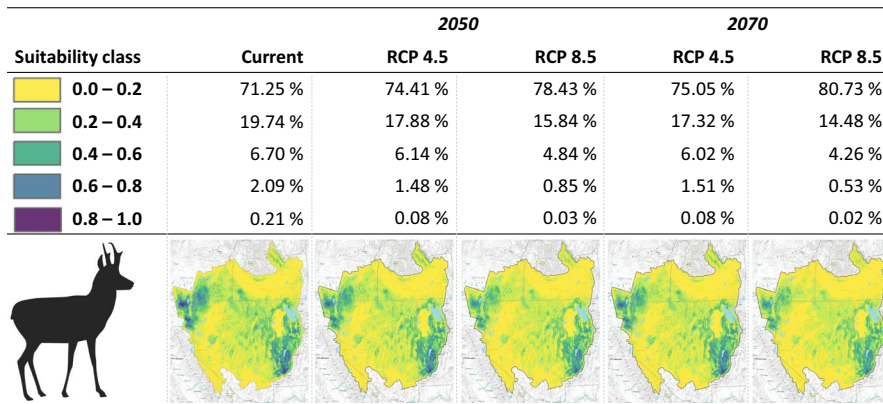


FIGURE 3 Per cent of Great Basin in each pronghorn habitat suitability class for the current time step and two future time steps (2050 and 2070) under two emissions scenarios (RCP 4.5 and 8.5). The ensemble species distribution model predictions were range rescaled from 0 to 1 and divided into five habitat suitability classes. Figures show spatial locations of each class. Abbreviation: RCP, representative concentration pathway

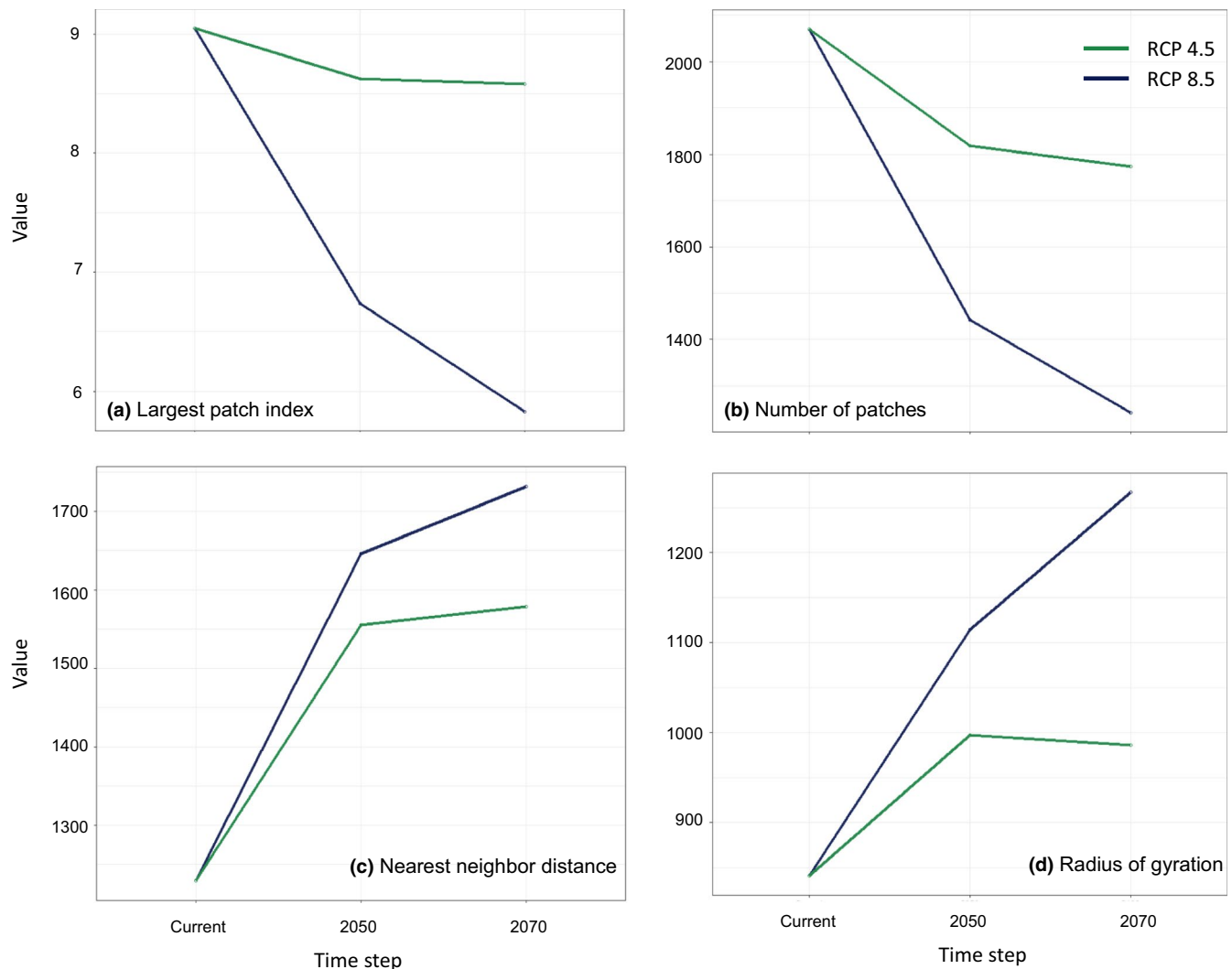


FIGURE 4 Landscape metrics of high-quality pronghorn habitat for the current time step and two future time steps (2050 and 2070) under two emissions scenarios (RCP 4.5 and 8.5). Abbreviation: RCP, representative concentration pathway

results indicate climate change will negatively affect pronghorn habitat and connectivity in the Great Basin. Assuming warming of 2°C by 2070, we observed a decline in areas of highly suitable habitat of 33.4%. Future patches of highly suitable habitat were fewer, smaller

and farther apart from one another than today. Therefore, to access critical habitat patches in the future, pronghorn will require areas of connectivity. However, areas of connectivity were less resilient to climate change than habitat patches. We found 47.2%–80% of

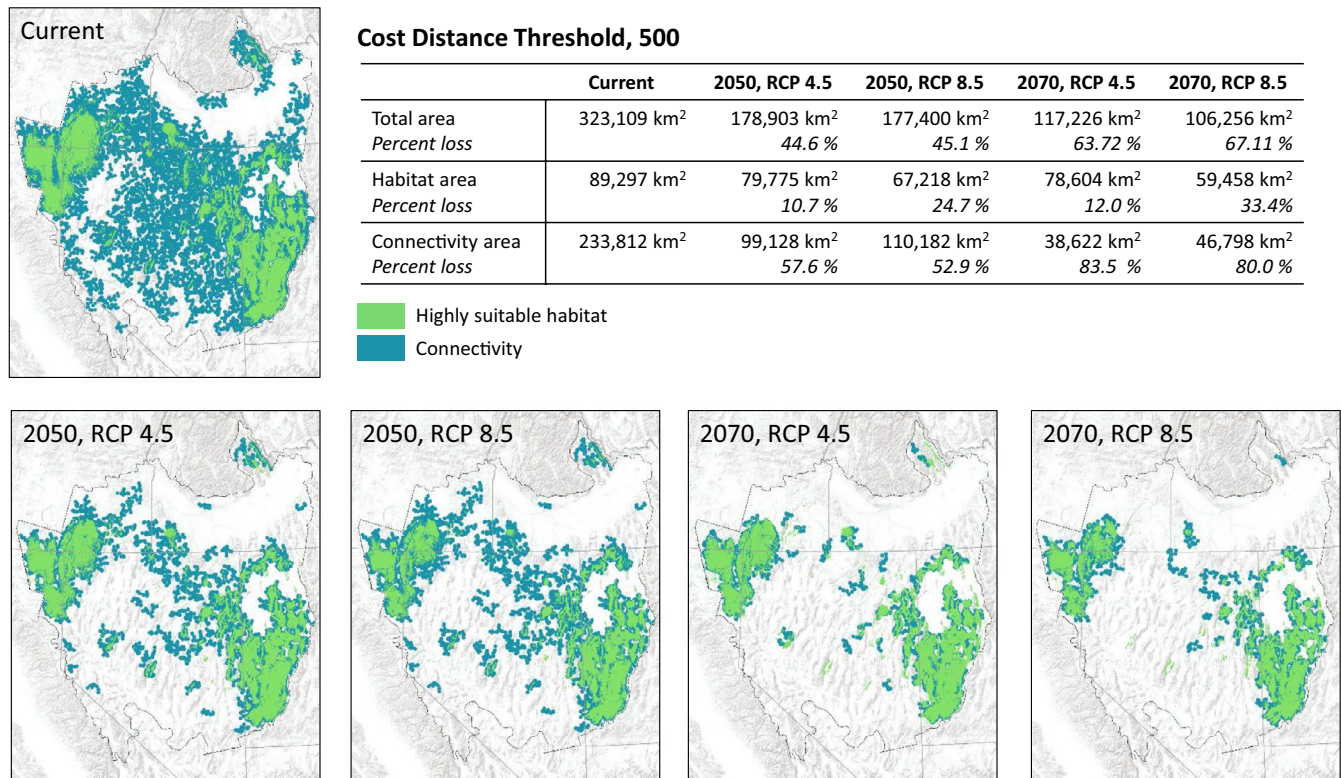


FIGURE 5 Pronghorn networks consisting of highly suitable habitat and areas of connectivity assuming a cost distance threshold of 500 for the current and two future time steps (2050 and 2070) under two emissions scenarios (RCP 4.5 and 8.5). Total area and changes in area are shown for the entire network as well as for highly suitable habitat and connectivity separately. Abbreviation: RCP, representative concentration pathway

pronghorn connectivity was lost in future scenarios, depending on the cost distance threshold used, indicating connectivity may be a limiting factor for future pronghorn populations in the Great Basin.

4.1 | Projected climate change impacts on the pronghorn habitat network

Although patches of highly suitable pronghorn habitat were more resilient to future climate change than connectivity, we observed an overall declining trend in habitat quality – highly suitable areas diminished over time whilst areas of low suitability increased. Across the Great Basin, projected future changes in precipitation are variable, and, whilst temperature is expected to increase, the magnitude of that increase will be highly dependent on topography (Chambers, 2008). The interacting effects of climate and temperature and their influence on pronghorn habitat and population growth are complex. For example, warmer temperatures and more precipitation can extend the growing season and result in more abundant forage and earlier spring green-up, but persistent warmer temperatures in the summer can also increase drought, decrease availability of highly nutritious forage and increase pronghorn mortality (Brown et al. 2006). We found temperature during the warmest quarter, annual precipitation and precipitation seasonality to all be important variables in our pronghorn models, with pronghorn having a

negative response to temperature and a slightly positive response to the precipitation variables. Gedir et al. (2015) modelled pronghorn population growth as a function of precipitation and temperature in 18 populations in the arid south-western United States. They found population growth of most populations was negatively influenced by higher temperatures and less precipitation, especially precipitation in the summer months. They also found that the growth rate of these populations was projected to decline with nine populations approaching extirpation by 2090, indicating the habitat decline we found could result in concurrent declines in pronghorn populations in the Great Basin. Lastly, because ungulates such as pronghorn have been shown to follow resource waves during migration, climatic changes can also affect timing and success of spring and fall migrations (Armstrong et al. 2016). For example, the window of time to migrate and access plants at their nutritional maximum decreased for elk in the Greater Yellowstone ecosystem following reduced winter precipitation and warmer temperatures (Middleton et al. 2013).

The negative impacts of climate change on connectivity of the overall habitat network were substantial. However, maintaining connectivity under a changing climate is key for allowing species to track changes in the location of habitat patches (Cross et al. 2012), and for maintaining functioning climate refugia (Morelli et al. 2017). Additionally, large stochastic disturbances brought on by climate change (e.g. extreme wildfires) may result in sudden losses of habitat patches, but connectivity can allow individuals to escape these

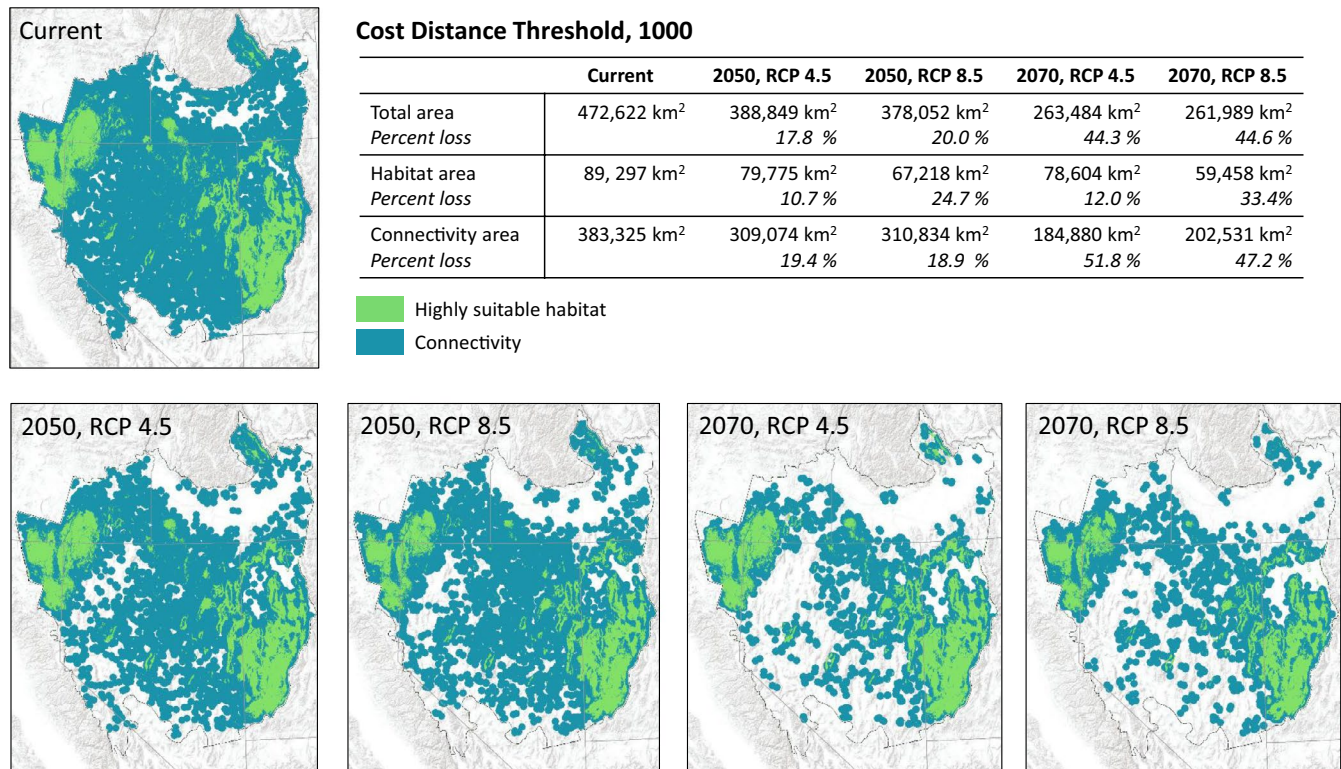


FIGURE 6 Pronghorn networks consisting of highly suitable habitat and areas of connectivity assuming a cost distance threshold of 1,000 for the current and two future time steps (2050 and 2070) under two emissions scenarios (RCP 4.5 and 8.5). Total area and changes in area are shown for the entire network as well as for highly suitable habitat and connectivity separately. Abbreviation: RCP, representative concentration pathway

disturbances and move to new resource areas relatively quickly. Because some pronghorn populations are migratory, maintaining areas of current and future connectivity will also allow these populations to migrate successfully, even if climate change results in shifts in summer and winter range areas.

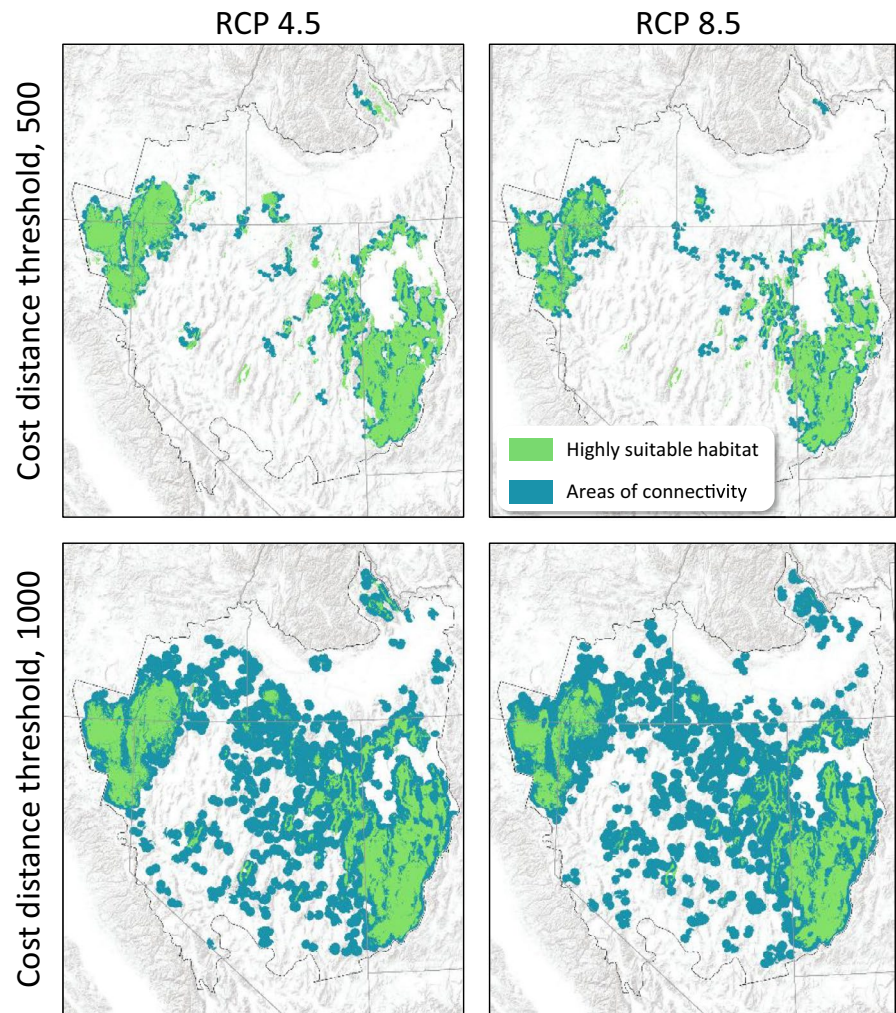
4.2 | Model limitations and caveats

Our models likely overestimated connectivity for pronghorn. Research has shown pronghorn are sensitive to linear features such as fences (Seidler et al. 2015; Xu et al. 2021), as fences can impede seasonal movements and restrain pronghorn to suboptimal habitat areas (Jones et al. 2019) and can cause direct mortality from entanglement with barbed wire (Harrington & Conover, 2006; Jones et al. 2018). In a study that included the Great Basin, the largest distance from a fence was 48 km with a mean distance of 3.1 km and the Great Basin consisted of low to moderate fence densities (McInturff et al. 2020), which likely represents a substantial impediment to movements of pronghorn within and amongst habitats in the Great Basin. However, we were unable to include fences directly in our models due to lack of accurate and consistent spatial data on their locations or structure. Therefore, the true level of fragmentation in the current landscape is likely higher than our estimates.

Another limitation of our models was our inability to parse out seasons and migratory behaviour from the data. We did not have adequate coverage from our telemetry data to model migratory movement across the entire Great Basin and had to pool data sources across years and seasons to cover our study extent. Therefore, our connectivity results reflect annual movements made by both resident and migratory pronghorn and should be interpreted as a coarse-scale connectivity analysis. Though many pronghorn populations are dependent on long-distance migrations, some are only partially migratory, migrate only short distances or are residents that do not migrate (Collins, 2016; Jakes et al. 2018; Kolar et al. 2011). In a study on pronghorn in the north-western Great Basin, 16% of individuals were residents, whilst the rest migrated distances from 10 to 160 km (Collins, 2016).

A final caveat to our models is that they relied upon future projections of climate and land use, which are difficult to validate and have a high level of uncertainty. We were able to counter some of this uncertainty by using two different emissions scenarios and multiple GCMs for the climate projections. We also used two different emissions scenarios for the land cover projections; however, we were not able to incorporate different land cover models due to the lack of data products in our study area at a fine spatial grain. If the land cover projections were prone to error (Sohl et al. 2016), this may have propagated through our identification of future pronghorn habitat suitability and connectivity.

FIGURE 7 Resilient areas of highly suitable habitat and connectivity. Areas of habitat and connectivity that persist from the current time step to 2070 are shown. Two emissions scenarios (RCP 4.5 and 8.5) and two cost distance thresholds (500 and 1,000) were modelled. Abbreviation: RCP, representative concentration pathway



4.3 | Protected status of pronghorn habitat network

Though we found suitable pronghorn habitat and areas of connectivity to decrease through time, the protection of the habitat networks remained relatively consistent into the future. Approximately 9%–12% of the pronghorn networks were protected by lands designated as IUCN categories 1–6, whilst 76%–79% of the networks were on other public lands. The Bureau of Land Management (BLM) the largest land holder in the Great Basin, covering 68%, manages its land for multiple uses. Energy production, in the form of oil, gas, geothermal and wind, is projected to increase on BLM lands in the Great Basin (Devoe, 2008). Oil and gas development has been shown to have a negative effect on pronghorn abundance (Christie et al. 2015), reduce winter range and areas available for migration (Beckmann et al. 2012; Jakes et al. 2020; Jones et al. 2019; Seidler et al. 2015) and fragment habitat (Christie et al. 2017). Actively managing the public-private lands matrix between protected areas as pronghorn habitat, corridors or migration routes could result in reducing the impacts of energy development and maintain resiliency of these areas in a changing climate (Cushman, Shirk, et al. 2012; Tack et al. 2019).

5 | CONCLUSIONS

Our results provide land and wildlife managers with information to help further the goals of Secretarial Order 3362 and guide future management decisions under future climate change scenarios. These models and maps can help managers prioritize resource investments and conservation efforts in areas most likely to be successful towards long-term pronghorn conservation. For example, with connectivity being more sensitive to climate change than highly suitable habitat, managers may choose to focus efforts (e.g. water enhancement, seeding) in those important connection corridors first. Furthermore, having identified pronghorn strongholds will help land managers make resource decisions to protect projected high value resource areas against development threats as well as prioritize conservation actions (fire rehabilitation, pinion-juniper removal, water/spring enhancement, etc.).

Management actions may become even more important to sustaining pronghorn populations in the Great Basin given the potential for compounding negative effects of climate change and linear features (i.e. roads, fences) on pronghorn. Our study found areas of highly suitable habitat decreased whilst suboptimal habitat increased with

climate change. Jones et al. (2019) found similar trends in habitat suitability when modelling the effect of fences on pronghorn. Together, the cumulative effects of climate change and fences may decrease pronghorn habitat even more than either of these studies in isolation found. With the addition of shifting vegetation, energy development, and roads, the cumulative effects on pronghorn populations in the Great Basin may be substantial. Additional research is needed on the combined effects of climate change and future development scenarios on pronghorn populations in the western United States.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13402>.

DATA AVAILABILITY STATEMENT

Pronghorn location data from California, Nevada, Oregon and Idaho is available on Figshare via: https://figshare.com/articles/dataset/Subset_of_pronghorn_location_data_in_the_Great_Basin_Ecoregion_USA/14787723. The pronghorn location data from the state of Utah is protected and cannot be shared in an online repository. Please contact the Utah Division of Wildlife Resources for data access.

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BIOSKETCH

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Authors' contributions: SC initiated the study. SC and KZ conceptualized the study. CS and GC helped to collect the data. KZ and HYW analysed the data and compiled the results. KZ wrote the manuscript with important contributions and edits from AJ, SC, HYW, CS, GC, and KD. All authors approved of the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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