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# Scale-dependent influence of the sagebrush community on genetic connectivity of the sagebrush obligate Gunnison sage-grouse

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## Abstract

Habitat fragmentation and degradation impacts an organism's ability to navigate the landscape, ultimately resulting in decreased gene flow and increased extinction risk. Understanding how landscape composition impacts gene flow (i.e., connectivity) and interacts with scale is essential to conservation decision-making. We used a landscape genetics approach implementing a recently developed statistical model based on the generalized Wishart probability distribution to identify the primary landscape features affecting gene flow and estimate the degree to which each component influences connectivity for Gunnison sage-grouse (*Centrocercus minimus*). We were interested in two spatial scales: among distinct populations rangewide and among leks (i.e., breeding grounds) within the largest population, Gunnison Basin. Populations and leks are nested within a landscape fragmented by rough terrain and anthropogenic features, although requisite sagebrush habitat is more contiguous within populations. Our best fit models for each scale confirm the importance of sagebrush habitat in connectivity, although the important sagebrush characteristics differ. For Gunnison Basin, taller shrubs and higher quality nesting habitat were the primary drivers of connectivity, while more sagebrush cover and less conifer cover facilitated connectivity rangewide. Our findings support previous assumptions that Gunnison sage-grouse range contraction is largely the result of habitat loss and degradation. Importantly, we report direct estimates of resistance for landscape components that can be used to create resistance surfaces for prioritization of specific locations for conservation or management (i.e., habitat preservation, restoration, or development) or as we demonstrated, can be combined with simulation techniques to predict impacts to connectivity from potential management actions.

**KEYWORDS**
connectivity, conservation genetics, gene flow, landscape genetics, landscape resistance

# 1 | INTRODUCTION

Landscape composition influences the way organisms navigate and distribute themselves (Fischer & Lindenmayer, 2007; Heinrichs et al., 2016; Sala et al., 2000) in space. When a species' habitat is fragmented or degraded conservation concern increases. The maintenance of connectivity, or movement of individuals among populations, reduces the risk of genetically structured populations, loss of genetic diversity to drift, inbreeding depression, and extinction risk (Burkey, 1989; Hoffmann et al., 2017; Soule et al., 1992). Despite the link to known genetic consequences, much of what we understand about connectivity is derived from direct observations of movement (Epps et al., 2005; Fahrig & Merriam, 1985; Frankham, 2003) and may misrepresent the effect on gene flow (Gubili et al., 2017; Levin, 1981; Spear et al., 2010). Direct observation of individual movement can provide insight about how organisms use or move through the landscape within a limited time-period. However, not all movements result in gene flow; a process which can occur over many generations and among populations not directly connected by dispersal events (Spear et al., 2010). Similarly, ecological processes shape populations differently across a spatiotemporal continuum (Johnson, 1980; Zeller et al., 2017). Yet few investigations of demographic or genetic connectivity have evaluated the influence of landscape components at more than one scale (Bissonette, 1997; Cushman & Landguth, 2010). Explicit characterization of the scale-dependent relationship between gene flow and the landscape would result in a better understanding of the potential impact of anthropogenic or climate-related landscape alteration on evolutionary capacity and provide more information for conservation and management decision-making (Holderegger & Wagner, 2008; Manel et al., 2003; Storfer et al., 2010).

The early 2000s has seen numerous applications of landscape genetic connectivity analyses for wildlife species, attempting to gain insight on how landscape composition affects gene flow (e.g Gerlach & Musolf, 2000; Row et al., 2015). However, many analytical approaches have significant limitations; namely a reliance on expert opinion-based parameterization of resistance, a lack of formal measures of uncertainty, and low statistical power (Bohonak, 1999; Graves et al., 2013; Keller et al., 2015; Koen et al., 2012; Landguth et al., 2010; Shirk et al., 2015; Zeller et al., 2016). Additionally, relatively few landscape genetic connectivity approaches consider more than a single scale (though see Galpern et al., 2012; Keller et al., 2013; Kozakiewicz et al., 2019). A recently developed statistical model of genetic connectivity extends the previous use of circuit theory as analogous to gene flow across a landscape (e.g McRae, 2006; Spear et al., 2010) and improves upon previous methods in multiple ways. Improvements include eliminating the use of expert opinion by directly estimating degree of impediment or facilitation for each considered landscape component, incorporating an estimate of uncertainty, providing a statistically supported framework for evaluating multiple variables in a single model, and allowing for model selection (Hanks & Hooten, 2013; Peterson et al., 2019). To date, this model has not been widely implemented.

One of the main goals of landscape genetics is to develop conservation planning tools, a goal frequently hindered by an inability to compare the relative influence of different actions (Keller et al., 2015). This formal statistical model for genetic connectivity lends itself to directly evaluating conservation actions. The best fit modelled relationship can be used to infer a resistance surface that reflects changes due to different potential conservation actions, proposed land-use change, or climate predictions and can be used in simulations to evaluate the potential impact to evolutionary capacity and to compare the consequences of alternative scenarios, analogous to other simulation-based conservation planning tools for wildlife (e.g Bennett et al., 2009; McRae et al., 2008). We utilized the statistical model for connectivity developed by Hanks and Hooten (2013) to evaluate the scale of influence for each landscape component and formed competing hypotheses of connectivity for two biologically relevant spatial scales. We subsequently extended the simulation approach described in Peterson et al. (2019) to predict impacts from hypothetical management actions using Gunnison sage-grouse (*Centrocercus minimus*) as an example of the utility of landscape genetic analyses for conservation and management decision-making.

Land-use change in the sagebrush steppe of western North America has been extensive (Bock & Webb, 1984; Braun, 1998; Knick et al., 2013). Over 50% of the sagebrush (*Artemisia* sp.) distribution has been removed or degraded (Connelly et al., 2004; Knick et al., 2013; Schroeder et al., 2004), imperiling the resident sagebrush obligate wildlife species (Anderson & Inouye, 2001). The Gunnison sage-grouse is one such sagebrush obligate species (Patterson, 1952; Young et al., 2000) impacted by the alteration of western landscapes (Oyler-McCance et al., 2001; Primack, 1993; Theobald et al., 1996). The species historically occupied the naturally rough terrain of the southeastern extent of sagebrush steppe as population centres connected by dispersal through intervening sagebrush corridors (Braun et al., 2014). Anthropogenic fragmentation and removal of sagebrush habitat is assumed to have led to significant range contraction around the population centres, low migration among populations, genetic differentiation, low genetic diversity (Oyler-McCance et al., 2005, 2015), and significant conservation concern (United States Fish and Wildlife Service, 2014). Currently the species occupies just 8% of the historical distribution (Braun et al., 2014; Schroeder et al., 2004) as a single, relatively large population in the Gunnison Basin of Colorado, USA (~85%–90% of remaining birds) and six smaller satellite populations (United States Fish and Wildlife Service, 2014). Individuals have relatively high fidelity for breeding grounds (i.e., leks) within populations, although movement among leks occurs relatively frequently (Aldridge et al., 2012; Oyler-McCance et al., 2005). The natural hierarchical structure of the species distribution (e.g., discrete breeding grounds nested within discrete populations) increases the likelihood of scale-dependent effects of the landscape on gene flow and reinforces the importance of considering scale when investigating gene flow patterns. Understanding the influence of landscape features on gene flow among and within populations can provide insights about conservation and management given that the human population is expected to continue growing for at least

the next three decades (Colorado Water Conservation, 2009) and landscape composition to continue changing (Theobald et al., 1996; United States Fish and Wildlife Service, 2014).

Previous work directly observing sage-grouse (*Centrocercus* spp.) habitat selection, or movement through the landscape (i.e., telemetry), provide some insight into the features likely to influence gene flow. For example, sage-grouse require sagebrush as a food source and for concealment from predators (Barnett & Crawford, 1994; Braun et al., 2005; Patterson, 1952; Sveum et al., 1998), while they generally avoid conifer cover (Baruch-Mordo et al., 2013; Hagen et al., 2011) and anthropogenic features (Aldridge et al., 2008, 2012; Blickley et al., 2012; Copeland et al., 2013). Additionally, a developed understory is important for sage-grouse brood rearing (Aldridge & Brigham, 2002; Barnett & Crawford, 1994) and nest concealment (Aldridge & Brigham, 2002; Webb et al., 2012). Gunnison sage-grouse populations, and leks within populations, are located within a variable range of climatic and topographic features, both of which are known to impact habitat use, movement, and persistence (Aldridge et al., 2008; Blomberg et al., 2012; Harju et al., 2013; Knick et al., 2013). Direct observation provides insight regarding short-term impacts to movement, but the degree to which these insights apply to long-term evolutionary impacts via gene flow is unknown (Levin, 1981; Roffler et al., 2016).

We fit a formal statistical model for genetic connectivity (Hanks & Hooten, 2013) to data for two biologically-relevant, hierarchical, spatial scales for the Gunnison sage-grouse, a species of conservation concern in an increasingly fragmented and degraded habitat. Our main objective was to identify the primary drivers of coarse-scale interpopulation and fine-scale intrapopulation genetic connectivity and directly estimate the degree of impediment or facilitation for each identified landscape component. We also wanted to illustrate the conservation applications of the identified relationships between genetic connectivity and landscape composition. We used our best fit models and simulations to demonstrate how hypothetical management actions might impact gene flow in future generations. We generally expected more contiguous sagebrush habitat to facilitate gene flow and rough terrain and anthropogenic modification to impede gene flow. An improved understanding of how the landscape influences genetic connectivity and how management actions might enable the achievement of specific targets for gene flow could ultimately result in better conservation outcomes.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We defined our two study areas by buffering known lek locations with Gunnison sage-grouse movement distances. We created the rangewide extent by applying a 54.68-km buffer around each known active lek to account for maximum observed dispersal distance (2 × 17.34 km; D. J. Saher, unpublished data) and an additional 20-km buffer to account for edge effects in our calculation of

moving window averages for pixels (see Spatial Covariates section below and Appendix S1). The resulting rangewide extent covered ~56,818 km$^2$ (Figure 1) of frequent changes in cover type, including anthropogenic features, land conversions (e.g., agriculture), and mountains (Gunnison sage-grouse Rangewide Steering, 2005). We evaluated rangewide connectivity among populations as a function of the intervening landscape within the described study area. The Gunnison Basin extent covered ~6282 km$^2$ and was previously created for development of seasonal resource selection models (Aldridge et al., 2012). Within the Gunnison Basin, we evaluated connectivity among leks within native sagebrush-steppe (dominated by big sagebrush, *Artemisia tridentata* ssp.) interrupted by anthropogenic features and variable topography (Gunnison sage-grouse Rangewide Steering, 2005).

### 2.2 | Genetic samples

Our rangewide data set was composed of 254 blood samples collected from birds captured using spotlight trapping methods (Giesen et al., 1992; Wakkinen et al., 1992) between 1996 and 2004 as part of a previous study (Oyler-McCance et al., 2005), avoiding confounding effects of translocations from the Gunnison Basin to the satellite populations that began in 2005 (United States Fish and Wildlife Service, 2014). Samples were distributed across populations as follows: Cimarron = 4, Crawford = 21, Dove Creek = 43, Gunnison Basin = 116, Piñon Mesa = 19, San Miguel = 51 (Figure 1). We excluded the recently re-established Poncha Pass population (Nehring & Apa, 2000). Our Gunnison Basin data set was composed of 624 unique samples representing 49 of the 70 leks considered active between 2006 and 2014 (92% of samples collected after 2010), also as part of a previous study (Zimmerman et al., 2019). In brief, samples were primarily noninvasively collected feathers, but also included mortalities, and blood samples collected from captured individuals. Leks not represented in our data could not be accessed or no feathers were found when searched. The number of samples collected at a lek ranged from 1 to 57 (See Appendix Table S2.1 for all lek sample sizes). The Gunnison Basin samples used for each extent are distinct.

Details on DNA extraction, microsatellite characterization, and duplicate sample elimination were previously published (Zimmerman et al., 2019). Samples were genotyped with 22 microsatellite loci (Caizergues et al., 2003; Fike et al., 2015; Oyler-McCance & St. John, 2010; Piertney & Höglund, 2001; Segelbacher et al., 2000; Taylor et al., 2003), using polymerase chain reaction (PCR) with components and concentrations as described in Oyler-McCance and Fike (2011) and thermal profiles as originally published. Duplicate noninvasive samples (Gunnison Basin only) were identified and removed using a combination of the R package *allelematch* (Galpern et al., 2012) and the stand-alone program Dropout (McKelvey & Schwartz, 2005). We calculated an individual-based pairwise absolute genetic distance matrix (**D**) based on a Manhattan distance in R (R Core Team, 2018) as in Hanks and Hooten (2013), for the rangewide and Gunnison Basin data sets. Genetic distance matrices were used as
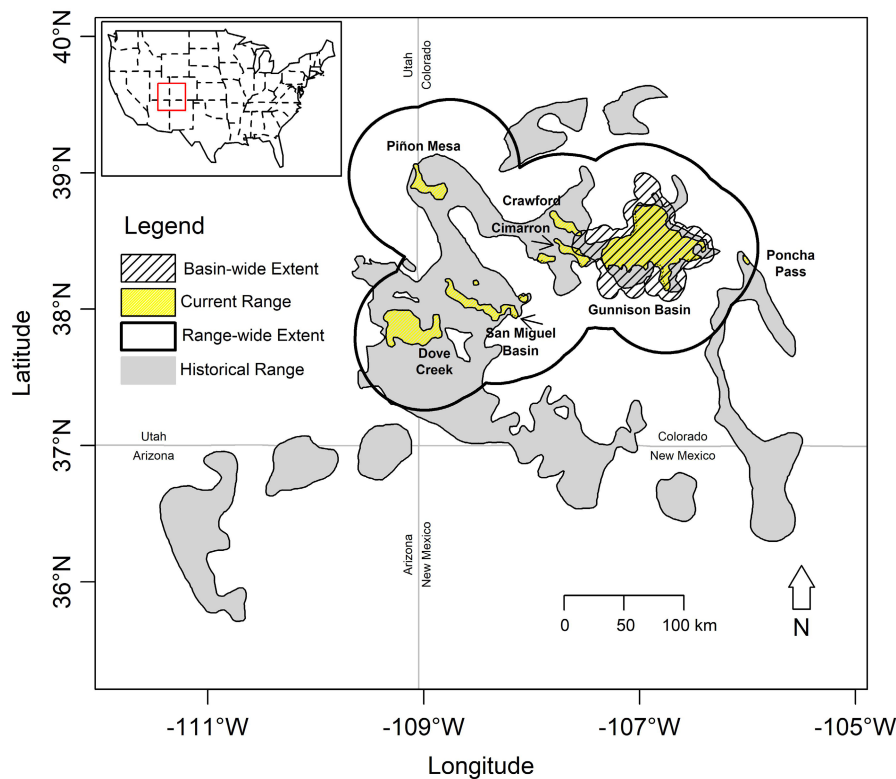
**FIGURE 1** Historical (grey) and current (yellow) distribution of Gunnison sage-grouse in the southwestern United States. Populations are labeled with respective names. Black polygon designates the rangewide study area and the hatched polygon delineates the Gunnison Basin study area. The historical and current distribution maps were developed by Schroeder et al. (2004); the two northernmost portions of the historical distribution correspond to an unknown species of sage-grouse and are not verified by Colorado Parks and Wildlife (Gunnison sage-grouse Rangewide Steering, 2005)

the dependent variable in our connectivity modelling as described in Hanks and Hooten (2013). Individuals sampled within the same population (rangewide analysis) or from the same lek (Gunnison Basin analysis) were treated as repeated samples at a location in our connectivity model.

## 2.3 | Spatial covariates

We identified spatial covariates likely to influence the ability of sage-grouse (*Centrocercus* spp.) to navigate the landscape based on existing literature. Thus we considered anything that affects dispersal, resource selection, survival, fecundity, occupancy, avoidance, or behaviour. The landscape components identified included the following: habitat structure (e.g., shrub height) and amount of sagebrush cover (Aldridge & Boyce, 2007; Aldridge et al., 2008, 2012; Baruch-Mordo et al., 2013; Doherty et al., 2010; Fedy et al., 2014; Harju et al., 2013; Knick et al., 2013; Oyler-McCance et al., 2001; Rice et al., 2017), amount of conifer cover (Baruch-Mordo et al., 2013; Commons et al., 1999; Fedy et al., 2014; Hagen et al., 2011; Knick et al., 2013; Severson et al., 2017), conifer configuration or aggregation (Baruch-Mordo et al., 2013), normalized difference vegetation index (NDVI) as a proxy for phenology (Aldridge & Boyce, 2007; Aldridge et al., 2012), soil wetness as described by compound topographic index or CTI (Aldridge & Boyce, 2007; Carpenter et al., 2010), seasonal habitat selection models for Gunnison sage-grouse (Aldridge et al., 2012), agricultural cover (Aldridge & Boyce, 2008; Beck & Maxfield, 2003; Bush et al., 2011; Fedy et al., 2014; Knick et al., 2013), proportion of anthropogenic

development (Aldridge et al., 2012; Knick et al., 2013; Rice et al., 2017), distance to development (Aldridge & Boyce, 2007; Aldridge et al., 2012), human population density (Aldridge et al., 2008), distance to human population density (Aldridge & Boyce, 2007; Aldridge et al., 2008), road density (Aldridge & Boyce, 2007; Aldridge et al., 2012; Fedy et al., 2014; Knick et al., 2013), distance to roads (Aldridge et al., 2012; Rice et al., 2017), oil and gas well density (Aldridge & Boyce, 2007; Blickley et al., 2012; Copeland et al., 2013; Green et al., 2017; Smith et al., 2014; Tack et al., 2011), distance to oil and gas wells (Aldridge & Boyce, 2007; Blickley et al., 2012; Copeland et al., 2013; Tack et al., 2011), slope (Harju et al., 2013; Knick et al., 2013), topographic roughness as described by the terrain ruggedness index or TRI (Fedy et al., 2014; Harju et al., 2013; Knick et al., 2013), annual precipitation (Blomberg et al., 2012; Fedy et al., 2014), mean maximum temperature (Blomberg et al., 2012), growing degree days, and a dryness index (Aldridge & Boyce, 2008; Table 1). Wind energy infrastructure can also impact movement and survival of sage-grouse (LeBeau et al., 2013, 2017). Presently, there are no major existing wind energy developments within the Gunnison sage-grouse range (United States Fish and Wildlife Service, 2014). We considered all identified landscape components influencers of connectivity.

Like other wildlife species, sage-grouse respond to different landscape components and characteristics in different ways and at different scales (Aldridge et al., 2012; Wiens, 1989; Wiens & Milne, 1989). Thus, we used a circular moving window to summarize the landscape variables in a neighbourhood larger than a single pixel to create versions of each landscape variable representing different scales. We used a circular moving window centred on

**TABLE 1** Covariates used to model connectivity

| Abv. | Covariate[a] | Source | Predicted impact |
|------|-----------|--------|------------------|
| *Habitat composition and configuration* | | | |
| AS | Proportion of all sagebrush cover | Landfire | + |
| BS | Proportion of big sagebrush cover | Landfire | + |
| CON | Proportion of conifer cover | Landfire | − |
| LS | Proportion of low sagebrush cover | Landfire | + |
| CC | Conifer configuration | Landfire derived | − |
| PBS | Percentage big sagebrush cover | NLCD shrubland product | + |
| PSB | Percentage all sagebrush cover | NLCD shrubland product | + |
| SBHT | Shrub height | NLCD shrubland product | + |
| *Habitat selection* | | | |
| N | Nest habitat RSF | Aldridge et al. (2012) | + |
| *Climate and phenology* | | | |
| MMT | Mean maximum temp. | PRISM | − |
| MAR | Mean annual rainfall | PRISM | + |
| DRI | Dryness index | Daymet derived | − |
| GDD | Growing degree days | Daymet derived | + |
| FNDVI | Fall NDVI | MODIS | + |
| SNDVI | Spring NDVI | MODIS | + |
| *Terrain morphology* | | | |
| CTI | Compound Topo. Index | EROS | + |
| S | Slope | DEM derived | − |
| TRI | Terrain Ruggedness Index | DEM derived | − |
| *Anthropogenic change* | | | |
| DI14 | Dist. To Class 1–4 Roads | NAIP derived | + |
| DI12 | Dist. To Class 1 & 2 Roads | NAIP derived | + |
| DI47 | Dist. To Class 4–7 Roads | NAIP derived | + |
| DIA | Dist. To All Roads | NAIP derived | + |
| DIB | Dist. To BLM Roads | NAIP derived | + |
| DID | Dist. To Development | NLCD | + |
| DILD | Dist. To Light Duty Roads | aerial imagery/TIGER derived | + |
| DIOG | Dist. To Oil & Gas Wells | States of CO & UT | + |
| DIP | Dist. To Pop. Dens. | LandScan | + |
| DOG | Dens. Of Oil & Gas Wells | States of CO & UT | − |
| DAG | Proportion Of Agriculture | NLCD | − |
| DA | Dens. Of All Roads | NAIP/TIGER dervied | − |
| DB | Dens. Of BLM Roads | NAIP derived | − |
| DD | Proportion Of Development | NLCD | − |
| DP | Dens. Of Population | LandScan | − |
| D14 | Dens. Of Roads Class 1–4 | NAIP/TIGER derived | − |
| D12 | Dens. Of Roads Class 1 & 2 | NAIP/TIGER derived | − |
| D2 | Dens. Of Roads Class 2 | TIGER | − |
| D47 | Dens. Of Roads Class 4–7 | NAIP derived | − |
| DLD | Dens. Of Light Duty Roads | aerial imagery/TIGER derived | − |

*Note:* The data source (source), abbreviation (Abv.), and predicted impact (positive [+] or negative [−]) to connectivity associated with each covariate are listed below. Covariates are organized into general categories (italic). The different sagebrush layers were based on different data types: Landfire derived layers are based on a binary landcover classification and the NLCD shrubland product layers are based on percentage of cover.

[a]Calculation of all covariates and details on data source are described in Appendix S1.

each pixel for all landscape variables calculating the mean within a radius of 564, 1000, 3000, 6400, 10,000, 15,000, and 20,000-m. Each considered radius had some support in the sage-grouse literature for actual movement distances up to 6400-m (e.g Aldridge et al., 2012; Fedy et al., 2012; Fremgen et al., 2016; Taylor et al., 2013). Additional radii were considered given potential differences in scale of direct observations versus gene flow. All spatial data processing was performed in ArcMap 10.1 (Environmental Systems Research, 2012). Details on covariate calculation and spatial data processing are included in Appendix S1. We predicted high sagebrush cover, high-quality habitat (as defined by resource selection models), more rain and growing degree days, and high CTI would facilitate gene flow. Conversely, we predicted high conifer cover and/or aggregation, high temperatures, drier climate, steeper slopes, rough terrain, and anthropogenic modification would impede gene flow (Table 1).

## 2.4 | Model fitting

We fit a formal statistical model based on circuit theory (Hanks & Hooten, 2013) to our genetic data to directly estimate the degree of resistance or facilitation to gene flow imposed by landscape covariates in a Bayesian framework. Our model was specified as follows:

$$- \mathbf{D} \sim \text{generalized Wishart} \, (1, 2\Psi) \tag{1}$$

$$\alpha_{i,j} = \begin{cases} \exp\left[ \dfrac{1}{d_{ij}} \left( \dfrac{\mathbf{x'}_i + \mathbf{x'}_j}{2} \right) \boldsymbol{\beta} \right] & , j \in N(i) \\ 0 & , j \notin N(i) \end{cases} \tag{2}$$

$$\boldsymbol{\beta} \sim \text{Normal} \, (\boldsymbol{\mu}_{\boldsymbol{\beta}}, \boldsymbol{\Sigma}_{\boldsymbol{\beta}}) \tag{3}$$

$$\log(\tau) \sim \text{Normal} \, (0, 1) \tag{4}$$

where $\mathbf{D}$ is the absolute genetic distance matrix for individuals (we used the Manhattan distance), $\Psi$ is the the covariance matrix of the observed nodes (i.e., populations/leks) accounting for variability ($\tau$) in repeated measures (i.e., multiple individuals) at a node. In the above model, $\mathbf{D}$ must be negated to use the mathematical relationships for estimation of edge weights as analogous to electrical conductance. The graph structure of the nodes connected by edges (i.e., effective dispersal or gene flow) is used to define the correlation structure ($\Sigma$) of the measured genetic distance ($\mathbf{D}$) among nodes (Equation 1). We obtained the covariance matrix $\Sigma$ by calculating edge weights ($\alpha_{ij}$) for each pair of nodes for a spatial covariate (i.e., raster layer) for the entire spatial extent of interest, and then found the inverse of the covariance matrix incorporating the influence of intervening nodes on the correlation structure. In calculating edge weights ($\alpha_{ij}$), $i$ and $j$ are locations of two nodes, $\mathbf{x}_i$ is the vector of values of spatial covariates at node $i$, $\mathbf{x}_j$ is the vector of values of spatial covariates at node $j$, and $d_{ij}$ is

the Euclidean distance between nodes $i$ and $j$. The edge weight ($\alpha_{ij}$) is the conductance between nodes and is proportional to the transition rate from one location ($i$) to another ($j$). The exponential link function (Equation 2) ensures intuitive interpretation of coefficients, where negative values denote degree of impediment and positive values degree of facilitation. If $i$ and $j$ are not first order neighbours ($j \notin N(i)$) the edge weight is zero; nodes not directly connected, however, may still be connected through intervening nodes. The covariance matrix of the observed nodes, $\Psi$, is calculated as $\mathbf{K\Sigma K^{T}} + \tau \mathbf{I}$, where $\mathbf{K}$ is a matrix relating each sample to a node, $\mathbf{I}$ is the identity matrix, and $\tau$ is a spatial nugget parameter representing the variability in repeated observations (i.e., individual birds) collected from the same location (i.e., node in the graph). We used functions in the *rwc* R package (Hanks, 2018) for data processing, the generalized Wishart probability distribution, to relate sample locations to raster grids, and to calculate covariance structure. Before fitting models to our data, we confirmed our model fitting approach could recover the true relationships with simulated data (see Appendix S1 for validation of our approach). Variability associated with coefficient estimates for each landscape covariate was typically large and credible intervals (*CRIs*) frequently included zero (Appendix S1 Table S2.2–2.5); however our modelling approach appropriately identified the true model and the mean of the coefficients approximated the true resistance values.

We first fit single covariate models for each scale (i.e., moving window radius) as both a linear and quadratic relationship. Each model fit included two independent chains of 50,000 Markov chain Monte Carlo (MCMC) iterations with the first 5000 iterations discarded as a burn-in period, using a random walk Metropolis-Hastings sampler. We evaluated convergence of independent chains through visual inspection of trace and density plots (not included here) and with the Gelman-Rubin diagnostic (Gelman & Rubin, 1992). We also fit a null hypothesis model based on an undifferentiated landscape (i.e., an intercept-only model) testing the isolation by distance null hypothesis (Wright, 1943) for comparison. We next fit multicovariate models using all combinations of covariates. Different forms of a single covariate were highly correlated (Pearson's $r > 0.8$). Consequently, we retained the form with the lowest deviance information criterion (*DIC*; Spiegelhalter et al., 2002) for combination in multicovariate models. Convergence was problematic when a model included moderately correlated covariates (Pearson's $r > |0.50|$), we therefore chose variables based on *DIC* rank and excluded lower ranked variables correlated at this level. We did not eliminate variables for combination with coefficient *CRIs* that included zero because our simulation-based evaluation of model fitting showed that coefficient *CRIs* frequently included zero but the mean coefficient value closely approximated the simulated true coefficient. Each model was fit and checked for convergence as described above, with the exception that our multicovariate models required longer runs for convergence resulting in 150,000 MCMC iterations, discarding the first 50,000 iterations as a burn-in period. The top model was chosen through *DIC* rank. All model fitting was accomplished in R.

We used a 5-fold cross-validation procedure to evaluate the generalizability of our models to unobserved data (Conn et al., 2018; Hooten & Hobbs, 2015). We split our data into five approximately equal partitions. We fit the model five times, each time withholding a different partition of individuals, using the withheld data to calculate the log predictive density (*lpd*) for each iteration. A cross-validation (*CV*) score based on the *lpd* for all five folds of the data was calculated as in Hobbs and Hooten (2015). We performed *CV* for the top 10 *DIC* ranked models for each spatial extent (rangewide and Gunnison Basin). The highest *CV* score corresponds to the model with the best predictive ability in the evaluated model set. We also evaluated the ability of the resistance surface created from our top ranked model to give rise to the observed data. We simulated genetic data from resistance surfaces created from the top ranked modelled relationship and an undifferentiated surface (isolation by distance or null hypothesis) for both the rangewide and Gunnison Basin extents using the PopGenReport R package (Adamack & Gruber, 2014) as described in Peterson et al. (2019). We simulated 4900 individuals (49 leks × 100 individuals) for Gunnison Basin and 5750 individuals for the rangewide analysis (6 subpopulations with 50, 200, 200, 4775, 175, and 350 individuals simulated representing true population estimates for Cimarron, Crawford, Dove Creek, Gunnison Basin, Piñon Mesa, and San Miguel, respectively; United States Fish and Wildlife Service, 2013). The true population sizes are highly variable; thus it was important to modify some functions in the R package to accommodate variable population size in our simulations (Appendix S3). For simulation parameters at both extents, we assumed a 1.6:1 female to male sex ratio (Gunnison sage-grouse Rangewide Steering, 2005), 22 loci with 11 alleles per locus (median alleles per locus in observed data), four offspring per reproductive event (based on the product of average clutch = 8 [Young et al., 2020], average hatchability = 82.5% [Young et al., 2020], average nest success = 46.7% [Davis, 2012; Stanley et al., 2019; Young et al., 1994] and rounded up to the nearest whole number), 0.01 as the percentage of individuals moving the maximum dispersal distance (proportion moved > the 99th percentile of all max distances in Aldridge et al., 2012), an empirical estimate of migrants per year (Wilson & Rannala, 2003), and simulated data for 1000 and 500 years for the rangewide and Gunnison Basin extents respectively. We then randomly subsampled an even number of individuals from each population ($n = 50$) or lek ($n = 15$) from the simulated data to approximate the dimensions of the observed data. We calculated a genetic distance matrix based on the individual-based Manhattan distance from the subsampled simulated data and fit the top 10 and bottom 10 ranked multicovariate models as described above. If the gene flow pattern observed in our original data was primarily shaped by the landscape variables we identified in our top model, we expected the model fitting process using simulated data from our top-ranked model to result in a *DIC* rank similar to the observed data, and *DIC* rank of models fit to data simulated from the undifferentiated surface to result in the opposite *DIC* rank order. We evaluated rank similarity with a Spearman's rank correlation coefficient ($\rho$).

## 2.5 | Conservation simulation

To illustrate the conservation potential of our modelled relationships we simulated management actions. We modified resistance surfaces based on the top ranked Gunnison Basin and rangewide modelled relationships. Rangewide we simulated actions via a modified surface (based on our best fit rangewide model—see Section 3) by maximizing the observed percentage of sagebrush cover (increasing to 26% in a 3000-m window) in an artificial 708-km$^2$ habitat corridor connecting the Gunnison Basin population to the Piñon Mesa population by way of Crawford (Figure 2b), an unmodified surface but with an artificial new population of 200 individuals (i.e., reintroduction) between Crawford and Piñon Mesa (Figure 2c), and the modified surface including the habitat corridor and new population combined (Figure 2d). For the Gunnison Basin, we artificially increased shrub height by 50% (to ~33 cm) in a 3000-m window over a 7.2-km$^2$ patch between two leks (Figure 3b), with the expectation that increased shrub height would result in greater cover of taller shrubs, and thus, increase gene flow between the two leks (based on our best fit Gunnison Basin model—see Section 3). We also modified the same area to decrease shrub height by 50% (Figure 3c). We used the above-described simulation procedure to simulate from the modelled resistance surface and the modified versions using the PopGenReport R package with 100 independent repetitions for 1000 and 150 years post landscape modification for the population and lek comparisons, respectively. We compared the change in Manhattan genetic distance (**D**) between the targeted leks or populations over time for the modified and unmodified resistance surfaces. This exercise was intended as an example of how our modelling approach can facilitate decision making and does not make any suggestion regarding management actions.

## 3 | RESULTS

### 3.1 | Rangewide model fitting

Individual pairwise Manhattan genetic distances for the rangewide analysis ranged between 8.00 and 92.00. The best fit scale (i.e., moving window radius) for each variable suggests habitat influenced gene flow primarily at a fine-moderate scale, where the best fit radius for proportions of conifer cover (CON) and low-statured sagebrush cover (LS) was 1000-m, percentage of sagebrush cover (PSB) was 3000-m, and proportion of big sagebrush cover (BS), percentage of big sagebrush cover (PBS), and shrub height (SBHT) was 6400-m (Table 1; see Appendix Table S2.2 for complete results). Climate and phenology also influenced gene flow at the fine-moderate scale, where mean annual rainfall (MAR), spring NDVI (SNDVI), and a dryness index (DRI) had a best fit radius of 1000-m, mean maximum temperature (MMT) and fall NDVI (FNDVI) with 3000-m, and growing degree days (GDD) with 6400-m. Anthropogenic and topographic variables influenced gene flow at more coarse scales: compound topographic index (CTI), density
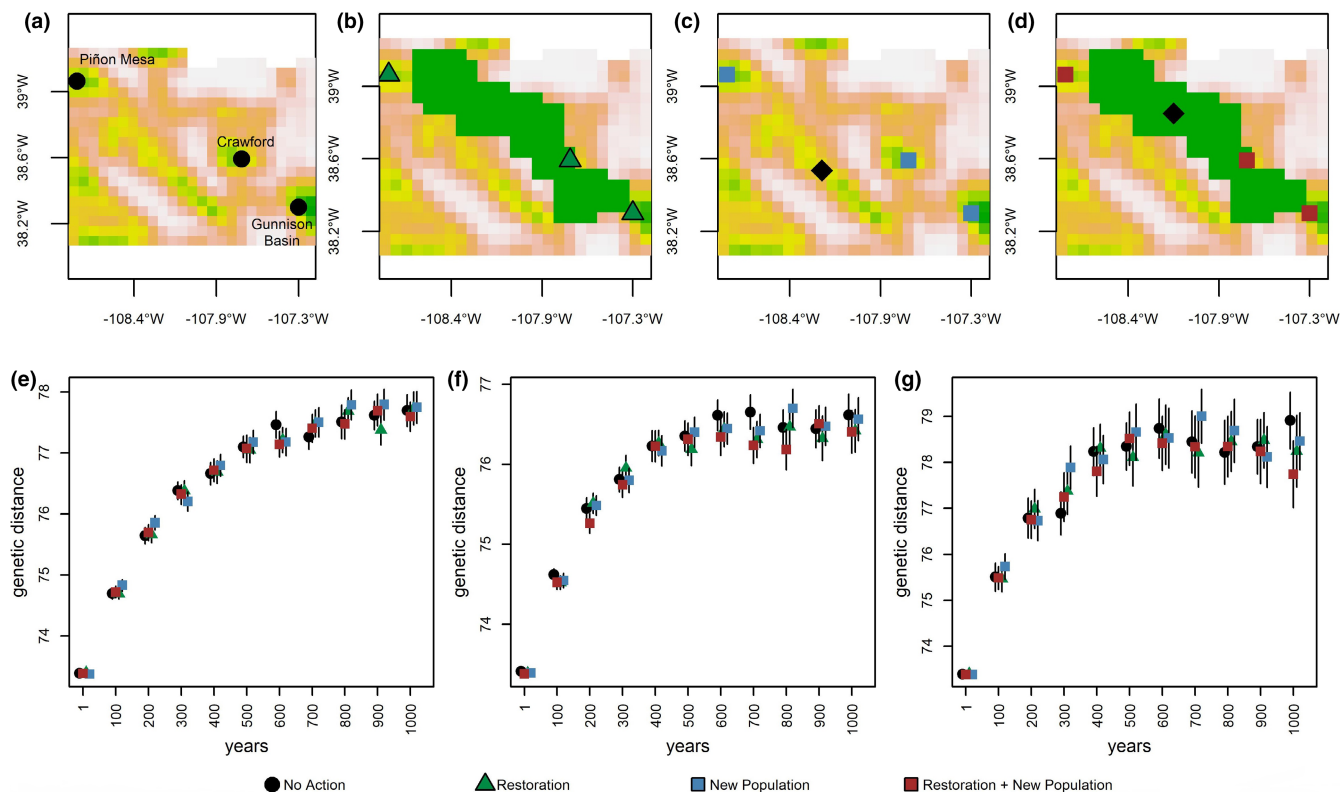
**FIGURE 2** The sagebrush cover surrounding three populations before (a) and after (b) a hypothetical management action increasing the intervening sagebrush cover by 26% in a 3000-m window over 708-km² (white = less, green = more), (c) establishing a new population (♦) in existing sagebrush habitat, and the combination of a sagebrush corridor and a new population (d). The average genetic distance (y-axis; Manhattan genetic distance) between Gunnison Basin and Piñon Mesa (e), Gunnison Basin and Crawford (f), and Piñon Mesa and Crawford (g) from simulations of gene flow based on a resistance surface developed with the original sagebrush cover raster (●), new sagebrush corridor (▲), and/or establishment of a new population (■, ■) and the relationships described by the top model. Vertical lines in panels (e–f) are 95% confidence intervals for the 100 independent simulations at each time step (1–1000 years)

of class 1 and 2 roads (D12, D2), proportion of agricultural cover (DAG) and development (DD), density of oil and gas wells (DOG), population density (DP), slope (S) ≥6400-m. Most of the modelled relationships match our predicted impact on gene flow (Table 1). The few notable exceptions included negative coefficient estimates for MAR, GDD, and SNDVI, and positive coefficient estimates for DAG, DA, DD, DP, D14, D12, D2.

Of the 33 variables considered in single covariate models, nine were retained for combination in multicovariate models after considering DIC rank and correlation: proportion of conifer cover (CON), density of class 2 roads (D2), proportion of development (DD), distance to population density (DIP), density of light duty roads (DLD), density of oil and gas wells (DOG), proportion of low-statured sagebrush cover (LS), mean maximum temperature (MMT), percent big sagebrush cover (PBS) (Figure 4; Appendix Table S2.2). We fit a total of 247 multicovariate models, the top 20 of which included a relatively large positive relationship with percent big sagebrush cover ($\beta_{PBS} = 2.3$ [–1.9, 7.0] in top model) and a smaller but consistent negative relationship with proportion of conifer cover ($\beta_{CON} = -0.5$ [–6.3, 3.9] in top model) indicating these 2 variables are consistently important in explaining observed variation in genetic distance (Table 2; Appendix Table S2.3). In addition to CON and PBS, the top ranked

multicovariate model (DIC = –72,497.79; lpd = 3842.39) also included three variables with a small but positive coefficient estimate: D2 ($\beta_{D2} = 0.5$ [–4.3, 5.9]), DLD ($\beta_{DLD} = 0.3$ [–5.0, 5.7]), DOG ($\beta_{DOG} = 0.2$ [–5.9, 6.3]). The conductance surface created from the top modelled relationships indicated relatively low gene flow rangewide with predicted high gene flow areas in population centres, primarily in the Gunnison Basin (Figure 5a). In our evaluation of whether the conductance surface from the top modelled relationship could result in our observed genetic distances, we found distance between populations probably plays a role in addition to landscape resistance. The rank of models fit to data simulated from the top modelled resistance surface (inverse of the conductance surface) closely approximated the DIC rank of the models based on observed data ($\rho = 0.90$). The DIC rank of models fit to data simulated from an undifferentiated surface also approximated DIC rank of models fit to the observed data; however, the correlation coefficient was smaller ($\rho = 0.83$) (Appendix Table S2.6).

## 3.2 | Gunnison Basin model fitting

Individual pairwise Manhattan genetic distance for Gunnison Basin ranged between 5.12 and 87.13. The shrub component influenced
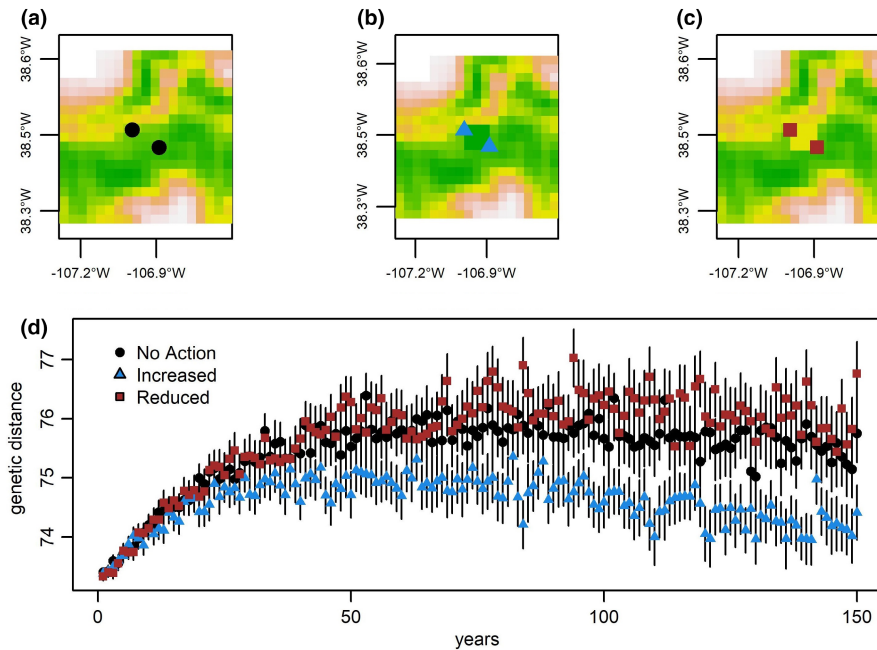
**FIGURE 3** The shrub height surrounding two leks within the Gunnison Basin before (a) and after (b) a hypothetical management action increasing the intervening shrub height by 50% in a 3000-m window over a 7.2-km² patch (white = shorter shrub, green = taller shrub), and (c) reducing shrub height in the same patch. The change in average genetic distance (y-axis; Manhattan genetic distance) between two selected leks from simulations of gene flow among active leks in the Gunnison Basin based on a resistance surface developed with the original shrub height raster (●), increased shrub height (▲), and decreased shrub height (■) and the relationships described by the top ranked model, mimicking management actions (d). Vertical lines in panel (d) are 95% confidence intervals for the 100 independent simulations at each time step (1–150 years)

gene flow across multiple scales with best fit radii ranging from 564-m to 10,000-m, while the conifer component had a best fit with a radius of 20,000-m (Appendix Table S2.4). All but a single climate variable was best fit at a coarse scale (15,000–20,000-m radius), the exception being MAR with a best fit to the 3000-m radius. Phenology variables were best fit at a fine-scale in the fall (FNDVI 3000-m radius) and coarse-scale in the spring (SNDVI 15,000-m). Similar to shrub variables, anthropogenic variables influenced gene flow across nearly all possible radii. Topographic variables were all best fit when averaged over a 20,000-m radius. As for the rangewide single covariate models, most of our predicted relationships for the effect of individual variables on gene flow were affirmed. Notably, we found negative coefficient estimates for LS, MAR, FNDVI, SNDVI, and CTI and positive coefficient estimates for MMT, DRI, GDD, S, and TRI when we predicted the opposite.

Of the 36 variables considered, seven were retained for combination after considering correlation and DIC rank: proportion of agriculture (DAG), density of class 1–4 roads (D14), proportion of low-statured sagebrush cover (LS), population density (DP), N (nesting habitat quality), shrub height (SBHT), and terrain ruggedness index (TRI) (Figure 6; Appendix Table S2.4). We initially evaluated habitat quality variables for the nesting, brood rearing, and winter seasons; only the nesting habitat quality variable was previously published. Data for the three seasons were highly correlated and the two unpublished seasonal habitat quality variables were poor predictors and excluded for further consideration. A total of 120 multicovariate models were fit to the

data. A single variable, shrub height (SBHT), was included in the top 62 DIC ranked models with a relatively large positive coefficient estimate (Appendix Table S2.5). The top ranked Gunnison Basin model (Table 3; DIC = −31,665.91, lpd = 9181.49) included shrub height ($\beta_{SBHT}$ = 2.95 [0.08, 6.22]), DP ($\beta_{DP}$ = 0.55 [−5.13, 5.83]), and nesting habitat quality ($\beta_N$ = 0.22 [−1.27, 1.72]). The conductance surface representing the top modelled Gunnison Basin relationship predicted high gene flow where there is a robust shrub community, with areas of low conductance near roads and significant development (Figure 5b). The coefficients for N, D14, and DP occasionally switch sign, possibly from multicollinearity. The coefficient for N is only negative when combined with DAG or D14 and a sagebrush cover variable (SBHT or LS) (Table3 and Appendix Table S2.5). The nesting habitat quality layer (N) was developed with some of the same spatial data sources we used here (Aldridge et al., 2012), notably the basin-wide road data and Landfire data. The covariance structure is calculated through matrix decomposition of covariates into a precision matrix for the observed nodes (i.e., populations or leks). We checked variables for correlation based on the entire raster for the study area, thus leaving the possibility that the observed nodes and directly intervening landscape are more correlated than was apparent at the study area scale. For DP, the coefficient is often small and CRIs bound zero nearly evenly suggesting the true effect of DP is either very small or zero. The DIC rank of the top and bottom 10 models fit to data simulated from the resistance surface and an undifferentiated surface, clearly show the data simulated from the resistance surface resulted in a DIC rank more closely aligned to the DIC rank based on the
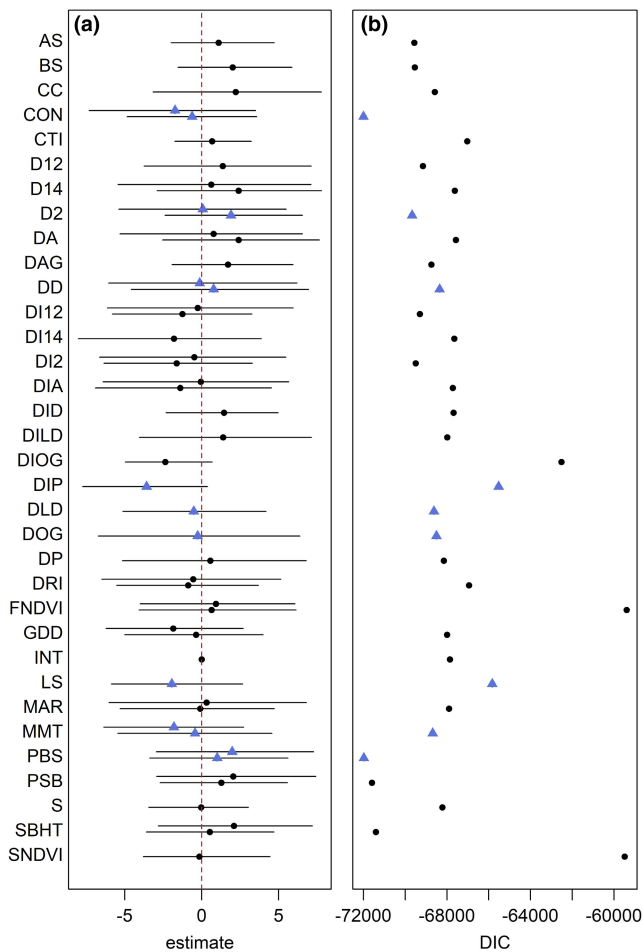
**FIGURE 4** Rangewide single-covariate model estimates (a) and associated deviance information criterion (*DIC*) (b). Coefficient estimates and 95% credible intervals (*CRI*) for each covariate and associated *DIC*. Only the top ranked version (moving window radius, linear vs. quadratic) for each covariate was included above. Only a subset of the above covariates (▲) were included in multicovariate model after considering correlation and *DIC* rank. Where appropriate, quadratic relationships were plotted just below the estimate for the linear term. Descriptions of covariates are provided in Table 1

observed data ($\rho = 0.72$) than the rank of models fit to data simulated from an undifferentiated surface ($\rho = -0.12$) and support the ability of our top ranked modelled relationships to have shaped the observed genetic distance patterns (Appendix Table S2.6).

## 3.3 | Conservation action simulation

Pairwise population comparison of genetic distance for simulation scenarios including an artificial sagebrush corridor were slightly lower, though not significantly, on average after 1000 years when compared to no action or a reintroduction alone (Figure 2e–g). Notably, differences in pairwise genetic distance were only observed after hundreds of years of simulation (~600 for comparisons between Gunnison Basin and Piñon Mesa [Figure 2e] or Crawford

[Figure 2f] and ~200 for the comparison between Crawford and Piñon Mesa [Figure 2g]). Variation around the mean genetic distance across years was high and scenarios that included an artificial habitat corridor did not consistently result in lower genetic distance relative to no action. The observed noise in relative change to genetic distance resulting from hypothetical management actions may be a result of the significant role of distance among populations in moderating gene flow. Our simulation of hypothetical management actions in the Gunnison Basin resulted in the expected effect: increasing shrub height in the area between two leks resulted in higher gene flow than if the shrub height were to remain the same and decreasing shrub height increased genetic distance (Figure 3). Twenty years after the hypothetical increase in shrub height, genetic distance between the two leks was lower than if no action were taken (Figure 3d). After approximately 60 years post shrub height increase, a slight decline in genetic distance was apparent. When the shrub height was decreased, genetic distance started to increase relative to no action at approximately 50 years and continued to increase slightly through 150 years (Figure 3d).

## 4 | DISCUSSION

We used a newly-developed formal statistical model to identify the main drivers of gene flow and estimate the degree of impact to genetic connectivity for Gunnison sage-grouse at two spatial scales. Our approach allowed us to identify the spatial scale at which each landscape feature was most likely to influence gene flow and characterize subtle differences in the primary drivers for long- and short-distance effective dispersal events. Our results reinforce the known importance of sagebrush-steppe habitat to the Gunnison sage-grouse, but also showed that interpopulation connectivity was primarily influenced by the amount of sagebrush cover on the landscape while intrapopulation connectivity was primarily facilitated by the height of the shrub community, mostly composed of sagebrush species. These findings highlight that different considerations may be necessary for conserving different biological processes (inter- vs. intrapopulation connectivity).

### 4.1 | The role of scale in gene flow

The landscape features influencing a species' behavior or movement capabilities vary across spatial scales (Wiens, 1989) and may determine corridors of gene flow and spatial genetic structure. Identification of the appropriate scale of impact to gene flow is crucial to understanding the underlying environmental drivers (Cushman & Landguth, 2010) and providing conservation insight. Our approach suggested different types of landscape variables impacted connectivity at different scales when considered individually. Among leks in the Gunnison Basin, we found that most habitat and anthropogenic variables best predicted the data at smaller scales (564–6400-m radius), while climate, topography, and other anthropogenic and

**TABLE 2** Rangewide top 10 Gunnison sage-grouse multicovariate model parameter estimates and associated 95% credible intervals (CRI). Covariates associated with each coefficient (β) estimate are abbreviated for clarity[a]

| Model no. | β_INT [95% CRI] | β_CON [95% CRI] | β_PBS [95% CRI] | β_D2 [95% CRI] | β_DLD [95% CRI] | β_DOG [95% CRI] | β_DD [95% CRI] | DIC | CV | DIC rank | CV rank |
|---|---|---|---|---|---|---|---|---|---|---|---|
| RW173 | −0.1 [−1.7, 1.6] | −0.5 [−6.3, 3.9] | 2.3 [−1.9, 7.0] | 0.5 [−4.3, 5.9] | 0.3 [−5.0, 5.7] | 0.2 [−5.9, 6.3] | | −72497.8 | 3842.39 | 1 | 1 |
| RW119 | 0.0 [−1.7, 1.6] | −0.5 [−6.1, 3.9] | 2.4 [−1.8, 7.2] | 0.5 [−4.3, 5.9] | 0.3 [−5.0, 5.9] | | | −72436.3 | 3842.36 | 2 | 2 |
| RW145 | 0.0 [−1.3, 1.5] | −0.5 [−6.2, 3.8] | 2.3 [−1.7, 7.1] | 0.5 [−4.1, 5.5] | | 0.1 [−6.2, 6.0] | | −72066.2 | 3842.33 | 8 | 3 |
| RW148 | 0.0 [−1.4, 1.5] | −0.5 [−6.1, 4.0] | 2.3 [−1.8, 7.1] | 0.5 [−4.2, 5.8] | | | 0.0 [−6.1, 6.1] | −72228.0 | 3842.31 | 6 | 4 |
| RW186 | 0.0 [−1.4, 1.5] | −0.4 [−6.2, 4.0] | 2.3 [−1.8, 7.0] | 0.5 [−4.3, 5.7] | | 0.2 [−5.9, 6.4] | −0.0 [−6.2, 6.1] | −72037.6 | 3842.26 | 10 | 5 |
| RW239 | −0.1 [−1.8, 1.6] | −0.5 [−6.2, 3.9] | 2.5 [−1.8, 7.3] | 0.4 [−4.4, 5.6] | 0.4 [−4.9, 5.9] | 0.1 [−6.3, 6.1] | −0.1 [−6.3, 6.2] | −72348.3 | 3842.16 | 3 | 6 |
| RW174 | −0.1 [−1.7, 1.6] | −0.5 [−6.2, 4.0] | 2.4 [−1.9, 7.1] | 0.5 [−4.5, 5.7] | 0.4 [−5.0, 6.0] | | −0.1 [−6.4, 6.3] | −72269.1 | 3842.07 | 4 | 7 |
| RW37 | 0.0 [−1.4, 1.4] | −0.4 [−6.2, 4.0] | 2.3 [−1.7, 7.0] | 0.5 [−4.1, 5.7] | | | | −72064.0 | 3842.05 | 9 | 8 |
| RW72 | 0.0 [−1.6, 1.6] | −0.6 [−5.9, 3.6] | 2.4 [−1.8, 7.2] | | 0.5 [−4.7, 5.9] | | | −72144.1 | 3841.84 | 7 | 9 |
| RW165 | 0.0 [−1.6, 1.6] | −0.6 [−6.0, 3.5] | 2.5 [−1.6, 7.2] | | 0.4 [−4.9, 5.8] | 0.1 [−6.0, 6.4] | 0.0 [−6.3, 6.2] | −72229.5 | 3841.79 | 5 | 10 |
| RW0 | 0.2 [−0.1, 0.5] | | | | | | | −67603.0 | | 216 | |

*Note:* Each model has an associated deviance information criterion (*DIC*) estimate, *DIC* rank, cross-validation score (*CV*), and *CV* rank. Estimates of τ are consistent across all models: 0.96 [0.92, 0.99].

[a]CON, proportion of conifer cover; D2, density of class 2 roads; DD, proportion of development; DLD, density of light duty roads; DOG, density of oil and gas wells; INT, intercept; PBS, percent big sagebrush.

habitat variables (D14, LS, CON) were more predictive at coarser scales (10,000–20,000-m radius). Among populations rangewide all but six variables (CON, DA, DLD, DRI, LS, MAR) were best fit at moderate-coarse scales (≥6400-m radius). The differences in best-fit scales for inter- and intrapopulation single covariate models support the role of hierarchical decisions in genetic connectivity, as previously described for Gunnison sage-grouse habitat selection (Aldridge et al., 2012; Saher et al., 2021). Our finding of primarily fine-scale drivers of intrapopulation gene flow within relatively contiguous sagebrush are in contrast to coarse-scale landscape effects on sage-grouse gene flow (Row et al., 2015) and large inter-seasonal movements (Fedy et al., 2012; Taylor et al., 2012) within similarly contiguous habitat patches. While the two species of sage-grouse have commonalities, Gunnison sage-grouse distribution has been described as naturally patchy, including decidedly nonhabitat barriers such as mountain passes and deep canyons (Braun et al., 2014; Gunnison sage-grouse Rangewide Steering Committee, 2005). The naturally patchy habitat of Gunnison sage-grouse may force effective dispersal behavior to be dependent on successive short-range movements within patches of favourable conditions.

The model best describing interpopulation gene flow included a positive relationship with percent big sagebrush cover and a smaller negative relationship with conifer cover (Table 2) suggesting interpopulation connectivity was primarily facilitated by relatively large, intact patches of sagebrush cover unobstructed by conifer. While small positive relationships with road and oil and gas well density (D2, DLD, DOG) were also included in the best fit model, this was probably due to the placement of these features within sagebrush habitat (e.g., low but positive correlation among sagebrush cover and these variables; Appendix Table S2.7) especially considering wildlife generally (Galpern, Manseau, & Wilson, 2012; Gerlach & Musolf, 2000), and sage-grouse specifically (Aldridge et al., 2012; Bush et al., 2010; Green et al., 2017; Kirol et al., 2015; Saher et al., 2021), avoid anthropogenic features. Sagebrush cover within the topographically diverse distribution of Gunnison sage-grouse coincides with areas that are less rugged and therefore more favorable sites for development. The positive correlation between sagebrush cover and some anthropogenic variables in addition to the positive coefficient estimates in our top model suggest that current densities of roads and energy extraction infrastructure do not inhibit gene flow completely, despite many documented instances of disruption to behaviour (e.g., Green et al., 2017), survival (e.gAldridge & Boyce, 2007; Holloran et al., 2010), and habitat quantity and quality (e.g Aldridge et al., 2012; Copeland et al., 2013). Much of the cited research on the negative impacts of anthropogenic development come from greater sage-grouse whose distribution encompasses significantly more human alteration. It is possible that presence of higher densities of some anthropogenic modifications can increase gene flow precisely because they create unfavorable conditions, prompting individuals to disperse through the area despite the lack of available resources (Ribe et al., 1998; Spear et al., 2010). These relationships highlight the importance of carefully considering the biological mechanism underlying modelled relationships for conservation insight, as
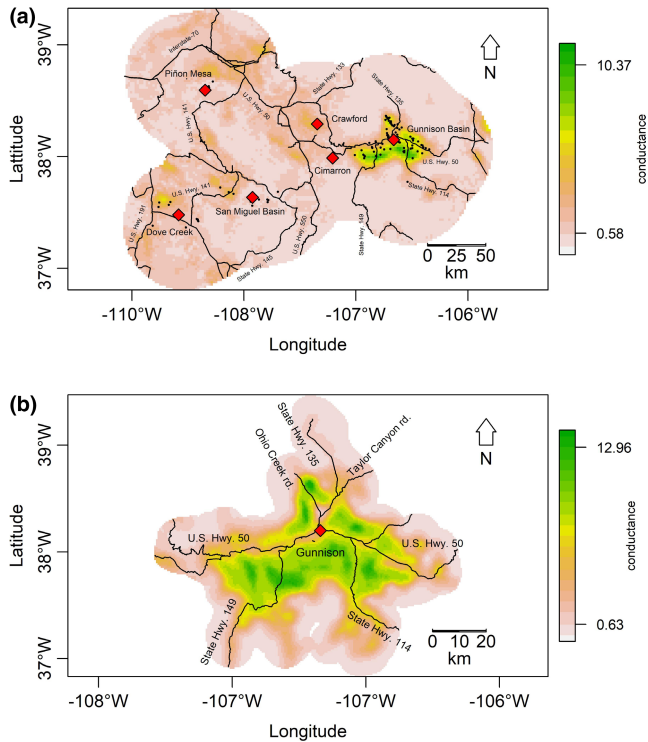
**FIGURE 5** Posterior mean conductance (gene flow) for the top rangewide multicovariate model (a) and across the Gunnison Basin (b). Rangewide conductance (i.e., gene flow) increased with percent big sagebrush cover (PBS), density of class 2 roads (D2), light duty roads (DLD) and oil and gas wells (DOG), and decreased with proportion of conifer cover (CON). Within the Gunnison Basin, conductance increased with shrub height (SBHT), population density (DP) and high-quality nesting habitat (N). For reference major roads, Gunnison sage-grouse population centres (a) and the city of Gunnison (b; ♦) were included



**FIGURE 6** Gunnison Basin single-covariate model estimates (a) and associated deviance information criterion (*DIC*) (b). Coefficient estimates and 95% credible intervals (*CRI*) for each covariate and associated *DIC*. Only the top ranked version (moving window radius, linear versus quadratic) for each covariate was included above. Only a subset of the above covariates (▲) were included in multicovariate model after considering correlation and *DIC* rank. Where appropriate, quadratic relationships were plotted just below the estimate for the linear term. Descriptions of covariates are provided in Table 1

increased anthropogenic footprint will necessarily remove and degrade sagebrush habitat essential for this species to persist (Young et al., 2020). Generally, our findings are consistent with previous assumptions that land alteration that removes or degrades sagebrush cover has contributed to the formation of physically isolated and genetically distinct populations via reduced gene flow (Oyler-McCance et al., 2005, 2015).

Among leks in the Gunnison Basin, our top model included a relatively large positive relationship between shrub height and gene flow, and smaller positive relationships with nesting habitat quality and human population density (Table 3). As in the rangewide model, the positive relationship of human population density with gene flow could be the result of one of the following: correlation with sagebrush habitat (Appendix Table S2.8) and a small anthropogenic footprint relative to locally available habitat with a small positive effect facilitating dispersal through unfavorable habitat, or a statistically zero effect given the large credible intervals evenly bounding zero. The inclusion of shrub height in the top 62 *DIC* ranked models (Appendix Table S2.5) further reinforces the primary importance of the shrub community in maintaining connectivity among leks. Protecting the remaining sagebrush habitat
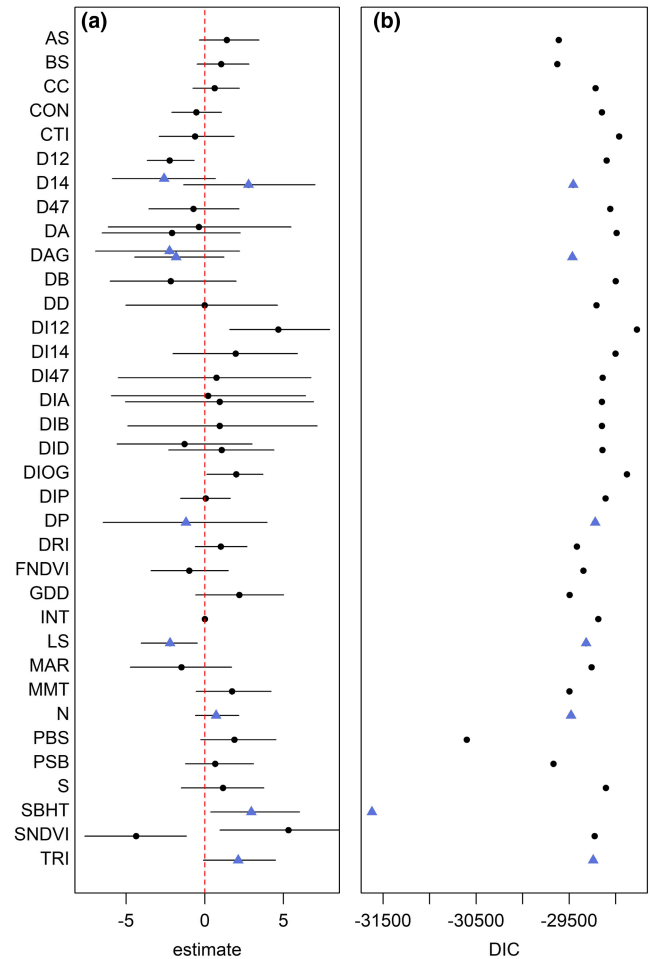
is considered essential to the survival of this sagebrush obligate species (Oyler-McCance et al., 2001). We found that shrub height (not sagebrush cover) was important to intrapopulation connectivity, as was previously observed in greater sage-grouse (Row et al., 2015). The multicovariate model including shrub height was a better fit to the data than when shrub height was replaced with sagebrush cover ($DIC_{SBHT} = -31,665.9$ versus $DIC_{PBS} = -30,735.2$), suggesting shrub height is capturing a pattern important to explaining gene flow that is not captured by sagebrush cover alone. However, sagebrush cover and shrub height are highly correlated in the region (Pearson's $r > 0.9$; Appendix Table S2.1) and any management efforts increasing the cover of tall sagebrush correspond to increased shrub height and should benefit genetic connectivity for Gunnison sage-grouse. Additionally, we know that locally abundant and essential landscape components may not be

**TABLE 3** Gunnison Basin top 10 Gunnison sage-grouse multicovariate model parameter estimates and associated 95% credible intervals (CRI). Covariates associated with each coefficient (β) estimate are abbreviated for clarity[a]

| Model no. | $\beta_{INT}$ [95% CRI] | $\beta_{D14}$ [95% CRI] | $\beta_{DP}$ [95% CRI] | $\beta_N$ [95% CRI] | $\beta_{SBHT}$ [95% CRI] | $\beta_{TRI}$ [95% CRI] | DIC | DIC rank | CV | CV rank |
|---|---|---|---|---|---|---|---|---|---|---|
| GB51 | −0.5 [−2.8, 1.5] | | 0.6 [−5.1, 5.8] | 0.2 [−1.3, 1.7] | 3.0 [0.1, 6.2] | | −31665.9 | 1 | 9181.49 | 1 |
| GB87 | −0.2 [−2.6, 1.6] | −0.5 [−1.7, 0.5] | 1.1 [−4.3, 6.2] | −0.4 [−2.4, 1.6] | 3.2 [0.3, 6.5] | | −31346.1 | 8 | 9181.19 | 2 |
| GB26 | −0.4 [−2.5, 1.4] | | | 0.2 [−1.2, 1.7] | 2.8 [0.1, 5.9] | | −31572.4 | 3 | 9181.07 | 3 |
| GB93 | −0.8 [−3.2, 1.0] | | 0.4 [−5.3, 5.4] | 0.2 [−1.4, 1.8] | 2.6 [−0.2, 5.9] | 1.9 [−0.8, 4.4] | −31402.7 | 7 | 9180.87 | 4 |
| GB45 | −0.2 [−2.6, 1.6] | −0.4 [−1.2, 0.5] | 1.2 [−4.6, 6.3] | | 2.9 [0.4, 6.3] | | −31564.4 | 4 | 9180.76 | 5 |
| GB16 | −0.5 [−2.7, 1.4] | | 0.4 [−5.2, 5.5] | | 3.0 [0.4, 6.3] | | −31642.5 | 2 | 9180.41 | 6 |
| GB6 | −0.4 [−2.5, 1.5] | | | | 2.8 [0.2, 6.0] | | −31523.0 | 5 | 9180.28 | 7 |
| GB52 | −0.8 [−3.1, 1.1] | | | | 2.6 [0.0, 6.0] | 1.8 [−0.8, 4.3] | −31442.1 | 6 | 9179.94 | 8 |
| GB27 | −0.8 [−3.0, 1.0] | | 0.1 [−5.6, 5.7] | | 2.5 [0.1, 5.7] | 1.9 [−0.7, 4.5] | −31343.8 | 9 | 9179.58 | 9 |
| GB20 | −0.1 [−2.3, 1.7] | −0.3 [−1.1, 0.5] | | | 2.7 [0.2, 5.7] | | −31314.8 | 10 | 9179.33 | 10 |
| GB0 | 1.6 [1.3, 1.8] | | | | | | −29155.2 | 114 | | |

*Note:* Each model has an associated deviance information criterion (DIC) estimate, DIC rank, cross validation score (CV), and CV rank. Estimates of τ are consistent across all models: 0.94 [0.92, 0.97].

[a]D14, density of road classes 1–4; DP, population density; INT, intercept; N, nesting habitat; SBHT, shrub height; TRI, terrain ruggedness index.

identified as a primary influencer of gene flow if heterogeneity is low (Shirk et al., 2010; Short Bull et al., 2011). The Gunnison Basin has some of the most contiguous sagebrush habitat within the species' range (Oyler-McCance et al., 2001), however it is not without fragmentation. While the shrub-steppe plant community is essential for the species, variables included in our top model suggest habitat structure and quality are important for inter-lek connectivity within relatively contiguous habitat.

## 4.2 | Conifer cover & gene flow

Conifer encroachment has displaced and degraded >170,000-km$^2$ of shrubland in western North America over the last 150 years (Miller et al., 2019; Romme et al., 2009). Thus, conifer removal has widely been suggested as a mechanism of habitat improvement for shrub-steppe species (Miller et al., 2017), including Gunnison sage-grouse (i.e., Doherty et al., 2018). Previous studies have shown negative population-level impacts from conifer cover for both greater (Coates et al., 2016; Severson et al., 2017) and Gunnison sage-grouse (Aldridge et al., 2012; Commons et al., 1999; Doherty et al., 2018; Saher et al., 2021). We expected high conifer cover to correspond to low gene flow. While we found the expected relationship in our top 20 rangewide models, conifer cover was not a significant influencer of gene flow within the Gunnison Basin. The nesting habitat quality layer included in our top Gunnison Basin model (N), however, included a negative relationship between habitat selection and conifer cover (Aldridge et al., 2012) suggesting increased conifer cover may play a role in influencing gene flow indirectly via nesting habitat quality. Although conifer cover has always been part of the naturally fragmented landscape encompassing the Gunnison sage-grouse distribution, encroachment has contributed to the displacement of sagebrush cover in recent decades (Bukowski & Baker, 2013). Productive, early-phase woodland sites, such as those formed by encroachment, may be attractive to sage-grouse despite the potential negative effects on vital rates, and may act as an ecological trap (Coates et al., 2016). We could not evaluate intra-lek connectivity for all satellite populations due to data limitations. Region specific impacts to gene flow from landscape components are not uncommon (Kozakiewicz et al., 2019; Row et al., 2018). Conifer encroachment and known presence of pinyon-juniper woodlands in some satellite populations may be important to consider in the future given the known hazards.

## 4.3 | Conservation applications

Development of conservation planning tools is a key goal of many landscape genetic analyses (Keller et al., 2015). The relationships identified in our findings could provide insight into areas of high connectivity that might be considered dispersal corridors, as well as areas that have low gene flow that might benefit from some

type of habitat improvement or restoration. We identified an area in the Gunnison Basin where our top model predicted low gene flow and evaluated alternative scenarios for impact to genetic distance if shrub height increased, shrub height decreased, or if no action was taken (Figure 3a–c). The predicted effects of our hypothetical management actions indicated that if the shrub height (i.e., tall sagebrush cover in this area) across the selected 7.2 km$^2$ area between the two leks was increased by 50% we should expect genetic divergence to continue for 20 years, remain approximately stable through 75 years and then begin to decrease (Figure 3d). Changes in genetic distance occur over multiple generations and lag behind changes in population dynamics, thus we expect genetic distance to continue increasing for a period of time post modification as we observed. If no action is taken, we expect genetic distance to increase and stabilize after 50 years. If shrub height was decreased by 50%, we expect genetic distance to increase for longer than if no action was taken for 150 years. We found a similar, although less pronounced, result when we simulated restoration of a sagebrush corridor between populations and the establishment of a new population; after ~200–600 years we might expect to see genetic divergence decrease among the targeted populations (Figure 2e–g). Notably, we did not see an effect from the establishment of a new population in the absence of the sagebrush corridor across the 1000 simulated years, variation in mean change across years was highly variable among different scenarios. Our example landscape alterations were arbitrarily chosen and depict a uniform increase in shrub height (between leks) or the establishment of dense sagebrush cover (among populations) over relatively large areas; conditions that may not be realistic for management actions but are useful for illustrative purposes. Predicted changes to the landscape from further anthropogenic alteration, climate change, or potential management actions or conservation could be used to evaluate a predicted response in connectivity. Similar approaches have been utilized for sage-grouse to prioritize habitat for conservation or potential management actions based on population size (Heinrichs et al., 2017) and lek persistence (Doherty et al., 2018); we showed how those concepts could be extended to a gene flow scenario.

## 5 | CONCLUSIONS

The ability to explicitly consider scale at every step of our landscape genetic analysis and estimate the degree of influence on gene flow are important steps to making conservation relevant inference (Keller et al., 2015). Similarly, the ability to compare relative impact of land-use change or conservation action underscores the usefulness of the modelled relationships for decision making. Our comparison of inter- and intrapopulation genetic connectivity highlights the necessity of understanding scale-dependent relationships between environment and gene flow. While sagebrush cover was important for Gunnison sage-grouse regardless of scale, we found that large patches of dense sagebrush cover free

from conifer cover was important for gene flow among populations, which contrasts with the importance of tall shrubs (primarily composed of sagebrush species) and high-quality nesting habitat among leks within the Gunnison Basin (Table 3 and Appendix Table S2.6). Like the indirect effect of conifer cover on gene flow via inclusion in the nesting habitat quality layer (N) in our top Gunnison Basin model, sagebrush cover had a positive relationship with nesting habitat selection supporting indirect effects of sagebrush cover to gene flow (Aldridge et al., 2012). Altogether this suggests the structure of the sagebrush habitat (i.e., shrub height) might be important within a population, while longer effective dispersal events appear to be governed more by the presence or absence of sagebrush habitat in general. Additionally, we found that landscape features observed to influence behaviour or movement for wildlife species generally (e.g., roads, agriculture), and including for sage-grouse, were not important direct influencers of Gunnison sage-grouse genetic connectivity, underscoring the potential follies of relying on direct observations as an indicator of gene flow. Future analyses could explore the impacts of lag effects in genetic signal from landscape change (Epps & Keyghobadi, 2015), relaxing the assumption of symmetric gene flow (Hanks, 2017; Peterson et al., 2019), allowing the coefficient to vary across the landscape using splines (Hanks & Hooten, 2013), considering the influence of natural selection (Peterson et al., 2019) or ways to incorporate behavior or fitness measures (Spear et al., 2010) to further refine our understanding of drivers of gene flow. Understanding and characterizing the primary drivers of gene flow can facilitate prediction of the impact of multiple conservation relevant scenarios and decision making.

## AUTHOR CONTRIBUTION

Shawna J. Zimmerman, Sara J. Oyler-McCance, Cameron L. Aldridge, and Mevin B. Hooten designed the study; Shawna J. Zimmerman analysed the data and wrote the first manuscript draft. All authors contributed to the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

Genetic data have been made available via USGS data release (https://doi.org/10.5066/P920WO0Q). Unpublished data (D.J. Saher, unpublished data) are either not available or have limited availability owing to restrictions regarding the sensitive nature of data for sensitive species listed as Threatened under the Endangered Species Act. Contact CLA for more information.

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## REFERENCES

Adamack, A. T., & Gruber, B. (2014). PopGenReport: simplifying basic population genetic analyses in R. *Methods in Ecology and Evolution*, 5(4), 384–387. https://doi.org/10.1111/2041-210X.12158

Aldridge, C. L., & Boyce, M. S. (2007). Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. *Ecological Applications*, 17(2), 508–526. https://doi.org/10.1890/05-1871

Aldridge, C. L., & Boyce, M. S. (2008). Accounting for fitness: Combining survival and selection when assessing wildlife-habitat relationships. *Israel Journal of Ecology & Evolution*, 54(July), 389–419. https://doi.org/10.1560/IJEE.54.3

Aldridge, C. L., & Brigham, R. M. (2002). Sage-grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management*, 66(2), 433–444. https://doi.org/10.2307/3803176

Aldridge, C. L., Nielsen, S. E., Beyer, H. L., Boyce, M. S., Connelly, J. W., Knick, S. T., & Schroeder, M. A. (2008). Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions*, 14(6), 983–994. https://doi.org/10.1111/j.1472-4642.2008.00502.x

Aldridge, C. L., Saher, D. J., Childers, T. M., Stahlnecker, K. E., & Bowen, Z. H. (2012). Crucial nesting habitat for Gunnison sage-grouse: A spatially explicit hierarchical approach. *Journal of Wildlife Management*, 76(2), 391–406. https://doi.org/10.1002/jwmg.268

Anderson, J. E., & Inouye, R. S. (2001). Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs*, 71(4), 531–556.

Barnett, J. K., & Crawford, J. A. (1994). Pre-laying nutrition of sage-grouse hens in Oregon. *Journal of Range Management*, 47(2), 114–118. https://doi.org/10.2307/4002817

Baruch-Mordo, S., Evans, J. S., Severson, J. P., Naugle, D. E., Maestas, J. D., Kiesecker, J. M., Falkowski, M. J., Hagen, C. A., & Reese, K. P. (2013). Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation*, 167, 233–241. https://doi.org/10.1016/j.biocon.2013.08.017

Beck, J. L., & Maxfield, B. D. (2003). Changes in the distribution and status of sage-grouse in Utah. *Western North American Naturalist*, 63(2), 203–214.

Bennett, V. J., Beard, M., Zollner, P. A., Fernández-Juricic, E., Westphal, L., & LeBlanc, C. L. (2009). Understanding wildlife responses to human disturbance through simulation modelling: A management tool. *Ecological Complexity*, 6(2), 113–134. https://doi.org/10.1016/j.ecocom.2008.08.002

Bissonette, J. A. (1997). Scale-sensitive ecological properties: historical context, current meaning. In J. A. Bissonette (Ed.), *Wildlife and landscape ecology: Effects of pattern and scale* (pp. 3–31). Springer-Verlag.

Blickley, J. L., Blackwood, D., & Patricelli, G. L. (2012). Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology*, 26(3), 461–471. https://doi.org/10.1111/j.1523-1739.2012.01840.x

Blomberg, E. J., Sedinger, J. S., Atamian, M. T., & Nonne, D. V. (2012). Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. *Ecosphere*, 3(6), 55. https://doi.org/10.1890/ES11-00304.1

Bock, C. E., & Webb, B. (1984). Birds as grazing indicator species in Southeastern Arizona. *Journal of Wildlife Management*, 48(3), 1045–1049. https://doi.org/10.2307/3801466

Bohonak, A. J. (1999). Dispersal, gene flow, and population structure. *The Quarterly Review of Biology*, 74(1), 21–45. https://doi.org/10.1086/392950

Braun, C. E. (1998). Sage-grouse declines in Western North America: what are the problems? *Proceedings, Western Association of Fish and Wildlife Agencies*, 78, 139–156.

Braun, C. E., Connelly, J. W., & Schroeder, M. A. (2005). Seasonal habitat requirements for sage-grouse: Spring , summer, fall, and winter. USDA Forest Service Proceedings RMRS-P-9-38, 38–42.

Braun, C. E., Oyler-McCance, S. J., Nehring, J. A., Commons, M. L., Young, J. R., & Potter, K. M. (2014). The historical distribution of Gunnison sage-grouse in Colorado. *The Wilson Journal of Ornithology*, 126(2), 207–217. https://doi.org/10.1676/13-184.1

Bukowski, B. E., & Baker, W. L. (2013). Historical fire in sagebrush landscapes of the Gunnison sage-grouse range from land-survey records. *Journal of Arid Environments*, 98, 1–9. https://doi.org/10.1016/j.jaridenv.2013.07.005

Burkey, T. V. (1989). Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos*, 55(1), 75–81. https://doi.org/10.2307/3565875

Bush, K. L., Aldridge, C. L., Carpenter, J. E., Paszkowski, C. A., Boyce, M. S., & Coltman, D. W. (2010). Birds of a feather do not always lek together: Genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. *The Auk*, 127(2), 343–353.

Bush, K. L., Dyte, C. K., Moynahan, B. J., Aldridge, C. L., Sauls, H. S., Battazzo, A. M., Walker, B. L., Doherty, K. E., Tack, J., Carlson, J., Eslinger, D., Nicholson, J., Boyce, M. S., Naugle, D. E., Paszkowski, C. A., & Coltman, D. W. (2011). Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics*, 12(2), 527–542. https://doi.org/10.1007/s10592-010-0159-8

Caizergues, A., Rätti, O., Helle, P., Rotelli, L., Ellison, L., & Rasplus, J. Y. (2003). Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Molecular Ecology*, 12(9), 2297–2305. https://doi.org/10.1046/j.1365-294X.2003.01903.x

Carpenter, J. E., Aldridge, C. L., & Boyce, M. S. (2010). Sage-grouse habitat selection during winter in Alberta. *Journal of Wildlife Management*, 74(8), 1806–1814. https://doi.org/10.2193/2009-368

Coates, P. S., Prochazka, B. G., Ricca, M. A., Gustafson, K. B., Ziegler, P., & Casazza, M. L. (2016). Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. *Rangeland Ecology & Management*, 70(1), 25–38. https://doi.org/10.1016/j.rama.2016.09.001

Colorado Water Conservation, B. (2009). 2050 population projections for the state of Colorado municipal and industrial water use projections. Final report prepared for Colorado Water Conservation Board, Appendix B in Colorado's water supply future: State of Colorado 2050 municipal and industrial water use projections. http://cwcb.state.co.us/IWMD/COsWaterSupplyFuture/

Commons, M. L., Baydack, R. K., & Braun, C. E. (1999). Sage-grouse response to pinyon-juniper management discussion. *USDA Forest Service Proceedings RMRS-P-9*, 97, 238–239.

Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., & Hooten, M. B. (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs*, 88(4), 526–542. https://doi.org/10.1002/ecm.1314

Connelly, J. W., Knick, S. T., Schroeder, M. A., & Stiver, S. J. (2004). *Conservation assessment of greater sage-grouse and sagebrush habitats*. Western Association of Fish and Wildlife Agencis. Unpublished Report. Cheyenne, Wyoming.

Copeland, H. E., Pocewicz, A., Naugle, D. E., Griffiths, T., Keinath, D., Evans, J. S., & Platt, J. (2013). Measuring the effectiveness of

conservation: A novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. *PLoS One*, *8*(6), e67261. https://doi.org/10.1371/journal.pone.0067261

Cushman, S. A., & Landguth, E. L. (2010). Scale dependent inference in landscape genetics. *Landscape Ecology*, *25*, 967–979. https://doi.org/10.1007/s10980-010-9467-0

Davis, A. J. (2012). *Gunnison sage-grouse demography and conservation* [PhD Dissertation]. Colorado State University.

Doherty, K. E., Hennig, J. D., Dinkins, J. B., Griffin, K. A., Cook, A. A., Maestas, J. D., Naugle, D. E., & Beck, J. L. (2018). Understanding biological effectiveness before scaling up range-wide restoration investments for Gunnison sage-grouse. *Ecosphere*, *9*(3), e02144. https://doi.org/10.1002/ecs2.2144

Doherty, K. E., Naugle, D. E., & Walker, B. L. (2010). Greater sage-grouse nesting habitat: The importance of managing at multiple scales. *Journal of Wildlife Management*, *74*(7), 1544–1553. https://doi.org/10.2193/2009-043

Environmental Systems Research Institute. (2012). *ArcGIS desktop release 10.1*.

Epps, C. W., & Keyghobadi, N. (2015). Landscape genetics in a changing world: Disentangling historical and contemporary influences and inferring change. *Molecular Ecology*, *24*, 6021–6040. https://doi.org/10.1111/mec.13454

Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., & McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert big-horn sheep. *Ecology Letters*, *8*(10), 1029–1038. https://doi.org/10.1111/j.1461-0248.2005.00804.x

Fahrig, L., & Merriam, G. (1985). Habitat patch connectivity and population survival. *Ecology*, *66*(6), 1762–1768. https://doi.org/10.2307/2937372

Fedy, B. C., Aldridge, C. L., Doherty, K. E., O'Donnell, M., Beck, J. L., Bedrosian, B., Holloran, M. J., Johnson, G. D., Kaczor, N. W., Kirol, C. P., Mandich, C. A., Marshall, D., McKee, G., Olson, C., Swanson, C. C., & Walker, B. L. (2012). Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. *Journal of Wildlife Management*, *76*(5), 1062–1071. https://doi.org/10.1002/jwmg.337

Fedy, B. C., Doherty, K. E., Aldridge, C. L., O'Donnell, M., Beck, J. L., Bedrosian, B., Gummer, D., Holloran, M. J., Johnson, G. D., Kaczor, N. W., Kirol, C. P., Mandich, C. A., Marshall, D., Mckee, G., Olson, C., Pratt, A. C., Swanson, C. C., & Walker, B. L. (2014). Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using greater sage-grouse in Wyoming. *Wildlife Monographs*, *190*(1), 1–39. https://doi.org/10.1002/wmon.1014

Fike, J. A., Oyler-McCance, S. J., Zimmerman, S. J., & Castoe, T. A. (2015). Development of 13 microsatellites for Gunnison sage-grouse (*Centrocercus minimus*) using next-generation shotgun sequencing and their utility in greater sage-grouse (*Centrocercus urophasianus*). *Conservation Genetics Resources*, *7*(1), 211–214. https://doi.org/10.1007/s12686-014-0336-z

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, *16*, 265–280. https://doi.org/10.1111/j.1466-8238.2006.00287.x

Frankham, R. (2003). Genetics and conservation biology. *Comptes Rendus Biologies*, *326*, S22–S29. https://doi.org/10.1016/S1631-0691(03)00023-4

Fremgen, A. L., Hansen, C. P., Rumble, M. A., Gamo, R. S., & Millspaugh, J. J. (2016). Male greater sage-grouse detectability on leks. *Journal of Wildlife Management*, *80*(2), 266–274. https://doi.org/10.1002/jwmg.1001

Galpern, P., Manseau, M., Hettinga, P., Smith, K., & Wilson, P. (2012). Allelematch: An R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. *Molecular Ecology Resources*, *12*(4), 771–778.

Galpern, P., Manseau, M., & Wilson, P. (2012). Grains of connectivity: Analysis at multiple spatial scales in landscape genetics. *Molecular Ecology*, *21*, 3996–4009. https://doi.org/10.1111/j.1365-294X.2012.05677.x

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511. https://doi.org/10.1214/ss/1177011136

Gerlach, G., & Musolf, K. (2000). Fragmentation of landscape as a cause for genetic subdivision in bank voles. *Conservation Biology*, *14*(4), 1066–1074. https://doi.org/10.1046/j.1523-1739.2000.98519.x

Giesen, K. M., Schoenberg, T. J., & Braun, C. E. (1992). Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin*, *10*(3), 224–231.

Graves, T. A., Beier, P., & Royle, J. A. (2013). Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. *Molecular Ecology*, *22*(15), 3888–3903. https://doi.org/10.1111/mec.12348

Green, A. W., Aldridge, C. L., & O'Donnell, M. S. (2017). Investigating impacts of oil and gas development on greater sage-grouse. *Journal of Wildlife Management*, *81*(1), 46–57. https://doi.org/10.1002/jwmg.21179

Gubili, C., Mariani, S., Weckworth, B. V., Galpern, P., McDevitt, A. D., Hebblewhite, M., Nickel, B., & Musiani, M. (2017). Environmental and anthropogenic drivers of connectivity patterns: A basis for prioritizing conservation efforts for threatened populations. *Evolutionary Applications*, *10*(2), 199–211. https://doi.org/10.1111/eva.12443

Gunnison Sage-Grouse Rangewide Steering Committee. (2005). *Gunnison sage-grouse rangewide conservation plan*. Colorado Division of Wildlife.

Hagen, C. A., Willis, M. J., Glenn, E. M., & Anthony, R. G. (2011). Habitat selection by greater sage-grouse during winter in southeastern Oregon. *Western North American Naturalist*, *71*(4), 529–538. https://doi.org/10.3398/064.071.0411

Hanks, E. M. (2017). Modeling spatial covariance using the limiting distribution of spatio-temporal random walks. *Journal of the American Statistical Association*, *112*(518), 497–507. https://doi.org/10.1080/01621459.2016.1224714

Hanks, E. M. (2018). *rwc: random walk covariance models. R package version 1.11*. https://CRAN.R-project.org/package=rwc

Hanks, E. M., & Hooten, M. B. (2013). Circuit theory and model-based inference for landscape connectivity. *Journal of the American Statistical Association*, *108*(501), 22–33. https://doi.org/10.1080/01621459.2012.724647

Harju, S. M., Olson, C. V., Dzialak, M. R., Mudd, J. P., & Winstead, J. B. (2013). A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). *PLoS One*, *8*(12), e82271. https://doi.org/10.1371/journal.pone.0082271

Heinrichs, J. A., Aldridge, C. L., O'Donnell, M. S., & Schumaker, N. H. (2017). Using dynamic population simulations to extend resource selection analyses and prioritize habitats for conservation. *Ecological Modelling*, *359*(10), 449–459. https://doi.org/10.1016/j.ecolmodel.2017.05.017

Heinrichs, J. A., Bender, D. J., & Schumaker, N. H. (2016). Habitat degradation and loss as key drivers of regional population extinction. *Ecological Modelling*, *335*, 64–73. https://doi.org/10.1016/j.ecolmodel.2016.05.009

Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Princeton University Press.

Hoffmann, A. A., Sgro, C. M., & Kristensen, T. N. (2017). Revisiting adaptive potential, population size, and conservation. *Trends in Ecology & Evolution*, *32*(7), 506–517. https://doi.org/10.1016/j.tree.2017.03.012

Holderegger, R., & Wagner, H. H. (2008). Landscape genetics. *BioScience*, *58*(3), 199–207. https://doi.org/10.1641/B580306

Holloran, M. J., Kaiser, R. C., & Hubert, W. A. (2010). Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management*, 74(1), 65–72. https://doi.org/10.2193/2008-291

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85(1), 3–28. https://doi.org/10.1890/07-1861.1

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61(1), 65–71. https://doi.org/10.2307/1937156

Keller, D., Holderegger, R., & vanStrien, M. J. (2013). Spatial scale affects landscape genetic analysis of a wetland grasshopper. *Molecular Ecology*, 33, 2467–2482. https://doi.org/10.1111/mec.12265

Keller, D., Holderegger, R., vanStrien, M. J., & Bolliger, J. (2015). How to make landscape genetics beneficial for conservation management? *Conservation Genetics*, 16, 503–512. https://doi.org/10.1007/s10592-014-0684-y

Kirol, C. P., Beck, J. L., Huzurbazar, S. N., Holloran, M. J., & Miller, S. N. (2015). Identifying greater sage-grouse sources and sink habitats for conservation planning in an energy development landscape. *Ecological Applications*, 25(4), 968–990.

Knick, S. T., Hanser, S. E., & Preston, K. L. (2013). Modeling ecological minimum requirements for distribution of greater sage-grouse leks: Implications for population connectivity across their western range, U.S.A. *Ecology and Evolution*, 3(6), 1539–1551. https://doi.org/10.1002/ece3.557

Koen, E. L., Bowman, J., & Walpole, A. A. (2012). The effect of cost surface parameterization on landscape resistance estimates. *Molecular Ecology Resources*, 12(4), 686–696. https://doi.org/10.1111/j.1755-0998.2012.03123.x

Kozakiewicz, C. P., Burridge, C. P., Funk, W. C., Salerno, P. E., Trumbo, D. R., Gagne, R. B., & Carver, S. (2019). Urbanization reduces genetic connectivity in bobcats (*Lynx rufus*) at both intra– and interpopulation spatial scales. *Molecular Ecology*, 28(23), 5068–5085. https://doi.org/10.1111/mec.15274

Landguth, E. L., Cushman, S. A., Schwartz, M. K., McKelvey, K. S., Murphy, M. A., & Luikart, G. (2010). Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology*, 19(19), 4179–4191. https://doi.org/10.1111/j.1365-294X.2010.04808.x

LeBeau, C. W., Beck, J. L., Johnson, G. D., & Holloran, M. J. (2013). Short-term impacts of wind energy development on greater sage-grouse fitness. *Journal of Wildlife Management*, 78(3), 522–530. https://doi.org/10.1002/jwmg.679

LeBeau, C. W., Johnson, G. D., Holloran, M. J., Beck, J. L., Nielson, R. M., Kauffman, M. E., Rodemaker, E. J., & McDonald, T. L. (2017). Greater sage-grouse habitat selection, survival, and wind energy infrastructure. *Journal of Wildlife Management*, 81(4), 690–711. https://doi.org/10.1002/jwmg.21231

Levin, D. A. (1981). Dispersal versus gene flow in plants. *Annals of the Missouri Botanical Garden*, 68(2), 233–253. https://doi.org/10.1017/CBO9781107415324.004

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18(4), 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

McKelvey, K. S., & Schwartz, M. K. (2005). DROPOUT: A program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes*, 5(3), 716–718. https://doi.org/10.1111/j.1471-8286.2005.01038.x

McRae, B. H. (2006). Isolation by resistance. *Evolution*, 60(8), 1551–1561.

McRae, B. H., Schumaker, N. H., McKane, R. B., Busing, R. T., Solomon, A. M., & Burdick, C. A. (2008). A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling*, 219(1–2), 77–91. https://doi.org/10.1016/j.ecolmodel.2008.08.001

Miller, R. F., Chambers, J. C., Evers, L., Williams, C. J., Snyder, K. A., Roundy, B. A., & Pierson, F. B. (2019). *The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the Great Basin and Northern Colorado Plateau of the western United States*. U.S. Depart of Agriculture, Forest Service, Rocky Mountain Research Station.

Miller, R. F., Naugle, D. E., Maestas, J. D., Hagen, C. A., & Hall, G. (2017). Special issue: Targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. *Rangeland Ecology & Management*, 70(1), 1–8. https://doi.org/10.1016/j.rama.2016.10.004

Nehring, J. A., & Apa, A. D. (2000). *Gunnison sage-grouse population augmentation to Poncha Pass, Saguache County & Sims Mesa, Montrose County*. Colorado Division of Wildlife.

Oyler-McCance, S. J., Zimmerman, S. J., Aldridge, C. L., & Apa, A. D. (2019). Sample collection information and microsatellite data for Gunnison sage-grouse pre and post translocation: U.S. Geological Survey data release. https://doi.org/10.5066/P920WO0Q

Oyler-McCance, S. J., Burnham, K. P., & Braun, C. E. (2001). Influence of changes in sagebrush on Gunnison sage-grouse in southwestern Colorado. *Southwestern Naturalist*, 46(3), 323–331. https://doi.org/10.2307/3672428

Oyler-McCance, S. J., Cornman, R. S., Jones, K. L., & Fike, J. A. (2015). Genomic single-nucleotide polymorphisms confirm that Gunnison and greater sage-grouse are genetically well differentiated and that the Bi-State population is distinct. *The Condor*, 117(2), 217–227. https://doi.org/10.1650/CONDOR-14-174.1

Oyler-McCance, S. J., & Fike, J. A. (2011). Characterization of small microsatellite loci isolated in endangered Indiana bat (*Myotis sodalis*) for use in non-invasive sampling. *Conservation Genetics Resources*, 3(2), 243–245. https://doi.org/10.1007/s12686-010-9332-0

Oyler-McCance, S. J., St John, J., Taylor, S. E., Apa, A. D., & Quinn, T. W. (2005). Population genetics of Gunnison sage-grouse: implications for management. *Journal of Wildlife Management*, 69(2), 630–637.

Oyler-McCance, S. J., & St. John, J. (2010). Characterization of small microsatellite loci for use in non-invasive sampling studies of Gunnison sage-grouse (*Centrocercus minimus*). *Conservation Genetics Resources*, 2(1), 17–20. https://doi.org/10.1007/s12686-009-9122-8

Patterson, R. L. (1952). *The Sage Grouse in Wyoming*. Wyoming Game and Fish Commission Sage Books Inc.

Peterson, E. E., Hanks, E. M., Hooten, M. B., Ver Hoef, J. M., & Fortin, M.-J. (2019). Spatially-structured statistical network models for landscape genetics. *Ecological Monographs*, 89(2), e01355.

Piertney, S. B., & Höglund, J. (2001). Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). *Molecular Ecology Resources*, 1(4), 303–304.

Primack, R. B. (1993). *Essentials of Conservation Biology*. Sinauer Associates Inc.

R Core Team. (2018). *R: A language and environment for statistical computing*.

Ribe, R., Morganti, R., Hulse, D., & Shull, R. (1998). A management drive investigation of landscape patterns of northern spotted owl nesting territories in the high Cascades of Oregon. *Landscape Ecology*, 13, 1–13.

Rice, M. B., Apa, A. D., & Wiechman, L. A. (2017). The importance of seasonal resource selection when managing a threatened species: targeting conservation actions within critical habitat designations for the Gunnison sage-grouse. *Wildlife Research*, 44(5), 407–417. https://doi.org/10.1071/WR17027

Roffler, G. H., Schwartz, M. K., Pilgrim, K. L., Talbot, S. L., Sage, G. K., Adams, L. G., & Luikart, G. (2016). Identification of landscape features influencing gene flow: How useful are habitat selection models? *Evolutionary Applications*, 9(6), 805–817. https://doi.org/10.1111/eva.12389

Romme, W. H., Allen, C. D., Bailey, J. D., Baker, W. L., Bestelmeyer, B. T., Brown, P. M., Eisenhart, K. S., Floyd, M. L., Huffman, D. W., Jacobs, B. F., Miller, R. F., Muldavin, E. H., Swetnam, T. W., Tausch, R. J., & Weisberg, P. J. (2009). Historical and modern disturbance regimes,

stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. *Rangeland Ecology & Management*, *62*, 203–222. https://doi.org/10.2111/08-188R1.1

Row, J. R., Doherty, K. E., Cross, T. B., Schwartz, M. K., Oyler-McCance, S. J., Naugle, D. E., Knick, S. T., & Fedy, B. C. (2018). Quantifying functional connectivity: The role of breeding habitat, abundance, and landscape features on range-wide gene flow in sage-grouse. *Evolutionary Applications*, *11*(8), 1305–1321. https://doi.org/10.1111/eva.12627

Row, J. R., Oyler-McCance, S. J., Fike, J. A., O'Donnell, M. S., Doherty, K. E., Aldridge, C. L., Bowen, Z. H., & Fedy, B. C. (2015). Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. *Ecology and Evolution*, *5*(10), 1955–1969. https://doi.org/10.1002/ece3.1479

Saher, D. J., O'Donnell, M. S., Aldridge, C. L., & Heinrichs, J. A. (2021). Balancing model generality and specificity in management-focused habitat selection models for Gunnison sage-grouse. *Global Ecology and Conservation*, *35*, e01935. https://doi.org/10.1016/j.gecco.2021.e01935

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L. R., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schroeder, M. A., Aldridge, C. L., Apa, A. D., Bohne, J. R., Braun, C. E., Bunnell, S. D., Connelly, J. W., Deibert, P. A., Gardner, S. C., Hilliard, M. A., Kobriger, G. D., McAdam, S. M., McCarthy, C. W., McCarthy, J. J., Mitchell, D. L., Rickerson, E. V., & Stiver, S. J. (2004). Distribution of sage-grouse in North America. *The Condor*, *106*(2), 363–376. https://doi.org/10.1093/condor/106.2.363

Segelbacher, G., Paxton, R. J., Steinbruck, G., Tronteljs, P., & Storch, I. (2000). Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). *Molecular Ecology*, *9*, 1934–1935.

Severson, J. P., Hagen, C. A., Maestas, J. D., Naugle, D. E., Forbes, J. T., & Reese, K. P. (2017). Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. *Rangeland Ecology & Management*, *70*(1), 50–58. https://doi.org/10.1016/j.rama.2016.07.011

Shirk, A. J., Schroeder, M. A., Robb, L. A., & Cushman, S. A. (2015). Empirical validation of landscape resistance models: Insights from the greater sage-grouse (*Centrocercus urophasianus*). *Landscape Ecology*, *30*(10), 1837–1850. https://doi.org/10.1007/s10980-015-0214-4

Shirk, A. J., Wallin, D. O., Cushman, S. A., Rice, C. G., & Warheit, K. I. (2010). Inferring landscape effects on gene flow: A new model selection framework. *Molecular Ecology*, *19*(17), 3603–3619. https://doi.org/10.1111/j.1365-294X.2010.04745.x

Short Bull, R. A., Cushman, S. A., Mace, R., Chilton, T., Kendall, K. C., Landguth, E. L., Schwartz, M. K., McKelvey, K., Allendorf, F. W., & Luikart, G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology*, *20*, 1092–1107. https://doi.org/10.1111/j.1365-294X.2010.04944.x

Smith, K. T., Kirol, C. P., Beck, J. L., & Blomquist, F. C. (2014). Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. *Ecosphere*, *5*(2), 15. https://doi.org/10.1890/ES13-00238.1

Soulé, M. E., Alberts, A. C., Bolger, D. T., & Soule, M. E. (1992). The effects of habitat fragmentation on chaparral plants and vertebrates. *Oikos*, *63*(1), 39–47. https://doi.org/10.2307/3545514

Spear, S. F., Balkenhol, N., Fortin, M.-J., McRae, B. H., & Scribner, K. T. (2010). Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, *19*(17), 3576–3591. https://doi.org/10.1111/j.1365-294X.2010.04657.x

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & van derLinde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B*, *64*(4), 583–639. https://doi.org/10.1111/1467-9868.00353

Stanley, T. R., Aldridge, C. L., Saher, D. J., & Childers, T. M. (2019). Daily nest survival rates of Gunnison sage-grouse (*Centrocercus minimus*): assessing local- and landscape-scale drivers. *The Wilson Journal of Ornithology*, *127*(1), 59–71.

Storfer, A., Murphy, M. A., Spear, S. F., Holderegger, R., & Waits, L. P. (2010). Landscape genetics: where are we now? *Molecular Ecology*, *19*(17), 3496–3514. https://doi.org/10.1111/j.1365-294X.2010.04691.x

Sveum, C. M., Edge, W. D., & Crawford, J. A. (1998). Nesting habitat selection by sage-grouse in south-central Washington. *Journal of Range Management*, *51*(3), 265–269. https://doi.org/10.2307/4003409

Tack, J. D., Naugle, D. E., Carlson, J. C., & Fargey, P. J. (2011). Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: A biological basis for international prairie conservation. *Oryx*, *46*(1), 64–68. https://doi.org/10.1017/S003060531000147X

Taylor, R. L., Tack, J. D., Naugle, D. E., & Mills, L. S. (2013). Combined effects of energy development and disease on greater sage-grouse. *PLoS One*, *8*(8), e71256. https://doi.org/10.1371/journal.pone.0071256

Taylor, R. L., Walker, B. L., Naugle, D. E., & Mills, L. S. (2012). Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management*, *76*(2), 336–347. https://doi.org/10.1002/jwmg.267

Taylor, S. E., Oyler-McCance, S. J., & Quinn, T. W. (2003). Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). *Molecular Ecology Notes*, *3*(2), 262–264. https://doi.org/10.1046/j.1471-8286.2003.00424.x

Theobald, D. M., Gosnell, H., & Riebsame, W. E. (1996). Land use and landscape change in the Colorado mountains II: A case study of the East River Valley. *Mountain Research and Development*, *16*(4), 407–418. https://doi.org/10.2307/3673990

United States Fish and Wildlife Service. (2013). Endangered and threatened wildlife and plants; Designation of critical habitat for gunnison sage-grouse, *Federal Register*, *78*(8), 2540–2570.

United States Fish and Wildlife Service. (2014). Endangered and threatened wildlife and plants; threatened status for gunnison sage-grouse. *Federal Register*, *79*(224), 69192–69310.

Wakkinen, W. L., Reese, K. P., Connelly, J. W., & Fischer, R. A. (1992). An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin*, *20*(4), 425–426.

Webb, S. L., Olson, C. V., Dzialak, M. R., Harju, S. M., Winstead, J. B., & Lockman, D. (2012). Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. *Ecological Processes*, *1*, 4. https://doi.org/10.1186/2192-1709-1-4

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397. https://doi.org/10.2307/2389612

Wiens, J. A., & Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, *3*(2), 87–96. https://doi.org/10.1007/BF00131172

Wilson, G. A., & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, *163*(3), 1177–1191.

Wright, S. (1943). Isolation by distance. *Genetics*, *28*(2), 114–138.

Young, J. R., Braun, C. E., Oyler-McCance, S. J., Aldridge, C. L., Magee, P. A., & Schroeder, M. A. (2020). Gunnison Sage-Grouse (*Centrocercus minimus*), version 1.0. In P. G. Rodewald (Ed.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.gusgro.01

Young, J. R., Braun, C. E., Oyler-McCance, S. J., Hupp, J. W., & Quinn, T. W. (2000). A new species of sage-grouse (Phasianidae: *Centrocercus*) from Southwestern Colorado. *The Wilson Bulletin*, *112*(4), 445–453.

Young, J. R., Hupp, J. W., Bradbury, J. W., & Braun, C. E. (1994). Phenotypic divergence of secondary sexual traits among sage

grouse, *Centrocercus urophasianus*, populations. *Animal Behaviour*, *47*, 1353–1362. https://doi.org/10.1006/anbe.1994.1183

Zeller, K. A., Creech, T. G., Millette, K. L., Crowhurst, R. S., Long, R. A., Wagner, H. H., Balkenhol, N., & Landguth, E. L. (2016). Using simulations to evaluate Mantel-based methods for assessing landscape resistance to gene flow. *Ecology and Evolution*, *6*(12), 4115–4128. https://doi.org/10.1002/ece3.2154

Zeller, K. A., Vickers, T. W., Ernest, H. B., & Boyce, W. M. (2017). Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLoS One*, *12*(6), e0179570. https://doi.org/10.1371/journal.pone.0179570

Zimmerman, S. J., Aldridge, C. L., Apa, A. D., & Oyler-McCance, S. J. (2019). Evaluation of genetic change from translocation among Gunnison sage-grouse (*Centrocercus minimus*) populations. *The Condor*, *121*(1), 1–14. https://doi.org/10.1093/condor/duy006

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