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Understanding biological effectiveness before scaling up range-wide restoration investments for Gunnison sage-grouse

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Abstract. Imperiled species recovery is a high-stakes endeavor where uncertainty surrounding effectiveness of conservation actions can be an impediment to implementation at necessary scales, especially where habitat restoration is required. Gunnison sage-grouse (*Centrocercus minimus*) represents one such species in need of large-scale habitat restoration. It is a federally threatened sagebrush (*Artemisia* spp.) obligate bird with a limited range in Colorado and Utah. Threats to recovery of Gunnison sage-grouse include conifer expansion into sagebrush along with additional habitat loss and degradation attributed to human development and agricultural conversion. Recovery of Gunnison sage-grouse and other sensitive species can be aided by spatial tools that forecast plausible outcomes of conservation actions. We illustrate this by using a novel framework for predicting outcomes of proactive tree removal and subsequent sagebrush restoration for the Gunnison sage-grouse. To assess threats on Gunnison sage-grouse lek presence, we developed a spatially explicit breeding habitat model to compare active lek and random pseudo-absence locations from 2015. Models identified land cover, climatic, and abiotic variables at landscape-level scales (0.56 and 4 km) most important for predicting breeding habitat. Our model correctly differentiated between lek and pseudo-absence locations 94% of the time. All but one of the active leks (n = 94) were in areas with >0.65 probability of lek occurrence. Using this probability value as a threshold, we predicted 15% of the current grouse range as high-quality breeding habitat. Simulated removal of trees in areas with ≤30% tree canopy cover (0.56-km scale) increased extent of high-quality habitat fourfold (59%). Hypothetical restoration of sagebrush cover in the same areas increased habitat quality an additional 11%. Our breeding habitat model indicated that targeted tree removal and sagebrush restoration have potential to improve Gunnison sage-grouse breeding habitat. While our habitat treatment scenarios were not meant to be prescriptive, they highlight that considerable uplift in Gunnison sage-grouse breeding habitat may be possible across much of its range with cooperation from multiple stakeholders and illustrates the utility of this approach for predicting biological return on investment.

Key words: *Centrocercus minimus;* Colorado; conifer expansion; habitat restoration; habitat selection; lek occurrence; juniper; pińyon pine; Utah.

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Introduction

Identifying and funding conservation practices to support broadscale restoration of ecosystems is a high-stakes investment, especially when landscape restoration efforts are conducted to support the recovery of an endangered species. Conservation plans are often challenged in the U.S. legal system when they are part of an evaluation of the Endangered Species Act. Conservation plans are more defensible under the United States Fish and Wildlife Service Policy for the Evaluation of Conservation Efforts when effectiveness of conservation actions, such as treatments or restoration, has greater certainty to be effective and implemented as a means to reduce or eliminate a threat (PECE 2003). Scientifically predicting the benefits of restoration actions to populations of species of conservation concern is difficult, and thus, conservation planners and managers often focus on protective measures with more certain conservation outcomes, such as an easement that prevents an action from occurring. Most (84%) of imperiled species are conservation-dependent wherein protective measures must be blended with proactive management to both conserve and enhance their habitats; lacking is science that proactively identifies opportunities to restore habitat quality before a species succumbs to degradation (Scott et al. 2010).

A prime example of the need to identify opportunities to restore ecosystem functionality and increase habitat is the sagebrush (*Artemisia* spp.) ecosystem, which hosts many priority wildlife species with low population numbers. Big sagebrush (*Artemisia tridentata*) are the keystone species of sagebrush ecosystems (Beck et al. 2012), and the sagebrush-obligate sage-grouse (*Centrocercus* spp.) serve as an umbrella for ~350 other species (Suring et al. 2005, Gamo et al. 2013). Sagebrush systems have been highly impacted by invasive plants such as cheatgrass (*Bromus tectorum*) that fuel catastrophic wildfires at lower elevations (Davies et al. 2011); conifer expansion into sagebrush communities at higher elevations (Miller et al. 2008, Davies et al. 2011); and anthropogenic changes including cropland cultivation (Smith et al. 2016), ex-urbanization (Copeland et al. 2013), and energy development (Naugle 2011). In total, about 56% of greater sage-grouse (*Centrocercus urophasianus*) and 90% of Gunnison sage-grouse (*Centrocercus minimus*) historic habitat have become unoccupied by sage-grouse since pre-European settlement (Schroeder et al. 2004, Miller et al. 2011).

Pińyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) have increased in spatial extent and density since Euro-American settlement in the Intermountain region of the western United States (Miller et al. 2008, Romme et al. 2009). About 90% of woodland expansion has occurred in sagebrush (Miller et al. 2011). Increasing dominance of trees results in decline of perennial grasses, forbs, and herbaceous productivity (Bates 2005, Roundy et al. 2014). Moreover, increasing woodland cover can reduce soil water availability, which in turn shortens growing seasons (Roundy et al. 2014) and limits prevalence of forbs and grasses used by sage-grouse for food and cover. These cumulative alterations reduce resilience to disturbances and resistance to invasive species, which can lead to ecosystem shifts to undesirable stable states that require management intervention to return to conditions prior to human induced disturbances (Miller et al. 2013).

Sage-grouse habitat quality and distribution have declined with increasing tree prevalence (Doherty et al. 2010, Aldridge et al. 2012, Baruch-Mordo et al. 2013, Knick et al. 2013), and conservationists have long suspected that targeted tree removal would benefit sage-grouse populations (Commons et al. 1999, Freese 2009). However, the nuanced understanding of impacts has just recently emerged (Miller et al. 2017). In the Bi-State greater sage-grouse population along the Nevada/California border, early-phase pińyon–juniper expansion functions as ecological traps that attract sage-grouse but adversely affect population vital rates (Coates et al. 2017). Additional evidence across 12 Great Basin study areas documented a behavioral mechanism of faster yet riskier movements associated with reduced survival, especially in juvenile birds, when navigating conifer-invaded sagebrush (Prochazka et al. 2017). In northwest Utah, most female sage-grouse (86%) avoided conifer-invaded habitats and those using restored habitats were more likely to raise a successful brood (Sandford et al. 2017). In a recent experiment with three years post-tree removal, Severson et al. (2017*a*) showed that probability of sage-grouse nesting in newly restored sites increased by 22% annually, and females were 43% more likely to nest near new cuts. Further, researchers in the Great Basin estimated a 25% increase in population growth rate in conifer treatment areas vs. control areas from 2010 to 2014 (Severson et al. 2017*b*). Together, these studies show conifer removal can increase habitat quality for nesting and brooding sage-grouse with potential demographic benefits. Reducing conifer expansion into sagebrush is one of the few scientifically defensible practices available to restore otherwise suitable habitats to increase sagebrush-obligate populations (Miller et al. 2017).

Gunnison sage-grouse share the same population biology and use similar habitat characteristics as greater sage-grouse, but were recognized as a new species in 2000 because of genetic differentiation and distinct differences in plumage, morphological characteristics, and mating behavior (Young et al. 2000). Gunnison sage-grouse inhabit the Colorado Plateau and have declined in Colorado and Utah (Braun et al. 2014), where they have retracted from a historical distribution that likely included birds inhabiting sagebrush in Arizona, Colorado, New Mexico, and Utah (Young et al. 2000, Schroeder et al. 2004). The entire Gunnison sage-grouse population is estimated at <5000 individuals with 94 active leks and was listed as threatened under the Endangered Species Act in 2010 (USFWS 2010). Declining and degraded habitat are identified as major threats to their recovery (USFWS 2010, Bi-State Technical Advisory Committee 2012).

Conifer cover on the landscape negatively impacts Gunnison sage-grouse nesting habitat (Aldridge et al. 2012) and piñyon–juniper removal has been recommended for habitat improvement (Commons et al. 1999, GSGRSC 2005). Yet, the historic presence of a variety of piñyon–juniper vegetation types (e.g., persistent woodlands, wooded shrublands, and savannas) and uncertainties about expected stand structure and disturbance regimes on the Colorado Plateau have made it challenging for land managers to determine appropriateness of tree removal (Romme et al. 2009). Nevertheless, increases in tree density and extent are known to have occurred at least locally (Eisenhart 2004), which may justify carefully targeted conifer management. After reconstructing historical landscapes using coarse land-survey records in the Gunnison sage-grouse range, Bukowski and Baker (2013) describe a landscape that once supported large contiguous expanses of mature sagebrush structured by variations in shrub density and patches of trees. However, when compared to current conditions, only 48% of Gunnison sage-grouse range remained sagebrush, with 30% having become piñyon–juniper woodland, and the remaining 22% having converted to other vegetation categories including different conifer (e.g., *Abies* spp.) and tall-shrub (e.g., *Quercus gambelii*) types (Bukowski and Baker 2013).

To be successful, tree removal projects must enhance attributes of productive sage-grouse habitat including increasing sagebrush, forbs, and grass for food and cover resources (Miller et al. 2014). Post-treatment compositional response of sagebrush stands following conifer removal range from greater resemblance of native shrub steppe, to little change from pre-treatment conditions, or worse yet, large increases in invasive annual grass dominance driven in large part by site conditions and dominance of trees in invaded communities prior to treatment (Miller et al. 2014, Roundy et al. 2014). In particular, restoration potential for sagebrush is highest in Phase I and II woodlands (i.e., early and mid-successional woodlands), because sagebrush is still dominant or co-dominant, prior to treatment, enabling recolonization following treatment (Roundy et al. 2014, Maestas et al. 2015, Bates et al. 2017). Phase III often lack shrub understory necessitating reseeding following conifer removal. Ensuring treatment areas have the capacity to regenerate into sagebrush-dominated cover is key to the long-term success of a range-wide coordinated conservation effort where conifers are removed.

Recovery of Gunnison sage-grouse and other sensitive species can be aided by spatial tools that forecast plausible outcomes of conservation actions such as tree removal and subsequent sagebrush restoration in tree removal areas. Active habitat restoration provides a singular opportunity to expand high-quality breeding habitat and potentially create habitat for new lek formation to ensure long-term persistence of Gunnison sage-grouse across their current range. Reducing woodland expansion by partnering within local communities to identify shared goals and collaborative conservation plans are key ingredients to scaling up voluntary proactive restoration (Duvall et al. 2017). Objectives of our study were to (1) use all known active lek locations to model the probability of occupied breeding habitat across the current distribution of Gunnison sage-grouse and then (2) use the resulting model to forecast biological outcomes of conservation actions (conifer removal and reestablishment of sagebrush).

Study Area

The extent of our analyses was delineated by placing a minimum convex polygon around range-wide Gunnison sage-grouse habitat which occurs in one main large population and six smaller satellite populations (Fig. 1). The analysis area was defined by Colorado Parks and Wildlife (CPW) as occupied range and linkage habitat, Utah Division of Wildlife Resources (UDWR) as occupied and vacant habitat, and U.S. Fish and Wildlife Service (USFWS) as critical habitat. Linkage areas were classified as lands that currently do not support Gunnison sage-grouse, but are thought to be important to maintaining connectivity of populations. The intent of the linkages was to provide focal areas where restoration and treatments may occur to facilitate movement and connectivity between current populations. We then buffered this polygon by 18 km, which is a reasonable approximation for the average distance a Gunnison sage-grouse might move annually to access seasonal resources (based on greater sage-grouse data, Fedy et al. 2012). We also chose this spatial extent to have a continuous surface between currently occupied areas, which could be used by stakeholders to identify areas with potential as movement pathways between currently occupied areas (Fig. 1). Areas currently designated as population and linkage habitat between occupied habitat total 10,037 km^2 (51% private, 48% federal, 1% state ownership). From 1981 to 2010, yearly mean precipitation was 538 mm (196–1857 mm) and yearly mean temperature was 6°C (−5° to 18°C). Mean elevation was 2497 m (range: 1221–4393 m). Big sagebrush (*Artemisia tridentata*) was the dominant shrub, and Engelmann spruce (*Picea engelmannii*),

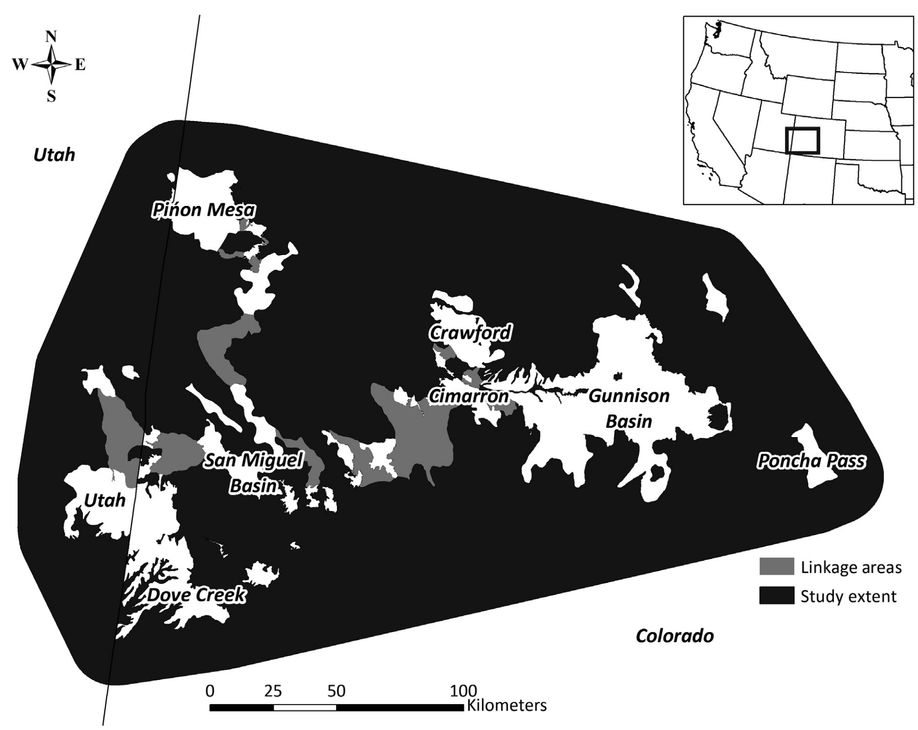

Fig. 1. Location of study area for Gunnison sage-grouse populations, and linkage areas, Colorado and Utah, USA.

Rocky Mountain (*Juniperus scopulorum*), Utah (*Juniperus osteosperma*) juniper, two-needle piñyon pine (*Pinus edulis*), and Douglas fir (*Pseudotsuga menziesii*) comprised the dominant conifer species.

Methods

We followed the exact statistical methodology used to create range-wide breeding habitat models for greater sage-grouse (Doherty et al. 2016) to create breeding habitat models for the range of Gunnison sage-grouse. We created a spatially explicit model of Gunnison sage-grouse breeding habitat to assist stakeholders in targeting conifer removal projects and quantify the effect of restoring sagebrush cover within tree removal areas. Our models provide a platform to assess likely biological outcomes of habitat treatments to expand or enhance the distribution of Gunnison sage-grouse. Other habitat restoration efforts, such as riparian and wet meadow restoration to promote brood rearing and juvenile survival, are also important components of an overall conservation strategy (Davis et al. 2016), but were beyond the scope of our analyses.

Breeding habitat model

We developed a binomial probabilistic model of occupied breeding habitat by quantifying habitat characteristics around active sage-grouse leks ($n = 94$) and pseudo-absence points ($n = 188$) using a classification instance of the non-parametric model random forests (Cutler et al. 2007, Olden et al. 2008, Evans et al. 2011, Baruch-Mordo et al. 2013). We used lek designations from 2015 for active, inactive, and historic Gunnison sage-grouse leks from Colorado provided by CPW (GSGRSC 2005) and by UDWR for Utah. There have been extensive efforts in Colorado and Utah to identify additional Gunnison sage-grouse lek locations over the last decade. While it is likely some unidentified leks exist, we are confident that the spatial processes governing lek locations were well represented in the data. To generate pseudo-absence (i.e., background) locations, we modeled the spatial process of active leks, employing an isotropic kernel estimate (Diggle 1985) and used the inverse of the density estimate to weight samples within the extent of our study area (Doherty et al. 2016).

Our breeding habitat model provided the probability of each 30-m grid cell containing sufficient habitat to support an occupied lek. Numerous publications have shown lek locations to be good predictors of important breeding areas for sage-grouse at landscape scales (Holloran and Anderson 2005, Doherty et al. 2010, 2011, Coates et al. 2013, Fedy et al. 2014). In this regard, we are modeling lek locations as a surrogate to represent the landscapes that support successful nesting and early brood-rearing habitat critical to recruitment and maintenance of sage-grouse populations. Nesting females exhibit strong site fidelity with much shorter distances between inter annual nest sites for successful nesters (e.g., average distances of 5.2 km vs. 1.6 km in Schroeder and Robb 2003, 0.5 km vs. 0.3 km in Holloran and Anderson 2005, and 1.2 km vs. 0.7 km in Dinkins et al. 2014). Through time, this spatial movement process promotes selection for less risky habitats as sage-grouse slowly move away from areas that do not support recruitment (Holloran et al. 2010). We therefore believe modeling lek locations as a surrogate to represent the landscapes which support nesting and early brood-rearing habitat is supported because persistent lek formation is unlikely to occur in landscapes that do not support recruitment through time. Potential components of Gunnison sage-grouse breeding areas were compiled into a GIS database representing abiotic and biotic variables of ecological relevance (Table 1).

Scale

Akin to Doherty et al. (2016), we evaluated landscape-scale breeding habitat across the geographic range of active Gunnison sage-grouse leks. We also included patch-scale metrics to evaluate trade-offs with future habitat restoration projects. Much of the Gunnison sage-grouse range is naturally fragmented by mountains or plateaus; therefore, we used the median distance of an active lek to non-habitat (4 km) as a reasonable distance to account for landscape context. We quantified habitat, landform, and disturbance variables within a 4-km buffer of each 30-m pixel (Table 1). This represented a finer scale than used in previous analyses for greater sage-grouse (Doherty et al. 2016); however, this was warranted because an analogous 6.4-km

Table 1. Description of explanatory variables used to predict occupied Gunnison sage-grouse breeding habitat across its range in Colorado and Utah, USA.

Name	Source (yr)	Native resolution	Description†	Justification and References
All sagebrush	LANDFIRE EVT 1.3 (2012)‡	30 m	Proportion of grid cells classified as sagebrush	Established positive relationship between sage-grouse abundance and sagebrush (Patterson 1952, Young et al. 2000 Oyler-McCance et al. 2001)
Tree canopy cover	Falkowski et al. (2017)	1 m	1 m binary estimate of canopy cover	Established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Aldridge et al. 2012, Baruch-Mordo et al. 2013, Fedy et al. 2014) and positive relationship to conifer removal (Commons et al. 1999)
Grassland/ herbaceous	LANDFIRE Fuels 1.2 (2010)	30 m	Proportion of grid cells classified as grassland/ herbaceous	Established negative relationship between sage-grouse abundance and grasslands (Patterson 1952, Aldridge et al. 2012)
Gross primary# production	MODIS NASA EODP (2009–2013)	1 km	Index of early brood-rearing habitat (mean of GPP from 5–15 through 6–15)	Forbs are important predictors of early brood survival and habitat selection (Crawford et al. 2004).
Compound topographic index	National Elevation Data NED (2013)	10 m	Index of wetness	Established positive relationship between sage-grouse populations and riparian habitats (Aldridge et al. 2012, Blomberg et al. 2014)
Degree days >5°C§, ‖	USFS (1961–1990; Rehfeldt et al. 2006)	1 km	Number of days that reach a temperature ≥5°C	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Guttery et al. 2013, Blomberg et al. 2014)
Mean annual§ precipitation	USFS (1961–1990; Rehfeldt et al. 2006)	1 km	Mean annual precipitation (mm)	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Blomberg et al. 2013, 2014)
Annual drought index§	USFS (1961–1990; Rehfeldt et al. 2006)	1 km	Ratio = dd5/map	Large-scale ecological driver of land types. Hypothesized regional scale relationship between sagebrush landscapes with higher production. Documented carry over effects (Guttery et al. 2013, Blomberg et al. 2014)
Roughness	National Elevation Data NED (2013)	10 m	Standard deviation in elevation within a buffer of the grid cell	Established negative relationship between sage-grouse and rough terrain (Doherty et al. 2008, Fedy et al. 2014)
Elevation‖	National Elevation Data NED (2013)	10 m	Average elevation within a buffer of the grid cell	Hypothesized relationship between sage-grouse populations and areas with higher productivity because of elevation.
Human disturbance index	NLCD Disturbed Classes¶ (2011)	1 km	Proportion of land cover types associated with human presence	Established negative relationship between sage-grouse and human activity (Tack 2009, Naugle et al. 2011, Aldridge et al. 2012)
Agriculture lands	NASS (2008–2014)	30 m	Proportion of grid cells classified as tilled agriculture	Established negative relationship between sage-grouse and cropland (Knick et al. 2013, Fedy et al. 2014)

Notes: All variables apart from the climate data predictor group were quantified using 0.56 and 4-km buffer moving windows.

† All variables were resampled to a 30-m pixel. All moving windows were calculated at a 0.56 and a 4-km buffer.

‡ Landfire vegetation groupings defined in Johnson et al. SAB (Johnson et al. 2011).

§ Because climate grids native resolution change at a 1-km scale and are highly spatially correlated, we did not resample the grids using a 0.56-km or 4-km moving window.

¶ NLCD Urban development classes: Developed-High Intensity, Developed-Low Intensity, Developed-Medium Intensity, Developed-Open Space, and NLCD impervious surfaces. The index also included roads (TIGER), oil and gas wells, wind turbines (FCC obstruction database), transmission lines (Ventyx), and pipelines (Ventyx).

\# Gross primary production (GPP) was removed because a joint negative correlation with sagebrush and positive correlation in conifer caused model instability.

‖ Variables removed from consideration because of high correlation with other variables.

buffer used in greater sage-grouse analyses placed around active Gunnison sage-grouse leks included approximately 37% non-habitat (e.g., forested mountains).

We also used a 0.56-km buffer to represent patch-scale habitat variables (Table 1). We specifically choose this scale, because it was the top-ranked spatial scale for both sagebrush and woodlands in past Gunnison sage-grouse analyses (Aldridge et al. 2012). We did not evaluate smaller buffer distances, such as 100-m buffer (Aldridge et al. 2012), because these scales are more suitable for studies modeling telemetry locations. Climatic variables had a native raster resolution of 1 km with a high degree of autocorrelation between adjacent grid cells; therefore, we simply queried the 1-km grid (Table 1) and resampled to a 30-m resolution (Table 1) to allow for spatial predictions in program R.

Statistical model

We modeled selection of breeding season habitat within the Gunnison sage-grouse range (Johnson 1980, Meyer and Thuiller 2006) using random forests, which is a bootstrapped Classification and Regression Tree approach (Hastie et al. 2008). Random forests is based on the principle of weak learning, where a set of weak subsample models converge on a stable global model. This method has been shown to provide stable estimates while being robust to many of the issues associated with spatial data (Cutler et al. 2007, Evans et al. 2011) such as autocorrelation and non-stationarity (i.e., non-constant mean and variance). It also fits complex, non-linear relationships, accounts for high dimensional interaction effects and accounts for hierarchically structured data inherent in non-stationary processes (Cutler et al. 2007, Evans et al. 2011). Analyses were conducted in program R (R Core Team 2012) using the rgdal (Bivand et al. 2013), sp (Bivand et al. 2008), and raster (Hijmans and Etten 2013) libraries to read spatial data, assign values from spatial covariates to the point observations of our dependent variable, and make spatial predictions. We used the implementation of random forests (Breiman 2001) in the R library randomForest (Liaw and Wiener 2002) and followed the model selection method introduced in Murphy et al. (2010) using the rfUtilities package (Evans and Murphy 2014).

Having a continuous surface between occupied areas was important for future conservation planning efforts. Use of a non-linear model allowed us flexibility to evaluate thresholds of non-habitat across a large extent, while simultaneously evaluating lek occurrence habitat selection within occupied areas. Random forests models partition data based upon nodes (Breiman 2001). In the classification instance of random forests, the nodes are, in essence, decision rules which partition variation in occurrence based upon node splits at different levels of covariates (i.e., Table 1 in this study). The use of a non-linear model affords flexibility because they allow diverse functional relationships at varying levels of habitat features (Breiman 2001, Evans et al. 2011). This is because node partitions, not a user defined link function and equation, such as a quadratic function with an identity link, define the shape of the functional relationships. For example, a threshold amount of tree canopy cover that causes habitat avoidance may serve as a major node split. However, random forests models can simultaneously have other major node splits that define the shape of the tree canopy cover relationship below threshold values. In other words, functional relationship shapes at habitat values above and below a node split are not structurally bound by a user defined equation and link function as they are in a traditional Generalized Linear Model (McCullagh and Nelder 1989). Our choice of statistical model allowed flexibility to model across the entire Gunnison sage-grouse range, while simultaneously understanding habitat relationships within currently occupied areas.

Evaluation of model fit and spatial predictions and graphical interpretation of habitat selection responses

To assess model fit, we used OOB error (out-of-bag) and confusion matrices (Liaw and Wiener 2002). We evaluated model stability and performance using cross-validation methods (Evans et al. 2011), where 10% of data were withheld from training the model and used as a validation dataset. Over-fitting was assessed by comparing error rates between OOB and cross-validation. We used partial probability plots to elucidate habitat relationships of the modeled covariates after partialling out (holding constant) the other variables in the model. The partial probability plots were derived using the rfUtilities library (Evans and Murphy 2014).

Forecasting outcomes of tree removal and sagebrush restoration

Our scenarios of tree removal and sagebrush restoration allow stakeholders a menu of possible alternatives to evaluate at local levels. Forecasts also highlight plausible outcomes of different strategies (i.e., tree removal vs. sagebrush restoration) for different populations. We emphasize that resulting forecasts are not intended to be prescriptive; instead, they quantify the potential and cumulative benefits of targeted tree removal and sagebrush restoration across the range of Gunnison sage-grouse.

To approximate how the amount of breeding habitat might change if tree cover was reduced, we simulated tree removal scenarios at ≤10%, ≤20%, and ≤30% landscape coverages of tree canopy cover. Tree cuts are typically implemented locally: So, we used the smaller 0.56-km scale to simulate treatment outcomes. We performed a moving window analysis on the 30-m tree canopy cover raster, which generated a value of percent tree canopy cover within a 0.56-km buffer for each 30-m grid cell. To be included in our scenario of cuts, two criteria had to occur simultaneously. First, a 30-m grid cell needed to be classified as containing tree cover. Second, the same grid cell needed to possess a value of ≤10% tree canopy cover within the surrounding 0.56-km buffer. The first criteria ensured a cell contained trees and the second criteria allowed for simulated treatments to occur in low-density stands preventing treatments from occurring in higher density conifer forests. If these conditions were met, the cell was turned to null. After all cells meeting these conditions were turned to null, we recomputed moving window analyses on the 30-m scenario-based tree canopy cover raster, which created new tree canopy cover rasters at 0.56 and 4-km buffer scales. Finally, we created a new Gunnison sage-grouse habitat prediction surface for each scenario by predicting the probability of each 30-m grid cell supporting an occupied lek using the tree removal-scenario rasters instead of the original tree canopy cover rasters. We repeated this process for tree canopy cover values of ≤20% and ≤30%. To evaluate the simulated response of restoring sagebrush in areas where trees were removed, we edited the 30-m sagebrush raster so that it was classified as sagebrush where null values were created by the simulated tree removal process. We followed the same processes to create new Gunnison sage-grouse habitat prediction surfaces using the sagebrush restoration-scenario rasters. Results are presented at range-wide scale (Tables 3, 4); however, linkage areas were removed from our summary tables because roughly a third of the targeted tree removal occurred within them despite an absence of birds. We present results of our scenarios at a range-wide scale; however, the results for each population, including linkages, are listed in Appendix S1: Table S1.

Results

Our final model included 16 variables with the top eight variables relating to habitat cover, topography, and a drought index (Table 2). We removed the gross primary production variable post hoc, but prior to model finalization, because a negative correlation with sagebrush and positive correlation with tree canopy cover caused instability in model predictions. The top three variables predicting the probability of an

Table 2. Selected variables to model occupied Gunnison sage-grouse breeding habitat in Colorado and Utah, USA.

Variable	Importance value
Sagebrush cover, 4 km	1.00
Sagebrush cover, 0.56 km	0.64
Tree canopy cover, 0.56 km	0.53
Annual Drought Index, 1 km	0.39
Tree canopy cover, 4 km	0.33
Topographic roughness, 0.56 km	0.21
Topographic roughness, 4 km	0.15
Compound topographic wetness index, 4 km	0.14
Compound topographic wetness index, 0.56 km	0.14
Tilled agriculture, 4 km	0.11
Mean annual precipitation, 1 km	0.09
Human disturbance, 4 km	0.05

Notes: Variable importance values were scaled so that the top variable equals 1 and the remaining variables are a proportion derived by dividing by the top variable. They were derived from probability scaled partial plots in the randomForest package in R.

occupied lek were sagebrush cover at 4 km, sagebrush cover at 0.56 km, and tree canopy cover at 0.56 km (Table 2).

Our model correctly classified 94.0% of lek and pseudo-absence locations across the entire Gunnison sage-grouse range. Error rates were low for both leks (9.6%) and pseudo-absence locations (4.3%), indicating the ability of our model to predict both sources of input data accurately. Our model correctly classified 93.3% of K-fold cross-validation hold-out data set locations (10%), which were correctly classified by a model built with 90% of the data set. When we compare internal model fit statistics generated via bootstrap resampling (OOB error = 6.0%) to K-fold cross-validation (93.3% correct), the general agreement displayed indicates lack of over-fitting and stability to predict independent data. All active leks within our analysis, apart from one, were in areas with predicted probabilities of breeding habitat ≥0.65 (Fig. 2A). When we used a 0.65 probability threshold to classify our prediction layers, we found 15% of the range-wide Gunnison sage-grouse habitat as defined by CPW, UDWR, and USFWS to be predicted breeding habitat. These area estimates ranged from 0.4% of linkage areas to 36% of the Gunnison Basin population.

Sage-grouse exhibited a strong functional habitat response to the amount of sagebrush cover at both the 4 and 0.56-km buffer scales (Figs. 3, 4). Despite having a variable importance of almost half that of sagebrush at 4 km, tree canopy cover within a 0.56-km buffer showed the steepest functional response of any predictor variable (Figs. 3, 4). Averaged across the entire range, tree canopy cover >0.8% at 0.56-km and 1.5% at 4-km buffer scales exceeded habitat thresholds for breeding Gunnison sage-grouse (Fig. 4). We documented a threshold relationship with the compound topographic wetness index (CTI) for both 0.56 and 4-km buffer scales. Areas below 8.97 CTI (0.56 km) and 8.78 CTI (4 km) were unlikely to have enough breeding habitat to support lek formation. Compound topographic index is a wetness index to biological processes such as annual net primary production and vegetation patterns. Areas with higher CTI values have higher net primary productivity because they have more access to water. Consistent with past literature (Doherty et al. 2010, Dzialak et al. 2011, Dinkins et al. 2014), areas with lower topographic roughness values at both scales were unlikely to contain enough breeding habitat to support lek formation.

Our conservation scenarios show a large potential increase in predicted occupied habitat following targeted tree removal (Table 3). Across the Gunnison sage-grouse range, removing trees in areas where cover is ≤10% at the 0.56-km scale would increase the amount of predicted occupied habitat by 46.4%. Up to a 58.8% increase would result if tree canopies ≤30% were removed. Land tenure indicates conifer removal on both public and privately owned land would greatly increase the habitat acreage predicted to be occupied (Table 3).

Positive effects of sagebrush restoration within conifer treatment areas were not as pronounced as the conifer removal treatments themselves. However, range-wide summaries can be misleading because the area of the Gunnison Basin is over 4.5 times larger than the combined area of the surrounding satellite populations (Table 4, Fig. 4A, B). Apart from the Cimarron population, which showed a 2.0–3.3% increase in habitat, the Gunnison Basin showed the lowest positive effects of sagebrush restoration because it already has the most intact sagebrush landscapes (3.7–9.0%, Fig. 2B). There were two general responses to combined conifer removal and sagebrush restoration. First, the Pińon Mesa, Dove Creek, San Miguel Basin, and Utah populations showed a 40.2% increase in predicted breeding habitat (range 27.1–59.4%) when tree canopy covers ≤30% were removed and sagebrush was restored (Fig. 5). Second, the Gunnison Basin, Cimarron, and Crawford populations exhibited an 8.4% increase in predicted breeding habitat with the addition of sagebrush restoration in conifer removal areas (range 3.3–13.0%). Further, the positive effects of sagebrush restoration were most pronounced at higher levels of tree removal (Fig. 5).

Discussion

We developed the first probabilistic breeding habitat model for Gunnison sage-grouse encompassing the entire breeding range within Colorado and Utah (Fig. 4A). Our model demonstrated high accuracy for both bootstrap hold-out

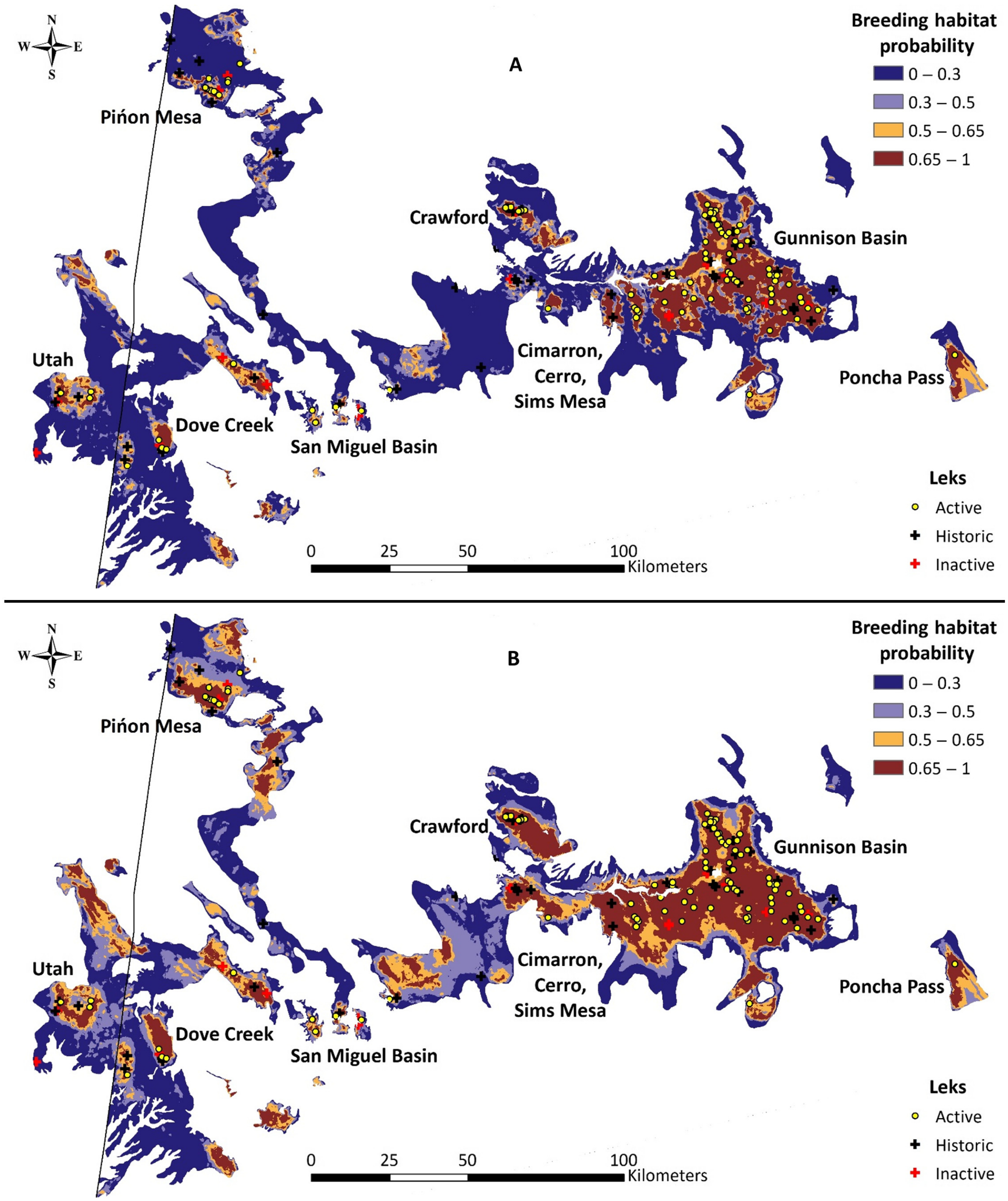

Fig. 2. Comparison of predicted breeding habitat probabilities across Gunnison sage-grouse populations and linkage areas between current land cover (A) and removal of tree canopy cover ≤30% and replacement with sagebrush (B), Colorado and Utah, USA.

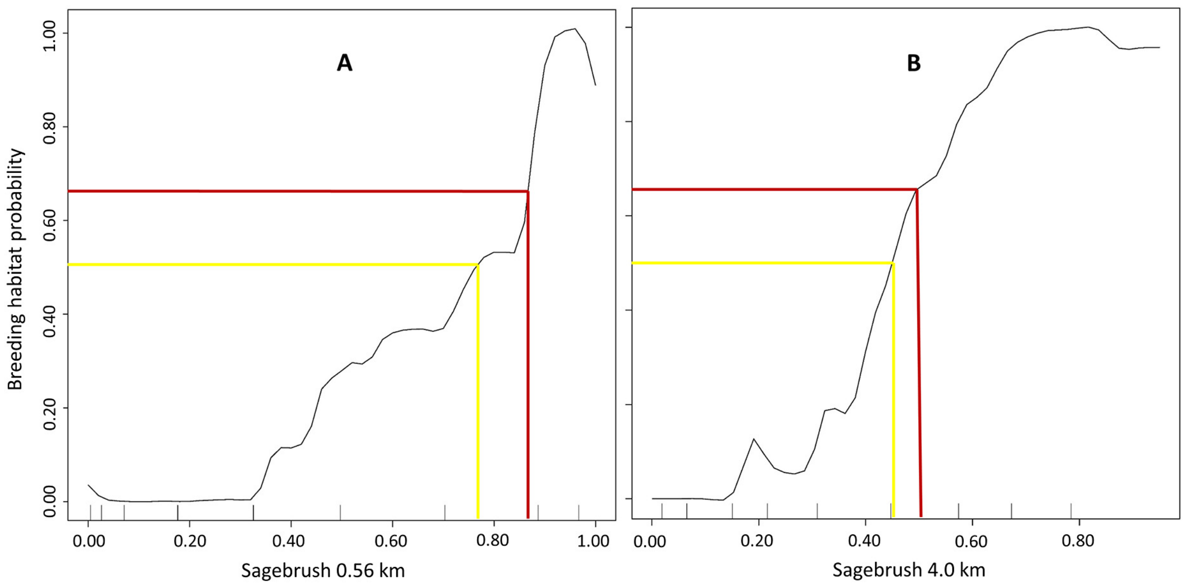

Fig. 3. Sagebrush cover partial probability plots. Breeding habitat probability threshold values at the 0.56-km scale (A) = 77% (0.50–0.65; yellow) and 87% (>0.65; red); threshold values at the 4-km scale (B) = 45% (0.50–0.65; yellow) and 48% (>0.65; red), Colorado and Utah, USA.

data (94%) and K-fold cross-validation (93.3%). The ability to reliably predict landscape-level breeding habitat gave confidence that our model was a reasonable tool to forecast the magnitude of different potential effects under differing levels of conservation effort (Tables 3, 4). These simple scenarios clearly demonstrate that large-scale, coordinated conservation efforts to remove

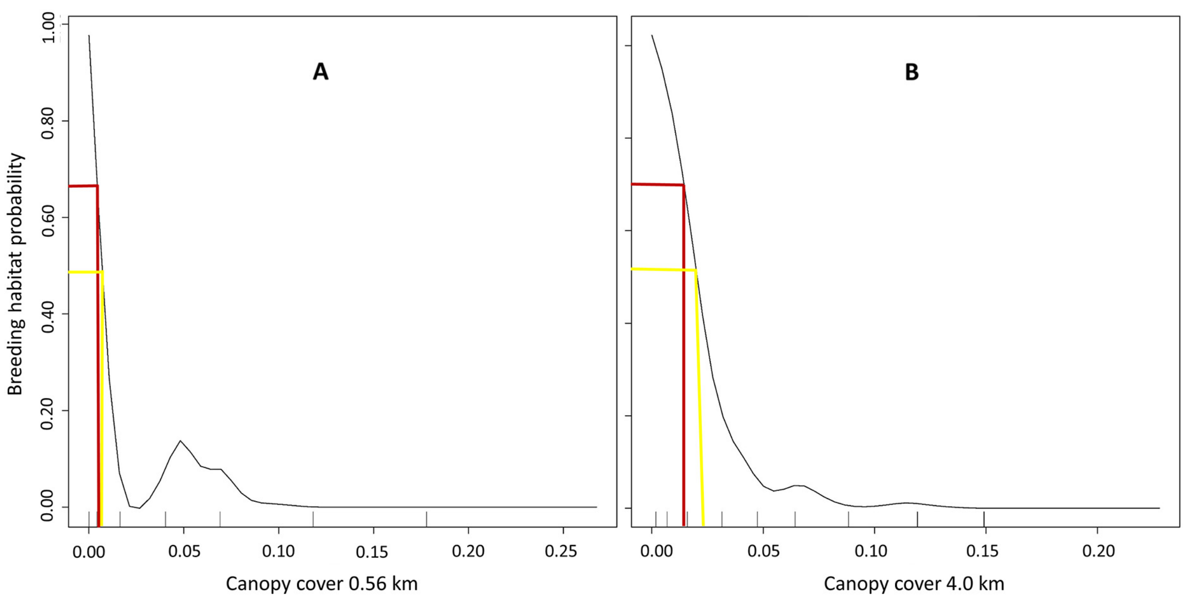

Fig. 4. Tree canopy cover partial probability plots. Probability threshold values at the 0.56-km scale = 1.6% (0.50–0.65; yellow) and 0.8% (>0.65; red); threshold values at the 4-km scale = 2.0% (0.50–0.65; yellow) and 1.5% (>0.65; red), Colorado and Utah, USA.

Table 3. Area removed (km^2) and the predicted increase (%) in breeding habitat probability across Gunnison sage-grouse populations from tree removal on private, public, and all lands for each scenario of conifer removal, Colorado and Utah, USA.

Tree canopy cover removal scenarios	Removed (km^2)		Percentage of increase in habitat predicted to be occupied ($P > 0.65$)		
	Private	Public	Public and private removal	Only private removal	Only public removal
≤10%	71	58	46.4	18.6	22.6
≤20%	136	194	57.0	20.9	27.4
≤30%	145	237	58.8	20.9	28.0

conifers, while ensuring treatment areas regenerate into sagebrush-dominated cover, could increase breeding habitat by 46–69% across the range of Gunnison Sage-grouse.

Functional habitat selection response curves allow for scientific and practical understanding of habitat selection and threshold responses. Simply put, steeper curves equate to stronger behavioral responses. Thus, curves provide insight into conservation actions most likely to yield highest return on conservation investment. In our analyses, negative association with tree canopy cover was steeper than the positive association with sagebrush (Figs. 3, 4), despite sagebrush explaining the most variation in active lek occurrence (Table 2). Not surprisingly, tree removal exhibited a larger proportional effect in conservation forecasting (Tables 3, 4). To state the obvious, Gunnison sage-grouse are a sagebrush-obligate bird and conducting conifer treatments in landscapes that do not have large expanses of sagebrush will not promote habitat use. One of the greatest advantages of using a landscape-scale model to help identify potential treatment areas is providing context for all variables that influence habitat selection and vital rates so that treatments are targeted to areas with the greatest potential benefit. Landscape context is accounted for in our scenarios because areas that are targeted for low-density conifer removal in our simulation which are not surrounded by large expanses of sagebrush will not result in increases in predicted Gunnison sage-grouse breeding habitat by our landscape-scale model.

Functional habitat responses also help guide restoration strategies, and our work demonstrates that benefits accrue more quickly when beneficial cuts transcend ownership boundaries. Grouping cuts regardless of land tenure matches scale of treatment to the birds' local intolerance (0.8% at 0.56 km) and landscape-scale avoidance of encroaching trees (1.5% at 4 km; Tables 3, 4). Locally, to place this in context, one clump of trees in an 11-ha area (0.56-km buffer) is enough encroachment for birds to avoid otherwise suitable breeding habitat. Low thresholds (1.5%) at much larger scales (4 km) have even larger implications for planning especially for comingled ownerships, where close coordination will ensure treatments reduce cumulative tree cover below critical thresholds. Accumulating knowledge suggests that clustering of treatments, their adjacency to intact sagebrush, retaining sagebrush within tree

Table 4. Area removed (km^2) and the predicted increase (%) in breeding habitat probability across Gunnison sage-grouse populations from conifer removal and subsequent restoration of treatment areas to a sagebrush-dominated state on private, public, and all lands for each scenario of tree removal and replacement with sagebrush, Colorado and Utah, USA.

Tree canopy cover removal scenarios	Removed (km^2)		Percentage of increase in habitat predicted to be occupied ($P > 0.65$)		
	Private	Public	Public and private removal	Only private removal	Only public removal
≤10%	71	58	49.2	19.9	23.7
≤20%	136	194	66.2	23.6	30.9
≤30%	145	237	69.8	23.7	32.1

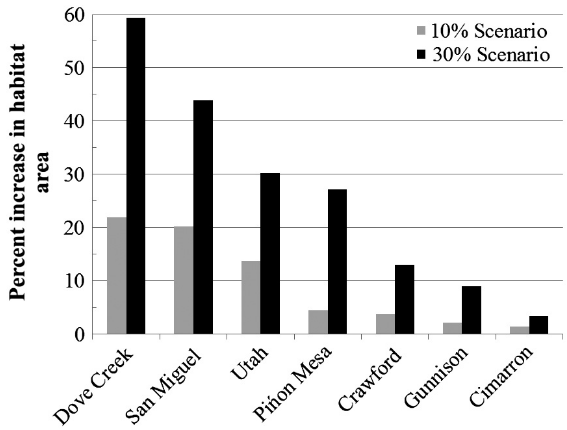

Fig. 5. Additional positive effects of the transition of conifer removal areas into a sagebrush-dominated state by Gunnison sage-grouse sub-population groupings, Colorado and Utah, USA. The predicted percent increase in habitat area was calculated as the percent additional area predicted to be habitat ($P \geq 0.65$) after sagebrush was the dominant state in conifer removal areas compared to area predicted to be habitat from just removing conifers. For graphical purposes, we only display the ≤10% and ≤30% tree cover removal scenarios.

cuts and removal of all post-settlement trees each help foster positive sage-grouse responses to tree removal (Severson et al. 2017*a*). Our findings corroborate those from eastern Oregon, where likelihood of maintaining greater sage-grouse breeding activity declined precipitously in the presence of very low amounts of conifer cover such that no leks remained active with >4% conifer cover (1-km buffer; Baruch-Mordo et al. 2013). Findings also support Coates et al. (2017) who found that greater sage-grouse along the California–Nevada border experienced reduced survival in high productivity areas with pińyon-juniper cover as low as 1.5%.

In our study area, pińyon–juniper woodlands and scattered trees were present historically (Bukowski and Baker 2013). Given the sensitivity sage-grouse have to expanding tree cover, spatial prioritization is necessary to maintain legacy trees while restoring large, relatively treeless landscapes. Designation of habitat treatment areas is inherently a local process in which landscape-scale models can help guide allocation of efforts and forecast potential benefits. Gunnison sage-grouse habitats exist across a broad and diverse spectrum of ecological conditions (GSGRSC 2005), so careful site-specific planning will be needed to determine ecological site potential, treatment needs, and techniques. For example, removal of pińyon–juniper tends to increase perennial grass, shrub, and forb cover, but can also increase annual plants, which could include the invasive cheatgrass (Bates et al. 2005, Coop et al. 2017). Therefore, ecological sites with low resilience and resistance, such as areas with warm and dry soils, low abundance of perennial herbaceous plants, and cheatgrass invasion (Chambers et al. 2016), may be poor choices for treatment, regardless of their potential as identified by our GIS-based analyses. At a minimum, these higher risk sites will require additional costs for herbicide, seed, and monitoring. Likewise, misclassification of GIS-based layers such as the high-resolution canopy cover layer used in our analyses, could identify other tall woody vegetation for potential treatment which are not likely to be socially acceptable or ecologically appropriate to treat such as aspen stands (*Populus tremuloides*), or mixed mountain shrub communities (e.g., *Amelanchier* spp.). In practice, our restoration benefit estimates are going to be biased high in these areas if conifer treatment areas are in fact other non-target community types. However, we have clearly identified large expanses with treatment potential for managers to consider, thus ample opportunities for restoration exist across the Gunnison sage-grouse range (168 km^2 for the ≤10% scenario and 606 km^2 for the ≤30% scenarios; Appendix S1: Table S1). Once the Gunnison partnership has verified the ecological appropriateness and sociological willingness of treatment areas through site-specific planning, our models can be refined to quantify cumulative benefits of locally defined treatment areas aimed at promoting large relatively treeless landscapes for Gunnison Sage-grouse.

Ecosystem benefits of targeted tree removal extend well beyond a single species and include conservation of non-target sagebrush-obligate avifauna (Donnelly et al. 2017, Holmes et al. 2017), enhancement of big game forage (Stephens et al. 2016), improved soil water availability (Roundy et al. 2014, Kormos et al. 2017), and promotion of ecosystem resilience to disturbance and resistance to invasive species (Chambers et al. 2016, Miller et al. 2017). Concomitant with the expansion of low-density conifer throughout the West, sagebrush obligates such as Brewer's Sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*) are in decline (Sauer et al. 2017). Several examples exist of how sage-grouse can serve as important flagship species catalyzing landscape-scale woodland management providing a host of ecosystem benefits (Miller et al. 2017).

Our placed-based science for Gunnison sage-grouse provides confidence to local partnerships that effective restoration, already demonstrated for greater sage-grouse (Severson et al. 2017*b*), can be replicated. But ultimate success is contingent on local communities' desire to rally around science in ways they deem socially acceptable and ecologically appropriate (Duvall et al. 2017). Science presented here is not a substitute for on-the-ground practitioners; rather, our scenarios provide the spatial context for Gunnison partnerships to infuse their ecological knowledge to delineate cuts and to invest in conservation actions. Enough watershed scale restorations have been completed to know that conifer restoration averages \$24,700–49,400 USD per km^2 depending on tree density, site conditions and mechanical treatment employed (Maestas et al. 2015). Most recently, a locally backed coalition of Bi-State greater sage-grouse partners along the California–Nevada border assembled a \$45 million USD investment to remove encroaching conifer, acquire conservation easements, and implement their action plan (USFWS 2015). In comparison, an investment of \$3.2–6.4 million USD would restore all habitats invaded by ≤10% tree canopy (130-km^2 area; Tables 3, 4) in Gunnison sage-grouse populations. A more aggressive strategy covering habitats invaded by ≤30% canopies would range from \$9.3 to \$18.7 million (~380 km^2).

Our framework demonstrates the utility of models for informing the local process of identifying specific areas for imperiled species habitat restoration and quantifying the potential cumulative effectiveness of individual on-the-ground habitat restoration projects. Coupled with recent scientific documentation of the biological effectiveness of conifer removal to sage-grouse (Miller et al. 2017), our models increase defensibility and certainty of investments aimed at recovering Gunnison sage-grouse. While our habitat treatment scenarios were not meant to be prescriptive, they highlight that considerable uplift in Gunnison sage-grouse breeding habitat may be possible across much of its range with cooperation from multiple stakeholders and more broadly illustrate the utility of this approach for predicting biological return on investment for large-scale restoration.

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Literature Cited

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Bates, J. D. 2005. Herbaceous response to cattle grazing following juniper cutting in Oregon. Rangeland Ecology & Management 58:225–233.

Bates, J. D., K. W. Davies, A. Hulet, R. F. Miller, and B. Roundy. 2017. Sage grouse groceries: forb response to piñon-juniper treatments. Rangeland Ecology and Management 70:106–115.

Bates, J. D., R. F. Miller, and T. Svejcar. 2005. Long-term successional trends following western juniper cutting. Rangeland Ecology and Management 58: 533–541.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology and Management 65:444–455.

Bi-State Technical Advisory Committee. 2012. Bi-state action plan: past, present, and future actions for the conservation of the greater sage-grouse bi-state distinct population segment. https://www.fws.gov/greatersagegrouse/Bi-State/Bi-State%20Action%20Plan.pdf

Bivand, R. S., T. Keitt, and B. Rowlingson. 2013. rgdal: bindings for the Geospatial Data Abstraction Library. R package version 0.8-9. http://CRAN.R-project.org/package=rgdal

Bivand, R. S., E. J. Pebesma, and V. Gomez-Rubio. 2008. Applied spatial data analysis with R. Springer, New York, New York, USA. http://www.asdar-book.org/

Blomberg, E. J., J. S. Sedinger, D. Gibson, P. S. Coates, and M. L. Casazza. 2014. Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. Ecology and Evolution 4:4488–4499.

Blomberg, E. J., J. S. Sedinger, D. V. Nonne, and M. T. Atamian. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. Journal of Avian Biology 44:149–158.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. Wilson Journal of Ornithology 126: 207–217.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Bukowski, B. E., and W. L. Baker. 2013. Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. Ecological Applications 23:546–564.

Chambers, J. C., et al. 2016. Using resilience and resistance concepts to develop a strategic approach for managing threats to sagebrush ecosystems, Gunnison sage-grouse, and greater sage-grouse in their eastern range. RMRS-GTR-356. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Coates, P. S., M. L. Casazza, E. J. Blomberg, S. C. Gardner, S. P. Espinosa, J. L. Yee, L. Wiechman, and B. J. Halstead. 2013. Evaluating greater sage-grouse seasonal space use relative to leks: implications for surface use designations in sagebrush ecosystems. Journal of Wildlife Management 77:1598–1609.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. B. Gustafson, P. Ziegler, and M. L. Casazza. 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology and Management 70:25–38.

Commons, M. L., R. K. Baydack, and C. E. Braun. 1999. Sage grouse response to pinyon-juniper management. Pages 229–234 *in* S. B. Monsen and R. Stevens, editors. Proceedings: Ecology and Management of Pinyon-Juniper Communities within the Interior West. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Coop, J. D., T. A. Grant, P. A. Magee, and E. A. Moore. 2017. Mastication treatment effects on vegetation and fuels in piñon-juniper woodlands of central Colorado, USA. Forest Ecology and Management 396:68–84.

Copeland, H. E., A. Pocewicz, D. E. Naugle, T. Griffiths, D. Keinath, J. Evans, and J. Platt. 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:e67261.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Rangeland Ecology and Management 57:2–19.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584.

Davis, A. J., M. L. Phillips, and P. F. Doherty Jr. 2016. Declining recruitment of Gunnison sage-grouse highlights the need to monitor juvenile survival. Condor 118:477–488.

Diggle, P. 1985. A kernel method for smoothing point process data. Applied Statistics 34:138–147.

Dinkins, J. D., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014. Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. Condor 116:629–642.

Doherty, K. E., J. S. Evans, P. S. Coates, L. M. Juliusson, and B. C. Fedy. 2016. Importance of regional variation in conservation planning: a range-wide example of the greater sage-grouse. Ecosphere 7:e01462.

Doherty, K. E., D. E. Naugle, H. E. Copeland, A. Pocewicz, and J. M. Kiesecker. 2011. Energy development and conservation tradeoffs: systematic planning for greater sage-grouse in their eastern range. Pages 505–516 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and

conservation of a landscape species and its habitats. Studies in avian biology. Volume 38. University of California Press, Berkeley, California, USA.
Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.
Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.
Donnelly, J. P., J. D. Tack, K. E. Doherty, D. E. Naugle, B. W. Allred, and V. J. Dreitz. 2017. Extending conifer removal and landscape protection strategies from sage-grouse to songbirds, a range-wide assessment. Rangeland Ecology and Management 70:95–105.
Duvall, A. L., A. L. Metcalf, and P. S. Coates. 2017. Conserving the greater sage-grouse: a social-ecological systems case study from the California-Nevada region. Rangeland Ecology and Management 70:129–140.
Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273.
Eisenhart, K. S. 2004. Historic range of variability and stand development in piñon-juniper woodlands of western Colorado. Dissertation. University of Colorado, Boulder, Colorado, USA.
Evans, J. S., and M. A. Murphy. 2014. rfUtilities. R package version 1.0-0. http://CRAN.R-project.org/package=rfUtilities
Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using Random Forests. Pages 139–159 *in* C. A. Drew, Y. F. Wiersman, and F. Huettmann, editors. Predictive species and habitat modeling in landscape ecology: concepts and applications. Springer, New York, New York, USA.
Falkowski, M. J., J. S. Evans, D. E. Naugle, C. A. Hagen, S. A. Carleton, J. D. Maestas, A. H. Khalyani, A. J. Poznanovic, and A. J. Lawrence. 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management 70:15–24.
Fedy, B. C., et al. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management 76:1062–1071.
Fedy, B. C., et al. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using greater sage-grouse in Wyoming. Wildlife Monographs 190:1–39.
Freese, M. T. 2009. Linking greater sage-grouse habitat use and suitability across spatiotemporal scales in central Oregon. Thesis. Oregon State University, Corvallis, Oregon, USA.
Gamo, R. S., J. D. Carlisle, J. L. Beck, J. A. C. Bernard, and M. E. Herget. 2013. Greater sage-grouse in Wyoming: an umbrella species for sagebrush dependent wildlife. Wildlife Professional 7:56–59.
GSGRSC [Gunnison Sage-grouse Range-wide Steering Committee]. 2005. Gunnison sage-grouse range-wide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.
Guttery, M. R., D. K. Dahlgren, T. A. Messmer, J. W. Connelly, K. P. Reese, P. A. Terletzky, N. Burkepile, and D. N. Koons. 2013. Effects of landscape-scale environmental variation on greater sage-grouse chick survival. PLoS ONE 8:e65582.
Hastie, T., R. Tibshirani, and J. Friedman. 2008. The elements of statistical learning. Second edition. Springer-Verlag, New York, New York, USA.
Hijmans, R. J., and J. V. Etten. 2013. raster: geographic data analysis and modeling. R package version 2.1-25. http://CRAN.R-project.org/package=raster
Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.
Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.
Holmes, A. L., J. D. Maestas, and D. E. Naugle. 2017. Bird responses to removal of western juniper in sagebrush-steppe. Rangeland Ecology and Management 70:87–94.
Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.
Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997–2007. Studies in Avian Biology 38:407–450.
Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. Ecology and Evolution 3: 1539–1551.
Kormos, P. R., D. Marks, F. B. Pierson, C. J. Williams, S. P. Hardegree, S. Havens, A. Hedrick, J. D. Bates, and T. J. Svejcar. 2017. Ecosystem water availability in juniper versus sagebrush snow-dominated

rangelands. Rangeland Ecology and Management 70:116–128.

Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. R News 2:18–22.

Maestas, J. D., B. A. Roundy, and J. D. Bates. 2015. Conifer removal in the sagebrush steppe: the why, when, where, and how. Great Basin Fact Sheet Series, no. 4, Sage-Grouse Initiative, http://www.sagegrouseinitiative.com/category/science-tosolutions/great-basin-factsheet-series/

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Monographs on statistics and applied probability 37. Chapman & Hall, Boca Raton, Florida, USA.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions 12:288–297.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, and C. J. Williams. 2013. A review of fire effects on vegetation and soils in the Great Basin Region: response and ecological site characteristics. RMRS-GTR-308. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in avian biology. Volume 38. University of California Press, Berkeley, California, USA.

Miller, R. F., D. E. Naugle, J. D. Maestas, C. A. Hagen, and G. Hall. 2017. Special issue: targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. Rangeland Ecology and Management 70:1–8.

Miller, R. F., J. Ratchford, B. A. Roundy, R. J. Tausch, A. Hulet, and J. Chambers. 2014. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. Rangeland Ecology and Management 67:468–481.

Miller, R. F., R. J. Tausch, E. D. MacArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the intermountain west. RMRS-RP-69. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–261.

Naugle, D. 2011. Energy development and wildlife conservation in Western North America. Island Press, Washington, D.C., USA.

Naugle, D. E., K. E. Doherty, B. L. Walker, H. E. Copeland, M. J. Holloran, and J. D. Tack. 2011. Sage-grouse and cumulative impacts of energy development. Pages 55–70 *in* D. Naugle, editor. Energy development and wildlife conservation in Western North America. Island Press, Washington, D.C., USA.

Olden, J. D., J. J. Lawler, and N. L. Poff. 2008. Machine learning without tears: a primer for ecologists. Quarterly Review of Biology 83:171–193.

Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage grouse in southwestern Colorado. Southwestern Naturalist 46:323–331.

Patterson, R. L. 1952. The sage grouse in Wyoming. Wyoming Game and Fish Commission, Sage Books, Denver, Colorado, USA.

PECE [Policy for Evaluation of Conservation Efforts When Making Listing Decisions]. 2003. U.S. Federal Register, Rules and Regulations. Volume 68, No. 60:15100–15115.

Prochazka, B. G., P. S. Coates, M. A. Ricca, M. L. Casazza, K. B. Gustafson, and J. M. Hull. 2017. Encounters with pinyon-juniper influence riskier movements in greater sage-grouse across the Great Basin. Rangeland Ecology and Management 70:39–49.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate Relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. Rangeland Ecology and Management 62:203–222.

Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Egget. 2014. Understory cover responses to piñon–juniper treatments across tree dominance gradients in the Great Basin. Rangeland Ecology and Management 67:482–494.

Sandford, C. P., M. T. Kohl, T. A. Messmer, D. K. Dahlgren, A. Cook, and B. R. Wing. 2017. Greater sage-grouse resource selection drives reproductive fitness under a conifer removal strategy. Rangeland Ecology and Management 70:59–67.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski Jr., K. L. Pardieck, J. E. Fallon, and W. A. Link. 2017. The North American breeding bird survey, results and analysis 1966–2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Schroeder, M. A., et al. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Scott, J. M., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel. 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3:91–97.

Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017*a*. Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. Rangeland Ecology and Management 70:50–58.

Severson, J. P., C. A. Hagen, J. D. Tack, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017*b*. Better living through conifer removal: a demographic analysis of sage-grouse vital rates. PLoS ONE 12:e0174347.

Smith, J. T., J. S. Evans, B. H. Martin, S. Baruch-Mordo, J. M. Kiesecker, and D. E. Naugle. 2016. Reducing cultivation risk for at-risk species: predicting outcomes of conservation easements for sage-grouse. Biological Conservation 201:10–19.

Stephens, G. J., D. B. Johnston, J. L. Jonas, and M. W. Paschke. 2016. Understory responses to mechanical treatment of pinyon-juniper in northwestern Colorado. Rangeland Ecology and Management 69:351–359.

Suring, L. H., M. M. Rowland, and M. J. Wisdom. 2005. Identifying species of conservation concern. Pages 150–162 *in* M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. Habitat threats in the sagebrush ecosystem—methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

Tack, J. 2009. Sage-grouse and the human footprint: implications for conservation of small and declining populations. Thesis. University of Montana, Missoula, Montana, USA.

USFWS [U.S. Fish and Wildlife Service]. 2010. Endangered and threatened wildlife and plants; determination for the Gunnison sage-grouse as a threatened or endangered species. Federal Register 75:59803–59863.

USFWS [U.S. Fish and Wildlife Service]. 2015. Endangered and threatened wildlife and plants; withdrawal of the proposed rule to list the bi-state distinct populations segment of the greater sage-grouse and designate critical habitat. Federal Register 80:22827–22866.

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

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2144/full