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Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin

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Abstract. A recurrent challenge in the conservation of wide-ranging, imperiled species is understanding which habitats to protect and whether we are capable of restoring degraded landscapes. For Greater Sage-grouse (*Centrocercus urophasianus*), a species of conservation concern in the western United States, we approached this problem by developing multi-scale empirical models of occupancy in 211 randomly located plots within a 40 million ha portion of the species' range. We then used these models to predict sage-grouse habitat quality at 826 plots associated with 101 post-wildfire seeding projects implemented from 1990 to 2003. We also compared conditions at restoration sites to published habitat guidelines. Sage-grouse occupancy was positively related to plot- and landscape-level dwarf sagebrush (*Artemisia arbuscula*, *A. nova*, *A. tripartita*) and big sagebrush steppe prevalence, and negatively associated with non-native plants and human development. The predicted probability of sage-grouse occupancy at treated plots was low on average (0.09) and not substantially different from burned areas that had not been treated. Restoration sites with quality habitat tended to occur at higher elevation locations with low annual temperatures, high spring precipitation, and high plant diversity. Of 313 plots seeded after fire, none met all sagebrush guidelines for breeding habitats, but approximately 50% met understory guidelines, particularly for perennial grasses. This pattern was similar for summer habitat. Less than 2% of treated plots met winter habitat guidelines. Restoration actions did not increase the probability of burned areas meeting most guideline criteria. The probability of meeting guidelines was influenced by a latitudinal gradient, climate, and topography. Our results suggest that sage-grouse are relatively unlikely to use many burned areas within 20 years of fire, regardless of treatment. Understory habitat conditions are more likely to be adequate than overstory conditions, but in most climates, establishing forbs and reducing cheatgrass dominance is unlikely. Reestablishing sagebrush cover will require more than 20 years using past restoration methods. Given current fire frequencies and restoration capabilities, protection of landscapes containing a mix of dwarf sagebrush and big sagebrush steppe, minimal human development, and low non-native plant cover may provide the best opportunity for conservation of sage-grouse habitats.

Key words: *Artemisia tridentata*; *Centrocercus urophasianus*; Greater Sage-Grouse; habitat management guideline; landscape; occupancy model; rangeland restoration; sagebrush; western USA; wildfire.

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INTRODUCTION

Habitat loss is a major barrier to recovery of many imperiled species. Yet, protection of intact habitats and restoration of degraded areas, which can be paramount to persistence, is often extremely challenging for species that have broad distributions, large home ranges, and complex habitat requirements. One such species, the Greater Sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), is a candidate for federal protection under the Endangered Species Act (U.S. Fish and Wildlife Service 2010). Sage-grouse populations have been declining across their range due to loss and fragmentation of sagebrush (*Artemisia* spp.) habitat, which once dominated arid landscapes in the western United States (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). Degradation and loss of sagebrush habitat is the result of decades of sagebrush removal efforts, invasion of non-native plants, expansion of woodlands, altered fire regimes, and persistent human influences such as roads, agricultural development, improper grazing practices, oil and gas extraction, and expansion of urban areas (Suring et al. 2005, Knick et al. 2011).

Persistence of sage-grouse depends on protecting or carefully managing remaining habitat and restoring areas that have degraded habitat quality (Stiver et al. 2006, Connelly et al. 2011*b*). Putting this "protect what's left and fix what's broken" paradigm into practice, however, requires understanding the characteristics of high-quality habitat and knowing whether we are capable of restoring those characteristics within degraded areas. Sage-grouse habitat associations have been well documented at local or state-scales (Connelly et al. 2011*c*) and although published guidelines of sage-grouse habitat requirements exist (Connelly et al. 2000, Stiver et al. 2010), the generality of these local-scale habitat associations and guidelines is not well documented.

Sage-grouse have large home ranges and select habitats at multiple scales (Wisdom et al. 2005, Doherty et al. 2010, Tack et al. 2012). They use sagebrush plants for cover and forage within breeding, brood-rearing, and wintering habitats, which can be spatially separated over large areas with diverse climates (Connelly et al. 2000, Crawford et al. 2004, Hagen et al. 2007). Individuals may move 10–160 km between seasonal habitats resulting in annual ranges of 2,500 km^2 or more (Patterson 1952, Connelly et al. 1988, Connelly et al. 2011*a*). Sage-grouse are strongly associated with landscapes where sagebrush is abundant and they utilize landscapes selectively, depending on the season and the bird's life stage (Connelly et al. 2011*c*). The species is thought to need large patches (e.g., >4,000 ha) where sagebrush canopy cover exceeds 15–20% in each seasonal range (Connelly et al. 2004). Nests are usually placed in small patches of high sagebrush cover (>20%) within a matrix of moderate sagebrush cover (Sveum et al. 1998, Aldridge and Brigham 2002). The understory of breeding, brood rearing, and summer habitats usually contains tall native bunchgrasses and forbs (Connelly et al. 2000, Aldridge and Brigham 2002, Crawford et al. 2004, Hagen et al. 2007). Collectively, overstory and understory conditions determine the quality of habitat patches for sage-grouse (i.e., conditions appropriate for individual or population persistence; sensu Hall et al. 1997), but the landscape context (i.e., composition and configuration) of those patches is also important.

Sage-grouse occupy diverse areas within the Great Basin and populations likely experience regional differences in habitat availability and preference, as evidenced by variations in the findings of past habitat studies (see Connelly et al. 2011*c* for review). Analyzing data collected throughout this range holds promise for elucidating habitat associations that transcend regional variability in availability and preferential use by sage-grouse. Further, habitats available to and used by sage-grouse on an annual basis are dynamic because large-scale disturbances (e.g., wildfire) can quickly alter large proportions of a population's home range.

To mitigate or reverse the loss of preferred sage-grouse habitat, restoration actions are being implemented throughout the region (Wisdom et al. 2005, Davies et al. 2011). Whether these restoration actions are successful in restoring sagebrush habitats, and benefit sage-grouse, is still unknown (Knick et al. 2003, Pyke 2011). For example, thousands of hectares of current and former sage-grouse habitat are impacted by wildfire each year (Baker 2011, Miller et al. 2011) and large portions of these burns are subsequently treated with restoration or rehabilitation projects (hereafter "restoration"). At least 1,600 post-fire restoration treatments have been conducted since 1990 within the Great Basin according to U.S. Geological Survey Land Treatment Digital Library (LTDL) data (Appendix: Fig. A1; Pilliod and Welty 2013). These post-1990 treatments alone represent 2.2 million ha or 6% of the land area of the region. The majority of these post-fire land treatments are funded through the Department of Interior's Emergency Stabilization and Burned Area Rehabilitation (hereafter ESR) program and occur on Bureau of Land Management lands.

Although the ESR program was not specifically designed to restore sage-grouse habitat, wildfire burns as much as 1 million ha per year in the Great Basin and 97% of ESR treated hectares in the region are within historic sage-grouse habitat. Thus, it is important to know whether ESR treatments provide an ancillary benefit to sage-grouse. Further, these projects represent an important sage-grouse conservation opportunity for three reasons: (1) ESR projects constitute by far the largest number of hectares treated and dollars spent on restoration in the Great Basin (e.g., $60 million in 2007), (2) most individual ESR projects (73%) cite a need to improve wildlife or sage-grouse habitat as specific project objectives or concerns (these projects account for 1.6 million ha, or 81% of all hectares treated since 1990 according to LTDL data), and (3) studies have found that native plant restoration in degraded areas is significantly more successful when preceded by non-native plant removal via fire or other means (Davies 2010, McAdoo et al. 2013, Miller et al. 2013).

The goal of our study was to determine plot- and landscape-scale habitat associations of sage-grouse and to use this information to quantify the effects of post-fire restoration treatments on habitat quality throughout the Great Basin. To address this goal, we first used empirical data on sage-grouse occupancy in the region to address the following questions: (1) what are the plot-scale habitat predictors of sage-grouse occupancy; and (2) how does landscape context (i.e., proportion of landcover types within 5 km) combine with plot-level conditions to influence occupancy? We then used models developed from these analyses to predict the probability of sage-grouse occupancy in plots at 101 restoration projects throughout the Great Basin to answer the following questions: (3) what is the probability of sage-grouse occupancy in or around restoration sites; and (4) what restoration treatment and environmental characteristics are associated with a high predicted probability of sage-grouse occupancy? Finally, we used an independent assessment, based on published sage-grouse habitat guidelines, to address two additional questions: (5) what proportion of plots in or around restoration sites meet published guidelines for seasonal sage-grouse habitat; and (6) what restoration treatment and environmental characteristics are associated with plots that meet habitat guidelines?

MATERIALS AND METHODS

Data collection

This study was conducted in the sagebrush biome of the Great Basin, western United States (Fig. 1). This 39.6 million ha region spans parts of five states and is dominated by arid and semi-arid grasslands, shrublands, and piñon-juniper woodlands. Empirical data on plot-level sage-grouse occupancy and habitat conditions were collected in 2006 at 211 plots (Fig. 1) that were randomly located on public land throughout the study area (Hanser and Knick 2011). At each of these 180 × 180 m plots, we measured the percent cover and height of plant species and abiotic habitat components (e.g., plant litter, rock, soil) using line-point intercept (LPI) on two parallel 50-m lines separated by 20 m. We recorded species or abiotic group intercepts at 0.5 m increments along transect lines (200 sampling points per plot). We conducted pellet surveys to identify plots that were used by sage-grouse (Boyce 1981, Hanser et al. 2011). Observers walked three parallel 120-m transect lines, which were connected by two 36-m transects, and searched within 2 m of each transect line for a total search area of 864 m^2 per plot. If one or

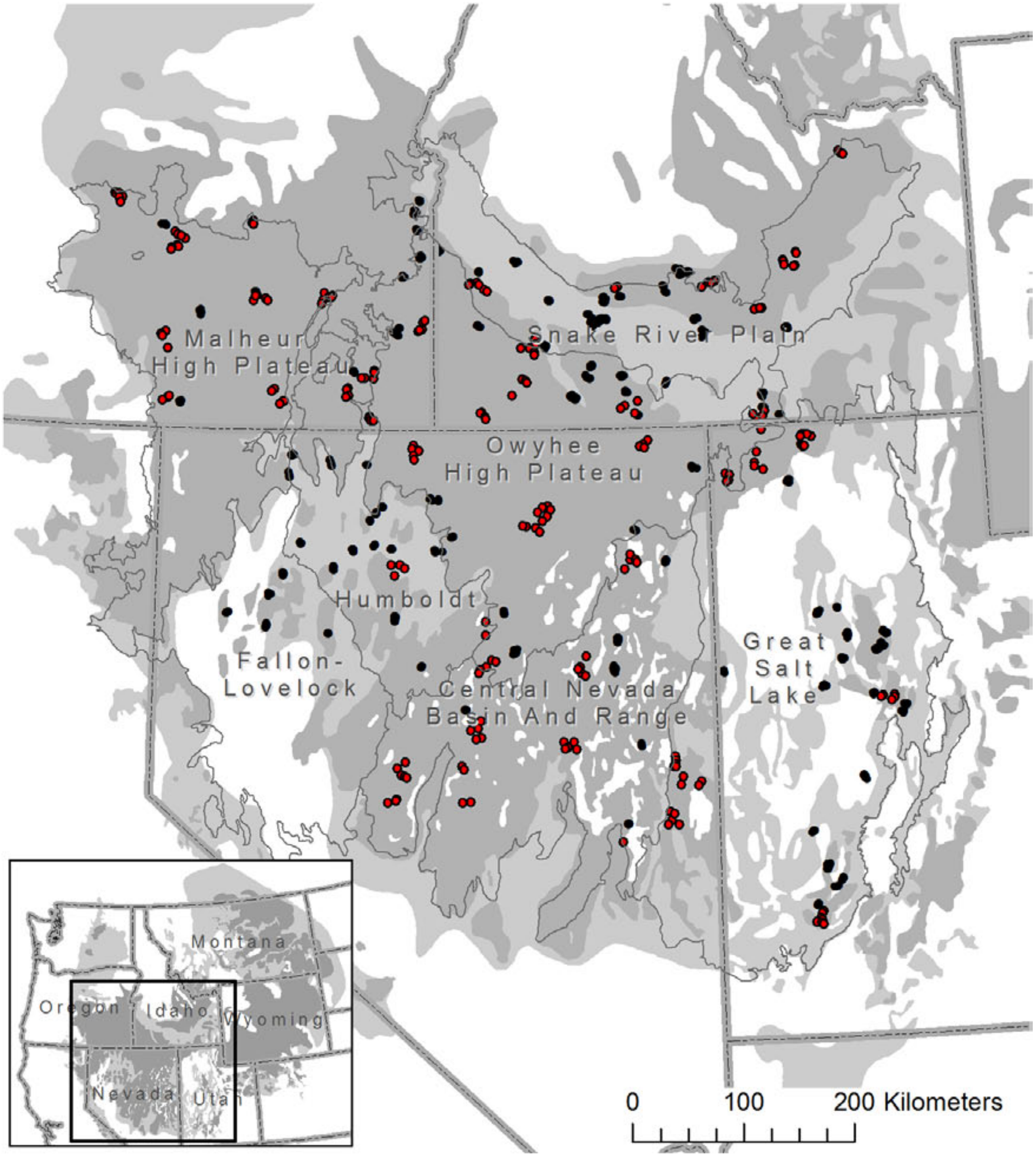

Fig. 1. Study area showing Major Land Resource Areas (MLRA; USDA Natural Resources Conservation Service) in the Great Basin, USA. Light and dark gray areas represent former and current Greater Sage-Grouse habitat, respectively (Schroeder et al. 2004). Black points indicate plots sampled at post-wildfire ESR projects that were implemented from 1990–2003, and red points represent plot locations where vegetation and sage-grouse occupancy surveys were conducted. The inset map shows the study area in relation to the distribution of Greater Sage-Grouse in western North America.

more sage-grouse pellets were found during this search, the plot was considered occupied by sage-grouse (Hanser and Knick 2011). This approach results in relatively high detection probabilities (sensu MacKenzie et al. 2006), especially when narrow search widths are used, regardless of vegetation cover (Dahlgren et al. 2006). Mean detection probability was >0.87 in all vegetation types where repeat sampling occurred (2–3 sampling events). Consequently, we used naïve estimates of occupancy in our analyses.

Vegetation composition data were also collected from 2010–2011 in plots ($n = 826$) associated with 101 Bureau of Land Management ESR sites throughout the Great Basin (Fig. 1; also see K. C. Knutson et al., *unpublished manuscript*, for a summary of treatment and environmental characteristics). Sites were selected using a random stratified design to gain inference for the population of all post-fire ESR projects conducted between 1990 and 2003 on loamy soil types (identified using SSURGO data and field verified) within seven of USDA Natural Resources Conservation Service's Major Land Resource Areas (MLRA; Fig. 1). Further, projects were in locations where only one wildfire and subsequent drill or aerial seeding rehabilitation project had occurred according to best available GIS data (LTDL data; Monitoring Trends in Burn Severity data [Eidenshink et al. 2007]). All sites received 203–304 mm precipitation per year (identified using GIS data; PRISM Climate Group 2011). After identifying ESR projects that met each of these criteria, we randomly selected projects until we obtained an equal number of all combinations of seeding type (i.e., Aerial, Drill, Mixed), MLRA, precipitation level, and years since treatment, where possible. ESR sites coincided with areas identified as current or former sage-grouse habitat (Fig. 1; Schroeder et al. 2004). At each site we sampled up to three (depending on availability of suitable treatment types and plot locations) randomly placed 1-ha plots in areas that: (1) had burned but were left untreated (Burned plots), (2) had burned and were subsequently seeded ("treated" plots include Aerial, Drill, or Mixed plots), (3) were 150–2000 m outside of the fire perimeter and were consequently unburned and untreated (Unburned plots). At each of the resulting plots ($n = 826$ total plots associated with ESR sites) in the above treatment categories (TREATMENT), we sampled vegetation cover and height using LPI on three 50-m transect lines arranged in a spoke design (Herrick et al. 2005) and recorded species intercepting pins at 1-m intervals for a total of 150 points per plot. We also quantified the density of cattle feces (COWDEN) within 2 m of each transect as a measure of plot-level cattle use (Jenkins and Manly 2008).

Landscape composition surrounding each plot was quantified using Landfire Existing Vegetation Type data (LANDFIRE 2009, 2011) within a 5-km radius (78.5 km^2). This distance corresponds to that recommended for the management of non-migratory sage-grouse populations (Connelly et al. 2000). Consequently, our results may provide a conservative view of the scale over which landscape composition influences migratory populations, as individuals from these populations may select habitats based on landcover over a greater area. Within each 5-km buffer, we calculated the proportion of 30-m pixels in each of 29 landcover types, which were reclassified from Landfire data (Appendix: Table A1). For empirical models developed using the 211 plots surveyed in 2006, we used Landfire Version 1.1.0 (2008 image date; LANDFIRE 2011), unless a portion of the 5-km buffer surrounding the plot burned between the time of field sampling in 2006 and the 2008 Landfire image date. In this case we used Landfire Version 1.0.0 (2001 image date; LANDFIRE 2009) because it would better represent the landscape surrounding these plots at the time of field sampling for sage-grouse occupancy. We used Landfire Version 1.1.0 for the 826 plots associated with ESR treatments.

Variable development

Using LPI data, we calculated canopy cover (%) and average height (cm) of each species or functional group (groups based on morphology, life history, and nativeness; for example, native perennial grass, non-native annual grass, shrub) to generate plot-level predictor variables. We also used LTDL data to produce variables representing treatment characteristics of each plot (Appendix: Table A2). Percent landcover (within 5 km) values for each landcover type were used as landscape-level predictor variables. To determine if certain combinations of landcover types were important predictors of sage-grouse occupancy, we performed a non-metric multi-dimensional scaling (NMS) ordination of landcover data for each plot using PC-ORD 6.09 software (McCune and Mefford 2011). This analysis was conducted as in Arkle and Pilliod (2010), but without transformations. We used the three axis scores generated for each plot (in addition to values of individual landcover variables) as potential predictors in subsequent analyses. This NMS analysis also provides evidence that landscapes sampled for sage-grouse occupancy and those sampled for restoration effectiveness are similar, suggesting that inferences drawn from occupancy rates at random sites are applicable to ESR sites (see Appendix: Fig. A2). PRISM data were used to generate climate variables for each plot (e.g., 30-year average monthly temperature and precipitation values). Using these climate variables, we took a similar NMS approach to generate ordination scores that described the combined monthly temperature and precipitation regime, or climate, of each plot. Digital elevation models were used to produce topographic variables. Appendix: Table A2 contains descriptions of all variables used in models and Appendix: Figs. A2–A4 provide additional information on NMS-derived variables.

Data analysis

We used non-parametric multiplicative regression (NPMR) in HyperNiche 2.22 (McCune and Mefford 2009) to determine how plot-level plant, landscape, environmental, and treatment variables interact in non-linear, multiplicative ways to influence response variables (McCune 2006). For each NPMR analysis, we used a local mean model (for binary response variables), or a local linear model (for quantitative response variables) and Gaussian weighting functions to conduct free search iterations of combinations of predictor variables (pre-screened to remove correlated predictors) and their tolerances (standard deviation of the Gaussian weighting function for each predictor) that maximized model fit and minimized overfitting. We controlled for overfitting through minimum average neighborhood size, minimum data-to-predictor ratio, and an improvement in fit criteria. Model fit for binary models was assessed with log likelihood ratios (logβ), which evaluate the improvement of each fitted model over the naïve model (i.e., the overall occupancy rate). For quantitative models, fit was assessed using cross-validated R^2 (xR^2). For each analysis, we identified the best fitting model as that which resulted in a $\geq$2.5% increase in fit (i.e., logβ or xR^2) over the next-best model with one less predictor variable. Since logβ and xR^2 are calculated using a "leave-one-out" cross validation, the training data error rate is expected to approximate that of validation data sets. Consequently, we did not withhold data for validation purposes. Instead, we used full datasets to maximize our ability to model relationships across large geographic and environmental gradients. Bootstrap resampling (each dataset resampled with replacement 100 times to generate 100 new datasets, each with $n - 1$ plots) was used to quantify the stability of models against the inclusion of particular plots in a given analysis by providing an average fit (±SE) between the final model and 100 resampled datasets.

In addition, we report the average neighborhood size (N^*; the average number of sample units contributing to the estimate of occupancy at each point on the modeled surface) and the results of a Monte Carlo randomization. This procedure tests the null hypothesis that the fit of the best model is no better than what could be obtained by chance using the same number of predictor variables in 100 free search iterations with randomly shuffled response variable values. Tolerance and sensitivity values are also given for each quantitative predictor variable. High tolerance values, relative to the range of the predictor, indicate that data points with a greater distance (in predictor space) from the point targeted for estimation contribute to the estimate of the response variable's value at the target point. Sensitivity, which generally ranges from 0 to 1, indicates the relative importance of each quantitative predictor in the model. A sensitivity of 1 indicates that, on average, changing the value of a predictor by ±5% of its range results in a 5% change in the estimate of the response variable, whereas a sensitivity of 0 indicates that changing the value of the predictor has no effect on the response variable.

Predictors of sage-grouse occupancy.—We developed a NPMR model to predict sage-grouse occupancy from plot-level vegetation data at the 211 randomly placed plots within the current range of the sage-grouse in the Great Basin ("Plot-level Model"). This model indicated the relative importance of vegetation predictors at the same spatial scale at which sage-grouse occupancy was assessed (Question 1).

We also developed a NPMR model of sage-grouse occupancy using potential predictor variables that describe both within-plot vegetation conditions (e.g., percent canopy cover or average height of a given species) and the landscape context surrounding each plot (e.g., percent landcover of a given type within a 5-km buffer) at the same 211 plots. This model ("Plot + Landscape Model") assessed the importance of patch and landscape scale habitat conditions to plot-level sage-grouse occupancy (Question 2).

Predicted probability of sage-grouse occupancy in post-fire restoration areas.—We applied the Plot-level Model (developed using the 211 randomly placed plots) to vegetation data from the 826 plots associated with ESR treatments to estimate the probability of sage-grouse occupancy based solely on within-plot vegetation characteristics (Question 3, in part). This indirect approach to quantifying sage-grouse habitat quality (i.e., a high probability of occupancy) reduced bias that could be created by sampling for sage-grouse exclusively in and around burned areas in need of ESR treatment. We repeated the above process using the Plot + Landscape Model to estimate the probability that plots at restoration sites would be occupied by sage-grouse on the basis of habitat variables at both plot and landscape scales. We used these model outputs to calculate the mean estimated probability of occupancy for plots in different treatment types (Question 3, in part).

Treatment and environmental predictors of sage-grouse occupancy.—To determine which restoration treatment and environmental characteristics are associated with a high predicted probability of sage-grouse occupancy, we developed an NPMR model using only treatment, species richness, cattle grazing, climate, topographic, and spatial variables (i.e., no vegetation cover or landcover variables) as potential predictors of estimated probability of sage-grouse occupancy in the 826 plots associated with ESR treatments ("Trt + Env Model"). The results of this model indicated which factors are associated with treatments that are likely to be occupied by sage-grouse (Question 4).

Meeting seasonal habitat guidelines.—Taking an alternative approach to quantifying habitat quality that explicitly recognizes the seasonal nature of sage-grouse habitat associations, we calculated the proportion of restoration plots that met the sage-grouse habitat management guidelines of Connelly et al. (2000) or Stiver et al. (2010) (Question 5; Table 3). We assigned each plot a binary value for each guideline criterion (e.g., percent canopy cover of sagebrush, or grass height) given for each season (i.e., breeding, brood-rearing, or winter), depending on whether the plot met the particular criterion. We also determined whether each plot met all understory (i.e., grass and forb), all overstory (i.e., sagebrush), and all combined criteria for a particular season. This allowed us to separate grass and forb components from sagebrush, which regenerates more slowly after wildfire (Wambolt et al. 2001). For each treatment (i.e., Aerial, Drill, Mixed, Burned, Unburned) we calculated the proportion of plots that met each guideline criterion for each season. Winter habitat guidelines are based solely on sagebrush canopy cover and height exposed above snow. Since we did not have snow depth data for each plot, we could not determine whether individual plots met winter habitat guidelines. However, if a given plot did not have at least 10% sagebrush cover or an average sagebrush height of at least 25 cm, the plot could not possibly meet winter habitat guidelines, even in the absence of snow cover. Thus, for winter habitat, we reported the maximum proportion of plots that potentially met winter habitat guidelines, assuming no snow cover. Appreciable snow cover would result in fewer plots meeting winter guideline criteria than suggested by our results.

Treatment and environmental predictors of meeting guidelines.—For each guideline criterion (Table 3), we developed an NPMR model using treatment, climate, topographic, and spatial location variables as potential predictors of whether plots met the guideline criterion (i.e., binary response). These models indicated which factors were associated with plots that had a high probability of meeting established habitat guidelines for each seasonal habitat type (Question 6).

RESULTS

Plot-scale predictors of sage-grouse occupancy

Sage-grouse occupancy (SGOCC) at the 1-ha plot level was best predicted by a non-linear interaction between dwarf sagebrush (*A. arbuscula, A. nova, A. tripartita*) cover, Wyoming big

Table 1. NPMR results for two models (Plot-level and Plot + Landscape) predicting sage-grouse occupancy (SGOCC) in randomly located 1-ha plots.

Response variable	*n* plots	logβ	Bootstrap results	*N**†	Predictor‡	Sensitivity	Tolerance
Plot-level							
SGOCC	211	9.4	10.7 ± 2.1	13.7	(∧) DWARFSAGEcov	0.65	2.45 (5%)
					(±) WYSAGEcov	0.16	6.23 (15%)
					(−) CHEATcov	0.13	18.8 (20%)
					(∧) WYSAGEht	0.10	35.4 (35%)
					(+) GRASScov	0.06	33.8 (50%)
Plot + Landscape							
SGOCC	211	12.2	14.6 ± 2.6	17.2	(−) EPGF5km	0.49	1.9 (5%)
					(∧) DWARFSAGEcov	0.44	4.9 (10%)
					(−) DEVELOPED5km	0.44	0.72 (10%)
					(−) LNDSCP3	0.37	0.38 (15%)
					(+) RIPARIAN5km	0.12	1.8 (20%)

Notes: Plot-level Model used only variables collected at each plot as potential predictors, whereas the Plot + Landscape Model used plot-level variables and variables representing the prevalence of landcover types within a 5 km radius of each plot as potential predictors. Bootstrap results are given as mean logβ ± SE. Variable names are defined in Appendix: Table A2.

† *N**, the average neighborhood size, is the average number of sample units contributing to the estimate of occupancy at each point on the modeled surface.

‡ Symbols in parentheses indicate the *general* direction of the relationship between each predictor and response variable: "+" indicates positive, "−" indicates negative, "±" indicates both negative and positive, and "∧" indicates a Gaussian relationship.

sagebrush (*A. tridentata wyomingensis*) cover and height, native grass cover, and cheatgrass cover ($p < 0.0001$; Table 1, Fig. 2). The logβ of this model was 13% better than that of the best four-predictor model. Based on bootstrap results, the Plot-level Model was robust against which plots were included in the dataset (logβ = 10.7 ± 2.1 [mean ± SE]). The probability of sage-grouse occupancy reached a maximum of 0.92 in areas with 10–20% dwarf sagebrush canopy cover (DWARFSAGEcov) combined with 10–15% Wyoming big sagebrush canopy cover (WYSAGEcov), 0–5% cheatgrass canopy cover (CHEATcov), 10–40% native grass canopy cover (GRASScov), and, intermediate Wyoming big sagebrush height (WYSAGEht; 40–55 cm average height). Plots with >10% CHEATcov, 0% DWARFSAGEcov, 0–5% WYSAGEcov, 0–5% GRASScov, and very short or very tall WYSAGEht were the least likely to be occupied. Plots with no shrub cover at all were occupied 33% of the time when they had high GRASScov and low CHEATcov. Based on sensitivity values, DWARFSAGEcov was by far the best predictor of occupancy (Table 1). Plots where any DWARFSAGEcov was detected had an observed occupancy rate of 0.51, whereas plots where WYSAGEcov was detected had an observed occupancy rate of 0.27 (see Appendix:

Table 2. NPMR results for two Trt + Env models predicting probability of occupancy (as estimated from empirical models) in plots associated with restoration treatments.

Response variable	*n* plots	xR^2	Bootstrap results	*N**	Predictor	Sensitivity	Tolerance
pSGPLOT	773	0.50	0.49 ± 0.01	41.5	(+) PLANTDIV	0.65	0.18 (20%)
					(+) PLANTEVEN	0.62	0.9 (10%)
					(−) DEGMONTH	0.39	2.5 (5%)
					(+) PLANTRICH	0.22	11.3 (45%)
					(−) COWDEN	0.14	0.22 (75%)
					(±) PROJYR	0.08	9.1 (70%)
pSGPLOT + LS	731	0.67	0.66 ± 0.003	41.5	(±) PROJYR	0.94	0.65 (5%)
					(+) ELEV	0.30	177.6 (15%)
					(+) CLIMATE1	0.25	0.79 (25%)
					(−) COWDEN	0.20	0.1 (35%)
					(+) PLANTRICH	0.18	16.3 (65%)
					(−) CLIMATE2	0.18	1.17 (40%)

Notes: Some of the 826 plots associated with restoration sites could not be used in Trt + Env model development because they occupied regions of predictor space with too few data points to derive reliable estimates of probability of sage-grouse occupancy, the response variable in Trt + Env models. Bootstrap results are given as mean xR^2 ± SE. Symbols are defined in Table 1. Variable names are defined in Appendix: Table A2.

Table 3. Proportion of 826 plots associated with ESR treatments meeting seasonal habitat guidelines (Connelly et al. 2000, Stiver et al. 2010) by treatment type.

Season	Criterion	Aerial (n = 90)	Drill (n = 120)	Mixed (n = 103)	Burned (n = 226)	Unburned (n = 287)
Breeding	Sagebrush cover (15–25%)	0	0.01	0.02	0	0.39
	Sagebrush height (30–80 cm)	0.09	0.06	0.06	0.09	0.74
	Perennial grass and forb height (≥18 cm)	0.56	0.58	0.71	0.46	0.49
	Perennial grass and forb cover (≥15%)†	0.72	0.64	0.81	0.62	0.66
	Perennial grass cover (>10%)†	0.76	0.65	0.92	0.65	0.68
	Forb cover (≥5%)†	0.30	0.20	0.41	0.33	0.38
	All understory (Connelly)	0.47	0.47	0.66	0.36	0.40
	All understory (Stiver)	0.19	0.10	0.32	0.17	0.18
	All overstory	0	0	0	0	0.32
	All (Connelly)	0	0	0	0	0.15
	All (Stiver)	0	0	0	0	0.08
Brood-rearing	Sagebrush cover (10–25%)	0.01	0.02	0.02	0.02	0.49
	Sagebrush height (40–80 cm)	0.09	0.04	0.02	0.06	0.51
	Perennial grass and forb cover (≥ 15%)	0.72	0.64	0.81	0.62	0.66
	All overstory	0.01	0.01	0	0.01	0.29
	All	0.01	0.01	0	0.01	0.21
Winter	Sagebrush cover (10–30% exposed above snow)	<0.02	<0.02	<0.02	<0.02	<0.86
	Sagebrush height (25–35 cm exposed above snow)	<0.09	<0.07	<0.08	<0.10	<0.85
	All	<0.02	<0.02	<0.01	<0.01	<0.76

Note: For winter habitat, we report the maximum proportion of plots that *potentially* met winter habitat guidelines in the absence of snow cover (see *Data analysis* for explanation).

† Criteria differ between the two guideline sources.

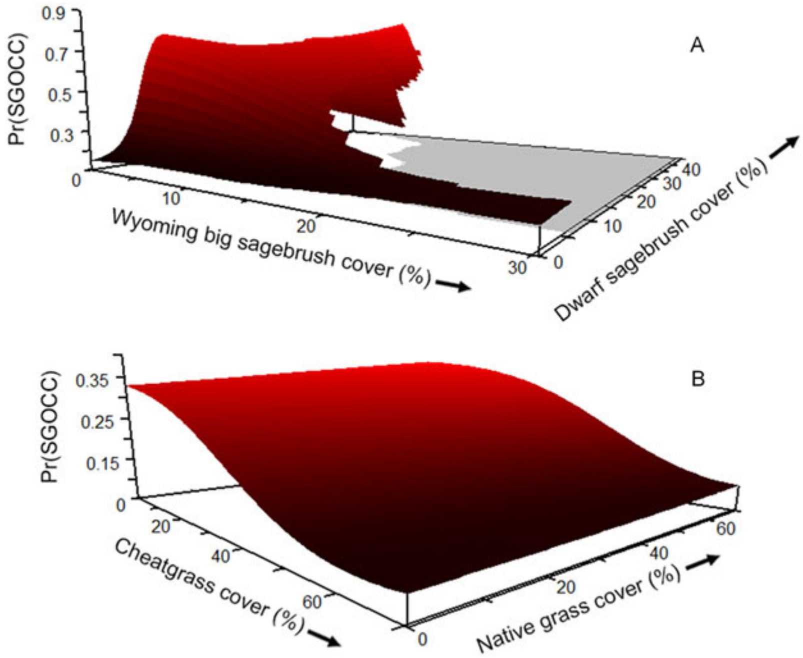

Fig. 2. NPMR modeled relationship between probability of sage-grouse occupancy (vertical axes) and (A) percent canopy cover of Wyoming big sagebrush and dwarf sagebrush and (B) percent canopy cover of cheatgrass and native grass. Gray areas indicate regions of predictor space with too few plots for reliable estimates to be made. Relationships are derived from the "Plot-level Model" created using 211 plots in the Great Basin. Note different scales of vertical axes.

Table A3 for occupancy rates by *Artemisia* species presence). However, occupancy was more likely in plots containing a mixture of dwarf and Wyoming big sagebrush. Predicted occupancy was moderately sensitive to low values of CHEATcov, but declined dramatically when CHEATcov exceeded approximately 10%. Occupancy estimates were less sensitive to WYSAGEht and GRASScov. See Appendix: Fig. A5 for additional information on this model.

Plot- and landscape-scale predictors of sage-grouse occupancy

Combining variables representing within-plot vegetation conditions with those representing the landscape-context (within 5 km) of each plot resulted in increased model fit over the Plot-level Model ($p < 0.0001$; Table 1, Fig. 3). Only one plot-level predictor variable, DWARFSAGEcov, was included in the Plot + Landscape Model, which also contained four landscape variables. The landcover of non-native perennial grass and forbs (EPGF5km) was the most influential predictor of SGOCC, followed by the landscape cover of human developed areas (DEVELOPED5km) and the plot-level DWARFSAGEcov. LNDSCP3, a synthetic variable, was an important predictor of SGOCC in the final model (Table 1, Fig. 3) and was the best single-variable predictor of occupancy ($\log\beta = 6.2$) during the model fitting process. LNDSCP3 represents landscapes containing a mixture of dwarf sagebrush (DWARFSAGE5km) and big sagebrush steppe (BSAGESTEPPE5km) (but not big sagebrush shrubland, BSAGESHRUB5km) landcover at the negative end of the gradient (both sagebrush landcover types have >10% shrub cover, but sagebrush shrubland has <25% herbaceous cover, while sagebrush steppe has >25%). At the positive end of the LNDSCP3 gradient, landscapes have a high proportion of non-native annual grass, agriculture, conifer, juniper, greasewood, and salt desert shrubland landcover (see Appendix: Fig. A3 for details on LNDSCP3). Riparian landcover (RIPARIAN5km) was associated with increased probability of occupancy, but occupancy probabilities were least sensitive to this predictor. The logβ of this model was 8.1% better than that of the best four-predictor model. Based on bootstrap results, the Plot + Landscape Model was unaffected by which plots were included in the dataset ($\log\beta = 14.6 \pm 2.6$). The probability of sage-grouse occupancy reached a maximum of 0.72 in areas with <0.5% exotic perennial grass and forb landcover (EPGF5km), 10–20% plot-level canopy cover of dwarf sagebrush species, 0–1% human development landcover, 0.2–2.8% riparian landcover, and in landscapes with low values of LNDSCP3 (i.e., 50–70% combined dwarf sagebrush and sagebrush steppe landcover and minimal non-native annual grass, agricultural, conifer, juniper, greasewood, or salt desert shrubland landcover). See Appendix: Fig. A6 for additional information on this model.

Predicted probability of sage-grouse occupancy in restoration areas

Based on plot-level vegetation characteristics alone, the predicted probability of sage-grouse occupancy at restoration plots (pSGPLOT) was low (treated plot average = 0.09) and was not substantially different from areas that were burned and untreated. However, Mixed plots were more likely to be occupied (average pSGPLOT = 0. 12) than Burned plots and certain Aerial and Drill plots had relatively high probabilities of occupancy (Fig. 4). Plots in unburned-untreated areas surrounding ESR sites had higher pSGPLOT values than other plot types ($F_{4,768} = 37.4$, $r^2 = 0.16$, $p < 0.0001$). Some of the 826 plots associated with restoration sites could not be assigned a predicted probability of occupancy (pSGPLOT or pSGPLOT+LS) value because they occupied regions of predictor space with too few data points to derive a reliable estimate of occupancy probability. These plots were omitted from subsequent analyses where these values were necessary.

After accounting for landscape context, the predicted probability of sage-grouse occupancy in treated plots (pSGPLOT+LS) averaged 0.09 (maximum = 0.41) and was not significantly different from that of burned plots (Fig. 4). Plots in unburned areas had a significantly higher average probability of occupancy (pSGPLOT+LS) than treated (Aerial, Drill, Mixed) plots and Burned plots ($F_{4,726} = 5.35$, $r^2 = 0.03$, $p = 0.0003$).

Treatment and environmental predictors of sage-grouse occupancy

The probability of sage-grouse occupancy in plots at ESR sites (pSGPLOT) was best predicted

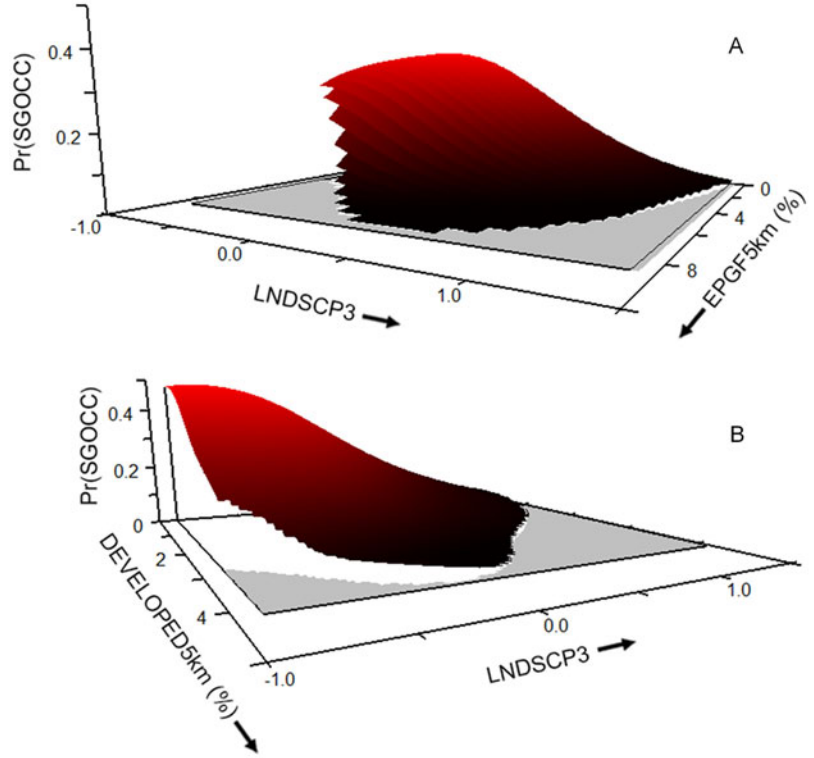

Fig. 3. NPMR modeled relationship between plot-level probability of sage-grouse occupancy (vertical axes) and (A) LNDSCP3 and percent landcover of non-native perennial grass and forb within 5 km of plots (EPGF5km) and (B) LNDSCP3 and percent human developed landcover within 5 km of plots (DEVELOPED5km). Low values of LNDSCP3 represent landscapes containing high combined big sagebrush steppe and dwarf sagebrush landcover types. High values of LNDSCP3 represent landscapes containing high proportions of non-native annual grass, agriculture, conifer, and juniper landcover types (see Appendix: Fig. A3 for details). Gray areas are as in Fig. 2. Relationships are derived from the "Plot + Landscape Model" created using 211 plots in the Great Basin.

by variables relating to plant species richness and diversity, annual duration of high temperatures (DEGMONTH), density of cattle feces (COWDEN), and the year of ESR project implementation (PROJYR; $p < 0.0001$; Table 2). The xR^2 of this model was 3% better than that of the best five-predictor model. Based on bootstrap results, this model was not sensitive to which plots were included in the dataset ($xR^2 = 0.49 \pm 0.01$ [mean ± SE]). Treatment characteristics (including TREATMENT) of plots were not important predictors of pSGPLOT, with the exception of PROJYR, which indicated that projects implemented in certain years (i.e., no general increase or decrease through time) were more likely to result in high quality sage-grouse habitat.

After accounting for landscape context, restoration plots with a high predicted probability of sage-grouse occupancy (pSGPLOT+LS) tended to be in similar locations as observed above ($p < 0.0001$; Table 2), with additional predictive capacity provided by elevation (ELEV) and two ordination derived climate variables. CLIMATE1 represented a spring/fall temperature and spring precipitation gradient and CLIMATE2 represented a winter versus monsoonal precipitation gradient (Appendix: Fig. A4). Treatment characteristics were not important predictors of plots with high pSGPLOT+LS, except for PROJYR, which exhibited the same pattern as described above. The xR^2 of this model was 3% better than that of the best five-predictor model. Based on bootstrap results, this model was not dependent on which plots were included in the dataset ($xR^2 = 0.66 \pm 0.003$).

These analyses indicate that plots with high

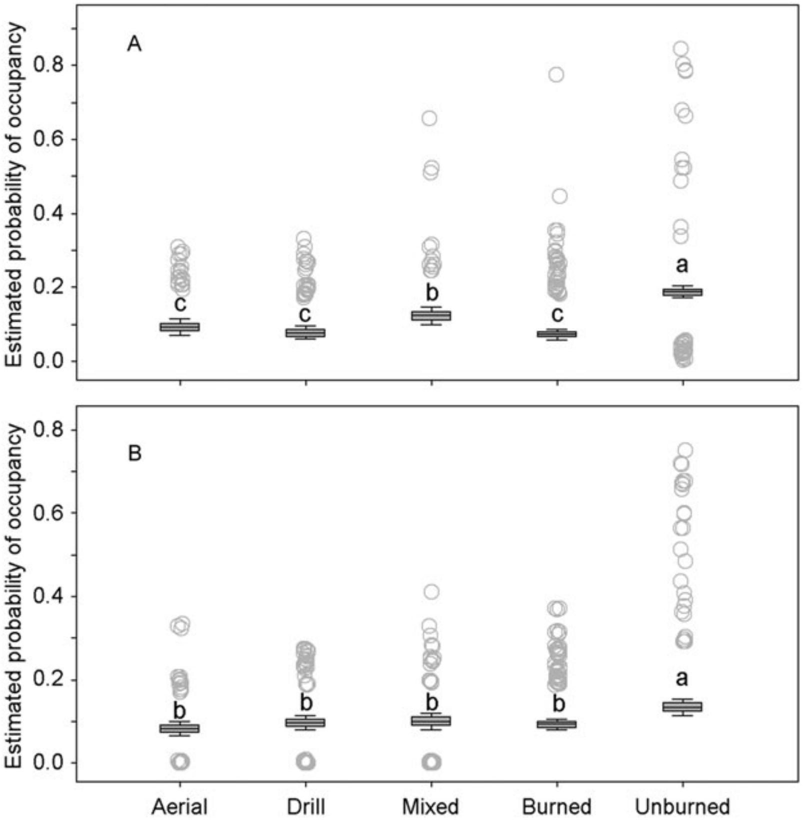

Fig. 4. Estimated probability of sage-grouse occupancy in ESR plots based on predictions from (A) Plot-level Model, and (B) Plot + Landscape Model. Boxes indicate ±1 SE and bars indicate ±2 SE of mean. To show the range of estimated values for each group, open circles indicate plots greater than 1 SD from mean. For each series, groups with different letters are significantly different according to Duncan's Multiple Range Test.

predicted probabilities of occupancy tend to occur in areas with lower annual temperatures (primarily cooler spring and fall temperatures), greater April–June precipitation (less reliance on summer monsoonal precipitation), greater total precipitation, higher elevation, higher plant species richness, lower cattle use, and at ESR projects conducted in years with greater post-seeding precipitation (Table 2).

Meeting seasonal habitat guidelines

None of the 313 treated plots met breeding season habitat guidelines for sagebrush (cover and height combined), but approximately 50% of treated plots met Connelly and other's (2000) breeding season guidelines for understory species, particularly for cover (Table 3). Fewer treated plots met forb canopy cover guidelines of Stiver et al. (2010), with Aerial and Drill plots meeting forb canopy guidelines less frequently than Burned plots. Only 8–15% of Unburned plots ($n = 287$) met all breeding season habitat guidelines. Brood-rearing habitat guidelines for sagebrush overstory were met by 2% of treated plots, but 68% met understory guidelines. Unburned plots met all brood-rearing habitat guideline criteria more frequently (21% of plots) than they met breeding season criteria. Less than 2% of treated plots potentially met winter habitat guidelines, even when zero cm snow depth was assumed. The proportion of treated plots and Burned plots meeting seasonal habitat guidelines did not differ substantially for most criteria examined.

Treatment and environmental predictors of meeting guidelines

The probability of meeting breeding season or brood-rearing habitat guidelines was influenced by a latitudinal gradient, climate conditions, and topographic variables (Appendix: Tables A4–A9). Variables related to treatment characteristics (e.g., TREATMENT or plant species seeded) were generally not significant predictors of whether plots met any particular guideline criteria, except PROJYR, which indicated that seedings implemented prior to certain high precipitation years were more likely to meet guidelines. Plots that were most likely to meet some or all guideline criteria for a given season tended to be farther north (except for the Snake River Plain MLRA, where plots were substantially less likely to meet guidelines than plots to the north or south), have specific climate regimes (e.g., more late winter to early spring precipitation, and less summer precipitation), and lower values of DEGMONTH and PDIR, two variables related to the amount of time each year with warm temperatures. Plots with an optimal set of these conditions had a relatively high (>0.93) probability of meeting understory habitat guidelines, whereas plots in the southern Great Basin that were at lower elevations and in warmer, drier locations had the lowest probability of meeting these guidelines.

DISCUSSION

Plot-scale predictors of sage-grouse occupancy

Sage-grouse are commonly perceived as being associated exclusively with big sagebrush dominated habitats, yet few empirical studies have examined which factors predict sage-grouse occupancy throughout the range of conditions present in a given region (Aldridge et al. 2008, Wisdom et al. 2011, Knick et al. 2013). Across the Great Basin, we found that recent, plot-level sage-grouse occupancy (based on pellet presence) was better predicted by plot-level canopy cover of dwarf sagebrush species (e.g., *A. arbuscula*, *A. nova*, *A. tripartita*) than by big sagebrush cover. However, sage-grouse occupancy was most likely in plots that contained both dwarf sagebrush and at least some big sagebrush.

Given the findings of recent research, this association with dwarf sagebrush should not be particularly surprising and may be attributed to at least two factors. First, contemporary studies spanning four western states and multiple seasons of sage-grouse habitat use have found that sage-grouse use dwarf sagebrush habitats disproportionately to their availability or more frequently than big sagebrush sites (Erickson et al. 2009, Atamian et al. 2010, Bruce et al. 2011, Hagen et al. 2011, Frye et al. 2013). This is likely because the leaves of dwarf sagebrush species have significantly lower monoterpene concentrations than those of Wyoming sagebrush (Frye et al. 2013). Monoterpenes are plant secondary metabolites that have deleterious effects on herbivores. In one study, Wyoming big sagebrush was browsed less than expected based on availability despite having higher crude protein levels and providing greater escape cover (Frye et al. 2013). Thus, it is likely that areas containing a mixture of dwarf and big sagebrush are desirable because dwarf sagebrush species provide a less toxic and metabolically costly food source, while the larger statured Wyoming big sagebrush provides structural cover and a secondary food source. Second, dwarf sagebrush species are often associated with higher elevation sites with rocky soils or with wind-swept ridges, while adjacent stands of higher elevation big sagebrush often have relatively high forb and native grass cover. These locations may provide quality habitat with low susceptibility to invasion by non-native plant species because of climate and soil constraints on establishment. Alternatively, because of fewer human impacts, these habitats may simply be the "best of what's left" for sage-grouse. For example, habitat associations of other organisms have shifted substantially in altered landscapes, where some species can persist by using marginal quality, isolated (e.g., from non-native species), or novel habitats (e.g., Pilliod et al. 2013). It is unclear what the plot-level habitat associations of sage-grouse were before European settlement, but our findings and those of other recent studies suggest that, currently, mixtures of dwarf and big sagebrush habitats are most likely to be occupied within the Great Basin.

We found a strong negative association between sage-grouse occupancy and cheatgrass, even at relatively low cover values. This relationship could be related to increased continuity of herbaceous cover following cheatgrass invasion (Klemmedson and Smith 1964, Billings 1990), a reduction of desirable, native herbaceous vegetation components (Harris 1967, Chambers et al. 2007), or increased likelihood that the surrounding landscape is also dominated by cheatgrass. Other studies have suggested that negative effects of cheatgrass on sage-grouse are primarily indirect and are mediated through impacts on native plant species (Miller et al. 2011). However, cheatgrass cover has been shown to increase as distances between perennial plants increases (Reisner et al. 2013). Consequently, areas with high cheatgrass cover may simply lack adequate hiding cover generated by perennial plants. Although our results do not provide a mechanism for this negative association, they do highlight the important influence of non-native annual grasses on sage-grouse habitat quality in the region.

Native perennial grass cover and Wyoming big sagebrush height were important predictors of occupancy, but sage-grouse were less sensitive to these variables than to dwarf sagebrush and cheatgrass cover. If native grass cover and big sagebrush height were near optimal values, occupancy rates tended to be relatively high, but if not, occupancy was still likely if there was little cheatgrass and a mix of dwarf and big sagebrush present. We also note that optimal model-derived values for sagebrush cover, sagebrush height, and perennial grass cover were mostly similar to values given in sage-grouse habitat management guidelines (Connelly et al. 2000, Stiver et al. 2010).

Plot- and landscape-scale predictors of sage-grouse occupancy

Landscape context had a strong influence on plot-level sage-grouse occupancy. With the exception of dwarf sagebrush canopy cover, plot-level vegetation variables were unimportant predictors of occupancy relative to landscape-level variables. This was not surprising given the large home ranges, migratory patterns, and discrete seasonal and life stage habitat requirements of this species (Connelly et al. 2004, 2011*c*). Sage-grouse tended to occupy plots in landscapes dominated (50–70% landcover) by a mixture of dwarf sagebrush landcover and big sagebrush steppe landcover. This finding is congruent with our plot-level findings and other studies that have shown selection for this type of habitat (Erickson et al. 2009, Atamian et al. 2010, Frye et al. 2013). Availability of even a small amount of riparian landcover (0.2–2.8% landcover within 5 km) increased the probability of sage-grouse occupancy, but occupancy was still likely in landscapes without this habitat element if other conditions were favorable. Riparian habitats are particularly important as sources of forbs and insects consumed during brood-rearing (Crawford et al. 2004, Connelly et al. 2011*c*).

Sage-grouse occupancy was strongly negatively affected by relatively small amounts (ca. 1%) of non-native perennial grass and forb landcover within 5 km. The negative association with planted non-native species [e.g., crested wheatgrass (*Agropyron cristatum* Gaertn.) which was common in ESR seed mixes] may be due to properties of the plants, the plants' effects on surrounding habitat conditions, or the confounding influence of high levels of disturbance, the undesirable perennial forb component of this landcover type, and low shrub cover in these landscapes. Since there was not an important negative effect of these species at the plot-level, further investigation of sage-grouse associations with non-native perennial grass and forb species is needed.

Our finding of strong, negative effects of even modest amounts of human development on sage-grouse occupancy is consistent with another recent study, which found that active lek sites tend to occur in landscapes containing less than 3% human development (Knick et al. 2013). We found that even in the highest quality landscapes (i.e., low values of LNDSCP3), sage-grouse were half as likely to occupy plots when just 2.5% of the surrounding landscape (within 5 km) was developed, as compared to similar landscapes with no human development. Non-native annual grass, juniper, other conifer, and agricultural landcover also negatively affected sage-grouse occupancy when these landcover types accounted for 5–18% of the landscape around a given plot. These findings, which largely concur with our plot-level results, suggest that certain landscapes are more likely to support sage-grouse and that habitat protection or restoration efforts specifically targeting sage-grouse could focus on these landscapes and on adjacent areas connecting them.

Predicted probability of sage-grouse occupancy in restoration plots

Based on plot-level vegetation characteristics alone (i.e., not accounting for the surrounding landscape, connectivity, or proximity to extant populations), sage-grouse are relatively unlikely to use many burned areas of the Great Basin for at least 20 years, regardless of whether post-fire seeding treatments were implemented. This low habitat quality was not simply due to a lack of shrub cover, because shrubless plots (i.e., those used for empirical modeling) were occupied up to 33% of the time when understory conditions were favorable. On average, aerial seeded and drill seeded areas were no more likely to support sage-grouse occupancy than burned-untreated areas, indicating that seeding techniques or seed sources used during this time period were generally ineffective at improving post-fire habitat conditions for sage-grouse within two decades. However, some treated plots were predicted to be occupied 65% of the time, and plots that received both drill and aerial (i.e., Mixed) seeding had significantly higher estimated habitat quality than burned-untreated plots. This success, however, appears to be more related to the conditions present in locations where these treatments tend to be implemented and less related to a positive effect of combining treatment types (these points are discussed further in the following section). Unburned-untreated areas had a significantly higher average probability of occupancy than the four other treatment types, but at 0.19, this value was 10% lower than the naïve occupancy rate for plots used to develop empirical models, suggesting degradation prior to wildfire, or that unburned plots were indirectly impacted by their proximity (150–2000 m) to the disturbed areas.

Accounting for landscape characteristics in estimates of sage-grouse occupancy probability resulted in lower maxima (maximum = 0.41) and lower average values for unburned and mixed treatment plots, but did not decrease the average values for aerial seeded, drill seeded, or burned-untreated plots. This indicates that, on average, the habitat quality of the latter three plot types is approximately equally limited by plot (i.e., native species regeneration or treatment success) and landscape conditions, whereas habitat quality in mixed-treatment and unburned areas is more limited by landscape composition. Treatment technique limitations are currently being addressed through using seeds with local genotypes, low- or no-till rangeland drills, novel approaches for seed application (e.g., using imprinters for seeds that should not be buried, coating seeds prior to sowing) (Monsen et al. 2004, Shaw et al. 2005, Madsen et al. 2012*a*, Madsen et al. 2012*b*), and planting seedlings (Dettweiler-Robinson et al. 2013, McAdoo et al. 2013). Landscape limitations on sage-grouse occupancy were not unexpected since ESR sites are, by definition, in need of restoration action and they are often imbedded in disturbance-prone locations. However, as restoration actions proceed in the Great Basin, it is important to consider that a high quality plot embedded in a low quality landscape is still unlikely to be occupied by sage-grouse. Consequently, if sage-grouse habitat restoration is a primary goal, land managers may want to evaluate the probability of restoration success at a given site *and* the quality of the surrounding landscape (see previous section), potentially focusing restoration dollars on relatively intact landscapes (Meinke et al. 2009), or implementing a triage-type strategy (Pyke 2011).

Treatment and environmental predictors of sage-grouse occupancy

ESR sites were more likely to have high-quality (i.e., high predicted probability of occupancy) sage-grouse habitat in higher elevation areas with particular climate regimes, high plant species richness, and low cattle grazing pressure regardless of how, or if, treatments were implemented. The year of project implementation was the only treatment characteristic that was an important predictor of estimated sage-grouse occupancy. However, there was no evidence that older projects had higher quality habitat as they matured, nor was there evidence that more recent projects were more successful due to advances in restoration techniques. Instead, projects implemented in certain years, particularly years preceding cool, wet growing seasons (i.e., spring-early summer), were more likely to result in high quality sage-grouse habitat.

In addition to post-treatment weather, climate plays a clear role in treatment effectiveness. Based on our sample, restoration practitioners can expect greater effectiveness in areas of the Great Basin with lower annual temperatures (especially cooler springs and falls), greater April-June (non-monsoonal) precipitation, and greater total precipitation. Sites at higher elevations often have these climate characteristics (even when surrounding lowlands have less-optimal conditions), which can result in greater native grass and forb abundance through increased resource (i.e., water) availability and higher native plant species richness because of lower susceptibility to dominance by non-native plant species. Whether higher plant diversity and lower cattle grazing pressure are causally related to, or simply correlated with, sage-grouse habitat quality is unknown, but ESR sites with these characteristics were more likely to provide quality sage-grouse habitat than were species-poor, heavily grazed restoration areas.

Meeting seasonal habitat guidelines

Within 20 years of treatment, none of the treated plots met breeding season overstory (sagebrush) guidelines, few (2 of 313) met brood-rearing overstory guidelines, and only 2% potentially met winter overstory guidelines. *Artemisia* spp. can be slow to reestablish dominance following disturbance, especially when seed sources are distant (Wambolt et al. 2001, Hemstrom et al. 2002, Lesica et al. 2007, Beck et al. 2009). However, despite up to 20 years since burning and *Artemisia* spp. being sown at 62% of our sites, *Artemisia* spp. struggled to reestablish at all, let alone to reestablish dominance (also see K. C. Knutson et al., *unpublished manuscript*). For example, *Artemisia* spp. were not detected at all in 76% of treated plots using LPI. In treated plots where *Artemisia* spp. were detected, the average canopy cover was 3.4% and only 4 of 313 plots had >10% sagebrush cover. Moreover, *Artemisia* spp. canopy cover did not increase with years since treatment, suggesting that within 20 years, time is not the principle limitation on reestablishment of sagebrush at post-wildfire restoration sites in the Great Basin. This finding has important implications for habitat protection and restoration decisions.

In contrast to sagebrush guidelines, ESR-treated areas met breeding and brood-rearing season guidelines for perennial grass cover fairly often. Native perennial grass cover and height are important for hiding nests and young during these seasons (Connelly et al. 2011*c*). Despite the relative success of native perennial grass recovery, it is important to consider that establishment of these grasses does not necessarily preclude an abundance of invasive plants. For example, of the 554 plots that met Connelly and others' (2000) criterion for perennial grass and forb cover, cheatgrass cover averaged 36% and non-native annual forb cover averaged 14% (i.e., 50% total non-native annual plant cover). Our habitat association models indicated that these plots are unlikely to be occupied by sage-grouse.

Few treated areas met Stiver and others' (2010) forb canopy cover guideline, and this understory component limited the proportion of plots meeting this set of breeding season understory guidelines in all plot types (including Unburned plots). Establishing native forbs is difficult because they are naturally sparse in many parts of the Great Basin and they often do not compete well with non-native plants, are difficult to procure, and can require specialized seeding application (Pyke 2011). Treated plots met all of Connelly and other's (2000) breeding season understory guidelines more frequently than did burned-untreated plots (indicating a positive treatment effect). A relatively high proportion of treated areas met brood-rearing understory habitat guidelines, but these plots often had high cheatgrass and non-native forb abundance. Surprisingly few unburned areas surrounding ESR sites met understory habitat guidelines, especially for the breeding season. A lack of native perennial grass cover and height was the main cause of this finding. Habitat management guidelines could be improved by incorporating our landscape-level findings and adding criteria regarding non-native plant canopy cover.

Treatment and environmental predictors of meeting guidelines

Restoration areas that met habitat guidelines tended to be farther north, have more late winter-spring precipitation (less summer precipitation), and lower annual temperatures. ESR sites that were farther south and in warm, dry, low elevation locations had the lowest probability of meeting understory habitat guidelines. Greater heat or water stress on seeded plants during key lifecycle phases (e.g., emergence, germination) likely impedes restoration efforts that could benefit sage-grouse habitat after wildfire. A study of seeded grass recruitment in the Great Basin found that seedling emergence (and likely environmental conditions) in March–May was the main barrier to recruitment, with spring-summer drought adding to mortality, but at lower levels (James et al. 2011). Sites within the Snake River Plain were an exception to the latitudinal trend we observed, but these locations were also typically low in elevation and total precipitation. Sites with poor environmental conditions for post-wildfire seeding treatments may require novel restoration methods to potentially meet sage-grouse habitat guidelines.

Conclusions

Post-wildfire restoration of Wyoming big sagebrush sites is only likely to result in quality sage-grouse habitat under a relatively narrow range of climate and environmental conditions. Where conditions are favorable, native perennial grass restoration is possible within 20 years of project completion, but establishing native forbs and obtaining ecologically significant reductions in non-native plant cover is unlikely under most conditions. Further, establishing sagebrush cover under any of our study conditions will likely require more than 20 years and substantial improvements to restoration methods. From a sage-grouse habitat perspective, even the most initially successful post-fire restoration projects in the Great Basin should be viewed as long-term investments rather than as short-term mitigation aimed at preserving particular sage-grouse populations because restoring high quality sage-grouse habitat may require a time span equivalent to several sage-grouse generations.

Given current fire frequencies, climate trajectories, and anthropogenic stressors, conservation and protection of "what's left" is increasingly important, especially in landscapes containing a mix of dwarf sagebrush and big sagebrush steppe with minimal human development and low non-native plant dominance. With respect to sage-grouse habitat, our ability to "fix what's broken" after large wildfires is currently limited in Wyoming big sagebrush habitats of the Great Basin. This suggests improvements to ESR restoration approaches (i.e., increasing sagebrush and native herb establishment, reducing non-native plant dominance) and prioritization of sage-grouse specific restoration funding for particular landscapes may be necessary to maximize conservation effectiveness.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. LANDFIRE reclassification scheme used to develop landcover variables describing landscape composition around each plot surveyed for sage-grouse and vegetation ($n = 211$ plots) and each plot associated with ESR restoration sites ($n = 826$ plots).

Landcover variable	LANDFIRE class name
AGRICULTURE5km	Agriculture-Cultivated Crops and Irrigated Agriculture Agriculture-General Agriculture-Pasture and Hay Agriculture-Pasture/Hay NASS-Close Grown Crop NASS-Fallow/Idle Cropland NASS-Orchard NASS-Pasture and Hayland NASS-Row Crop NASS-Row Crop-Close Grown Crop NASS-Vineyard Recently Disturbed Pasture and Hayland
ASPEN5km	Rocky Mountain Aspen Forest and Woodland
ASPENCONIFER5km	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland
BARREN5km	Barren Inter-Mountain Basins Sparsely Vegetated Systems Northern Rocky Mountain Avalanche Chute Shrubland Rocky Mountain Alpine Fell-Field Rocky Mountain Alpine/Montane Sparsely Vegetated Systems Snow/Ice
BSAGESHRUB5km	Inter-Mountain Basins Big Sagebrush Shrubland
BSAGESTEPPE5km	Inter-Mountain Basins Big Sagebrush Steppe
BURNED5km	Recently Burned Herbaceous Wetlands Recently Burned-Herb and Grass Cover
CONIFER5km	Abies concolor Forest Alliance Abies grandis Forest Alliance Inter-Mountain Basins Subalpine Limber-Bristlecone Pine Woodland Middle Rocky Mountain Montane Douglas-fir Forest and Woodland Northern Rocky Mountain Conifer Swamp Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest Northern Rocky Mountain Foothill Conifer Wooded Steppe Northern Rocky Mountain Mesic Montane Mixed Conifer Forest Northern Rocky Mountain Ponderosa Pine Woodland and Savanna Northern Rocky Mountain Subalpine Woodland and Parkland Pseudotsuga menziesii Forest Alliance Rocky Mountain Lodgepole Pine Forest Rocky Mountain Poor-Site Lodgepole Pine Forest Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland Rocky Mountain Subalpine-Montane Limber-Bristlecone Pine Woodland Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland Southern Rocky Mountain Ponderosa Pine Savanna Southern Rocky Mountain Ponderosa Pine Woodland
DECIDSHRUB5km	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland Northern Rocky Mountain Subalpine Deciduous Shrubland Quercus gambelii Shrubland Alliance Rocky Mountain Bigtooth Maple Ravine Woodland Rocky Mountain Gambel Oak-Mixed Montane Shrubland
DEVELOPED5km	Developed-General Developed-High Intensity Developed-Low Intensity Developed-Medium Intensity Developed-Open Space Developed-Roads Developed-Upland Deciduous Forest Developed-Upland Evergreen Forest Developed-Upland Herbaceous Developed-Upland Mixed Forest

Table A1. Continued.

Landcover variable	LANDFIRE class name
	Developed-Upland Shrubland
	Quarries-Strip Mines-Gravel Pits
	Recently Disturbed Developed Upland Deciduous Forest
	Recently Disturbed Developed Upland Evergreen Forest
	Recently Disturbed Developed Upland Herbaceous
	Recently Disturbed Developed Upland Mixed Forest
	Recently Disturbed Developed Upland Shrubland
DWARFSAGE5km	Colorado Plateau Mixed Low Sagebrush Shrubland
	Columbia Plateau Low Sagebrush Steppe
	Columbia Plateau Scabland Shrubland
	Great Basin Xeric Mixed Sagebrush Shrubland
	Wyoming Basins Dwarf Sagebrush Shrubland and Steppe
EFORB5km	Introduced Upland Vegetation-Annual and Biennial Forbland
EPGF5km	Introduced Upland Vegetation-Perennial Grassland and Forbland
EXOTICANN5km	Introduced Upland Vegetation-Annual Grassland
GRASSLAND5km	Columbia Basin Palouse Prairie
	Columbia Plateau Steppe and Grassland
	Inter-Mountain Basins Semi-Desert Grassland
	Northern Rocky Mountain Lower Montane-Foothill-Valley Grassland
	Northern Rocky Mountain Subalpine-Upper Montane Grassland
	Rocky Mountain Alpine Dwarf-Shrubland
	Southern Rocky Mountain Montane-Subalpine Grassland
GRESEWOOD5km	Inter-Mountain Basins Greasewood Flat
HERBACEOUS5km	Herbaceous Semi-dry
	Herbaceous Semi-wet
JUNIPER5km	Colorado Plateau Pinyon-Juniper Woodland
	Columbia Plateau Western Juniper Woodland and Savanna
	Great Basin Pinyon-Juniper Woodland
	Inter-Mountain Basins Juniper Savanna
	Juniperus occidentalis Woodland Alliance
	Rocky Mountain Foothill Limber Pine-Juniper Woodland
MAHOGANY5km	Inter-Mountain Basins Curl-leaf Mountain Mahogany Woodland and Shrubland
MTGRASS5km	Rocky Mountain Alpine Turf
MTSHRUB5km	Rocky Mountain Lower Montane-Foothill Shrubland
MTSAGE5km	Artemisia tridentata ssp. vaseyana Shrubland Alliance
	Inter-Mountain Basins Montane Sagebrush Steppe
RABBITBRUSH5km	Inter-Mountain Basins Semi-Desert Shrub-Steppe
OTHERSHRUB5km	Arctostaphylos patula Shrubland Alliance
	Coleogyne ramosissima Shrubland Alliance
	Grayia spinosa Shrubland Alliance
	Great Basin Semi-Desert Chaparral
RIPARIAN5km	Inter-Mountain Basins Montane Riparian Systems
	Introduced Riparian Vegetation
	Rocky Mountain Montane Riparian Systems
	Rocky Mountain Subalpine/Upper Montane Riparian Systems
	Western Great Plains Floodplain Systems
SALTDESERT5km	Inter-Mountain Basins Mat Saltbush Shrubland
	Inter-Mountain Basins Mixed Salt Desert Scrub
	Mojave Mid-Elevation Mixed Desert Scrub
UNKNOWN5km	(blank)
OPENWATER5km	Open Water
WETLAND5km	Herbaceous Wetlands
	Rocky Mountain Subalpine-Montane Mesic Meadow
	Western Great Plains Depressional Wetland Systems

Table A2. Descriptions of variables included in models by variable type.

Variable	Units	Source	Description
Response			
SGOCC	binary	field survey	Observed occupancy of sage-grouse, where 0 = pellet(s) not detected and 1 = pellet(s) detected in Random Plots
pSGPLOT	probability	Plot-level Model	Estimated probability of sage-grouse occupancy in Chronosequence Plots based on applying Plot-level Model to Chronosequence vegetation data
pSGPLOT+LS	probability	Plot + Landscape Model	Estimated probability of sage-grouse occupancy in Chronosequence Plots based on applying Plot + landscape Model to Chronosequence vegetation and landcover data
GUIDELINEMET	binary	field data	Based on plant data, whether plots met various habitat guideline criteria (see Table 3), where 0 = plot did not met criterion and 1 = plot met criterion
Plot-level predictor			
DWARFSAGEcov	percent	LPI survey	Percent canopy cover of *Artemisia arbuscula*, *A. nova*, *A. tripartita*
WYSAGEcov	percent	LPI survey	Percent canopy cover of *Artemisia tridentata* var. *wyomingensis*
WYSAGEht	cm	LPI survey	Average height of *Artemisia tridentata* var. *wyomingensis*
GRASScov	percent	LPI survey	Percent canopy cover of native perrenial grasses
CHEATcov	percent	LPI survey	Percent canopy cover of *Bromus tectorum*
PLANTRICH	n species	calculated	Number of plant species detected using LPI sampling
PLANTDIV	...	calculated	Shannon diversity of vegetation, based on LPI data
PLANTEVEN	...	calculated	Evenness of vegetation, based on LPI data
COWDEN	number/m^2	field count	Density of cattle fecal groups within 1 m of transect lines
Landscape-level predictor			
EPGF5km	percent	LANDFIRE	Within 5 km of plot, percent landcover of exotic perennial grasses and forbs
DEVELOPED5km	percent	LANDFIRE	Within 5 km of plot, percent landcover of human developed areas
RIPARIAN5km	percent	LANDFIRE	Within 5 km of plot, percent landcover of riparian areas
LNDSCP3	...	NMS ordination	Ordination axis score, where negative values correspond to landscapes containing high proportions of DWARFSAGE5km and BSAGESTEPPE5km and positive values correspond to landscapes containing high proportions of EXOTICANN5km, AGRICULTURE5km, CONIFER5km, and JUNIPER5km
Treatment predictor			
TREATMENT	categorical	LTDL	Whether a Chronosequence Plot was burned-aerial seeded (AERIAL), burned-unseeded (BURNED), burned-drill seeded (DRILL), burned-seeded with aerial and drill treatments (MIXED), or unburned (UNBURNED)
PROJYR	year	LTDL	The year that a restoration project was conducted; always in the Fall-Winter following wildfire
SEEDSP	categorical	LTDL	Whether a particular plant species was seeded on a given restoration project (a separate binary variable for each seeded species)
Topographic predictor			
ELEV	meters	DEM	Mean elevation of the plot
SLOPE	degrees	DEM	Mean slope of the plot
HEATLOAD	...	DEM	Relative amount of heat gain in location (0 = coolest, to 1 = warmest), based on slope, aspect, and latitude. (Calculated as in McCune and Keon [2002].)
PDIR	$\mathrm{MJ\ cm^{-2}\ yr^{-1}}$	DEM	Potential direct incident radiation, calculated as in McCune and Keon (2002).
Climate predictor			
DEGMONTH	degree·months	PRISM	Sum of monthly average temperatures, based on 30 year PRISM average for each month
PRECIP	cm/yr	PRISM	Average annual precipitation, based on 30 year PRISM average for each month
CLIMATE1	...	NMS ordination	Ordination axis score, where negative values correspond to high DEGMONTH and warm winters and positive values correspond to high May–June and total annual precipitation
CLIMATE2	...	NMS ordination	Ordination axis score, where negative values correspond to high Nov–Dec precipitation and positive values correspond to high monsoonal (July–Oct) precipitation

Table A2. Continued.

Variable	Units	Source	Description
Location predictor			
MLRA	categorical	GIS	One of seven Major Land Resource Areas where the plot was located
STATE	categorical	GIS	One of four states where the plot was located
NORTHING	meters	GIS	Northing coordinate
EASTING	meters	GIS	Easting coordinates

Table A3. For each *Artemisia* species detected in 211 randomly located plots, the canopy cover range, the number of plots where each shrub species was detected during LPI sampling, and the naïve probability of sage-grouse occupancy at those plots where the shrub species was detected.

Species	Common name	Canopy cover range (%)	No. plots with shrub detected	Naïve probability of SGOCC
Artemisia arbuscula	Low sagebrush	1–49	35	0.57
A. nova	Black sagebrush	0.5–44	41	0.40
A. tripartita	Threetip sagebrush	1–23	8	0.75
A. tridentata spp. *vaseyana*	Mountain big sagebrush	5–25	5	0.20
A. tridentata spp. *wyomingensis*	Wyoming big sagebrush	0.5–41.5	160	0.27
A. tridentata spp. *tridentata*	Basin big sagebrush	0.5–25	17	0.35

Table A4. Results of eight separate NPMR models describing relationships between environmental or treatment characteristics and whether AERIAL, DRILL, MIXED, and BURNED plots met published seasonal sage-grouse habitat guideline criteria for breeding season habitat (Connelly et al. 2000, Stiver et al. 2010).

Criterion (response variable)	*n* meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover (15–25%)	4	. . .	. . .	na‡
Sagebrush height (30–80 cm)	40	18.9	28	(±) PROJYR, (±) STATE, (∧) CLIMATE3
Perennial grass and forb height (≥18 cm)	295	22.5	27	(+) NORTHING, (−) HEATLOAD, (−) PDIR, (±) MLRA
Perennial grass and forb cover (≥15%)§	365	42.3	27.3	(+) PRECIP, (+) CLIMATE1, (+) NORTHING, (−) PDIR
Perennial grass cover (>10%)§	376	39.9	27.6	(+) NORTHING, (±) CLIMATE3, (+) PRECIP, (+) PDIR
Forb cover (≥5%)§	166	42.7	29.1	(−) CLIMATE2, (∧) PRECIP, (∧) ELEV
All understory (Connelly et al. 2000)	244	31.1	27.3	(+) NORTHING, (−) CLIMATE2, (−) DEGMONTH, (−) PDIR, (+) PRECIP
All understory (Stiver et al. 2010)	99	34.8	27.2	(∧) CLIMATE2, (±) PROJYR, (−) DEGMONTH

Note: Variable names are defined in Appendix: Table A2.

† Symbols in parentheses indicate the general direction of the relationship between each predictor and response variable: "+" indicates positive, "−" indicates negative, "±" indicates both negative and positive, and "∧" indicates a Gaussian relationship.

‡ Models were not run for a given guideline criterion if fewer than 20 plots met the criterion.

§ Criteria differ between the two guideline sources.

Table A5. Results of 11 separate NPMR models describing relationships between environmental or treatment characteristics and whether UNBURNED plots met published seasonal sage-grouse habitat guideline criteria for breeding season habitat (Connelly et al. 2000, Stiver et al. 2010).

Criterion (response variable)	*n* meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover (15–25%)	107	5.8	29.6	(+) CLIMATE3, (−) CLIMATE2, (−) HEATLOAD
Sagebrush height (30–80 cm)	207	8.6	15.7	(∧) CLIMATE1, (∧) PDIR, (−) PROJYR
Perennial grass and forb height (≥18 cm)	138	14.9	14.6	(−) DEGMONTH, (∧) CLIMATE2, (+) PRECIP, (+) ELEV
Perennial grass and forb cover (≥15%)§	179	26.6	15.3	(+) NORTHING, (−) DEGMONTH, (+) PRECIP, (−) PROJYR, (∧) SLOPE, (+) CLIMATE3
Perennial grass cover (>10%)§	190	26.5	15.3	(+) NORTHING, (±) PROJYR, (+) SLOPE, (±) STATE
Forb cover (≥5%)§	102	28.6	15.5	(−) CLIMATE2, (−) HEATLOAD, (+) PRECIP, (+) CLIMATE1, (+) CLIMATE3
All understory (Connelly et al. 2000)	110	17.6	14.4	(−) DEGMONTH, (−) CLIMATE2, (+) NORTHING, (∧) SLOPE, (+) PRECIP
All understory (Stiver et al. 2010)	52	16.2	17.3	(−) DEGMONTH, (+) CLIMATE3, (±) MLRA
All overstory	91	3.2	24.6	(−) DEGMONTH, (−) CLIMATE2, (−) SLOPE
All breeding season (Connelly et al. 2000)	38	7.7	17.4	(−) DEGMONTH, (+) SLOPE, (−) ELEV
All breeding season (Stiver et al. 2010)	22	8.5	17.5	(−) DEGMONTH, (+) NORTHING

Note: Symbols are defined in Appendix: Table A4 and variable names are defined in Appendix: Table A2.

Table A6. Results of five separate NPMR models describing relationships between environmental or treatment characteristics and whether AERIAL, DRILL, MIXED, and BURNED plots met published seasonal sage-grouse habitat guideline criteria for brood-rearing season habitat (Connelly et al. 2000, Stiver et al. 2010).

Criterion (response variable)	*n* meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover (10–25%)	9	...	...	na‡
Sagebrush height (40–80 cm)	28	15.9	34.8	(±) STATE, (±) PROJYR
Perennial grass and forb cover (≥15%)	365	42.3	27.3	(+) PRECIP, (+) CLIMATE1, (+) NORTHING, (−) PDIR
All overstory	4	...	...	na‡
All summer	4	...	...	na‡

Note: Symbols are defined in Appendix: Table A4 and variable names are defined in Appendix: Table A2.

Table A7. Results of five separate NPMR models describing relationships between environmental or treatment characteristics and whether UNBURNED plots met published seasonal sage-grouse habitat guideline criteria for brood-rearing season habitat (Connelly et al. 2000, Stiver et al. 2010).

Criterion (response variable)	*n* meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover (10–25%)	129	12.6	16.5	(∧) PDIR, (−) CLIMATE2, (+) CLIMATE3, (−) CLIMATE1, (+) SLOPE
Sagebrush height (40–80 cm)	142	15.8	15	(±) DEGMONTH, (+) NORTHING, (±) MLRA, (±) STATE
Perennial grass and forb cover (≥15%)	179	26.6	15.3	(+) NORTHING, (∧) DEGMONTH, (+) PRECIP, (±) PROJYR, (+) SLOPE, (+) CLIMATE3
All overstory	79	11.7	14.4	(∧) DEGMONTH, (∧) PDIR, (±) MLRA, (±) STATE
All brood-rearing	58	8.1	15.6	(∧) DEGMONTH, (−) PDIR, (−) CLIMATE2, (+) NORTHING

Note: Symbols are defined in Appendix: Table A4 and variable names are defined in Appendix: Table A2.

Table A8. Results of three separate NPMR models describing relationships between environmental or treatment characteristics and whether AERIAL, DRILL, MIXED, and BURNED plots met published seasonal sage-grouse habitat guideline criteria for winter season habitat (Connelly et al. 2000, Stiver et al. 2010). Winter models predict the probability of *not meeting* habitat guideline criteria assuming no snow cover (see main text for explanation).

Criterion (response variable)	*n* not meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover above snow (10–30%)	529	. . .	. . .	na‡
Sagebrush height above snow (25–35 cm)	491	19.4	27	(−) PRECIP, (+) CLIMATE2, (±) STATE, (±) PROJYR
All winter	531	. . .	. . .	na‡

Note: Symbols are defined in Appendix: Table A4 and variable names are defined in Appendix: Table A2.

Table A9. Results of three separate NPMR models describing relationships between environmental or treatment characteristics and whether UNBURNED plots met published seasonal sage-grouse habitat guideline criteria for Winter season habitat (Connelly et al. 2000, Stiver et al. 2010). Winter models predict the probability of *not meeting* habitat guideline criteria assuming no snow cover (see main text for explanation).

Criterion (response variable)	*n* not meeting criterion	logβ	*N**	Predictor variables†
Sagebrush cover above snow (10–30%)	40	12.7	15.4	(+) CLIMATE2, (−) ELEV, (±) CLIMATE3
Sagebrush height above snow (25–35 cm)	41	6.1	16.5	(+) CLIMATE1, (+) PDIR, (±) PROJYR, (−) NORTHING
All winter	64	11.6	15.7	(+) CLIMATE2, (+) PDIR, (−) NORTHING, (+) DEGMONTH

Note: Symbols are defined in Appendix: Table A4 and variable names are defined in Appendix: Table A2.

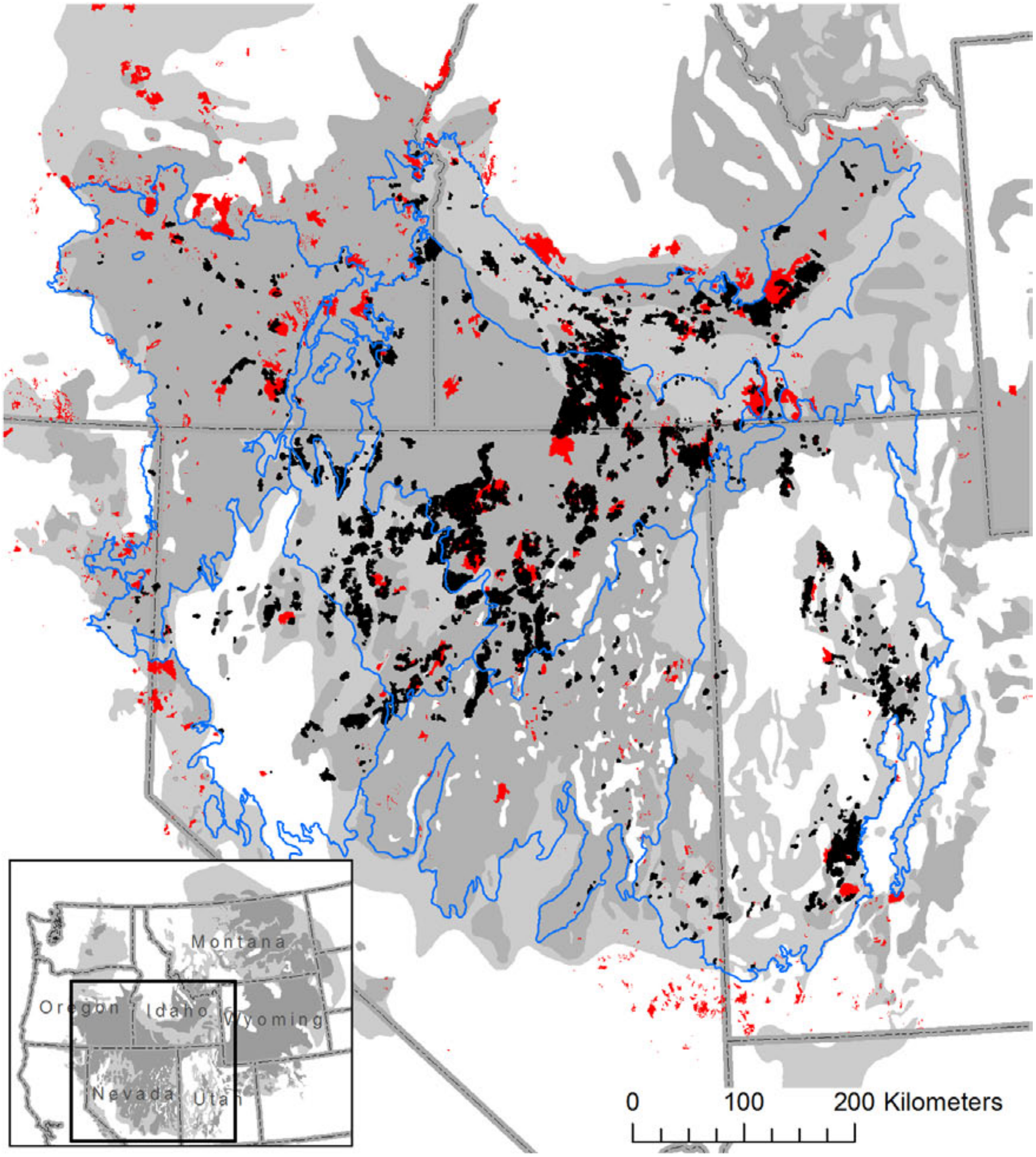

Fig. A1. Study area, with blue lines showing Major Land Resource Areas (USDA Natural Resources Conservation Service) within the Great Basin of the western United States. Light and dark gray areas are as in Fig. 1. Black polygons are all post-wildfire seeding treatments conducted since 1990 (total area = 2.2 million ha, or 6% of the study area) and red polygons represent other types of land treatments. Over 800 post-wildfire treatments conducted between 1935 and 1990 are not shown. The inset map shows the study area in relation to the distribution of the Greater Sage-Grouse in western North America.

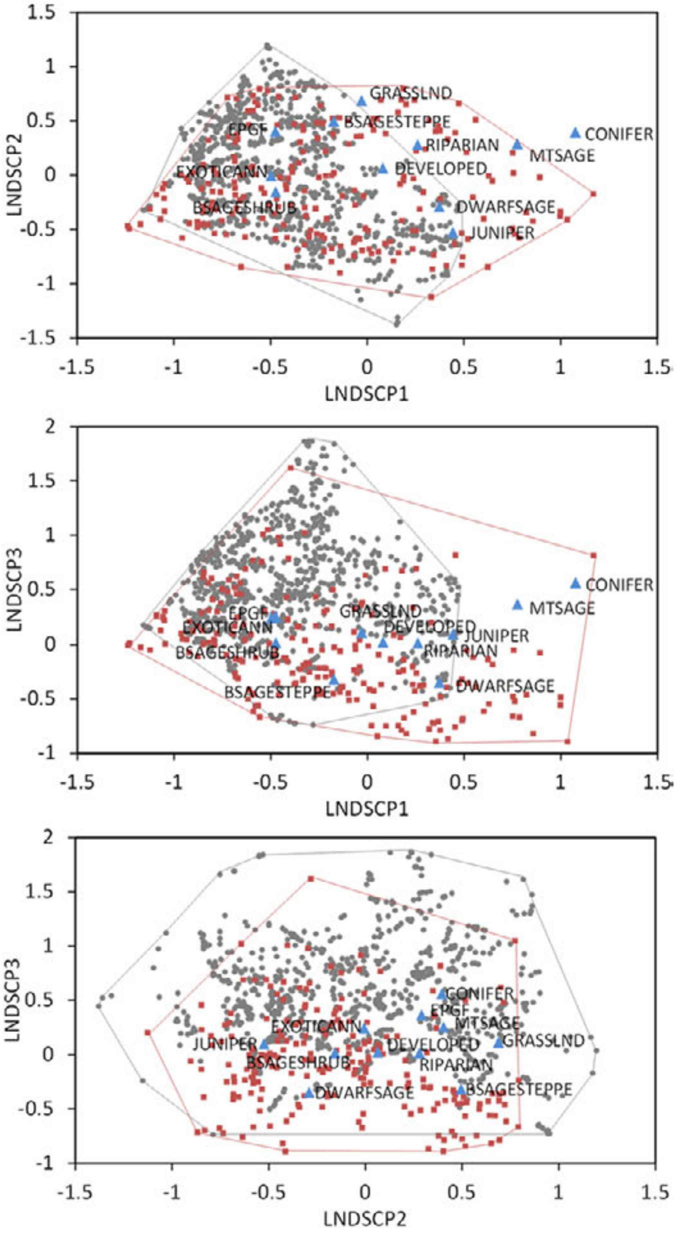

Fig. A2. NMS biplots, each showing 211 plots sampled for sage-grouse occupancy and habitat (red) and 826 plots associated with ESR projects (gray) in two-dimensional landcover space. Plots closer together in ordination space have more similar landscape compositions (within a 5 km radius) to one another. Centroids for certain landcover types are shown (blue triangles) and are labeled as in Table A1. The remaining landcover types were used in the NMS analysis, but were omitted from these figures for clarity. As expected (based on our ESR site selection and stratification approach and the location of these plots within burned landscapes), ESR plots predominantly occupy a subset (albeit a large subset) of the landscapes where sage-grouse occupancy and habitat were assessed in randomly placed plots. Ninety-four percent of ESR plots fall within the ordination space occupied by random plots. Thus, landscapes similar to those of our ESR plots are well represented in the sage-grouse occupancy and habitat data. Consequently, occupancy rates in these randomly located plots should provide inference for occupancy rates in ESR plots.

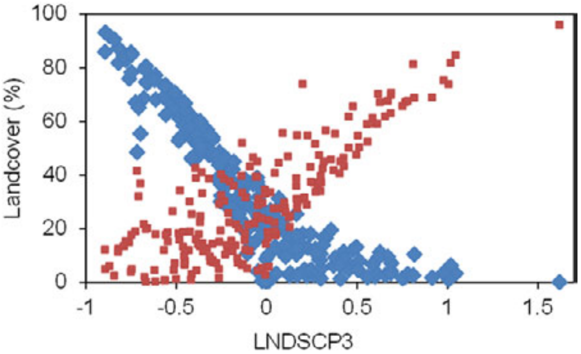

Fig. A3. Correlation between LNDSCP3 (x-axis) and landcover variables (y-axis) obtained from LANDFIRE data within 5 km of each plot and used in empirical model development. LNDSCP3 values were derived from NMS ordination of landcover data for each plot. Blue points ($n = 211$) represent the combined percent landcover of DWARFSAGE5km and BSAGESTEPPE5km (y-axis). This indicates that negative values of LNDSCP3 are strongly associated with landscapes containing a combination of DWARFSAGE5km and BSAGESTEPPE5km (linear $r^2 = 0.79$). Red points are the same 211 plots (with the same values for LNDSCP3), but plotted on the y-axis is the combined percent landcover of EXOTICANN5km, AGRICULTURE5km, CONIFER5km, JUNIPER5km, GREASEWOOD5km, and SALTDESERT5km (linear $r^2 = 0.67$). This shows that positive values of LNDSCP3 are strongly associated with landscapes that contain a combination of the above landcover types.

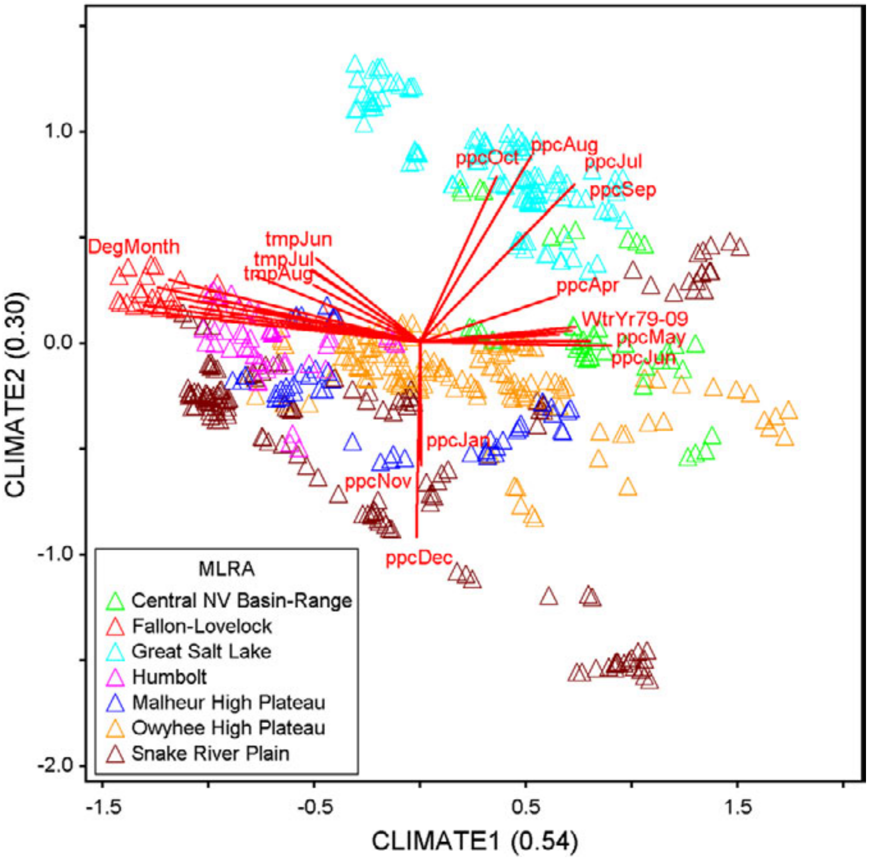

Fig. A4. NMS ordination biplot of 826 plots associated with ESR sites plotted in climate space. Plots closer together have more similar climates based on 30 year average monthly temperature and precipitation values derived from PRISM climate data. Plots are color coded by MLRA. Some MLRAs exhibit substantial climate gradients (e.g., Snake River Plain). Plots with negative CLIMATE1 scores have relatively high values of DEGMONTH, indicating that they have the greatest cumulative annual temperature, mostly because of warmer spring and fall seasons. Positive values of CLIMATE1 are associated with high May-June precipitation and high total annual precipitation. CLIMATE2 represents a gradient of high winter precipitation (negative values of CLIMATE2) to high summer, or monsoonal precipitation from July-October (positive values of CLIMATE2). NMS ordination was accomplished through relativizing each month's temperature or precipitation data by the maximum value, such that, after transformations, each plot had 12 temperature and 12 precipitation variables, each of which ranged from 0 to 1. NMS ordination was performed on these 24 variables and the resulting axis scores for each plot were used in subsequent analyses. CLIMATE1 represented 53.5% of the variance in the transformed data and CLIMATE2 and CLIMATE3 (not shown) represented 30.2% and 12.7%, respectively, for a total of 96.5%.

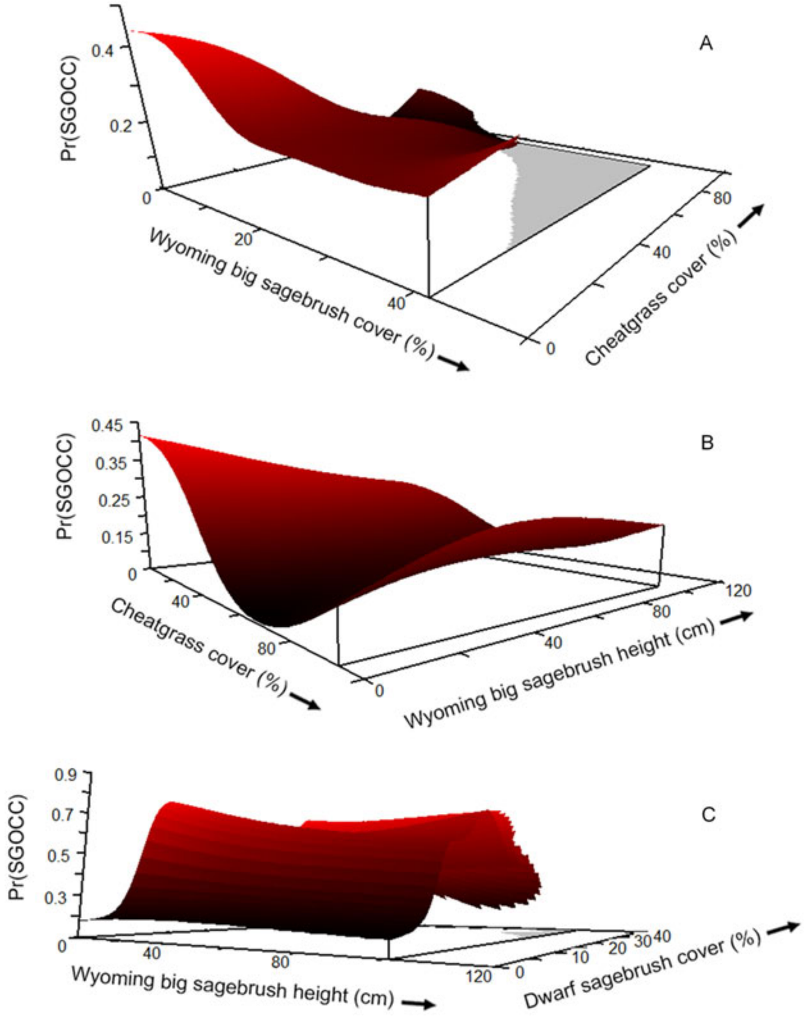

Fig. A5. NPMR modeled relationship between plot-level probability of sage-grouse occupancy (vertical axes) and (A) percent cover of Wyoming big sagebrush and cheatgrass, (B) cheatgreass cover and average Wyoming big sagebrush height, and (C) average Wyoming big sagebrush height and percent canopy cover of dwarf sagebrush. Gray areas indicate regions of predictor space with too few plots for reliable estimates to be made. Relationships are derived from the "Plot-level Model" created using 211 plots in the Great Basin.

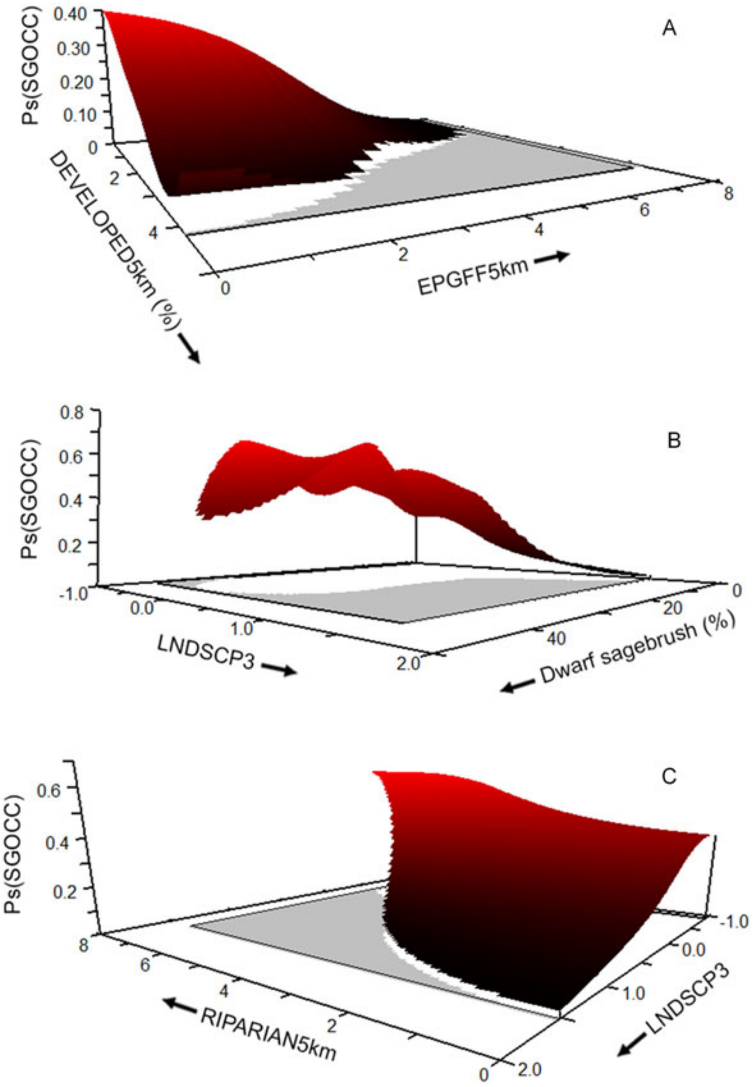

Fig. A6. NPMR modeled relationship between plot-level probability of sage-grouse occupancy (vertical axes) and percent landcover (within 5 km of plots) of (A) human development (DEVELOPED5km) and exotic perennial grass and forb (EPGF5km), (B) LNDSCP3 and plot-level canopy cover of dwarf sagebrush species, and (C) riparian areas (RIPARIAN5km) and LNDSCP3. Low values of LNDSCP3 represent landscapes containing high combined big sagebrush steppe and dwarf sagebrush landcover types. High values of LNDSCP3 represent landscapes containing high proportions of exotic annual grass, agriculture, conifer, and juniper landcover types. Gray areas indicate regions of predictor space with too few plots for reliable estimates to be made. Relationships are derived from the "Plot + Landscape Model" created using 211 plots in the Great Basin.